

# Plant community dynamics in an urban forest fragment of the São Paulo Metropolitan Area, Brazil<sup>1</sup>

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**ABSTRACT** - (Plant community dynamics in an urban forest fragment of the São Paulo Metropolitan Area, Brazil). We present a synthesis (2006-2012) of plant community dynamics in an area (1 ha) of the largest remnant of Atlantic Rain Forest surrounded by São Paulo city. Plants with  $\geq 2.5$  cm dbh, including the climbers, were sampled in 10 transects ( $2 \times 50$  m), and the smaller ( $> 1$  m height,  $< 2.5$  cm dbh) in 10 subtransects ( $1 \times 50$  m). We sampled 901 individuals, 125 species (38 families), 83 classified as late-successional species, 12 threatened with extinction and 56 absent in the area management plan, some Endangered (EN) species. The climbers were the most dynamics, they had the largest decrease in basal area; and the larger ( $> 5.0$  cm dbh) and shorter ( $< 2.5$  cm dbh) trees had the highest mortality rates of the shrub-tree synusia. Late species regeneration was predominant. The studied forest showed progression towards more mature successional stages in the monitoring period.

**Keywords:** climbing plants, demography, permanent plots, secondary forest, understory

**RESUMO** - (Dinâmica da comunidade vegetal em um fragmento florestal urbano da área metropolitana de São Paulo, Brasil). Nós apresentamos uma síntese (2006-2012) da dinâmica da comunidade vegetal em uma área (1 ha) do maior remanescente de Mata Atlântica cercado pela cidade de São Paulo. As plantas com  $\text{dap} \geq 2,5$  cm, incluindo as trepadeiras, foram amostradas em 10 transectos ( $2 \times 50$  m) e as menores (altura  $> 1$  m,  $\text{dap} < 2,5$  cm) em 10 subtransectos ( $1 \times 50$  m). Nós amostramos 901 indivíduos, 125 espécies (38 famílias), 83 classificadas como tardias, 12 ameaçadas e 56 ausentes no plano de manejo da área, algumas Em Perigo (EN) de extinção. As trepadeiras foram as mais dinâmicas, com a maior redução de área basal; e as árvores maiores ( $\text{dap} > 5,0$  cm) e menores ( $\text{dap} < 2,5$  cm) tiveram a maior mortalidade da sinússia arbórea. A regeneração de espécies tardias foi a predominante. No período monitorado, a floresta estudada apresentou progressão para estádios sucessionais mais maduros.

**Palavras-chave:** demografia, floresta secundária, parcelas permanentes, plantas trepadeiras, sub-bosque

## Introduction

Human activities and climate fluctuations have been influencing the functioning of ecosystems (Holmgren *et al.* 2001, O'Brien *et al.* 2012, Seneviratne 2012), altering their natural regeneration and promoting unknown dynamics in plant communities (Hubbell & Foster 1992). Forest cycles may be shorter, communities may be more dynamic (Körner 2004, Laurance *et al.* 2009) and species distributions may be changing (Hubbell 2004, Colombo & Joly

2010, Machado & Oliveira-Filho 2010, Feeley *et al.* 2011). The functioning of plant communities need to be further studied; this becomes especially important when considering the upward trend in the frequency of environmental changes (Lavell *et al.* 2012), the speed with which these changes have occurred (Feeley *et al.* 2011) and their influence on the remaining ecosystems.

Secondary forests in different regenerative processes, like the disturbed forests, are among one of the main remaining ecosystems from tropical forests. Much of the biodiversity, such as endangered and

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rare species, are restricted to fragments of this forest (Brown & Lugo 1990, FAO 2010, Farah *et al.* 2017). Different disturbance histories, local conditions, and local resources have directed these environments in unknown directions, making forecast and diagnosis difficult, for management purposes (Chazdon *et al.* 2007, Rodrigues *et al.* 2009, Norden *et al.* 2009). One example is Parque Estadual das Fontes do Ipiranga (PEFI), the largest Atlantic Forest remnant with completely urbanized surroundings in the Metropolitan Region of São Paulo, one of the most populous regions in the world (SMA 2008).

Subject to numerous disturbances, such as fragmentation, isolation, biological invasion, fires, pollution, edge effect and heat island (Struffaldi-De-Vuono 1985, Gomes *et al.* 2003, SMA 2008), the PEFI is an important laboratory for the study of forest dynamics, besides the significant climate changes seen over the past 85 years (EM-IAG 2017). Studies on the plant communities in different parts of PEFI showed heterogeneous vegetation cover with patches of heavily impacted forest (Struffaldi-De-Vuono 1985, Costa & Mantovani 1992, Gomes & Mantovani 2001, Pivello & Peccinini 2002, Gomes *et al.* 2003, Davison 2009, Eisenlohr *et al.* 2009, Hirata *et al.* 2010, Villagra & Romaniuc-Neto 2011, Tanus *et al.* 2012), some in evident recovery process and some relatively little disturbed (Pivello & Peccinini 2002, Gomes *et al.* 2003).

Variations in the dynamics of plant communities can be evaluated and monitored using permanent transects in environments with different historical disturbances (Gomes & Mantovani 2001, Oliveira 2001). Many studies in tropical forests have recorded the mortality and recruitment rates of trees in order to gather information on the dynamics and structure of these communities (Phillips & Gentry 1994, Sheil 1995a,b, Gomes *et al.* 2003, Oliveira-Filho *et al.* 2007, Machado & Oliveira-Filho 2010, Laurance *et al.* 2014). However, the majority have been done in continuous, well-preserved forests and have focused on trees (Gomes 1998).

In this paper, we decided to evaluate the plant community dynamics of different layers and life forms over the period of 6.5 years, in an urban forest remnant from the PEFI, a protected area surrounded by one of the largest urban areas of the world (CONDEPHAAT 2018). Smaller individuals, such as those found in the understory, are representative of forest regeneration and may be more sensitive in disturbed environments (Gomes *et al.* 2003, Salles & Schiavini 2007) and more

dynamic (Condit *et al.* 1996b, Machado & Oliveira-Filho 2010, Feeley *et al.* 2011). Similarly, other life forms, such as climbers, can be more dynamic when compared to shrubs and trees, as shown by ecological studies done with this life form (Wright *et al.* 2004, Phillips *et al.* 2005, Schnitzer 2005, Nepstad *et al.* 2007, Laurance *et al.* 2014, Nogueira *et al.* 2014), as we hypothesize to the plant community studied. Therefore, we expect smaller individuals to have higher mortality and recruitment rates, and the climbing plants to have the highest dynamics (mortality and recruitment) compared to shrub-tree synusia.

Differentiated dynamics are also expected in relation to successional groups from rainforest (Budowski 1965, Swaine *et al.* 1987, Whitmore 1989, Gomes *et al.* 2003, Schorn & Galvão 2009) such as the PEFI forest, which constitute a mosaic of secondary areas at different successional stages (Nastri 1992, Struffaldi-De-Vuono 1985, Costa & Mantovani 1992, Gomes & Mantovani 2001, Pivello & Peccinini 2002, Gomes *et al.* 2003). Thus, additionally, we present the status of successional groups, for which we expect differences between mortality and recruitment of early and late-successional plants.

## Material and methods

**Study Area** - This study was carried out in Parque Estadual das Fontes do Ipiranga (PEFI), 23°38'08"S - 23°40'18"S and 46°36'48"W - 46°38'00"W), city of São Paulo - São Paulo State, Brazil (Fernandes 2002, CONDEPHAAT 2018). PEFI is located on the São Paulo Plateau on crystalline basement rocks and sedimentary rocks. Its relief is characterized by rounded tops and altitudes ranging from 760 to 837 m. The predominant types of soils are Haplic Cambisols and Red-Yellow Podzolic Latosol (Oxisol) (SMA 2008).

The PEFI is considered the third-largest state park in the São Paulo Metropolitan Region, but it is the largest in the metropolis whose surroundings are completely urbanized and which contains remnants of the Atlantic Rain Forest (SMA 2008). The forest remnants occupy approximately 70% of its 495 hectares, according to the current limit (CONDEPHAAT 2018), and its predominant vegetation is classified as regeneration of the Dense Montane Ombrophylous Forest in different successional stages (Barros *et al.* 2002). The remnant is a secondary and disturbed forest, in a long recovery process (Peccinini & Pivello 2002). The area was

occupied by 12 lots of farmers and ranchers and its expropriation began in 1893. Since it is isolated in one of the largest metropolitan regions in the world it is subject to disturbances such as edge effect, biological invasion, pollution, fires and heat island effect (Struffaldi-De-Vuono 1985, Gomes *et al.* 2003, SMA 2008).

Flora has been described in a series of monographs by the Botanical Institute (Barros *et al.* 2002), located inside the Park, which has one of the largest herbariums in the country. In addition, the park has one of the oldest meteorological stations in the country and it has carried out measurements without interruption since 1932. Comparing the normals from 1933-1960 and 1991-2017, it was observed a local increase of approximately 1.7 °C in the average annual temperature and 320.1 mm increase in the average annual rainfall (EM-IAG 2017). The annual average temperature is 18.7 °C (1933-2017) with average monthly variations varying from 15.3 °C (July) to 21.9 °C (February). The average total annual precipitation is 1,412.3 mm, more than half of it concentrated between December and March (EM-IAG 2017).

**Procedures** - Data was collected from 10 transects measuring 2 × 50 m (0,1 ha) laid out in the first half of 2006 (Davison 2009). The permanent transects were randomly distributed along a perpendicular 200 m line, totaling a sample universe of 1 ha, in a conserved area on Botanical Institute, in a recovery process of past disturbances, however, that has not been occupied, nor the use thereof been changed, for at least 65 years (Peccinini & Pivello 2002). The area is located at an average altitude of 831 m, on Oxisol soil, and more than 100 m away from Cursino Avenue (District of Água Funda - São Paulo - SP). In each transect, shrubs, trees, vines, palms, tree ferns individuals with a stem diameter at breast height (dbh), *i.e.* 1.30 m from the soil, of at least ≥ 2.5 cm were measured and identified, the same for the growing roots of hemiepiphytes at ≤ 1.30 m from the soil (Gentry's protocol 1982, Phillips & Miller 2002). In 10 subtransects (1 × 50 m), all plants with < 2.5 cm dbh and > 1 m height (h) were sampled (figure 1).

All individuals were marked with numbered plastic plates and fixed with galvanized wire around the stem leaving room for the plant to grow. The height of each individual was estimated using a graduated ruler and an electronic measuring tape. The diameter at breast height (dbh) of individuals, including all branches with a dbh of at least ≥ 2.5 cm, was measured

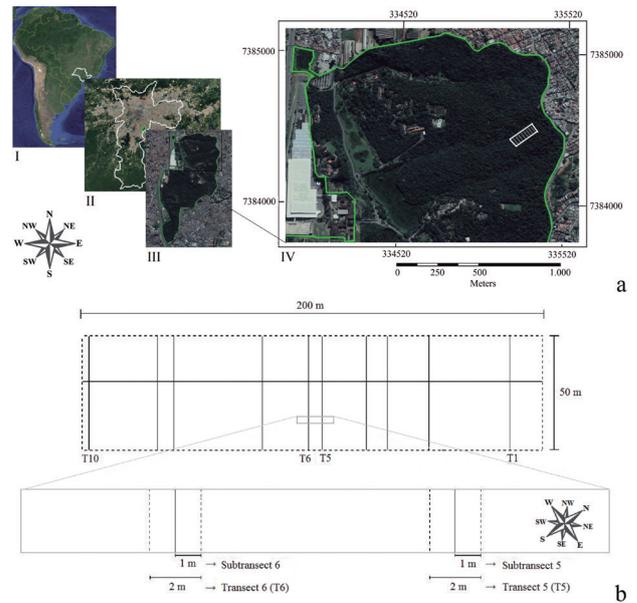


Figure 1. a. Location of the Parque Estadual das Fontes do Ipiranga (III), in the capital of São Paulo (II), SP, Brazil (South America, I), and the Botanical Institute area, zoomed in on the right (IV), with location of sample universe (white rectangle) of 1 ha. b. Scheme of the random distribution of the 10 transects (T, 2 × 50 m), detailing of the transects and subtransects 6 and 5. Source: Adapted of Google Earth, 2019, Image Landsat/Copernicus, Data SIO, NOAA, U.S Navy, NGA, GEBCO. DATUM/Projection: SIRGAS 2000/UTM zone 23S.

in late winter, between the second half of August and the first half of September 2012, which is the driest period of the year. That is, 6.5 years after the first measurement that was performed on March 2006 (Davison 2009).

Vegetative or fertile branches were collected, when present, from shrubs and trees for herborization and identification. Climbers were not botanically identified in order to avoid interference from the collection of stem on the climbers' dynamics, a single collection could cause the death of the monitored individual (Sheil 1995a). This means that only the structure and dynamics of this synusia, as a whole, were evaluated, without performing floristic study for this synusia.

Shrubs and trees individuals sampled in 2006 and those recruited during the study period were identified via comparison with herbarium specimens, references in the relevant literature and confirmation with researchers from the Herbarium of the São Paulo Botanical Institute (SP) and from the São Paulo Forestry Institute (SPSF). The botanical nomenclature from the Brazilian Flora Species List (Flora do Brasil 2020 under construction 2019) was used, according

to the APG IV system (APG IV 2016). Vouchers have been deposited in the Herbarium of the São Paulo Botanical Institute (SP, Maria Eneyda, P. K. Fidalgo).

The identified individuals were classified into two successional groups: Early and Late. This classification was based on field observations as well as by using some papers that adapted classical concepts (Budowski 1965, Denslow 1980, Swaine & Whitmore 1988, Whitmore 1989) to Brazilian forests (Gandolfi *et al.* 1995, Ivanauskas *et al.* 1999, Gandolfi 2000, Paula *et al.* 2004, Bernacci *et al.* 2006, Catharino *et al.* 2006, Guaratini *et al.* 2008, Ramos *et al.* 2011).

**Data Analysis** - Calculations were carried out to determine mortality and recruitment for the plant community, as well as growth rates and the proportion of dead and recruited basal area for the plants with  $\geq 2.5$  cm dbh over the period of 6.5 years (March 2006 to September 2012). The relative growth and the distribution of shrub and tree diameters were also evaluated. For the dynamics of the basal area, recruiting was considered as the sum of the relative value to the basal area of plants recruited in 2012 and the relative value to the growth of the remaining plants from 2006.

Demographic rates were calculated for plants with  $< 2.5$  cm dbh ( $> 1$  m height) and  $\geq 2.5$  cm dbh. Three class sizes were also considered for the shrub-tree synusia: I)  $< 2.5$  cm dbh ( $> 1$  m height), II)  $2.5 \leq$  dbh  $\leq 5$  cm and III)  $> 5$  cm dbh.

Significant differences between rates were assessed using the Student's t-test for normally distributed data (means and standard error were presented) or the Mann-Whitney test (medians = Mdn were presented). One-way Analysis of Variance (ANOVA) and *post-hoc* test of Tukey - Kramer were used to compare the three tree and shrub size classes. The assumptions were checked with the Shapiro-Wilk tests and Q-Q plot for normal distribution and Levene's test for homogeneity of variance. The degree of spatial dependence of the values was quantified by analysis of correlations according to Legendre & Fortin (1989), with later adjustment (decrease of two degrees of freedom). Mortality (Mr) and recruitment (Rr) rates were calculated algebraically and not logarithmically, as recommended by Sheil and colleagues (1995):

$$\begin{aligned} Mr &= \{1 - [(N_o - m)/N_o]^{1/\Delta t}\} \times 100 \\ Rr &= \{[(N_o + r)/N_o]^{1/\Delta t} - 1\} \times 100 \end{aligned}$$

$N_o$  = initial number of individuals,  $m$  = number of deaths in the period between censuses ( $\Delta t = t_1 - t_0$ ),

$r$  = number of individuals recruited, excluding recruited dead, between censuses (Gomes *et al.* 2003).

In order to evaluate mortality versus recruitment, the proportions of the dead and recruited throughout the period (6.5 years) were used. To this end, the formulas used were:

$$\begin{aligned} M_{\text{total}} &= (m/N_o) \times 100 \\ R_{\text{total}} &= (r/N_o) \times 100 \end{aligned}$$

Differences in the distribution of individuals' diameters between 2006 and 2012 were evaluated using the Kolmogorov-Smirnov Test. Based on the diameter differences, relative growth rates (RGR, Welden *et al.* 1991) of shrubs and trees were determined by:

$$\text{RGR} = \{[(\text{dbht} / \text{dbht}_0)^{1/\Delta t}] - 1\} \times 100$$

Calculations were automated by function developed in the R software environment (R Core Team 2019). The help page and function script can be found at Kondrat (2014).

## Results

**Composition and Structure in 2012** - A total of 901 individuals were sampled (survivors from 2006 and the dead and recruited during the study period, table 1), out of which 708 belong to the shrub-tree synusia, 190 to the climbers and three to the hemiepiphytes (two recruited and one survivor). Of the three ferns, which existed in 2006 and were included in the shrub-tree group, one survived until 2012. The growth rate for the group of all plants and sizes reflected an increase in the total number of individuals ( $\lambda > 1$ , 95% CI =  $1.003 \pm 0.003$ ).

On the other hand, results showed a decrease in the number of individuals ( $\lambda < 1$ ) of the shrub-tree synusia (95% CI =  $0.993 \pm 0.005$ ) and climbers (95% CI =  $0.951 \pm 0.003$ ) with  $\geq 2.5$  cm dbh (table 1). Similarly, all early-successional plants showed a decrease in the number of individuals ( $\lambda < 1$ , 95% CI =  $0.982 \pm 0.015$ , table 1).

The total number of identified species was 129, 125 belonging to the shrub-tree synusia (one exotic species - *Coffea arabica* L.), one to the hemiepiphyte synusia (*Philodendron appendiculatum* Nadrusz & Mayo) and three of the climber synusia which, in 2006, had been included in the shrub-tree group (*Hippocratea volubilis* L., *Salacia elliptica* (Mart.) G. Don and *Machaerium brasiliense* Vogel). A total of 39 families

Table 1. Number of sampled individuals (living plants in 2006 -  $N_{2006}$ , and 2012 -  $N_{2012}$ ; and the dead and recruited in the period), and growth rates ( $\lambda$ ): from the shrub-tree synusia, climbing plants, hemiepiphytes, and Early and Late-successional groups. Individuals separated by size class: diameter at breast height (dbh)  $< 2.5$  cm and  $\geq 2.5$  cm dbh. Note: Four individuals moved from the smaller to the larger class (in parenthesis).

GROUPS	$N_{2006}$	$N_{2012}$	Dead	Recruited	$\lambda$
Shrub-tree synusia					
$< 2.5$ cm dbh	243	265 (- 4)	28	50	1.013
$\geq 2.5$ cm dbh	401	381 (+ 4)	34	14 (+ 4)	0.993
Subtotal	644	646	62	64	1.000
Climbing plants					
$< 2.5$ cm dbh	66	92	28	54	1.052
$\geq 2.5$ cm dbh	63	53	17	7	0.951
Subtotal	129	145	45	61	1.018
Hemiepiphytes					
$< 2.5$ cm dbh	1	3	0	2	1.184
Early-successional plants					
$< 2.5$ cm dbh	45	40	8	3	0.982
$\geq 2.5$ cm dbh	105	98	9	2	0.989
Subtotal	150	138	17	5	0.982
Late-successional plants					
$< 2.5$ cm dbh	198	225 (-4)	20	47	1.020
$\geq 2.5$ cm dbh	293	283 (+4)	22	12 (+4)	0.997
Subtotal	491	508	42	59	1.005
Total	774	794	107	127	1.003

were identified. Myrtaceae (29 species), Lauraceae (15 species), Rubiaceae (10 species) and Fabaceae (8 species) were the families with the highest number of species. With the collection of vegetative and fertile material, it was possible to identify 56 species that did not appear on the Park Management Plan (table 2).

A total of 155 individuals (42 species) sampled in the shrub-tree synusia were classified into the early-successional group and 550 individuals (83 species) into the late-successional group (table 1). The two ferns and one Myrtaceae with  $\geq 2.5$  cm dbh (dead and without material for identification at the species level) were not classified or considered in this count.

In 2006 and 2012, 122 and 118 species were identified in the shrub-tree synusia, respectively; most species (115 species) were present in both surveys (table 2). In 2012, this synusia was composed of 37 families, but the Asteraceae and Clusiaceae families were not present. The most abundant species in 2006 and 2012 were (table 2): *Geonoma gamiova* Barb.Rodr. (Relative Density - RD = 6.06 and 6.82%, respectively for 2006 and 2012), *Calyptanthes grandifolia* O.Berg (RD = 6.06 and 5.74%), *Cordia myrciifolia* (K.Schum.) C.H. Perss. & Delprete

(RD = 4.35 and 4.19%), *Rudgea jasminoides* (Cham.) Müll.Arg. (RD = 4.50 and 3.88%) and *Pouteria reticulata* (Engl.) Eyma (RD = 3.88 and 4.34%).

The maximum height recorded in the community was 18 m for a specimen of *Aspidosperma olivaceum* Müll.Arg. (Apocynaceae), the median dbh value for shrub-tree synusia was 5 cm and the biggest dbh was 43.3 cm referring to a specimen of *Tapirira guianensis* Aubl. (Anacardiaceae). The median dbh value for the climbers was 4.6 cm and the maximum observed value was 22.3 cm. The distribution of diameters (dbh) of live plants in 2012 did not differ from that in 2006 (Kolmogorov-Smirnov Test,  $n_1 = 367$ ,  $n_2 = 385$ ,  $D = 0.05$ ,  $p = 0.81$ , figure 2a). The mean relative diameter growth of the plants in the shrub-tree synusia was 1.14% year<sup>-1</sup> (Mdn = 0.58% year<sup>-1</sup>), the minimum growth was zero and the maximum 9.05% year<sup>-1</sup> in regards to a specimen of *Cryptocarya mandioccana* Meisn. (Lauraceae). The diameter growth of plants with  $2.5 \leq \text{dbh} \leq 5$  cm (Mdn = 0.48% year<sup>-1</sup>) did not differ from that of plants with  $> 5$  cm dbh (Mdn = 0.7% year<sup>-1</sup>, Mann-Whitney Test,  $n_1 = 185$ ,  $n_2 = 166$ ,  $z = 1,549$ ,  $p = 0.12$ , figure 2b).

Table 2. Species, families and successional groups identified in a forest remnant in the Parque Estadual das Fontes do Ipiranga (PEFI), São Paulo, São Paulo State, Brazil. SG/H: Successional Group/Habit (L: Late, E: Early, CP: climbing plant, He: Hemiepiphyte). N° Col: H. Kondrat collector number (SP). RD: relative density, RF: relative frequency. Total Density: 2006 = 6,440 ind.ha<sup>-1</sup>; 2012 = 6,460 ind.ha<sup>-1</sup>. Total Frequency: 2006 = 3,400%, 2012 = 3,390%. Threatened Species Categories: Endangered: \*; Vulnerable: \*\* (Martinelli & Moraes 2013, MMA 2014, SMA 2016, IUCN 2019); Exotic: #. Absent in the PEFI Management Plan: +++.

Species	Family	SG/H	N° Col.	RF (%)		RD (%)	
				2006	2012	2006	2012
<i>Geonoma gamiova</i> Barb.Rodr. +++	Arecaceae	L	-	2.65	2.65	6.06	6.82
<i>Calyptanthes grandifolia</i> O.Berg	Myrtaceae	L	78	2.94	2.95	6.06	5.74
<i>Pouteria reticulata</i> (Engl.) Eyma +++	Sapotaceae	L	1	2.35	2.36	3.88	4.34
<i>Dendropanax exilis</i> (Toledo) S.L.Jung +++	Araliaceae	L	105	2.35	2.95	3.42	4.19
<i>Cordia myrciifolia</i> (K.Schum.) C.H.Perss. & Delprete	Rubiaceae	L	151	2.65	2.65	4.35	4.19
<i>Cupania oblongifolia</i> Mart.	Sapindaceae	E	171	2.35	2.65	3.88	3.88
<i>Rudgea jasminoides</i> (Cham.) Müll.Arg.	Rubiaceae	L	11	2.35	2.06	4.50	3.88
<i>Eugenia pruinosa</i> D.Legrand * +++	Myrtaceae	L	129	2.94	2.95	4.19	3.72
<i>Guarea macrophylla</i> Vahl	Meliaceae	E	15	2.35	2.36	3.73	3.57
<i>Eugenia excelsa</i> O.Berg	Myrtaceae	L	7	2.06	2.36	2.33	2.64
<i>Eugenia handroana</i> D.Legrand +++	Myrtaceae	L	33	2.06	2.06	2.33	2.33
<i>Actinostemon klotzschii</i> (Dir.) Pax +++	Euphorbiaceae	L	6	1.18	1.47	2.17	2.17
<i>Cryptocarya mandioccana</i> Meisn. +++	Lauraceae	L	2	2.06	1.77	1.71	1.86
<i>Myrcia multiflora</i> (Lam.) DC.	Myrtaceae	E	96	1.76	1.47	2.02	1.86
<i>Euterpe edulis</i> Mart. **	Arecaceae	L	-	0.88	2.06	0.62	1.71
<i>Neomitranthes glomerata</i> (D.Legrand) D.Legrand +++	Myrtaceae	L	83	1.47	1.47	1.71	1.71
<i>Eugenia brevistyla</i> D.Legrand +++	Myrtaceae	L	5	1.18	1.77	0.93	1.55
<i>Myrcia tijucensis</i> Kiaersk. +++	Myrtaceae	L	147	1.76	1.77	1.71	1.55
<i>Faramea montevidensis</i> (Cham. & Schltdl.) DC. +++	Rubiaceae	L	18	1.76	1.77	1.55	1.55
<i>Myrcia aethusa</i> (O.Berg) N.Silveira +++	Myrtaceae	L	163	1.47	1.47	1.55	1.55
<i>Cordia sellowiana</i> Cham.	Boraginaceae	E	197	2.35	1.77	2.02	1.40
<i>Myrcia pubipetala</i> Miq. +++	Myrtaceae	L	99	1.47	1.47	1.55	1.24
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	E	-	1.18	0.88	1.40	1.24
<i>Trichilia silvatica</i> C.DC. **	Meliaceae	L	130	0.88	0.88	1.40	1.24
<i>Calyptanthes lucida</i> Mart. ex DC. +++	Myrtaceae	L	79	1.47	1.47	1.09	1.09
<i>Sloanea obtusifolia</i> (Moric.) Schum. * +++	Elaeocarpaceae	L	14	1.18	1.18	0.93	1.09
<i>Aspidosperma olivaceum</i> Müll.Arg.	Apocynaceae	L	184	1.76	1.77	0.93	0.93
<i>Podocarpus sellowii</i> Klotzsch ex Endl. *	Podocarpaceae	L	172	1.47	1.47	0.78	0.93
<i>Geonoma schottiana</i> Mart.	Arecaceae	L	-	0.59	0.59	0.93	0.93
<i>Amaioua intermedia</i> Mart. ex Schult. & Schult.f.	Rubiaceae	E	167	1.47	1.47	0.78	0.78
<i>Ocotea odorifera</i> (Vell.) Rohwer *	Lauraceae	L	196	1.18	1.18	0.78	0.78
<i>Eugenia copacabanensis</i> Kiaersk. +++	Myrtaceae	L	169	1.18	1.18	0.78	0.78
<i>Ecclinusa ramiflora</i> Mart.	Sapotaceae	L	221	0.88	1.18	0.62	0.78
<i>Xylopia brasiliensis</i> Spreng.	Annonaceae	L	27	0.59	0.88	0.62	0.78
<i>Trichilia emarginata</i> (Turcz.) C.DC. ** +++	Meliaceae	L	134	0.88	0.88	0.78	0.78
<i>Psychotria suterella</i> Müll.Arg.	Rubiaceae	L	215	1.18	0.29	1.40	0.78
<i>Sloanea hirsuta</i> (Schott) Planch. ex Benth.	Elaeocarpaceae	L	195	1.18	1.18	0.62	0.62

continue

Table 2 (continuation)

Species	Family	SG/H	N° Col.	RF (%)		RD (%)	
				2006	2012	2006	2012
<i>Myrcia laxiflora</i> Cambess. +++	Myrtaceae	L	153	1.18	1.18	0.62	0.62
<i>Ocotea teleiandra</i> (Meisn.) Mez +++	Lauraceae	L	193	0.88	0.88	0.78	0.62
<i>Mouriri chamissoana</i> Cogn. +++	Melastomataceae	L	101	0.88	0.88	0.62	0.62
<i>Piper solmsianum</i> C.DC.	Piperaceae	E	194	0.88	0.88	0.62	0.62
<i>Casearia sylvestris</i> Sw.	Salicaceae	E	62	0.88	0.88	0.47	0.62
<i>Schefflera calva</i> (Cham.) Frodin & Fiaschi +++	Araliaceae	L	56	0.59	0.59	0.62	0.62
<i>Ocotea venulosa</i> (Nees) Baitello +++	Lauraceae	L	189	0.59	0.59	0.62	0.62
<i>Eugenia neoglomerata</i> Sobral +++	Myrtaceae	L	165	0.59	0.59	0.62	0.62
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	L	139	1.18	0.59	0.93	0.62
<i>Protium widgrenii</i> Engl.	Burseraceae	E	188	0.88	0.88	0.62	0.47
<i>Machaerium nyctitans</i> (Vell.) Benth.	Fabaceae	E	190	0.88	0.88	0.47	0.47
<i>Ocotea brachybotrya</i> (Meisn.) Mez +++	Lauraceae	L	57	0.59	0.88	0.31	0.47
<i>Posoqueria latifolia</i> (Rudge) Schult. +++	Rubiaceae	E	207	0.88	0.88	0.47	0.47
<i>Cordia ecalyculata</i> Vell.	Boraginaceae	E	200	0.59	0.59	0.47	0.47
<i>Sloanea guianensis</i> (Aubl.) Benth.	Elaeocarpaceae	L	58	0.59	0.59	0.31	0.47
<i>Nectandra oppositifolia</i> Nees +++	Lauraceae	L	204	0.59	0.59	0.47	0.47
<i>Cabralea canjerana</i> (Vell.) Mart.	Meliaceae	L	170	0.59	0.59	0.47	0.47
<i>Trichilia lepidota</i> Mart. +++	Meliaceae	E	181	0.59	0.59	0.47	0.47
<i>Mollinedia schottiana</i> (Spreng.) Perkins	Monimiaceae	L	71	0.29	0.59	0.16	0.47
<i>Brosimum glaziovii</i> Taub. **	Moraceae	L	13	0.59	0.59	0.31	0.47
<i>Coffea arabica</i> L. # +++	Rubiaceae	L	41	0.00	0.59	0.00	0.47
<i>Hirtella hebeclada</i> Moric. ex DC.	Chrysobalanaceae	L	202	0.29	0.29	0.47	0.47
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	E	205	0.59	0.59	0.31	0.31
<i>Maprounea guianensis</i> Aubl.	Euphorbiaceae	E	168	0.59	0.59	0.47	0.31
<i>Inga sellowiana</i> Benth. *	Fabaceae	E	192	0.59	0.59	0.31	0.31
<i>Cinnamomum triplinerve</i> (Ruiz & Pav.) Kosterm. +++	Lauraceae	L	107	0.59	0.59	0.31	0.31
<i>Ocotea glaziovii</i> Mez +++	Lauraceae	L	142	0.59	0.59	0.31	0.31
<i>Ocotea silvestris</i> Vattimo-Gil +++	Lauraceae	L	64	0.00	0.59	0.00	0.31
<i>Virola bicuhyba</i> (Schott ex Spreng.) Warb. *	Myristicaceae	L	74	0.59	0.59	0.31	0.31
<i>Myrcia strigipes</i> Mart. +++	Myrtaceae	L	125	0.59	0.59	0.31	0.31
<i>Myrcia coelosepala</i> Kiaersk. +++	Myrtaceae	L	154	0.59	0.59	0.31	0.31
<i>Heisteria silvianii</i> Schwacke	Olacaceae	L	166	0.59	0.59	0.31	0.31
<i>Pera glabrata</i> (Schott) Baill.	Peraceae	E	75	0.59	0.59	0.31	0.31
<i>Rudgea gardenioides</i> (Cham.) Müll.Arg. +++	Rubiaceae	L	160	0.59	0.59	0.31	0.31
<i>Matayba juglandifolia</i> (Cambess.) Radlk.	Sapindaceae	E	201	0.59	0.59	0.31	0.31
<i>Solanum pseudoquina</i> A.St.-Hil.	Solanaceae	E	80	0.59	0.59	0.31	0.31
<i>Gonatogyne brasiliensis</i> (Baill.) Müll.Arg. +++	Phyllanthaceae	L	85	0.29	0.29	0.31	0.31
<i>Annona cacans</i> Warm.	Annonaceae	E	141	0.29	0.29	0.16	0.16
<i>Duguetia salicifolia</i> R.E.Fr. ** +++	Annonaceae	L	176	0.29	0.29	0.16	0.16
<i>Ilex paraguariensis</i> A.St.-Hil.	Aquifoliaceae	E	183	0.29	0.29	0.16	0.16
<i>Citronella paniculata</i> (Mart.) R.A.Howard	Cardiopteridaceae	L	177	0.29	0.29	0.16	0.16
<i>Monteverdia evonymoides</i> (Reissek) Biral	Celastraceae	L	186	0.29	0.29	0.16	0.16

continue

Table 2 (continuation)

Species	Family	SG/H	N° Col.	RF (%)		RD (%)	
				2006	2012	2006	2012
<i>Licania hoehnei</i> Pilg.	Chrysobalanaceae	L	191	0.29	0.29	0.16	0.16
<i>Cyathea delgadii</i> Sternb. +++	Cyatheaceae	L	187	0.29	0.29	0.16	0.16
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	Euphorbiaceae	E	213	0.29	0.29	0.16	0.16
<i>Andira anthelmia</i> (Vell.) Benth.	Fabaceae	E	98	0.29	0.29	0.16	0.16
<i>Dalbergia brasiliensis</i> Vogel +++	Fabaceae	E	63	0.29	0.29	0.31	0.16
<i>Inga capitata</i> Desv. +++	Fabaceae	E	118	0.29	0.29	0.16	0.16
<i>Inga sessilis</i> (Vell.) Mart.	Fabaceae	E	59	0.00	0.29	0.00	0.16
<i>Machaerium villosum</i> Vogel	Fabaceae	E	173	0.59	0.29	0.31	0.16
<i>Beilschmiedia emarginata</i> (Meisn.) Kosterm. +++	Lauraceae	L	217	0.29	0.29	0.16	0.16
<i>Cryptocarya saligna</i> Mez +++	Lauraceae	L	224	0.29	0.29	0.16	0.16
<i>Ocotea aciphylla</i> (Nees & Mart.) Mez +++	Lauraceae	L	161	0.29	0.29	0.16	0.16
<i>Ocotea catharinensis</i> Mez ** +++	Lauraceae	L	90	0.29	0.29	0.16	0.16
<i>Ocotea dispersa</i> (Nees & Mart.) Mez	Lauraceae	L	203	0.29	0.29	0.16	0.16
<i>Ocotea laxa</i> (Nees) Mez +++	Lauraceae	L	175	0.29	0.29	0.16	0.16
<i>Cariniana estrellensis</i> (Raddi) Kuntze	Lecythidaceae	L	174	0.29	0.29	0.16	0.16
<i>Leandra variabilis</i> Raddi +++	Melastomataceae	E	76	0.59	0.29	0.31	0.16
<i>Campomanesia phaea</i> (O.Berg) Landrum	Myrtaceae	E	226	0.29	0.29	0.16	0.16
<i>Eugenia cerasiflora</i> Miq.	Myrtaceae	L	216	0.29	0.29	0.16	0.16
<i>Eugenia cereja</i> D.Legrand +++	Myrtaceae	L	156	0.29	0.29	0.16	0.16
<i>Eugenia supraaxillaris</i> Spring +++	Myrtaceae	L	149	0.29	0.29	0.16	0.16
<i>Myrcia reitzii</i> (D.Legrand) Mazine +++	Myrtaceae	L	209	0.29	0.29	0.16	0.16
<i>Myrcia citrifolia</i> (Aubl.) Urb. +++	Myrtaceae	L	152	0.29	0.29	0.16	0.16
<i>Myrcia oblongata</i> DC. +++	Myrtaceae	E	212	0.29	0.29	0.16	0.16
<i>Myrcia splendens</i> (Sw.) DC.	Myrtaceae	E	228	0.29	0.29	0.16	0.16
<i>Myrcia tenuivenosa</i> Kiaersk. +++	Myrtaceae	L	155	0.29	0.29	0.16	0.16
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	Myrtaceae	L	227	0.29	0.29	0.16	0.16
<i>Psidium cattleianum</i> Sabine	Myrtaceae	E	115	0.29	0.29	0.16	0.16
<i>Psidium rufum</i> Mart. ex DC. +++	Myrtaceae	E	214	0.29	0.29	0.16	0.16
<i>Siphoneugena densiflora</i> O.Berg +++	Myrtaceae	L	88	0.29	0.29	0.16	0.16
<i>Cybianthus cuneifolius</i> Mart. +++	Primulaceae	E	179	0.29	0.29	0.16	0.16
<i>Myrsine umbellata</i> Mart.	Primulaceae	E	220	0.29	0.29	0.16	0.16
<i>Prunus myrtifolia</i> (L.) Urb.	Rosaceae	E	223	0.29	0.29	0.16	0.16
<i>Ixora gardneriana</i> Benth. +++	Rubiaceae	L	127	0.29	0.29	0.16	0.16
<i>Psychotria vellosiana</i> Benth. +++	Rubiaceae	L	182	0.29	0.29	0.16	0.16
<i>Xylosma glaberrima</i> Sleumer	Salicaceae	E	93	0.29	0.29	0.16	0.16
<i>Allophylus edulis</i> (A.St.-Hil. et al.) Hieron. ex Niederl.	Sapindaceae	E	81	0.29	0.29	0.16	0.16
<i>Cupania vernalis</i> Cambess.	Sapindaceae	E	222	0.29	0.29	0.16	0.16
<i>Matayba elaeagnoides</i> Radlk.	Sapindaceae	E	225	0.29	0.29	0.31	0.16
<i>Vochysia magnifica</i> Warm.	Vochysiaceae	L	208	0.29	0.29	0.16	0.16
<i>Guatteria australis</i> A.St.-Hil.	Annonaceae	L	230	0.29	0.00	0.16	0.00
<i>Piptocarpha</i> sp.	Asteraceae	E	-	0.29	0.00	0.16	0.00
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	Clusiaceae	L	111	0.29	0.00	0.16	0.00

continue

Table 2 (continuation)

Species	Family	SG/H	N° Col.	RF (%)		RD (%)	
				2006	2012	2006	2012
<i>Cyatheales</i> sp.1	Cyatheales	L	-	0.59	0.00	0.31	0.00
<i>Mollinedia triflora</i> (Spreng.) Tul.	Monimiaceae	L	229	0.29	0.00	0.16	0.00
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger <i>et al.</i>	Moraceae	E	-	0.29	0.00	0.16	0.00
Myrtaceae sp.1	Myrtaceae	-	-	0.29	0.00	0.16	0.00
<i>Philodendron appendiculatum</i> Nadruz & Mayo	Araceae	He	91	-	-	-	-
<i>Hippocratea volubilis</i> L.	Celastraceae	CP	128	-	-	-	-
<i>Salacia elliptica</i> (Mart.) G.Don	Celastraceae	CP	12	-	-	-	-
<i>Machaerium brasiliense</i> Vogel	Fabaceae	CP	16	-	-	-	-

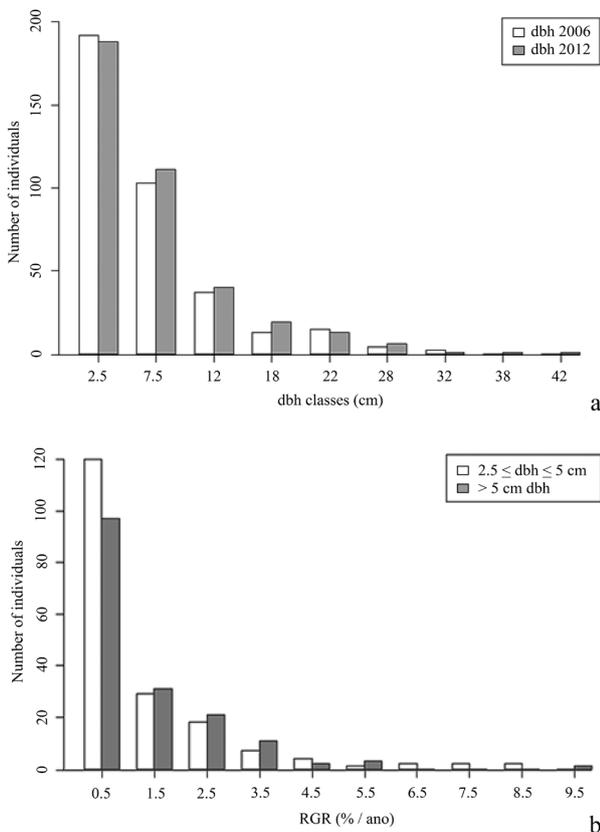


Figure 2. a. Distribution of individuals measured in 2006 (white bars) and in 2012 (gray bars) in classes of diameter at breast height (dbh, cm). Class Intervals = 5 cm. b. Distribution of individuals with diameter at breast height  $2.5 \leq \text{dbh} \leq 5$  cm (white bars) and  $> 5$  cm dbh (gray bars) in classes of relative growth rates (RGR, % year<sup>-1</sup>). Class Intervals = 1% year<sup>-1</sup>.

In 6.5 years, the increase in the basal area of the shrub-tree synusia ( $\geq 2.5$  cm dbh) was significantly higher than the reduction, leading to an increase in the total basal area from 24.32 to 27.10 m<sup>2</sup> ha<sup>-1</sup> (table 3) and to a significant difference between gain (Mdn = 14.71%) and loss (Mdn = 4.95%) of basal

area (Mann-Whitney Test,  $U = 11$ ,  $p = 0.002$ ,  $\lambda > 1$ , 95% CI =  $1.015 \pm 0.007$ ). The basal area of climbers decreased from 1.564 m<sup>2</sup> ha<sup>-1</sup> to 1.559 m<sup>2</sup> ha<sup>-1</sup> (table 3) with no significant difference between gain (Mdn = 27.48%) and loss (Mdn = 49.87%) in the period (Mann-Whitney Test,  $U = 45$ ,  $p = 0.734$ ). On the other hand, their basal area reduction was greater than that of the plants in the shrub-tree community (Mann-Whitney Test,  $U = 12$ ,  $p = 0.003$ ,  $\lambda < 1$ , 95% CI =  $0.970 \pm 0.009$ ).

Plant Dynamics - Concerning the shrub-tree versus climbers dynamics, the annual mortality of climbers was greater than that of plants in the shrub-tree synusia in both classes,  $< 2.5$  cm dbh (Mann-Whitney Test,  $U = 7$ ,  $p = 0.0004$ ) and  $\geq 2.5$  cm dbh (Mann-Whitney Test,  $U = 16$ ;  $p = 0.009$ ; figure 3 and table 4).

Likewise, the annual recruitment of climbers in the class with  $< 2.5$  cm dbh was also greater than of plants in the shrub-tree synusia (Mann-Whitney Test,  $U = 7.5$ ,  $p = 0.0005$ , figure 3). However, the annual recruitment of climbers in the class with  $\geq 2.5$  cm dbh did not differ from the annual recruitment of shrubs and trees in this size class (Mann-Whitney Test,  $U = 45$ ,  $p = 0.73$ , figure 3).

The annual mortality of plants with  $< 2.5$  cm dbh did not differ from that of plants with  $\geq 2.5$  cm dbh in the shrub-tree synusia (Mann-Whitney Test,  $U = 31.5$ ,  $p = 0.171$ ) and in the climbers synusia (Mann-Whitney Test,  $U = 41.5$ ,  $p = 0.538$ ). However, the annual plant recruitment in the smallest class ( $< 2.5$  cm dbh) was greater than that of plants with  $\geq 2.5$  cm dbh both in the shrub-trees synusia (Mann-Whitney Test,  $U = 0$ ,  $p = 0.00001$ ) and in the climbers synusia (Mann-Whitney Test,  $U = 8$ ,  $p = 0.0006$ , figure 3).

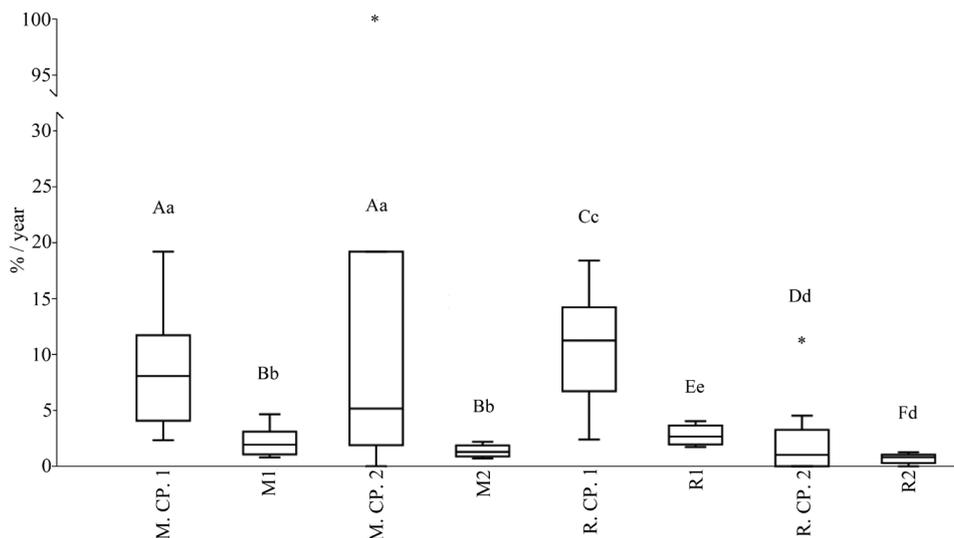
The division of the shrub-tree synusia into three class sizes showed that the annual mortality rates

Table 3. Basal Area dynamics ( $\text{m}^2 \text{ha}^{-1}$ ) of sampled individuals with the diameter at breast height (dbh)  $\geq 2.5$  cm in 2006 and 2012, and growth rates ( $\lambda$ ): from the shrub-tree synusia and climbing plants.

Groups	Basal Area ( $\text{m}^2 \text{ha}^{-1}$ )				$\lambda$
	2006	2012	Decrease	Increase	
Shrub-tree community	24.32	27.10	1.07	3.85	1.015
Climbing plants	1.564	1.559	0.599	0.594	0.970

Table 4. Median rates (% year<sup>-1</sup>) of Mortality (M) and Recruitment (R) from the shrub-tree synusia, climbing plants, and Early and Late-successional plants. Individuals separated by size class: diameter at breast height (dbh)  $< 2.5$  cm and  $\geq 2.5$  cm dbh.

Groups	M (% year <sup>-1</sup> )		R (% year <sup>-1</sup> )	
	$< 2.5$	$\geq 2.5$	$< 2.5$	$\geq 2.5$
Shrub-tree synusia	1.94	1.31	2.67	0.82
Climbing plants	8.08	5.18	11.25	1.04
Early-successional plants	3.34	1.48	0	0
Late-successional plants	1.09	1.32	2.84	0.84

Figure 3. Distribution of the annual mortality (M) and recruitment (R) rates of the shrubs and trees,  $< 2.5$  cm dbh (M1 or R1),  $\geq 2.5$  cm dbh (M2 or R2); and of climbers,  $< 2.5$  cm dbh (M.CP. 1 or R. CP. 1),  $\geq 2.5$  cm dbh (M. CP. 2 or R. CP. 2), in the 10 permanent transects. Capital letters represent the comparison of mortality or recruitment between size classes of the same life form; lowercase letters represent the comparison of mortality or recruitment between trees and climbers. Letters that are the same represent medians that are not significantly different according to the Mann-Whitney test, at a significance level of 5%.

were different among the classes ( $F = 6.30$ ,  $df = 23$ ,  $p = 0.007$ , figure 4). Class II ( $2.5 \leq \text{dbh} \leq 5$  cm) had average ( $\pm$  SE) of  $0.65 \pm 0.25\%$  year<sup>-1</sup>, lower mortality than the Class I ( $< 2.5$  cm dbh) average of  $2.32 \pm 0.41\%$  year<sup>-1</sup> ( $p = 0.01$ , *post-hoc* test of Tukey - Kramer) and lower than the Class III (dbh  $> 5$  cm) average of  $2.12 \pm 0.29\%$  year<sup>-1</sup> ( $p = 0.02$ , *post-hoc* test of Tukey - Kramer). The annual recruitment rates also differed in the three studied classes ( $F = 6.15$ ,  $df = 23$ ,  $p = 0.008$ , figure 4). Class I had an average ( $\pm$  SE) of  $2.99 \pm 0.26\%$  year<sup>-1</sup>, higher than the average

recruitment of Class II of  $1.37 \pm 0.25\%$  year<sup>-1</sup> ( $p = 0.01$ , *post-hoc* test of Tukey - Kramer) and higher than the average of Class III of  $1.47 \pm 0.44\%$  year<sup>-1</sup> ( $p = 0.02$ , *post-hoc* test of Tukey - Kramer).

Comparing mortality and recruitment rates in the total period (6.5 years), the class of shrubs and trees with  $\geq 2.5$  cm dbh showed average ( $\pm$  SE) mortality ( $= 8.68 \pm 0.96\%$ ) greater (t-test,  $df = 7$ ,  $t = 3.03$ ,  $p < 0.02$ ) than average recruitment ( $= 4.56 \pm 0.96\%$ ). In relation to the climbers with  $\geq 2.5$  cm dbh, there was a trend towards increased mortality (Mdn = 28.75%)

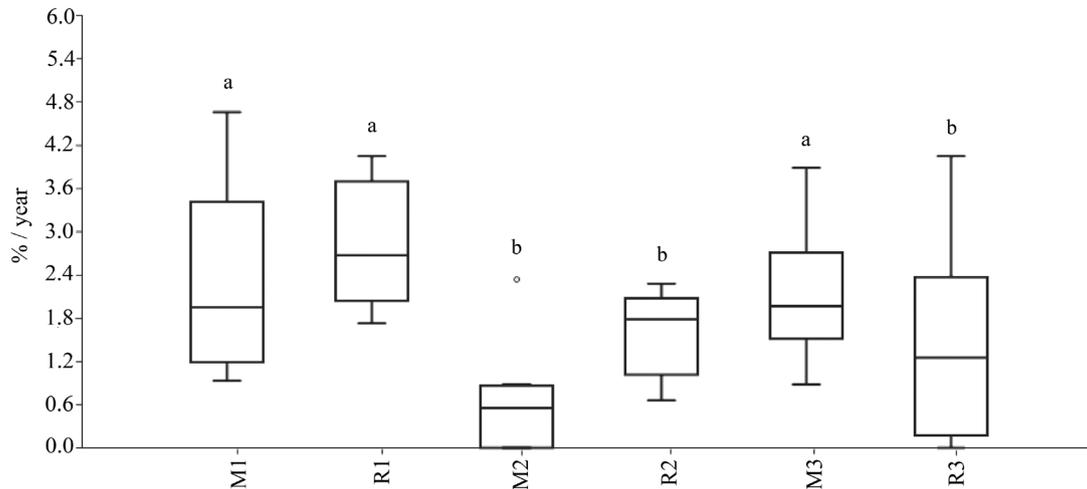


Figure 4. Distribution of the annual mortality (M) and recruitment (R) rates of the shrubs and trees with  $< 2.5$  cm dbh (M1 or R1),  $2.5 \leq$  dbh  $\leq 5$  cm (M2 or R2) and  $> 5$  cm dbh (M3 or R3) in 10 permanent transects. Letters on the boxes represent the comparison of mortality or recruitment between size classes. Letters that are the same represent averages that are not significantly different according to the *post-hoc* Tukey test, at a significance level of 5%.

compared to recruitment (Mdn = 7.14%, Mann-Whitney Test,  $U = 28$ ,  $p = 0.097$ ). Excluding the extreme values of an area where there was 100% mortality and recruitment, mortality (Mdn = 20%) was significantly greater than recruitment (Mdn = 0%, Mann-Whitney Test,  $U = 18.5$ ,  $p = 0.05$ ). In this period, recruitment of shrubs and trees with  $< 2.5$  cm dbh ( $= 19.65 \pm 2.03$ ) did not differ from the mortality ( $= 12.96 \pm 2.22\%$ , t-test,  $df = 7$ ,  $t = 2.22$ ,  $0.05 < p < 0.10$ ), despite the trend. However, climbers with  $< 2.5$  cm dbh showed greater recruitment (Mdn = 100%, Mann-Whitney test,  $U = 17$ ,  $p = 0.011$ ) than mortality (Mdn = 41.67%).

Successional Group Dynamics - Mortality (Mdn = 9.19%) was greater (Mann-Whitney Test,  $U = 18$ ,  $p = 0.007$ ) than recruitment (Mdn = 0%) in early-successional plants with  $\geq 2.5$  cm dbh during the 6.5-year period, and there was no significant difference between rates in early-successional plants with  $< 2.5$  cm dbh. Late-successional plants with  $\geq 2.5$  cm dbh did not present significant differences (t test,  $t = 1.21$ ,  $p = 0.24$ ) between mortality ( $= 7.67 \pm 1.24\%$ ) and recruitment ( $= 5.53 \pm 1.26\%$ ), whereas those with  $< 2.5$  cm dbh had higher (Mann-Whitney Test,  $U = 16$ ,  $p = 0.026$ ) recruitment (Mdn = 20.0%) than mortality (Mdn = 7.14%) during the same period.

Comparing the dynamics of the two successional plant groups with  $\geq 2.5$  cm dbh showed that the annual mortality of early-successional plants did not differ from that of late-successional plants (Mann-Whitney Test,  $U = 45$ ,  $p = 0.73$ , table 4), whereas the annual

recruitment of late-successional plants was higher than that of early-successional plants ( $U = 22$ ,  $p = 0.02$ , figure 5).

When the dynamics of both successional plant groups with dbh  $< 2.5$  cm were compared, no significant differences were found between the annual mortality rates of successional groups (Mann-Whitney Test,  $U = 31$ ,  $p = 0.16$ ). However, annual recruitment rate of late-successional plants was higher than that of early-successional plants ( $U = 11.5$ ,  $p = 0.003$ , figure 5).

## Discussion

In 2006 and 2012 the most abundant species, considering all sampled sizes, were late-successional species representative of the main families appearing in later successional stages of the Dense Ombrophylous Forest (Tabarelli & Mantovani 1999, Catharino 2006, Arzolla 2011). Myrtaceae, Lauraceae, Rubiaceae, and Fabaceae were the richest families (around 50% of the total species found, table 2), the first two with the greatest richness which is characteristic of mature Dense Montane Ombrophylous Forest (Tabarelli & Mantovani 1999, Franco *et al.* 2007, Arzolla *et al.* 2011).

In this study, Fabaceae, which is characteristic of environments at earlier successional stages and seasonal forests, was not among the first three richest and most abundant families. This result differed from what has been shown in other previous studies done in the park (Struffaldi-De-Vuono 1985, Nastri *et al.*

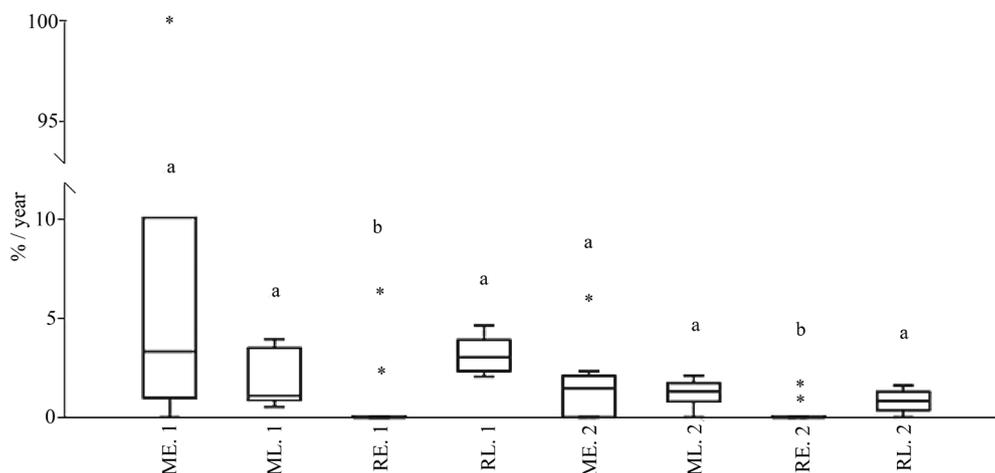


Figure 5. Distribution of the annual mortality (M) and recruitment (R) rates of plants with  $<2.5$  cm dbh (1) and  $\geq 2.5$  cm dbh (2), classified in Early (E) and Late (L) successional categories, in the 10 permanent transects. The letters represent the comparisons of mortality or recruitment of size classes between successional categories. Letters that are the same represent medians that are not significantly different according to the Mann-Whitney test, at a significance level of 5%.

1992, Gomes & Mantovani 2001, Pivello & Peccinini 2002, Eisenlohr *et al.* 2009, Hirata *et al.* 2010, Tanus *et al.* 2012). Similarly, the family Euphorbiaceae was not among the most represented families. The study area is in a more mature successional stage, with low abundance and richness of early-successional species such as those of the genus *Machaerium* (Fabaceae) and *Alchornea* (Euphorbiaceae) which are common in less mature areas of the park. The highest recruitment and predominance of late-successional species and higher mortality in the early-successional group in the area, seem to point to the progression of forest regeneration, the same results obtained in an area (Gomes *et al.* 2003) and different from other areas of the park (Struffaldi-De-Vuono 1985, Knobel 1995).

Of the 125 species identified in the area from the shrub-tree synusia, 12 are listed in the threatened categories “Endangered” or “Vulnerable” (Martinelli & Moraes 2013, MMA 2014, SMA 2016, IUCN 2019). Among the Endangered, one species (*Eugenia pruinosa* D.Legrand, Myrtaceae) is among the ten most abundant. In the set of species identified, we also highlight *Gonatogyne brasiliensis* (Baill.) Müll. Arg. (Phyllanthaceae), a rare species with only 52 records for the State of São Paulo (Arzolla 2011, CRIA 2019). This demonstrates the importance of remnants of secondary forest, like urban forests in a recovery process, as a shelter for rare and endangered species (Brown & Lugo 1990, Norden *et al.* 2009, FAO 2010). Comparing the list from this paper and that from the Park Management Plan (SMA 2008), we

observed that 56 species identified in this study are not included in the plan, out of which, five are listed in some threatened category. These are important information to strengthen the protection of forest remnants and contribute to the updating information of the Parque Estadual das Fontes do Ipiranga.

Despite the existence of other exotic species in fragments of the park (SMA 2008, Petri *et al.* 2018), just *Coffea arabica* L. (coffee) was present in the sampling units (recruited in 2012, table 2). The presence of this species is related to the history of the park area, it was previously grown in small farms located where the park now stands (SMA 2008). This species is dispersed by animals and develops in shaded areas, such as the understory studied (Instituto Hórus 2019). Currently, the species is classified as Non-Dominant Invader in the study area (Petri *et al.* 2018) and presents intermediate priority for extirpation from protected areas (Durigan *et al.* 2013). Therefore, the permanent monitoring of the park fragments will contribute to the correct management of this species.

As shown in other studies in the park (Struffaldi-De-Vuono 1985, Natri *et al.* 1992, Knobel 1995, Gomes & Mantovani 2001, Tanus 2012), the community trees are small in relation to others tropical forests, what is related to the dynamics and growth of plants (Lieberman *et al.* 1990, Condit *et al.* 1999). A large proportion of the specimens showed slow growth (Mdn =  $0.58\%$  year<sup>-1</sup>,  $\bar{X}$  =  $1.14\%$  year<sup>-1</sup>), lower than in another patch of the same park in recovery process (Mdn =  $0.72\%$  year<sup>-1</sup>,

$\bar{x} = 1.52\% \text{ year}^{-1}$ , Gomes 1998). There was no relative growth difference recorded between the size classes, despite the tendency observed in some studies (Swaine *et al.* 1987, Silva *et al.* 1995, Gomes *et al.* 2003). Growth is related to the prevalence of a continuous canopy and the predominance of small clearings in the area (Costa & Mantovani 1992, Davinson 2009) with abundance of late-successional plants and understory individuals, which generally have slower growth (Worbes 1989, Welden *et al.* 1991, Felfilli 1995, Condit *et al.* 1999). Lieberman and colleagues (1990) found that many plants had no diameter growth over the course of 30 years in Neotropical forests. Growth rates are quite variable; this is related to the different environmental conditions as well as to the species' and individuals' life history and phenotypes (Swaine *et al.* 1987, Worbes 1989, Sheil 1995a, Silva *et al.* 1995).

The short stature of canopy trees in mountain tropical forests is also due to high turnover (Herwitz & Young 1994). As expected and shown in other studies (Condit *et al.* 1996b, Machado & Oliveira-Filho 2010, Feeley *et al.* 2011, Laurance *et al.* 2014), the smallest plants were the most dynamic, with the largest recruitment. However, the larger ones also had the highest mortality rates, as observed in another area of the park (Gomes *et al.* 2003). The highest mortality rates, quantified in the extreme size classes (< 2.5 cm and > 5 cm dbh), may reflect the fragility of small plants (Salles & Schiavini 2007), more prone to lethal damage (Sheil *et al.* 2000), and of larger trees, as senescent pioneers, in competition with other plants in the community (Felfilli 1995, Schorn & Galvão 2009). However, late-successional plants predominate the community, and even though early-successional plants show an evident decline, it is not correct to state that overall mortality is due only to the death of this plants, given that the death of late-successional plants also represented a considerable percentage of deaths during the study period.

The death of large specimens caused by some disturbance in the past, as noted in other areas of the park (Struffaldi-De-Vuono 1985, Gomes & Mantovani 2001, Peccinini & Pivello 2002, Gomes *et al.* 2003) may have facilitated light reaching the lower layer of the forest and promoted higher turnover of smaller plants, influencing the establishment of climbers, mainly the woody climbers (lianas). The maintenance of lianas depends on the availability of large trees in the forest (Engel *et al.* 1998, Phillips *et al.* 2005, Sfair *et al.* 2013).

Climbers were the most dynamic life form, as was also observed by Wright (2004), Phillips *et al.* (2005) and Laurance *et al.* (2014). Penhalber & Mantovani (1997) noticed that plants of that synusia were the ones that produced the largest number of propagules in the park, which would favor higher recruitment. On the other hand, their low seedling establishment, especially in more mature forests (Engel 1998, Schnitzer 2005), would reduce, in the long term, recruitment to classes of larger sizes, as noted herein. Although less abundant, climbers had the largest decrease in basal area, accounting for 36% of the total decrease in the community, unlike plants from the shrub-tree synusia which had higher recruitment than loss in the basal area during the period. This decrease in lianas could be related to the maturing of the area. However, only the largest lianas, already established ( $\geq 2.5$  cm dbh), had higher mortality than recruitment and a tendency to decrease ( $\lambda < 1$ ).

The observed dynamism seems to be associated with local conditions and environmental resources. The park area has been protected since 1893 and the use of the sampled area has not changed for at least 65 years (Peccinini & Pivello 2002). Variations in water availability, temperature (Feeley *et al.* 2011), light and mineral nutrients are correlated with changes in the dynamics of plant communities (Laurance *et al.* 2009, Machado & Oliveira-Filho 2010).

The soil of the park is very acidic and poor in nutrients (Struffaldi De Vuono 1985, Gomes & Mantovani 2001); however, it is similar to that of other forests in Southeastern Brazil (Gomes & Mantovani 2001). Moraes (2002) in a study of litter production and decomposition in the 1990s found no abnormalities in a preserved area of the park. An important fact to consider is that the park vegetation was exposed to gas emissions from a nearby steel mill for about 60 years. These gases were responsible for the pollution of the forest, death of trees and the degraded state of part of the vegetation, according to Struffaldi-De-Vuono (1985). Nagaoka & Marcelli (1989) also attributed the considerable decrease of lichens in the park to this factor. The area is still exposed to air pollution from its fully urbanized surroundings. Domingos *et al.* (2002) found some evidence of atmospheric pollution in herbaceous bioindicator plants located outside the forest. Therefore, specific studies are needed in the current decade, considering trees and lianas developing in forest soil, to test the cumulative and current effects of pollution on plant dynamics.

Another important factor that has a relation with local conditions and resources and we suggest for research is the climate, associated with the effects of urbanization and the formation of heat islands (Marengo 2007, Dias *et al.* 2013). Ecological studies have shown an increasing relationship between the high mortality of trees and climbers and climate extremes (Hubbell & Foster 1992, Condit *et al.* 1996a,b, Curran *et al.* 1999, Nepstad *et al.* 2007, Feeley *et al.* 2011). Rainfall monitoring in the park itself over the course of 85 years (1933-2018) reveals irregularities in short periods of time, as in the studied period, which had the driest month (July 2008) and even the wettest month and the second wettest year (January 2010) of the whole historical series (EM-IAG 2017). Even though lianas have greater competitive advantage (Schnitzer 2005), and the smaller shows increasing abundance (Laurance *et al.* 2014), as well as observed, they depend on well-developed phorophytes to transition to larger size classes and to thrive (Phillips *et al.* 2005, Sfair *et al.* 2013, Nogueira *et al.* 2014). As shown, the study area presents small trees with slow growth, and the larger ones ( $\geq 2.5$  cm) presented higher mortality in comparison to the recruitment, which is critical for the maintenance of the abundance and basal area of the larger lianas (Nogueira *et al.* 2014).

Although the studied area shows progress toward a mature stage of regeneration as discussed initially, specific studies are needed to directly assess the influence of the factors mentioned here on forest dynamics. For an isolated forest fragment as the one in the present study, within a highly urbanized area, without any nearby forest fragments, what is expected is an erosion of species in time (Turner *et al.* 1995, Turner 1996). On the other hand, the local history (Chazdon *et al.* 2007, Norden *et al.* 2009), more protective actions in the area in relation to removal of flora and fauna specimens, fewer occurrences of fire and especially cessation of emissions from the neighboring steel mill have favored the regeneration of the vegetation cover, as also shown in another area of the Park (Gomes *et al.* 2003). Despite it is isolated and has fully urbanized surroundings, the remnant is an important source of propagules and shelter of various endangered species, besides providing ecosystem services. This reinforces the importance of this urban forest, in the face of the numerous anthropic pressures. The permanent monitoring of the community and of existing populations of this and other areas of the

fragment, including the climbing plants, may explain how diversity relates to ecosystem resilience and to local factors that can influence forest health.

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