VARIATIONS IN PRECIPITATION AND THE EQUILIBRIUM DYNAMICS OF A TROPICAL FOREST TREE COMMUNITY IN SOUTH-EASTERN BRAZIL

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Tropical forests are dynamic communities where stochastic and unpredictable events such as climate change affect key ecological processes. The objective of this study was to describe the dynamic behaviour of a semideciduous seasonal forest during 15 years of monitoring, with four sampling intervals, in order to verify if fluctuations in forest dynamics are related to precipitation variations. The work was carried out based on diameter at breast height measured in 25 plots of 400 m² each in four forest inventories (2000, 2005, 2009, 2015). To evaluate the direction of forest dynamic changes over time, we performed analyses of mortality rates, recruitment and net changes in number of individuals and rates of loss and gain in basal area. The results suggested that the forest was undergoing a rhythmic cycle characterised by the imbalance in forest dynamics, with rates of mortality and gain in basal area greater than those of recruitment and loss in basal area respectively. However, this natural cycle may be influenced by variation in precipitation, since in the periods characterised as dry, mortality rates increased and there was less increment in basal area.

Keywords: Fragment, forest dynamics, rhythmic cycle, climate changes, semidecidual seasonal forest, temporal changes

INTRODUCTION

Tropical forests are higly dynamic systems where stochasticity and unpredictable events affect many ecological processes that occur in its communities (Roitman & Vanclay 2015). In forests under natural disturbances, tree community dynamic equilibrium is reached after periods of instability or imbalance between dynamics rates, where periods with predominance of mortality events and/or loss in the basal area are counterbalanced by recruitment phases and/or biomass gain (Swaine 1990, Felfili 1995a).

Imbalance occurrs due to the nature of silvigenic processes, where mortality occurs first followed by the occorence of recruitment, thus creating an imbalance over a short period of time (Felfili 1995b). In addition to causing density reduction, high mortality can also result in considerable losses in basal area (Sheil et al. 2000), although open space in the tree community may favour the growth of individuals and increased basal area. The dynamic imbalance is influenced by the type, intensity and frequency of disturbances in the community and may cause fluctuations of dynamic rates, resulting in instability periods (Rolim et al. 1999). Among these disturbances, current climate changes have led to massive reorganisation of floristic composition, structure and dynamics of tropical forests (Wright et al. 2005, Lewis et al. 2009, Fauset et al. 2012).

Changes in precipitation patterns have direct consequences on many species, resulting in changes in floristic composition and functioning of the forests (Engelbrecht et al. 2007). Severe droughts in tropical forests have been associated with high rates of tree mortality and rotation, and reduction in recruitment, growth and accumulation of biomass (Rolim et al. 1999, Bonal et al. 2016). High temperatures associated with drought also have great consequences on plant functions due its influence on photosynthesis and respiration, as well as on stomatal regulation. This physiological restriction may lead to limitation in carbon assimilation, which can cause death of trees during dry season (Santiago et al. 2016).

In order to assess the effects of severe drought events on tropical forests, tree communities must be monitored during low rainfall events (Fauset et al. 2012). Periods with significant precipitation deficits were observed in south-eastern Brazil in 1953, 1971, 2001 and more recently in 2013–2014 (Marengo et al. 2015), with recent events demonstrating increased severity and duration.

Thus, in this work, our objective was to describe the dynamic behaviour of a semideciduous seasonal forest during 15 years of monitoring, with four sampling intervals. From the data on community dynamics and precipitation, we sought to verify if fluctuations in dynamics of the forest were related to variations in precipitation.

MATERIALS AND METHODS

The study area is a semideciduous seasonal forest fragment located on the banks of the Ingaí River (21° 24' S, 44° 55' W), in the municipality of Ingaí, southern region of Minas Gerais. The fragment has a total area of 16.85 ha, with altitude varying between 870 and 890 mm (Figure 1). The study area presents occupation history associated with selective cut of trees at the edge of the fragment in 1950 and presence of domestic animals such as cattle and horses that were very common until 2009 (Botrel et al. 2002). Some trails in the fragment are probably associated with sporadic presence of these animals and fishermen visits. The adjacent matrix is formed by other small fragments and anthropic areas (e.g. pastures and eucalyptus).

The climate in this region is classified as Koppen's Cwa (subtropical with dry winter and rainy summer), with average annual rainfall of 1476 mm (Dantas et al. 2007). Average annual temperature is 20 °C, with maximum of 28.1 °C and minimum, 9.3 °C (Oliveira-Filho 2014).

In order to evaluate the seasonal behaviour of rainfall and to detect dry and rainy periods, we calculated the annual rainfall anomaly index (RAI). For this we used precipitation of the historical data from 1968 till 2015 obtained from the meteorological station in the municipality of Lavras, Minas Gerais, 30 km from the municipality of Ingaí, Minas Gerais (INMET 2015). For calculation of RAI we only used years with complete monthly averages of precipitation. We used equations proposed by Van Rooy (1965):

Positive anomalies:
$$RAI = 3 \times [(N - N_m) / (M_m - N_m)] \qquad (1)$$

Negative anomalies:
$$RAI = -3 \times [(N - N_m) / (X_m - N_m)] \qquad (2)$$
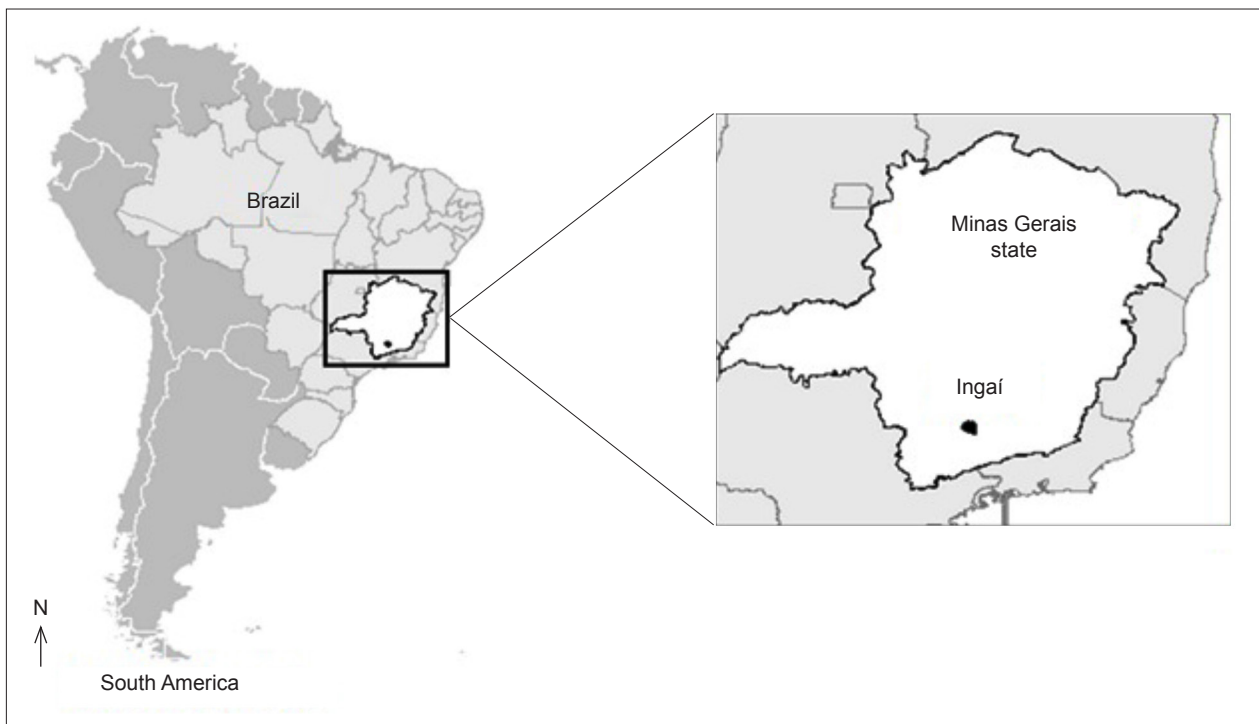
Figure 1   Location of study area, Ingaí in the state of Minas Gerais, Brazil

where: N = current annual precipitation (mm), N_m = average annual precipitation (mm) of the historical series, M_m = mean of 10 largest annual precipitations of the historical series (mm) and X_m = average of 10 lowest annual precipitations of the historical series (mm). Positive anomalies were represented by values above mean and negative, below it. We determined the RAI of monitoring intervals from the average annual precipitation of years that composed each monitoring interval. One interval ended and the next began the same year, e.g. the year 2005 in the first interval represented the final stage of the forest, while in the second interval, the same data represented the initial stage of the forest. The RAI intensity was determined according to the intensity classes presented in Table 1.

Table 1   Rainfall anomaly index (RAI) intensity classes

RAI band	Intensity classes
> 4	Extremely rainy
2 – 4	Very rainy
0 – 2	Rainy
0	Normal
0 – -2	Dry
-2 – -4	Very dry
< -4	Extremely dry

Sorce: Marcuzzo et al. (2011)

There were three arboreal community inventories in the study fragment. The first survey was carried out between August 1999 and August 2000, when 25 permanent plots of 20 m × 20 m were allocated, totalling 1 ha of sample area (Figure 2). The plots layout is detailed in Botrel et al. (2002). All tree individuals with DBH (diameter at breast height) ≥ 5 cm in each plot were sampled and marked with numbered aluminum tags (Botrel et al. 2002). Individuals with multiple stems were recorded when the root of the squares of DBH was ≥ 5 cm. When this single DBH exceeded the inclusion criterion, the individual was includeded in the inventory (Scolforo & Mello 2006). The plots were resurveyed in 2005, 2009 and 2015 and all surviving trees were remeasured. New individuals that reached the inclusion criterion (recruits) were identified until species level, measured for DBH and height and marked with numbered

aluminum tags. Dead individuals were also recorded.

We evaluated the tree community dynamics from rates of individual mortality (M, equation 3), recruitment (R, 4), as well as loss (L, 5) and gain (G, 6) in basal area (Sheil et al. 1995, Sheil & May 1996):

$$M = \left\{ 1 - \left[\frac{N_0 - N_m}{N_0} \right]^{\frac{1}{t}} \right\} \times 100 \tag{3}$$

$$R = \left\{ 1 - \left[1 - \left(\frac{N_r}{N_t} \right) \right]^{\frac{1}{t}} \right\} \times 100 \tag{4}$$

$$L = \left\{ 1 - \left[\frac{(Ab_0 - (Ab_d + Ab_m))}{Ab_0} \right]^{\frac{1}{t}} \right\} \times 100 \tag{5}$$

$$G = \left\{ 1 - \left[1 - \left(\frac{Ab_r + Ab_g}{Ab_t} \right) \right]^{\frac{1}{t}} \right\} \times 100 \tag{6}$$

We used the net change in the number of trees (7) and basal area (8) (Ch_N and Ch_{Ab} respectively), which were determined from the formulae described by Korning and Balslev (1994).

$$Ch_N = \left[\left(\frac{N_t}{N_0} \right)^{\frac{1}{t}} - 1 \right] \times 100 \tag{7}$$

$$Ch_{Ab} = \left[\left(\frac{Ab_t}{Ab_0} \right)^{\frac{1}{t}} - 1 \right] \times 100 \tag{8}$$

In the equations, N_0, N_t, N_m and N_r = numbers of initial, final, dead and recruited trees respectively in the time interval (t), Ab_0, Ab_t, Ab_m, Ab_d, Ab_r and Ab_g = respectively, the basal areas of the initial live, final and dead living trees, the basal area lost by the decrease of survivors, the basal area of the recruits and the basal area gained by survivors. We corrected mortality rates and recruitment of individual trees according to Lewis et al. (2004) (equation 9) due to irregularities between sampling time periods:

$$\lambda' = \lambda \times t^{0.08} \tag{9}$$

where λ' = rate of corrected dynamics and λ = verified dynamics rates.
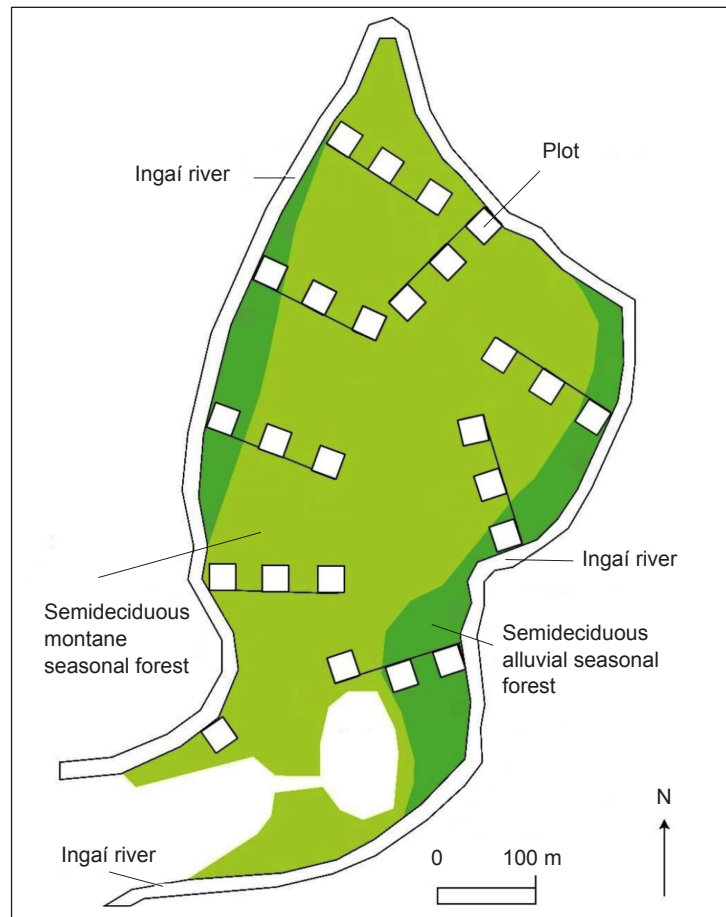
Figure 2   Map of the semideciduous seasonal forest fragment in Brazil showing the distribution of 20 m × 20 m sample plots

We also tested whether the data obtained were normally distributed using Shapiro-Wilk test (Zar 2010). In order to verify the existence of differences over time in the structural parameters of basal area and density, we used the paired *t*-test, with significance level of 5%. We verified the temporal changes in number of deaths, recruits, loss (basal area of the dead plus decrement) and gain (basal area of the recruits plus increment) by Kruskal–Wallis non-parametric test with Mann–Whitney test, using 5% as significance level.

RESULTS

Precipitation data showed temporal alternations, but the number of dry years predominated throughout the monitoring period (Table 2). In the first interval (2000–2005) four dry (2001, 2002, 2003 and 2005) and two rainy (2000 and 2004) years occurred and the greatest inflection point of the dry period occurred in 2002, with RAI of -3.41, characterising it as very dry. The greatest inflection point of the rainy years in this

interval occurred in 2004 (0.40, rainy). Thus, the overall period between 2000 and 2005 was characterised as a dry period. In the second interval (2005–2009), three rainy and two dry years occurred. The greatest RAI in the rainy year was 1.74, and the driest year had a RAI of -2.20 (very dry). However, the average period was classified as rainy (Table 2). In the third interval (2009–2015) the number of dry years was higher compared with rainy years (Table 2). Higher drought intensity was observed during this period, such as in 2014 when RAI was -4.03 (extremely dry). The greatest inflection point for rainy years was observed in 2011 (1.65, rainy). The overall monitoring interval was characterised as dry. Highest precipitation (85% of the total) was between October and March, while from April till September, monthly precipitation did not exceed 100 mm.

Tree density significantly (p < 0.001) reduced throughout the period of monitoring, especially between 2009 and 2015, i.e the third interval (Table 3). The number of dead trees was

Table 2   Annual precipitation and rainfall anomaly index (RAI) of the municipality of Lavras, Minas Gerais, Brazil between 1999 and 2015

Year	Precipitation (mm year^{-1})	RAI	Intensity	Interval	Precipitation average (mm year^{-1})	RAI	Intensity
1999	1491.0	0.40	Rainy	2000–2005	1372.6	-0.80	Dry
2000*	1469.7	0.23	Rainy	2005–2009	1485.2	0.40	Rainy
2001	1324.0	-1.34	Dry	2009–2015	1342.4	-1.10	Dry
2002	1142.4	-3.41	Very dry				
2003	1222.0	-2.50	Very dry				
2004	1489.0	0.40	Rainy				
2005*	1433.7	-0.10	Dry				
2006	1461.2	0.16	Rainy				
2007	1248.2	-2.20	Very dry				
2008	1646.0	1.74	Rainy				
2009*	1623.6	1.55	Rainy				
2010	1131.8	-3.53	Very dry				
2011	1635.2	1.65	Rainy				
2012	1291.4	-1.71	Dry				
2013	1380.6	-0.70	Dry				
2014	1087.6	-4.03	Extremely dry				
2015*	1246.0	-2.23	Very dry				

* = community measurements were conducted; one interval ends and the next begins the same year, e.g. the year 2005 in the first interval represent the final stage of the forest, while in the second interval, the same data represent the initial stage of the forest

Table 3   Structural and dynamic parameters of arboreal community at the fragment of the semideciduous seasonal forest located in Íngaí, Minas Gerais, Brazil

Parameter	Total sample			
	2000	2005	2009	2015
Structure				
Density (indivivual ha^{-1})	2683	2618	2575**	2331**
Basal area (m² ha^{-1})	28.37**	30.47**	32.91**	33.12
Dynamics				
Mortality rate (% year[-1])		2.30	3.02	3.78
Recruitment rate (% year[-1])		1.75	2.57	1.91
Number of dead trees		260 a	272 a	466 b**
Number of recruits		195 a	229 a	222 a
Loss rate (% year[-1])		2.06	2.22	2.52
Gain rate (% year[-1])		3.50	4.09	2.63
Loss[+] (m²)		-2.89 a	-2.62 a	-4.68 b**
Gain[+] (m²)		5.00 a	5.06 a	4.90 a
Net change in individuals (% year[-1])		-0.49	-0.41	-1.65
Net change in basal area (% year[-1])		1.44	1.94	0.11

* and ** represent values of $p < 0.05$ and < 0.01 respectively after paired analyses (*t*-test and Wilcoxon pairwise); lowercase letters represent significant statistical differences by the Kruskal–Wallis with Mann–Whitney tests; Loss[+]: decrease in basal area of the survivors + baseline area of death in m², Gain[+]: increase in basal area of survivors + basal area of recruits in m²

significantly higher during this time (mortality 3.78% year^{-1}), while the number of recruits did not show differences when compared over time (Table 3). With mortality rate higher than recruitment, net change values in number of individuals in the three periods were negative.

Accumulated basal area increased during the monitoring period, presenting significant differences in the first two monitoring intervals, i.e. 2000– 2005 and 2005–2009 (p = 0.001 and p < 0.001 respectively). Increase in basal area was contributed by the higher basal gain rates compared with loss rates, especially in the first two intervals. This imbalance resulted in positive values for net change in basal area in all three monitoring periods. Loss in basal area was significantly higher in the third interval (2.52% year^{-1}), while basal area gains did not show any significant changes between successive years (Table 3).

DISCUSSION

Dry years prevailed in the periods of monitoring tree community. Dry years have been more frequent in Brazil south-eastern region, where since the 1999/2000 summer, occurrences of lower annual precipitations than historical averages have become common (Coelho et al. 2016b, Getirana 2016). The dry period between 2000 and 2005 coincided with the 2001 drought that occurred in south-eastern region of Brazil (Marengo et al. 2015) and it extended until 2003 in the southern region of Minas Gerais as indicated by low RAI values (Table 2). Drought lasting several years is common because these events have longer time scales and may extend for decades (Cavalcanti 2012).

The wettest monitoring period was between 2005 and 2009. In 2009, a strong precipitation event occurred in Minas Gerais southern region. These high precipitation rates in Minas Gerais during this period were caused by the formation of South Atlantic Convergence Zone (SACZ) over Brazil south-eastern region (Alvarenga 2012). The formation of SACZ is one of the most important mechanisms of rainfall formation in this Brazilian region (Coelho et al. 2016a, Marengo et al. 2015).

The highest drought intensy occurred between 2012 and 2015. During this period, precipitation rates were 16% lower than annual average for south-east Brazil and the rainy season

of 2013–2014 recorded the lowest volume of rain in the historical series (Marengo et al. 2015, Getirana 2016). The main cause for the occurrence of this drought was an anomalously intense and prolonged high pressure system located on the Atlantic Ocean that avoided the formation of SACZ (Coelho et al. 2016a).

The tree community presented an ecological behaviour characterised by an imbalance between the rates of dynamics. This imbalance in dynamics is characteristic of undisturbed semideciduous seasonal forest fragments. It is due to the occurrence of natural rhythmic cycles of forests, which consist of compensatory dynamics where dead trees are replaced by new individuals and/or growth of remnants (Felfili et al. 1995b, Silva & Araújo 2009, Mews et al. 2011). In the fragment, the rhythmic cycle has caused negative changes in the number of trees but positive changes for basal area, describing self-harvesting of the forest. In this case, the maintenance of the growth of trees occurs to the detriment and mortality of numerous other trees (Higuchi et al. 2008).

Dynamic imbalance also may be influenced by transient disturbances such as climatic fluctuations, which can alter the forests rhythmic cycles and implying periods of instabilities. Thus, the predominance of dry years may have influenced the forest fragment rhythmic cycle by intensifying the tree community self-thinning process. The combination between increased mortality and reduced recruitment and growth of individuals has been described as one of the main tropical forest responses towards occurrence of drought events. These responses result in changes in the speed of structural modifications of tropical forests (Phillips et al. 2010, Roitman et al. 2016).

The response to drought events depends on the event severity and on the current species composition, since species composition may present different adaptations to drought (Corlett 2016, Singh & Kushwaha et al. 2016). Long-term droughts lead to changes in species composition that may favour drought-tolerant species via selective mortality of arboreal individuals, as observed in 2001 and 2013/2014 in the region (Feeley et al. 2011, Fauset et al. 2012). Thus the drought observed during the monitored period, i.e. mainly between 2012 and 2015, may have potentiated the restrictions for some species associated with the unfavourable season, causing

the death of species adapted to conditions of greater water availability and also of trees already naturally weakened. In the latter case water stress may have accelerated the predestined mortality of competitively suppressed trees, disease affected trees, and/or those in senescence stage (Itoh et al. 2012, Feldpausch et al. 2016). High mortality rates can still be observed in the years following severe droughts (Itoh et al. 2012, Doughty et al. 2015), which would keep mortality rates higher than recruitment for a few more years in the fragment. Mortality event occurs due to reduced investment in maintenance and/or defense of tissue by plants during dry season, which increases their vulnerability to pests and pathogens (Franklin et al. 2012, Doughty et al. 2015) and may boost early post-dry mortality. In this case, periodic monitoring is needed to check whether dry effects remain in the fragment over the subsequent years.

In addition to drought events, periods with intense precipitation can also influence community dynamics in other ways, such as via landslides and floods (Alvarenga 2012, Cavalcanti 2012). In the study fragment, there was one landslide event at one plot in the third interval (2009–2015), which resulted in the loss of this sample unity. This event had little influence on tree community dynamics, since the mortality rate still remained high in relation to previous intervals even after the removal of this plot. High mortality demonstrated a differentiated dynamic in the fragment margin that can be influenced by intense precipitations.

Besides causing density reduction, high mortality can also result in considerable losses in basal area (Sheil et al. 2000). However, in the study fragment mortality did not result in high loss rates, with the imbalance occurring in favour of basal area gain rates. This fact may indicate that mortality was more intense among small trees, which present a lower basal area. Small trees are subject to fierce competition for basic resources such as space, light, nutrients and water for their growth and development. Water availability is considered the most important factor for tree growth in semideciduous forests (Lisi et al. 2008). In the study area, the rates of gain were higher in the interval between 2005 and 2009 when rainfall indices were above the historical average. During the dry season, these species had their growth suppressed in order to survive the water deficit, shedding leaf as an important evolutionary adaptation to resist periods of low humidity (Lohbeck et al. 2013). Stem growth is one of first processes to be reduced by plants under stress conditions (Dobbertin 2005). Limitation in carbon assimilation imposed by drought can lead to increased mortality in tree species (Santiago et al. 2016). In the studied fragment the rates of basal area gain were lower in periods of drought occurrence. Growth deceleration was more pronounced in third monitoring period (2009–2015), when gain rates were in balance with basal area loss.

Low recruitment rates were expected due to advanced succession of forest fragment and its protection status. Forest maturation process increases plant cover by reducing recruitment of pioneer species (Lebrija-Trejos et al. 2010). Recruitment rates are thus maintained mainly by non-pioneer species that have low but steady recruitment throughout the entire process of forest development. The occurrence of the disturbance and the intensity of this disturbance will determine the size of the clearing; for example, larger gaps result in higher recruitment rates (Lima 2005). Pionner species recruitment is restricted mainly to clearings formed by tree falls or isolated trees (Paula et al. 2004), resulting in the growth of only few new individuals in the tree community.

Drought events may also influence tree recruitment in advanced stages of succession. Water availability is one of main factors regulating tree recruitment in seasonally dry climate, where greater recriutment occurs in higher humidity periods (Morton et al. 2011, Silveira et al. 2017). Although the number of recruited individuals was not significant accross the three intervals, the highest recruitment rate of the study was observed in 2005–2009, which coincided with the wettest period evaluated.

Dynamics of the tree community were described by fluctuations in rates of mortality and gain in basal area. These rythmic cycles in the fragment may be influenced by the advanced stage of forest succession and intensified by variations in precipitation.

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