Temporal changes in tree community structure and richness in a seasonally dry tropical forest in Minas Gerais, southeastern Brazil

Cambios temporales en la estructura y riqueza de la comunidad arbórea
en un bosque tropical estacionalmente seco en Minas Gerais, sudeste de Brasil

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SUMMARY

Seasonally Dry Tropical Forests (SDTF) are gaining recognition as a habitat of global conservation significance. However, these forests often occur on rich soils, and are therefore prone to disturbance by agricultural activities. Across their range, many SDTFs are in various stages of regeneration, although little is known about their regeneration dynamics and temporal change in general. To fill this knowledge gap, we studied the changes in species diversity and community structure of an SDTF tree community with a history of past selective logging located in northern Minas Gerais, Brazil. We hypothesized an increase in species diversity and biomass-related parameters, along with a reduction in stem density for the community after five years of regeneration. In 2005, we measured all trees (diameter ≥ 3.18 cm at 1.3 m) within twenty 20 x 20 m (400 m²) plots in the patch, and we remeasured the trees in 2010. Between the two censuses, we found no significant changes in species richness and diversity, suggesting that species accumulation had leveled out. However, we found significant gains in tree basal area and recruitment, suggesting continual regeneration. Diameter class distributions of the five most abundant tree species showed similar patterns. We conclude that past disturbances can have ongoing effects on SDTF vegetation, although inter-annual variations may also play a regulatory role on community dynamics.

Key words: forest ecology, ecosystems dynamics, forest regeneration, remnant vegetation, tropical tree diversity.

RESUMEN

Los Bosques Tropicales Secos Estacionales (BTSE) gozan de reconocimiento como hábitat de importancia global para la conservación. Sin embargo, estos bosques se encuentran a menudo en suelos ricos, y, por lo tanto, son propensos a perturbación por actividades agrícolas. En su rango de distribución, muchos BTSE están en varias etapas de regeneración, pero se sabe poco acerca de su dinámica de regeneración y cambio temporal en general. Para llenar este vacío de conocimiento, se estudiaron cambios en la diversidad de especies y la estructura de una comunidad de árboles de un BTSE con una historia de tala selectiva en el norte de Minas Gerais, Brasil. Se hipotetizó un aumento en la diversidad de especies y parámetros relacionados con la biomasa, junto con una reducción de la densidad para la comunidad después de cinco años de regeneración. En 2005, todos los árboles (diámetro ≥ 3,18 cm a 1,3 m) fueron medidos dentro de veinte parcelas de 20x20 m (400 m²), y fue repetido el mismo procedimiento en 2010. Entre ambos censos, no hubo cambios significativos en riqueza de especies ni diversidad, lo que sugiere que la acumulación de especies se había estabilizado. Sin embargo, hubo ganancias significativas en área basal y en el reclutamiento, lo que sugiere una regeneración continua. Las distribuciones diamétricas de las cinco especies de árboles más abundantes mostraron patrones similares. Se concluyó que los disturbios pasados pueden tener efectos continuos sobre la vegetación del BTSE, aunque las variaciones interanuales también pueden desempeñar un papel regulador en la dinámica de la comunidad.

Palabras clave: ecología de bosque, dinámica de ecosistemas, regeneración de bosques, vegetación remanente, diversidad de árboles tropicales.

INTRODUCTION

Seasonally dry tropical forests (STDFs) are increasingly being recognized for their global presence, ecological diversity, and socio-economic significance (de Albuquerque *et al.* 2012). At the same time, these ecosystems are considered among the most threatened in the world (Apgaua *et al.* 2014b). In South America for example, the

principal threat to STDFs is agricultural activities, because areas where SDTF occurs have fertile soils, and are typically cultivated intensively for a number of years and subsequently abandoned due to reduced productivity. This has led to fragmentation of SDTF in many areas and to a growing extent of SDTFs in a state of regeneration or succession (Chazdon 2003, Coelho *et al.* 2016).

The process of forest regeneration typically involves changes in floristics and structural dynamics (Chazdon 2003, Coelho *et al.* 2016). An area with post-disturbance tree regeneration is characterized by high stem abundance and basal area turnover rates, followed by a reduction in the number of individuals and increased biomass at late successional stages (Werneck and Franceschinelli 2004, Machado and Oliveira-Filho 2010). However, anthropogenic activities can affect these natural processes and thereby influence forest successional trajectories, resulting in very different ecosystems from those that previously existed (Lebrija-Trejos *et al.* 2010).

Studies on natural regeneration in Neotropical STDFs have been conducted variously in Mexico (Lebrija-Trejos *et al.* 2010), Nicaragua (Marín *et al.* 2005) and Brazil (Werneck and Franceschinelli 2004). However, there have been comparatively little studies for the Caatinga domain (de Albuquerque *et al.* 2012), an important phytogeographical region of SDTF vegetation in Brazil.

In northern areas of Minas Gerais State, Brazil, SDTF vegetation occurs in an ecotonal region wedged between savanna and rainforest (Apgaua *et al.* 2014b). Here, the integrity of SDTFs is threatened by agricultural expansion, mining activities and timber extraction (Santos *et al.* 2011). Long-term monitoring of tree communities in this region is therefore urgently needed to provide an improved understanding of the floristic and structural patterns of SDTFs, and to underpin their conservation and management.

We aimed at filling this gap of knowledge regarding SDTF forest dynamics by investigating the demographic and structural changes of the tree component in an SDTF community located in southeast Brazil, five years after an initial vegetation description in the area in 2005 (Santos *et al.* 2012). Following known patterns of SDTF vegetation succession (Lebrija-Trejos *et al.* 2010, Coelho *et al.* 2016), we hypothesized an increase in tree biomass, richness and diversity, along with a reduction in stem density for the community. Based on tree diameter class patterns observed in other studies (*e.g.* Apgaua *et al.* 2014a, Coelho *et al.* 2016) for late successional SDTF forest, we also predicted that there would be higher recruitment and mortality rates for trees in the smaller size class diameters, and a higher gain in biomass in intermediate classes.

METHODS

Study site. The study was conducted in a ~80 ha remnant of seasonally dry tropical forest (SDTF) located at Vale Verde Farm (14°24'88'' S and 44°09'79'' W, 658 m a.s.l.)

in the municipality of Juvenília, northern Minas Gerais, Brazil. The SDTF in the area has a seasonally deciduous tree component with discontinuous canopy which varied in both height (3–9 m) and density (Santos *et al.* 2012, Apgaua *et al.* 2014a). The flora comprises mostly succulent cacti and non-succulent shrubs and trees, many of which are armed with either thorns or prickles and bear microphyllous foliage, though they are leafless during periods of drought (Santos *et al.* 2012).

Interviews with the farm owners and local inhabitants in the area revealed that parts of the area were selectively logged 40 years ago for commercially valuable species of trees including *Handroanthus ochraceus*, *Myracrodruon urundeuva* and others. However, some individual trees in specific sections of the forest were preserved. Currently, trampling by livestock is the main source of disturbance to the forest fragment, and the adjacent areas are composed of pastures and abandoned fields undergoing natural regeneration (Santos *et al.* 2011).

The terrain is slightly hilly with gentle slopes in limestone outcrop areas. This area occurs in a region with most part of annual rainfall occurring in the summer. Annual average temperature exceeds 20 °C and annual average rainfall is 1,000 mm with the rainy season occurring between November and January (Santos *et al.* 2011). Soil at our sampling sites includes eutrophic red-yellow argisols and eutrophic red nitosols.

Sampling. We surveyed the tree community of the site initially in 2005 (Santos *et al.* 2011) and subsequently in 2010. We used twenty 20 × 20 m (400 m²) sampling plots distributed along a transect within and parallel to the widest edge of the forest fragment (sampling area totaling 8,000 m²). The plots were arranged 10 m apart from each other along the transect. This amounted to a total sampling area of 0.8 ha of SDTF. All living trees with a diameter at breast height (DBH or 1.3 m height) ≥ 3.18 cm were tagged with numbered aluminum tags, identified at the species level, and had their DBH and height measured. During the second survey, in January 2010, the DBH of all surviving individuals was remeasured, the number of dead individuals was determined and the individuals (recruits) that reached a DBH ≥ 3.18 cm (new recruits) were identified, tagged and measured.

To analyze the changes in species richness and diversity (Shannon diversity index) of the trees between 2005 and 2010 surveys, we computed species accumulation curves using EstimateS 8.2 software (Colwell 2013). Curves were generated using 999 randomizations of sampling units and means and standard deviations were used for comparisons. To determine the evenness of the vegetation, we also calculated Pielou's evenness indices (Kent 2011).

Tree community structure and population dynamics. Tree community structure of the SDTF community was visualized by plotting bar plots showing the size class distribu-

tions of the overall tree community and the top five most representative and abundant species (henceforth "important species"). The selection of the five important species was based on their importance value (IV) in both surveys – an index that accounts for species density, dominance and cover (Kent 2011). We classified stem sizes into eight equal DBH classes of 6 cm intervals each: $3 \leq DBH_1 < 9$; $9 \leq DBH_2 < 15$, $15 \leq DBH_3 < 21$, $21 \leq DBH_4 < 27$, $27 \leq DBH_5 < 33$, $33 \leq DBH_6 < 39$, $39 \leq DBH_7 < 45$ and $DBH_8 > 45$ cm.

Population dynamics and the changes in tree community structure were determined in terms of annual recruitment and mortality rates of individuals (demographic parameters) and annual basal area increment and loss rates (biomass-related parameters). Dynamics parameters were calculated for the total sample and for each diameter class according to exponential formulas by Sheil and May (1996). The rate and direction of structural changes were determined by analyzing turnover rates and net changes in the number of individuals and basal area – BA (*sensu* Korning and Balslev 1994).

We, therefore, used the following formulas to calculate parameters of mortality (M), recruitment (R), basal area loss (L), basal area increment (G), turnover in abundance (TN) and basal area (TBA), and net changes in abundance (ΔN) and basal area (ΔBA):

$$M = \{1 - [(N_0 - m)/N_0]^{1/t}\} \times 100 \qquad [1]$$

$$R = [1 - (1 - r/N_t)^{1/t}] \times 100 \qquad [2]$$

$$L = \{1 - [(BA_0 - (BA_m + BA_d)/BA_0]^{1/t}\} \times 100 \qquad [3]$$

$$G = \{1 - [1 - (BA_r + BA_g)/BA_t]^{1/t}\} \times 100 \qquad [4]$$

$$TN = (M + R)/2 \qquad [5]$$

$$TBA = (P + G)/2 \qquad [6]$$

$$\Delta N = [(N_t/N_0)^{1/t} - 1] \times 100 \qquad [7]$$

$$\Delta BA = [(BA_t/BA_0)^{1/t} - 1] \times 100 \qquad [8]$$

In the formulas, t corresponds to the time between surveys; N_0 and N_t correspond to the initial and final number of trees; m and r are the number of dead trees that were alive in the first measurement, though not in the second, and new recruits that reach the minimum size class diameter and therefore were included in the survey, respectively. Lastly, BA refers to basal area in the 2005 (BA_0) and 2010 (BA_t) surveys, of dead (BA_m) and recruited (BA_r) individuals, and of individuals with basal area decrease (BA_d) and gain (BA_g). To determine possible structural changes between surveys, we compared the values found in 2005 and 2010 using a *G* test (Zar 2010).

RESULTS

Species richness and diversity indices. In 2005, we recorded 1,321 tree individuals in our vegetation survey, consisting of 67 species within 19 families (Santos *et al.* 2012). Species richness in individual plots ranged between 12–25 species. In 2010, we observed 3.1 % increase in stem abundance (1,363 individuals) and reduction in species richness (65 species) across our plots. Eighteen species were represented by single individuals, and these constituted over 25 % of the species richness of the tree community in 2005. Meanwhile, four of these species were not recorded in 2010 due to mortality of individuals of the species *Bauhinia cheilantha* (Bong.) Steud., *Cnidoscolus oligandrus* (Müll.Arg.) Pax, *Jatropha mollissima* (Pohl) Baill., and *Senna spectabilis* (DC.) H.S. Irwin *et* Barneby. However, two new species *Bauhinia catingae* Harms and *Terminalia fagifolia* Mart. were included in the survey in 2010. Species represented by two or more individuals were all present in the 2010 survey.

There were no conspicuous differences in species richness (figure 1A), Shannon diversity index (figure 1B), or Pielou's evenness index (not plotted) between the two sampling periods (table 1).
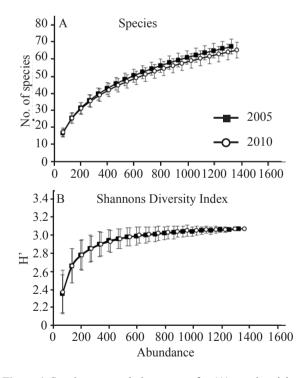

Figure 1. Species accumulation curves for (A) species richness and (B) Shannon diversity index (H') in a seasonally dry tropical forest tree community at Vale Verde farm, Juvenília, Minas Gerais, southeast Brazil in 2005 and 2010.

Curvas de acumulación de especies para (A) riqueza de especies y (B índice de diversidad de Shannon (H') en una comunidad de bosques tropicales estacionalmente secos en la granja Vale Verde, Juvenília, Minas Gerais, sudeste de Brasil en 2005 y 2010.

Table 1. Vegetation parameters of a seasonally dry tropical forest tree community in a long-term study in Minas Gerais, southeast Brazil in 2005 and 2010. Standard deviations are indicated where applicable and different alphabets indicate significant differences between years based on G-tests (Zar 2010) at α = 0.05.

Parámetros de vegetación de una comunidad de bosques tropicales estacionalmente secos en un estudio a largo plazo en Minas Gerais, sudeste de Brasil en 2005 y 2010. Las desviaciones estándar son indicadas donde sea aplicable y diferentes alfabetos indican diferencias significativas entre años basados en pruebas G (Zar 2010) en α = 0,05.

Vegetation parameter	2005	2010
Overall species richness	67	65
Overall Shannon's diversity index	3.06[a]	3.07[a]
Overall Pielou's Evenness index	0.73[a]	0.73[a]
Total no. of stems	1321	1363
Mean no. of Stems (plot^{-1})	66.1 (± 20.52)	68.25 (± 21.19)
Total basal area (m^2 ha^{-1})	16.49	18.34
Basal area (m^2 plot^{-1})	0.66[a] (± 0.16)	0.73[b] (± 0.17)

Tree community structure and population dynamics. Across the two surveys, the tree diameter distribution of the overall community did not show very large differences. The tree community represented in the total sample showed a reduction in abundance only in the first diameter class, and there was a slightly higher abundance of stems in the second diameter class ($6 \leq DBH_2 < 12$ cm; figure 2A). In addition, over 80 % of individuals remained in their size class, except for the first diameter class, in which only 63.9 % of original individuals remained in the class.

Annual recruitment in the tree community was higher than mortality, with 123 and 81 tree individuals recruited and dead respectively in 2010. This resulted in a positive net increase in the number of individuals in the community (tables 1, 2). The percentage of surviving individuals in 2010 was 90.97 %, whereas annual turnover rate was 1.57 %. The monitoring of tree community structure and composition showed faster basal area turnover rates, mainly due to high gain rates (table 2). Annual gain (3.79 % year^{-1}) was mainly due to the growth of surviving individuals, and loss rates (1.40 % year^{-1}) due to losses caused by the death of individuals. The higher rates of annual gain compared to loss, resulted in positive net changes in biomass with increased basal area in the tree community (tables 1, 2).

Recruitment and mortality events occurred mainly in the first two size classes (table 3); the first three diameter classes showed differences between the abundance of dead individuals and recruits when cross-compared. The first diameter class had a high number of recruits, whereas the first two size classes falling between 3 and 15 cm DBH had the highest mortality. Of the total number of dead individuals (79 individuals), 93.7 % were recorded in these first two size classes, while the trees with DBH ≥ 15 cm accounted for only 6.3 % of dead individuals (5 individuals) (table 3).

The five species of higher abundance and importance value (IV) were the same in both survey periods (figure 2) and consisted of *Anadenanthera colubrina* (Vell.) Brenan, *Poincianella pluviosa* (DC.) L.P. Queiroz, *Myracrodruon urundeuva* Allemão, *Handroanthus ochraceus* (Cham.) Mattos, and *Schinopsis brasiliensis* Engl. In 2005, *H. ochraceus*, *P. pluviosa*, and *S. brasiliensis* exhibited high density of small-sized individuals, which formed the lower strata under the canopy (figure 2B, C, F). The other two species, *A. colubrina* and *M. urundeuva*, exhibited high densities, however they also presented high dominances due to the presences of larger individuals (figure 2D, E).

As observed in the total sample, the most abundant tree species exhibited higher annual increment in basal area than losses due to mortality, resulting in net positive changes, especially in *H. ochraceus* and *M. urundeuva* (table 2). This accentuated the net positive changes (table 2) associated with an increase in cover value in *M. urundeuva* (table 4). The basal area gain observed in *M. urundeuva* accentuated its relative dominance (table 3), and as a result, the species had the second highest importance value (IV) in 2010, moving up one position from 2005.

The five important species showed more differing patterns in recruitment than in mortality: *Handroanthus ochraceus* was the only species which showed significantly higher recruitment than mortality events (table 2), whereas *A. colubrina* and *S. brasiliensis* showed an opposite pattern (table 2). In *P. pluviosa* and *M. urundeuva* (table 2), mortality rates were higher than recruitment, although the number of dead individuals and recruits did not differ significantly. Therefore, with the exception of *H. ochraceus*, there was an overall reduction in the number of individuals and absolute densities between surveys among the important species (table 2).

DISCUSSION

We surveyed a Seasonally Dry Tropical Forest fragment in northern Minas Gerais in 2005 and 2010 to examine the successional dynamics of the tree community. Our study represents one of the few, to date, to examine the temporal vegetation dynamics of SDTF vegetation in Brazil (Werneck and Franceschinelli 2004). In general we found a number of changes in tree demography and vegetation dynamics patterns in line with a later successional forest.

Species richness and diversity. The species richness of the community we sampled is typical of seasonally dry Brazilian ecosystems, which ranges between 36 and 110 species per hectare (Apgaua *et al*. 2014a, Reis *et al*. 2017), and
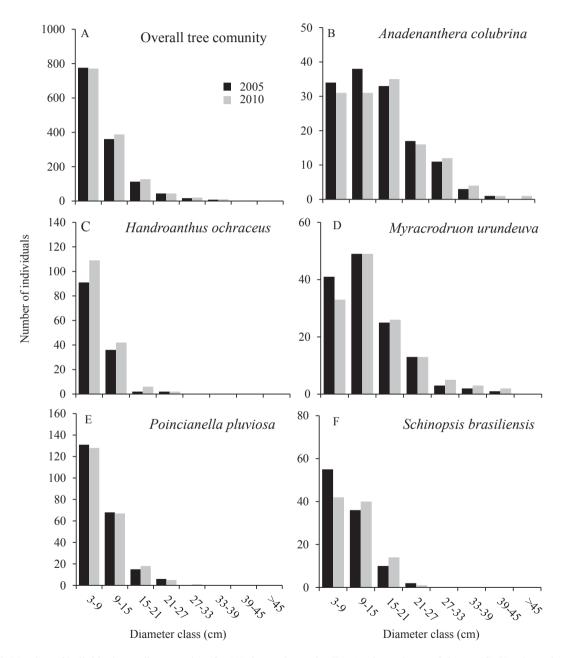

Figure 2. Number of individuals per diameter class for (A) the total sample; (B) *Anadenanthera colubrina*; (C) *Handroanthus ochraceus*; (D) *Myracrodruon urundeuva*; (E) *Poincianella pluviosa*; and (F) *Schinopsis brasiliensis* in a Seasonally Dry Tropical Forest tree community in Minas Gerais, southeast Brazil in 2005 and 2010.

Número de individuos por clase de diámetro para (A) la muestra total; (B) *Anadenanthera colubrina*; (C) *Handroanthus ochraceus*; (D) *Myracrodruon urundeuva*; (E) *Poincianella pluviosa*; y (F) *Schinopsis brasiliensis* en una comunidad de bosques tropicales estacionalmente secos en Minas Gerais, sudeste de Brasil en 2005 y 2010.

Table 2. Dynamics parameters and abundance of dead and recruited individuals for the total sample and for the most abundant species of a seasonally dry tropical forest tree community in Minas Gerais, southeast Brazil in 2005 and 2010. The abbreviations M and R correspond to the number of dead and recruited individuals, and BA_m and BA_r to the basal area (m^2) of these dead and recruited individuals respectively; N_0 and N_t to stem abundance, and BA_0, BA_t to the basal areas of these individuals in the 2005 and 2010 surveys respectively; TN and ΔN to turnover, and net changes in abundance; BA_g, and BA_d to basal area gain and decrease respectively; L, G, TBA and ΔBA correspond, respectively, to annual rates of basal area loss (%), gain (%), and turnover and net change in basal area; G-test to the G-test statistic (Zar 2010) and ns: non-significant at $\alpha = 0.05$.

Parámetros de dinámica y abundancia de individuos muertos y reclutados para la muestra total y para las especies más abundantes de una comunidad de bosques tropicales estacionalmente secos en Minas Gerais, sudeste de Brasil en 2005 y 2010. Las abreviaturas M y R corresponden al número de los individuos muertos y reclutados, y BA_m y BA_r al área basal (m^2) de estos individuos muertos y reclutados, respectivamente; N_0 y BA_t para la abundancia y BA_0, BA_t a las áreas basales de estos individuos en los estudios de 2005 y 2010, respectivamente; TN y ΔN al tasa de rotación, y cambios netos en la abundancia; BA_g y BA_d a la ganancia y disminución del área basal, respectivamente; L, G, TBA y ΔBA corresponden, respectivamente, a las tasas anuales de pérdida de área basal (%), ganancia (%) y tasa de rotación, y cambio neto en el área basal; prueba G a la pruebas estadística G (Zar 2010) y ns: no significativas a $\alpha = 0,05$.

	Abundance				Dynamics parameters				Poisson counts	
	M	R	N_0	N_t	M	R	TN	ΔN	G-test	P
Total sample	81	123	1,321	1,363	1.26	1.87	1.57	0.63	2.94	< 0.01
Anadenanthera colubrine	8	1	137	130	1.20	0.15	0.68	-1.04	2.33	< 0.05
Poincianella pluviosa	12	10	220	218	1.12	0.93	1.03	-0.18	0.43	Ns
Myracrodruon urundeuva	4	1	135	132	0.60	0.15	0.38	-0.45	1.34	Ns
Handroanthus ochraceus	1	29	131	159	0.15	3.95	2.05	3.95	5.11	< 0.001
Schinopsis brasiliensis	7	1	103	97	1.40	0.21	0.80	-1.19	2.12	< 0.05

	Basal area						Dynamics parameters			
	BA_m	BA_r	BA_0	BA_t	BA_g	BA_d	L	G	TBA	ΔBA
Total sample	0.53	0.21	13.20	14.91	2.41	0.37	1.40	3.79	2.59	2.42
Anadenanthera colubrina	0.13	0.002	3.39	3.67	0.48	0.04	1.01	2.81	1.91	1.62
Poincianella pluviosa	0.07	0.01	1.68	1.77	0.20	0.05	1.53	2.51	2.02	1.01
Myracrodruon urundeuva	0.04	0.001	2.64	3.01	0.43	0.02	0.46	3.07	1.77	2.69
Handroanthus ochraceus	0.0009	0.05	0.71	0.96	0.21	0.0007	0.05	5.93	2.99	6.25
Schinopsis brasiliensis	0.02	0.0008	0.90	0.95	0.11	0.04	1.39	2.43	1.91	1.07

Table 3. The number of remaining, recruited and dead individuals per diameter class between 2005 and 2010 in a seasonally dry tropical forest tree community in Minas Gerais, southeast Brazil.

Número de individuos remanentes, reclutados y muertos por clase de diámetro entre 2005 y 2010 en una comunidad de bosques tropicales estacionalmente secos en Minas Gerais, sudeste de Brasil.

Size classes (cm)	Individuals remaining	Recruitment	Mortality
3-9	632	121	59
9-15	298	85	15
15-21	92	33	2
21-27	30	13	3
27-33	11	9	0
33-39	5	5	0
39-45	1	1	0
>45	1	1	0

Table 4. Density, dominance and cover values for the most abundant tree species in a seasonally dry tropical forest tree community in Minas Gerais, southeast Brazil in 2005 and 2010. Absolute values of density and dominance refer to the number of stems and basal areas (m^2) respectively, and the relative values to the percentages of these values as a function of the total. Cover values are expressed as a percentage of the total cover.

Valores de densidad, dominancia y cobertura de las especies de árboles más abundantes en una comunidad de bosques tropicales estacionalmente secos en Minas Gerais, sudeste de Brasil en 2005 y 2010. Los valores absolutos de densidad y dominancia se refieren al número de tallos y áreas basales (m^2) respectivamente, y los valores relativos a los porcentajes de estos valores en función del total. Los valores de la cobertura se expresan como un porcentaje de la cobertura total.

Species	Density				Dominance				Cover value	
	Absolute		Relative		Absolute		Relative			
	2005	2010	2005	2010	2005	2010	2005	2010	2005	2010
Anadenanthera colubrina	171.25	162.5	10.37	9.54	4.18	4.59	25.36	24.61	17.86	17.07
Poincianella pluviosa	275	272.5	16.65	15.99	2.1	2.21	12.75	11.87	14.7	13.93
Myracrodruon urundeuva	168.75	165	10.22	9.68	3.26	3.77	19.77	20.21	14.99	14.95
Handroanthus ochraceus	163.75	198.75	9.92	11.67	0.89	1.21	5.4	6.47	7.66	9.07
Schinopsis brasiliensis	128.75	121.25	7.8	7.12	1.12	1.18	6.81	6.36	7.3	6.74

we found no significant changes in species richness and diversity between the two survey periods.

The lack of change in species richness and diversity was not surprising considering that species recovery can often occur on the scale of centuries (Chazdon 2003), and that our plots were only recensused after five years. Nevertheless, the lack of differences in species richness and diversity and evenness between surveys probably reflects that the SDTF vegetation at the study site is not at an early successional phase, although the short time period between surveys could have made it less likely that new species were recruited.

Tree demography and population dynamics. Contrary to our hypothesis that there would be a reduction in stem density, we found a small increase in stem abundance after five years. This slight change was again probably due to the short time period between surveys; nevertheless, the slight increase is much lower than what would be expected for an early successional forest. Similar findings have been reported for mature Amazonian and Atlantic forests (Lewis *et al.* 2004, Saiter *et al.* 2011) because tree population dynamics in late successional forests is characterized by slow growth and recruitment rates, and thus low turnover rates (Swaine and Whitmore 1988). In deciduous and ombrophilous forests subjected to more frequent anthropogenic and natural disturbances, other works have found a higher turnover in abundance (Lewis *et al.* 2004, Werneck and Franceschinelli 2004, Fontes and Walter 2011).

The tree community in our study exhibited a low mortality rate compared to riparian rain forests (Guilherme *et al.* 2004, Fontes and Walter 2011), and also some seasonal tropical forests (Werneck and Franceschinelli 2004), which was contrary to our expectations considering that

seasonal drought may be a cause of high mortality in SDT-Fs. However, more data will be needed to validate this point.

In terms of basal area, the tree basal area turnover rates of the tree community in our study were high, considering that rates above 2 % have been reported in more dynamic, seasonal forest fragments often subjected to natural disturbances (Guilherme *et al.* 2004) or with recent natural regeneration (Machado and Oliveira-Filho 2010). Lewis *et al.* (2004) reported high basal area turnover rates in Amazonian moist forests at late successional stages and showed that mature forests may have accelerated biomass dynamics. Likewise, the high turnover rate in basal area in our study was mainly due to the high basal area gain, which appears to be related to the high percentage of surviving individuals and their increase in basal area. In particular, this is a result of the increment of larger diameter trees. The basal area gain of recruits represented only 12.2 % of total basal area increment, which is slightly lower than the value observed in more humid tropical rain forests, where recruits may represent on average 15 % of the basal area increment (Lewis *et al.* 2004).

In terms of demography and diameter size class distributions, tree populations in tropical rain forests often exhibit a reverse J-shaped diameter size class curve (Sheil and May 1996), due to continuous recruitment and gap-phase dynamics favoring a large number of stems in the smallest size classes. Likewise, our tree size class distributions show that the overall tree community and some of the most abundant species exhibit a similar reverse J-shaped diameter size class curve, perhaps reflecting continuous recruitment during wet seasons. However, we also found that in a number of key species (*A. colubrina*, *H. ochraceus* and *M. urundeuva*), the largest number of individuals

was concentrated in the second DBH size class (9-15cm). The absence of a typical reverse J-shaped diameter curve in these species has been reported in other similar sites (Apgaua *et al.* 2014a), and may reflect an inherent difference in the demography of humid forest and some seasonal forest tree populations. It is also possible that past human use may have played a role in these patterns, although this needs to be further validated.

The occurrence of seasonal drought in SDTF habitats is possibly the key driver of differences in these demographic and dynamic patterns. For some species, the lower abundance of trees in the first, compared to the second diameter class at our site, may reflect the strategies of lower size classes in response to seasonal water shortage, which is more likely to lead to mortality in younger individuals (Fauset *et al.* 2012). Particularly in areas with seasonally dry soils, the shallow root systems of smaller-sized plants may limit their ability to tap into deeper soil water reservoirs. Individuals and species that can grow fast during favorable periods would therefore have a chance of survival, and therefore move into a larger size class.

Demography of important species. Our five important species, *Anadenanthera colubrina*, *Handroanthus ochraceus*, *Myracrodruon urundeuva*, *Poincianella pluviosa* and *Schinopsis brasiliensis*, represent the most frequent and abundant species that characterize Seasonally Dry Tropical Forests in northern Minas Gerais (Santos *et al.* 2012) and in Brazil in general (Särkinen *et al.* 2011), and can, therefore, provide important insights in the long-term dynamics of SDTFs.

The patterns of change in the demography of these species reflect the changes in community structure and species hierarchy of the tree community, highlighting the dynamic equilibrium of tropical forests. For instance, the reduction in density of *A. colubrina*, *P. pluviosa*, *S. brasiliensis* and *M. urundeuva* (accompanied by a reduction in dominance in the first three species) was probably associated with an increase in density or dominance of other species, although there was very little or no change in the overall diversity or evenness in the community across survey periods. Moreover, the increment in abundance and basal area of *H. ochraceus* and the increased dominance of *M. urundeuva*, which are representative of the subcanopy and canopy respectively, reflect an increased vertical complexity in the tree community. This increase in abundance and basal area of *H. ochraceus* and the biomass accumulation of *M. urundeuva* may represent the recovery of these tree populations from exploitation since the area was demarcated for protection.

CONCLUSIONS

After a five-year period between surveys in a remnant patch of seasonally dry tropical forest, we found no significant differences in species richness and diversity. In addition, the patterns of evenness and natural regeneration that we found during our 5-year study period suggest that our tree community is at a late successional stage, although continuous monitoring over longer time periods would be needed to validate this point further. In general, we observed a high proportion of stems at the smallest stem size classes of our tree community due to high recruitment; nevertheless, at the same time, this class of small-stemmed individuals also exhibited high mortality. This demographic pattern reflects stable vegetation dynamics in agreement with previous studies. Our study fills a knowledge gap on temporal studies in seasonally dry tropical forest, and will have implications for the conservation and management of seasonally dry forests in the region. Future studies may benefit from modelling the demography of important seasonally dry tropical forest species across a wider geographical extent.

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