

Dynamics and Edge Effect of an Atlantic Forest Fragment in Brazil

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ABSTRACT

The woody plants in an edge area formed approximately 35 years ago in an Atlantic Forest fragment in northeastern Brazil were examined, and three environments defined: edge, intermediate, and interior. Canopy tree densities and basal areas were found to be similar in all three environments, and also similar to previous published studies in the same region; species richness was greatest at the forest edge. The understory showed greater species richness in the forest interior, but greater diversity and equitability in the intermediate environment. Understory environments close to the forest edge demonstrated larger stem diameters than in the forest interior, although at lesser densities and with smaller total basal areas. Our results indicated the existence of distinct patterns in canopy and understory that most likely reflect differences in the response times of these two vegetation layers, with the understory being more sensitive to alterations in environmental structure.

Keywords: canopy, tropical rain forest, understory.

Dinâmica e Efeito de Borda de um Fragmento de Floresta Atlântica no Brasil

RESUMO

As plantas lenhosas foram examinadas em uma borda formada há aproximadamente 35 anos em um fragmento de Floresta Atlântica. Foram examinados três ambientes: borda, intermediário e interior. A densidade e a área basal de árvores foram semelhantes entre os três ambientes e também próximas à de outros estudos publicados com dados da mesma região. A riqueza de espécies foi maior na borda. Sub-bosque mostrou grande riqueza de espécies no interior da floresta, mas grande diversidade e equitabilidade no ambiente intermediário. Os sub-bosques dos ambientes próximos à borda da floresta possuem mais indivíduos com diâmetros maiores que no interior, embora com densidade e área basal menores. Os resultados indicam a existência de padrões distintos para o dossel e para o sub-bosque, que provavelmente resultaram dos diferentes tempos de resposta desses dois estratos da vegetação, com o sub-bosque mostrando-se mais sensível a alterações na estrutura ambiental.

Palavras-chave: dossel, floresta tropical úmida, sub-bosque.

1. INTRODUCTION

Neotropical forests demonstrate exceptional species richness as well as high levels of endemism, but they have been subjected to accentuated destruction and alterations due to human activities since colonial times (Myers et al., 2000). These habitat losses have had the direct effect of exposing remnant areas to novel environment conditions, reducing population sizes as well as altering migration and dispersal patterns that contribute to biodiversity losses (Murcia, 1995; Cadenasso et al., 2003).

Edge and area effects are the most important factors driving alterations in fragmented communities (Fahrig, 2003; Harper et al., 2005). Numerous studies have shown that the long-term maintenance of animal and plant populations in fragmented areas will depend on the existence of networks of fragments functioning as sources and sinks (Laurance et al., 2002; Ries et al., 2004; Nascimento & Laurance, 2006) - and there will be a tendency for local extinctions if these conditions cannot be maintained. Hanski & Ovaskainen (2002) demonstrated that many species respond rapidly to the environmental changes resulting from fragmentation, while others show much slower responses. From the community perspective, Tilman et al. (1994) used the term "extinction debt" to refer to situations following habitat loss in which suitable conditions for the survival and/or reproduction of some species no longer exist, although they can continue to survive within the community due to lag times in responding to those environment changes.

As an example of this type of delayed response, Metzger (1998) reported that species richness in the understory of an Atlantic Forest area in southeastern Brazil appeared to be more sensitive to alterations in environmental structure than canopy tree richness, as the latter took much longer to express significant changes in richness or diversity. According to Metzger et al. (2009), the mechanisms involved in these delayed responses are still poorly understood, and it will be necessary to examine in detail the long-term evolution of landscape structures and species-dependent plant responses in order to address this subject.

Within the context of fragmentation, there is a general consensus that analyses of population dynamics and succession (*sensu* Pickett et al., 2008) will aid in

determining how ecological processes (expressed as fluctuations of the values of mortality and recruitment and the growth of individuals) and disturbances influence the spatial and temporal patterns of plant populations (Lundberg & Ingvarsson, 1998; Lewis et al., 2004) - aspects that are fundamental to the analysis of fragmentation effects.

Regarding the speed of forest structure recuperation, a number of studies have indicated that there is an initial recuperation of tree density followed by basal area, species richness, and species composition recoveries (Finegan, 1996; Guariguata & Ostertag, 2001; Letcher & Chazdon, 2009). Forest edges tend to become structurally more open in the first years following fragmentation - and therefore more permeable to heat, light, and wind fluxes (Gascon et al., 2000; Laurance et al., 2002). Over time, however, the edges gradually begins to seal through the proliferation of colonizing trees and vines, and these plants will have a substantial influence on the microclimate (Camargo & Kapos, 1995; Didham & Lawton, 1999) as well as on the structure and dynamics of the local vegetation (Laurance et al., 1998; Mesquita et al., 1999; Marín et al., 2007). Edge sealing continues with the passage of more time, although the precise speed of this process is still being debated (Harper et al., 2005).

As edge sealing progresses, there may be disassociations between structural and floristic responses to those border influences, and tropical forests may demonstrate different recuperation responses depending on which plant parameters are analyzed. The present work examined a forest edge formed approximately 35 years ago in a 91 hectare fragment of Atlantic Forest in northeastern Brazil and its influence on the structure, composition, and population dynamics (2005 and 2008) of the canopy and understory vegetation. Previous studies of edge effects have led us to expect the canopy and understory areas closest to the forest edge to demonstrate structural and floristic parameters most strongly influenced by edge effects.

2. MATERIAL AND METHODS

Study area - The forest fragment studied here is located on the grounds of the Usina São José (USJ), situated in the municipality of Igarassu, Pernambuco State, Brazil. This sugar producing farm ("Usina") has

106 forest fragments in the Atlantic Forest domain (IBGE, 2012) that cover a total area of approximately of 6660 ha; 44.2% of these fragments have areas of between 10 and 100 ha (Trindade et al., 2008). The farm retains 24% of its original forest cover, with the most recent clearing having occurred in the mid 1970's when the federal government encouraged sugarcane crops to boost alcohol production (Kimmel et al., 2008; Trindade et al., 2008).

The forest fragment examined is known locally as the "Mata de BR" (7°47'14"-7°48'06"S and 34°56'39"-34°55'60"W), with altitude ranging from 20 to 85 m above sea level. Examinations of aerial photographs from the 1960s, 70s and 80s confirmed that the fragment edges were established 35 years before the present study began and no signs of any fires or recent tree cutting were observed in the forest.

The hot and humid regional climate is classified as As' in the Köppen system (Kottek et al., 2006), with a mean annual rainfall of 1687 mm (concentrated between March and August) and a mean annual temperature of 24.9 °C (data collected for the years 1998 to 2007 at the USJ meteorological station). The predominant winds in the area come from the southwest. This forest fragment grows on a generally flat tableland formation (on the Barreiras geological formation, dating from the Plio-Pleistocene age) that is defined by deep and narrow valleys.

Study design and data analysis - Initial surveys of the canopy and the woody understory of the "Mata de BR" forest were undertaken in the second half of 2005 by Lins-e-Silva (2010) and Gomes et al. (2009) respectively. These authors defined the "edge" as extending up to 50 m into the fragment interior, followed by an "intermediate" environment extending from 50 to 100 m farther in, with the "interior" forest environment being more than 150 m from the forest edge. The edge and intermediate environments were sampled using a methodology modified from Oosterhoorn & Kappelle (2000) that consisted of laying out two 10 × 100 m transects perpendicular to (and starting at) the forest edge. These transects were then divided into a sequence of 10 contiguous 10 × 10 m plots (0.1 ha). The forest interior was sampled using ten 10 × 10 m plots in a single 20 × 50 m block (0.1 ha). Transects were laid out with a southwestern orientation in order to exclude variables related to the orientation of the sun; ground inclinations were similar in all plots.

The canopy trees were sampled in each plot considering all live individuals with trunk diameters > 4.77 cm at 1.3 m above ground level (DBH). To sample the woody understory plants, 5 × 5 m sub-plots were installed in the upper left corners of the canopy plots, considering all plants with stem diameter at ground level (DGL) between 0.96 and 4.77 cm.

A second survey was undertaken during the second half of 2008 that measured the heights and diameters of all of the live individuals originally sampled in 2005, as well as new individuals that had reached the threshold inclusion criteria by 2008. The individuals that were alive in 2005 but could not be found in the 2008 survey were recorded as dead. The diameters of all canopy and understory individuals that surpassed the inclusion criteria used previously were measured and included in the 2008 survey; the heights of the woody understory plants were also recorded. The plants that fell between the two inclusion categories (>4.77 cm DGL and <4.77 cm DBH) in 2005 were measured and then added to the woody understory to avoid any discontinuity between the two classes.

The specimens collected were identified using the technical literature, by comparisons with material deposited in the Dárdano de Andrade Lima Herbarium at the Instituto Agronômico de Pernambuco, and by consulting specialists. These collections were subsequently deposited in the Geraldo Mariz Herbarium at the Universidade Federal de Pernambuco. The spelling of the species and the authors' names were verified by consulting the site www.ipni.org.

We collected 500 g samples from the superficial soil layer (0-20 cm) at the center of each 10 × 10 m plot for both chemical and textural analyses using standard protocols (EMBRAPA, 1997). The variables examined were: soil pH in suspension, the levels of phosphorous (P), potassium (K⁺), calcium (Ca²⁺), magnesium (Mg²⁺), and aluminum (Al³⁺), and the proportions of sand, silt, and clay.

The general parameters of density, basal area, diameter, and average heights of the communities were calculated for the two surveys (2005 and 2008); diameter histograms were prepared using 5 cm intervals for canopy trees and 1 cm intervals for understory plants; height histograms for the understory plants were elaborated using 1 m intervals. Vegetation structures were analyzed by calculating the absolute densities of

the species. Species diversities (in 2005 and 2008) were analyzed using the Shannon diversity index (H' , in nats./ind.) and Pielou's equitability (J'). All parameter were calculated using Mata Nativa 2 software (Souza et al., 2006). Sørensen's index was used to evaluate the floristic similarities between the edge, intermediate, and interior environments.

To compare the plant physiognomies between and within the three environments and at different times (2005 and 2008) we evaluated the numbers of individuals, basal area, height and average diameter, species richness, diversity, and equitability per plot. The comparisons of the environments at the two different times were performed using the "t" test (unilateral) for paired samples. Comparisons between the different environments themselves were performed by first using the Kolmogorov-Smirnov test to examine data normality; data showing normal distributions were submitted to one criterion ANOVA that was complemented by the "t de Tukey" test when the ANOVA results indicted differences between the environments at a significance level of 0.05 (Zar, 1999). When the parameters did not show normality, the non-parametric Kruskal-Wallis test was employed, complemented by Dunn's test. Diameter classes were compared using the Kolmogorov-Smirnov test for independent samples. The chemical and physical variables of the soil were compared between the different environments using the same statistical analyses employed for vegetation structure and physiognomy. All analyses were performed using Bioestat 5.0 software (Ayres et al., 2007).

The data from 2005 and 2008 were used to calculate the recruitment rates ($R = \{[(N0 + r)/N0]1/\Delta t - 1\} \times 100$), mortality ($M = \{1 - [(N0 - m)/N0]1/\Delta t\} \times 100$), and trunk diameter growth rates ($RGR = \{[(DAP1 - DAP0)/DAP0]1/\Delta t - 1\} \times 100$) of the plant communities in the three environments using the formula described by Welden et al. (1991) and Sheil et al. (1995), within the time interval (Δt) of three years.

The correlations between the numbers of individuals of each species and the environmental variables in the canopy and understory plots were examined using canonic correspondence analysis. The principal matrix was composed of species abundances and secondarily by soil variables. Rare species were eliminated as recommended by Ter Braak (1995) and only species with abundances > 5 individuals were considered. The data

was log-transformed before analysis to compensate for biases caused by a few elevated values, and the analyses were performed using PC-Ord 4 software (McCune & Mefford, 1999).

3. RESULTS

Canopy - The results of the canopy survey undertaken in 2008 indicated that there were no significant differences between the three forest environments. There were increases in the numbers of individuals between 2005 and 2008, with recruitment being significantly superior to deaths in all environments. The increase in basal area in the environments nearest the forest edge occurred as a function of increasing plant densities. The basal area in the interior site diminished (in spite of an increase in the absolute number of individuals there) due to the decrease in the average diameter (which was greatly influenced by the death of a very large tree - with a DBH of 22 cm). The average trunk diameter in the intermediate environment did not increase between 2005 and 2008; the edge environment demonstrated a decrease in this parameter due to the inclusion of new individuals with smaller diameters (Table 1). Approximately 60% of the individuals (2008) in the three environments were included within the smallest diameter class (4.77-9.77 cm) (Table 2).

Recruitment was greater than mortality in all three environments. The two environments closest to the forest edge had approximately twice the mortality rate (0.9-0.95%/year) of the interior environment (0.5%/year) (Table 1). The greatest recruitment rate was observed in the interior environment (3.6%/year) while the values for the edge and intermediate environments were 2.40 and 2.74%/year respectively. All of the environments had similar trunk diameter growth rates (0.15 to 16 cm/year) (Table 1).

The edge environment had a higher number of tree species in 2008 (38) than the other environments (intermediate = 32 and interior = 29), and showed greater diversity ($H' = 3.16$ versus 2.85 and 2.80 nats./ind.). The similarities between species compositions of the three environments were low, with values ranging from 0.29 to 0.33.

Understory - Our results demonstrated that there were notable differences between the three understory environments in 2008. The interior area was distinct

Table 1. General parameters, dynamics, species richness, and diversity and equitability indices for the edge, intermediate, and interior environments for canopy trees (0.1 ha per environment) and the woody understory plants (0.025 ha per environment) in Igarassu, Pernambuco State, Brazil, for 2005 and 2008.

Parameters	Edge		Intermediate		Interior	
	2005	2008	2005	2008	2005	2008
CANOPY						
Numbers of individuals	149 ^B	156 ^A	142	150	138 ^B	153 ^A
Density (ind./ha)	1490	1560	1420	1500	1380	1530
Basal area (m ² /ha)	26.1	26.6	19.1 ^B	20.2 ^A	30.2	24.4
Average diameter (cm)	12.6	12.5	10.9	10.9	12.7	11.9
Number of deaths	-	4	-	4	-	1
Number of recruits	-	11	-	12	-	16
Mortality rate (%/year)	-	0.9	-	0.95	-	0.5
Recruitment rate (%/year)	-	2.4	-	2.74	-	3.6
Diameter growth (cm/year)	-	0.16	-	0.15	-	0.15
Number of species	36 ^a	38 ^a	30 ^b	32 ^b	28 ^c	29 ^b
Diversity (H' nats./ind.)	3.1 ^a	3.16 ^a	2.79 ^b	2.85 ^b	2.8 ^b	2.8 ^b
Equitability (J)	0.87	0.87	0.82	0.82	0.84	0.83
WOODY UNDERSTORY						
Numbers of individuals	306 ^{Bb}	401 ^{Ab}	263 ^{Bb}	386 ^{Ab}	770 ^{Ba}	911 ^{Aa}
Density (ind/ha)	12240	16040	10520	15440	30800	36440
Basal area (m ² /ha)	4.3 ^{Bb}	8.7 ^{Ab}	3.7 ^{Bb}	6.3 ^{Ab}	7.4 ^{Ba}	10.4 ^{Aa}
Average diameter (cm)	1.81 ^{ab}	2.18 ^a	1.89 ^a	2.11 ^a	1.55 ^b	1.7 ^b
Average height (m)	1.66	1.94	1.69	1.96	1.68	1.62
Number of deaths	-	24	-	19	-	64
Number of recruits	-	104+(15)	-	130+(12)	-	197+(8)
Mortality rate (%/year)	-	2.7	-	2.5	-	2.8
Recruitment rate (%/year)	-	10.24	-	14.3	-	7.8
Diameter growth (cm/year)	-	0.05	-	0.05	-	0.05
Number of species	35 ^b	40 ^b	36 ^b	43 ^b	48 ^a	55 ^a
Diversity (H' nats./ind.)	2.18 ^b	2.23 ^b	2.88 ^a	2.8 ^a	2.6 ^a	2.65 ^a
Equitability (J)	0.61	0.6	0.8	0.74	0.67	0.66

Numbers within parentheses correspond to individuals of the diameter class not sampled in 2005; Upper case letters indicate significant statistical differences ($p \leq 0.05$) between 2005 and 2008, and lower case letters indicate significant statistical differences ($p \leq 0.05$) between edges, intermediate and interior environments in 2005 and 2008.

from the two environments nearest the forest edge (Table 1), having a greater number of individuals (36,440; *versus* 16,440 and 15,440 ind./ha). This larger number of individuals likewise resulted in a higher area basal (10.4; *versus* 8.7 and 6.3 m²/ha) in spite of the smaller average diameters of those interior individuals (1.7; *versus* 2.2 and 2.1 m²/ha). The basal area values in the two environments nearest the forest edge were found to have practically doubled in relation to those encountered in 2005 (Table 1), with the greatest proportions of individuals occurring in the smallest diameter class (0.96-1.96 cm) ($p < 0.05$) (Table 2).

The classes > 4.96 DGL and < 4.77 DBH had 35 individuals that would not have been tallied if the discontinuity of the inclusion criterion used in the 2005

survey had been maintained (refer to the Methods section). Of these 35 individuals, 19 were located in the edge environment. The intermediate and interior environments had greater numbers of individuals in the second height class (1.1 to 2 m), while the greatest number of individuals in the edge environment occurred in the smallest height class (0.1 to 1 m).

Growth rates were similar in all three environments (2.5 to 2.8%), although the interior environment had almost three times the number of individuals present in the other environments. The three environments showed similar values for trunk diameter growth (0.05 cm/year) (Table 1), and recruitment was greater than mortality in all of them. The number of recruited individuals was greater in the interior (197)

Table 2. Number of canopy (0.1 ha per environment) and woody understory (0.025 ha) individuals in 2005 and 2008 by diameter and height class in three environments in the Mata de BR, Igarassu, Pernambuco State, Brazil.

CANOPY Class of Diameter at Breast Height (cm)	NUMBERS of INDIVIDUALS					
	Edge		Intermediate		Interior	
	2005	2008	2005	2008	2005	2008
4.77-1 9.77	74	79	86	94	75	86
9.77-114.77	37	37	30	27	26	27
14.77-119.77	14	18	13	16	14	19
19.77-124.77	10	5	4	4	8	8
24.77-129.77	8	8	4	4	6	5
>29.77	6	9	5	5	9	8
Total	149	156	142	150	138	153

WOODY UNDERSTORY Class of diameter at ground level (cm)	WOODY UNDERSTORY					
	2005	2008	2005	2008	2005	2008
0.96 1.96	215	252	184	249	614	694
1.96 2.96	47	59	39	65	107	137
2.96 3.96	35	50	30	38	41	48
3.96 4.96	7	21	10	20	8	23
> 4.96 DGL and < 4.77 DBH	2	19	0	14	0	9
Total	306	401	263	386	770	911

HEIGHT CLASSES (m)	WOODY UNDERSTORY					
	2005	2008	2005	2008	2005	2008
0.1 1	111	149	58	114	145	308
1.1 2	127	130	143	139	435	354
2.1 3	33	50	49	71	141	140
3.1 4	12	17	8	26	39	68
4.1 5	15	31	2	15	6	21
5.1 6	3	16	2	9	3	14
>6	5	8	1	12	1	6
Total	306	401	263	386	770	911

than in the two environments nearest the forest edge (104 and 130 individuals in the edge and intermediate environments respectively).

The forest interior differed from the other two environments by having a greater species richness (55; *versus* 43 and 40), while diversity was greatest in the intermediate environment ($H^2=2.8$) (Table 1). The Sørensen indexes were low and similar in all three environments (0.44 to 0.55).

3.1. Multivariate analyses

Of the nine chemical and textural characteristics of the soil examined, two (silt and K^+) did not show any variation among the three environments (Table 3) (and likewise did not demonstrate any significant correlations with the axes of the canonic correspondence analysis for the canopy or understory) and were therefore eliminated from further consideration. (Table 4).

The characteristics that composed axes 1 and 2 were not the same for the canopy and the understory. Of these, only two differed between the three environments and were inversely correlated: pH (which was greater in the interior site) and Al^{3+} (highest in the intermediate environment). The sand content of the soil samples was significantly greater in the interior environment, while clay was better represented at the edge.

Regarding the canopy, of the seven edaphic characteristics analyzed, only three demonstrated any significant correlation with the axes: Al^{3+} , Ca^{2+} and clay content. All three had low eigenvalues (<0.3), however, for both the first (0.21) and second (0.08) axes. These two axes together explained only 13.1% (axis 1, 9.6% and axis 2, 3.5%) of the observed variation in the data, indicating that a large part of the variance could be stochastic or could not be explained by the characteristics analyzed (Table 4).

Table 3. Chemical and textural variables of the three environments in the Mata de BR, Igarassu, Pernambuco State, Brazil.

Variables	Edge	Intermediate	Interior	Auto values			
				Canopy		Woody Understory	
				1	2	1	2
pH in H ₂ O	5 ± 0.5ab	4.7 ± 0.1b	5.2 ± 0.2a	-	-	0.599	-1.593
P – Mehlich (mg.dm ⁻³)	5.4 ± 4.8	4.6 ± 0.5	3.3 ± 1.2	-	-	-0.192	-0.361
Ca ²⁺ (cmolc.dm ⁻³)	1.4 ± 1.4	0.6 ± 0.3	0.9 ± 0.5	-0.900	-0.452	-0.463	-0.132
Mg ²⁺ (cmolc.dm ⁻³)	0.9 ± 0.7	0.6 ± 0.1	0.7 ± 0.1	-	-	-0.100	0.77
Al ³⁺ (cmolc.dm ⁻³)	0.9 ± 0.8ab	1.2 ± 0.2a	0.4 ± 0.2b	-0.900	-0.425	-0.424	-1.686
Sand (%)	64.4 ± 1.9b	67.8 ± 2.1ab	72.8 ± 7.7a	-	-	0.040	-0.463
Clay (%)	29.2 ± 3.3b	27.0 ± 2.2b	21.2 ± 4.9a	-0.654	0.528	-0.289	0.269

The values are averages ± standard deviation for 30 samples; Letters indicate statistically significant differences ($p \leq 0.05$) between the edge, intermediate and interior environments.

Table 4. Canonic correspondence analysis of the abundance of 18 canopy species distributed among thirty 10 × 10 m plots, and 37 understory species distributed among thirty 5 × 5 m plots, in relation to soil factors in the Mata de BR, Igarassu, Pernambuco State, Brazil. The results of the first two ordination axes are provided.

AXES	Canopy		Woody Understory	
	1	2	1	2
Eigenvalues	0.22	0.08	0.31	0.14
Correlation species × environment factors	9.6	3.5	14.0	6.4
Cumulative percentage variations (%) of the species × environment factors	9.6	13.0	14.0	20.5
Monte Carlo permutation tests	0.01	0.14	0.01	0.03

In terms of the understory, all of the seven the characteristics considered (P, pH, Al³⁺, Ca²⁺, Mg²⁺, sand, and clay) demonstrated significant correlations with the first two axes, with eigenvalues greater than 0.3 on axis 1 (0.31) but lower on axis 2 (0.13). Axes 1 and 2 explained 14% and 6.4%, respectively, of the variance observed for the three environments, indicating that a large fraction of the variance demonstrated by the species could not be explained by the soil characteristics analyzed. As such, and considering that both the topography and the orientations of the plots in relation to the sun were controlled for, we can assume that edge effects, associated with the time of edge formation, were the principal agents modulating the species richness and structures of the environments studied here (Table 4).

4. DISCUSSION

Canopy - As the edge environment in the present study (which was established approximately 35 years ago) had a density (1490-1560 ind./ha) similar to

that of the interior site and was, in turn, very similar to the values reported for other general quantitative surveys undertaken in northeastern Brazil (ranging from 1471 to 1657 ind./ha) using the same basic methodology (Siqueira et al., 2001; Rocha et al., 2008; Silva et al., 2008a, b) – it can be concluded that no edge effect (*sensu* Harper et al., 2005) was detectable at the study site. Basal area values were likewise very similar to those reported in other surveys of lowland forest areas in the region using the same inclusion criteria (which varied from 26.8 to 30.1 m²/ha) (Siqueira et al., 2001; Alves-Júnior et al., 2006; Silva et al., 2008b), and the species composition, species richness, and diversity of the canopy trees in the edge environment did not demonstrate marked differences from the interior environment.

Regarding the speed of forest structure recuperation, reports in the literature indicate that there is usually an initial recuperation of plant density, which is followed by the recuperation of basal area, species richness, and species composition (Finegan, 1996; Guariguata &

Ostertag, 2001; Letcher & Chazdon, 2009). Our results indicated, however, that the forest edge studied here had not yet demonstrated any responses to edge effects.

Studies examining the dynamics of the different factors that act on edge and interior canopy components have been scarce, making interpretations of our results more difficult. In an attempt to address this problem, the data from the interior environment studied here were compared to other studies undertaken in mature tropical forests - as these would be expected to have grown under similar environmental conditions. The mortality rate observed in the present study (0.5%/year) was close to the lower limits reported for humid tropical and semideciduous forests (which vary from 0.9 to 3.2%/year) (Swaine et al., 1987; Condit et al., 1992; Phillips et al., 1994; Condit et al., 1999; Oliveira-Filho et al., 2007; Laurance et al., 2009), and the recruitment rate (3.6%/year) observed here was greater than the rates reported for other humid tropical forests (1.65 to 2.87%/year) (Condit et al., 1999). These results suggest that the interior environment examined in the present study had been disturbed.

Understory - In relation to the woody understory, the two environments nearest the forest edge had lower densities, basal areas, and diameters. The interior site differed from the other two environments in terms of its greater species richness (55; *versus* 43 and 40), while diversity was greater in the intermediate environment ($H^2=2.8$ nats/ind.) (Table 1). In terms of species composition, the Sørensen indexes of the three environments were all low and very similar - possibly due to the small sample sizes involved.

As for population dynamics, the environments nearest the forest edge demonstrated greater recruitment rates, while greater understory species richness and diversity was observed in the environments farthest from the edge.

5. FINAL CONSIDERATIONS

In examining the question of whether different recuperation responses to forest edge formation might be observed in terms of different phytosociological parameters, we analyzed the density, basal area, species richness, and composition of the canopy and understory plants in an Atlantic Forest fragment whose edges had been established approximately 35 years earlier. As such, it appears that only the understory was responding to

edge effects - although it is important to remember that the canopy trees in the interior environment were still in their growth (not mature) phase.

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