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Edge effects on the structure and dynamics of an Atlantic Forest fragment in northeastern Brazil

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ABSTRACT

Edge effects on the structure and dynamics of the canopy and understory of a forest fragment were examined in Igarassu, PE, Brazil. Two 10 × 100 m transects perpendicular to the forest edge (and divided into 10 × 10 m plots) were separated into outer (0-50 m) and inner edges (50-100 m) and their vegetations compared to those of 10 plots in a 20 × 50 m transect in the forest interior (280 m from the edge). The plots were the sampling units. All woody plants with stem perimeters at breast height (PBH) > 15 cm (canopy) were identified and measured within each plot. Plants with PBH < 15 cm and perimeter at soil level > 3 cm (understory) were also identified and measured in the 5 × 5 m subplots. Measurements were made in 2005 and repeated in 2008. Higher numbers of canopy species (39 in both edge) and plant densities (2020 and 2280, for inner and outer edge, respectively, in 2005. Similar results were observed in 2008) were encountered along the forest border, while higher understory species numbers (50), plant densities (9960 in 2005 and 13800 in 2008), and basal areas (2.8 in 2005 and 5.2 in 2008) were encountered in the forest interior. The number of recruited understory plants was lower along the forest border (55 individuals) and their mortality rate was higher (6.65 %yr^{-1}). The results indicated that canopy and undergrowth at the edge of the forest fragment studied were not totally recovered in structural terms, for most of the parameters analyzed.

Key words: canopy, mortality, plant, recruitment, understory

Efeito de borda na estrutura de dinâmica de um fragmento de Floresta Atlântica no nordeste do Brasil

RESUMO

Os efeitos de borda foram determinados no dossel e no sub-bosque de um fragmento florestal em Igarassu, PE, Brasil. Dois transectos de 10 × 100 m, perpendiculares à borda da floresta e divididos em parcelas de 10 × 10 m foram separados em borda externa (0-50 m) e borda interna (50-100 m) e a vegetação foi comparada com as parcelas de um transecto de 20 × 50 m no interior da floresta (280 m de distância da borda). Dentro de cada parcela, todas as plantas lenhosas com diâmetro do caule à altura do peito (DAP) > 4,77 cm (dossel) foram identificadas e medidas. Em sub-parcelas de 5 × 5 m, plantas com DAP < 4,77 cm e diâmetro ao nível do solo > 0,96 cm (sub-bosque) também foram identificadas e medidas. As amostras de solo foram coletadas em cada parcela e analisadas textura e propriedades químicas. As medições foram feitas em 2005 e repetidas em 2008. O dossel teve maior número de espécies e densidade de plantas na borda, enquanto o sub-bosque apresentou maior número de espécies, densidade de plantas e área basal no interior. Recrutamento e aumento em diâmetro ao longo dos três anos foram maiores no interior, tanto no dossel quanto no sub-bosque. A análise de correspondência canônica mostrou que as características do solo não afetaram a distribuição das espécies. Considerando que alguns resultados encontrados para o dossel pode ser dito que a borda do fragmento é selada, mas o sub-bosque está ainda na fase de recuperação.

Palavras-chave: dossel, mortalidade, plantas, recrutamento, sub-bosque

Introduction

Tropical forests have the greatest plant diversity in the world but are critically threatened by fragmentation (Pardini et al., 2009). One of the most important aspects of fragmentation is the formation of borders and the edge effects associated with them (Harper et al., 2005). Different physical and ecological processes occur on borders than in the interiors of large forests (Murcia, 1995; Schleuning et al., 2011). Microclimatic characteristics, vegetation structure, species composition, and population dynamics are altered by the formation of borders (Hagen & Kraemer, 2010; Laurance et al., 2011), and the intensities of those changes depend on the sizes and shapes of the fragments (Fahrig, 2003; Ewers et al., 2007). Decreasing fragment sizes and the consequent increases in the areas influenced by edge effects may jeopardize the success of conservation efforts (Harper et al., 2005).

Edge effects also depend on the time elapsed since border formation. The number of species increases along newly created edges, mainly plants adapted to high light intensities (Pütz et al., 2011) and having high photosynthetic and growth rates but short life cycles (Poorter et al., 2008). The densities and biomasses of canopy trees near edges become reduced, while those same parameters increase among understory plants and show faster dynamics than seen in forest interiors (Harper et al., 2005).

Although these general trends have been established, the actual number of studies in remnant forest areas has been relatively small and some aspects have received less attention and conflicting results have undermined the determination of broadly accepted patterns. Comparisons of mortality and recruitment rates along the borders and in the interiors of fragments of different sizes (especially of understory plants) have been scarce (Laurence et al., 1998a; 1998b) and have considered borders of different ages (see Harper et al., 2005). Little data has been gathered from the extremely fragmented Brazilian Atlantic coastal forest in the northeastern region of that country (Oliveira et al., 2004; Santos et al., 2008). Laurance et al. (1998a) reported greater tree mortality along the forest border than in the interior of 10 and 100 ha fragments in the Amazon region, while mortality and recruitment in both the canopy and understory were found to be similar along the border and in the interior of 14 (Costa et al., 2012) - which could have resulted from the homogenization of the vegetation in those highly fragmented sites (Tabarelli et al., 2008).

We report here on the influence of a 40 year-old edge on the dynamics and structures of canopy and understory plants in a large fragment (388 ha) of Atlantic Forest in northeastern Brazil. We expected the canopy of the edge environment to show lower densities and basal areas than the interior environment, and the understory of the edge environment to have higher densities and basal areas than seen in the interior. Both the canopy and the understory edge environments were found to have lower evenness and higher species richnesses, as well as higher rates of mortality and recruitment.

Materials and Methods

We examined a 388 ha fragment of Atlantic Forest (07°42'47"S x 34°59'26"W), known as the Zambana forest, in the municipality of Igarassu, Pernambuco State, in northeastern Brazil. This fragment was formed about 40 years before initiating the present study by the partial clearing of a larger fragment (5090 ha). The study fragment is now completely surrounded by sugar cane fields and is at least 500 m from the nearest remnant forest area (remnant forest of 87 ha). The forest extends across a depression 115 m a.s.l. along one edge and 20 m a.s.l. in the fragment center; it shows no obvious signs of recent disturbances. The soil the edges and interior have similar particle size and chemical characteristics.

The regional climate is of the AS' type (Köppen), hot and humid, with 1687 mm of average annual rainfall concentrated from March to August, and an average annual temperature of 24.9 ºC, with only small daily and monthly variations (meteorological data collected at the Usina São José Station, from 1998 to 2006). The area belongs to the Barreiras geological formation, dating from the Plio-Pleistocene, and has predominantly sandy soils and a flat to gently rolling topography (CPRH, 2003).

In 2005, Lins-e-Silva (2010) conducted a survey in the Zambana forest using 10 × 10 m plots delimited within two 10 × 100 m transects perpendicular to the forest edge; one 20 × 50 m plot, 280 m distant from the edge, was established in the fragment interior. The transects were subsequently considered to be composed of outer (0 to 50 m from the forest border) and inner edge areas (50 to 100 m from the forest border) based on canopy and understory plant densities, basal areas, and average stem diameters.

All living woody plants with stem circumferences (at 1.3 m above the ground) ≥15 cm were marked, identified, and had their stem diameters recorded (in 2005) by Lins-e-Silva (2010), and were treated as canopy plants. A 5×5 m sub-plot was installed in one corner of each plot and all plants with stem circumferences at breast height (1.3 m) >3 cm and <15 cm at ground level were tagged, identified, and had their stem diameters recorded, and were treated as the understory.

Species identifications were based on weekly collections (during 18 months) of plant material (preferentially fertile) that were prepared as herbarium vouchers and incorporated into the Geraldo Mariz Herbarium collection. Identifications were made by consulting the specialized literature, comparisons with specimens incorporated in regional herbaria, and by sending vouchers to experts at several Brazilian institutions. The adopted classification system was APG III (APG III, 2009).

Community characteristics (density, basal area, and average diameter measurements in the same season) were calculated for each plot in each survey (outer and inner edge, and interior of fragment). The Shannon diversity indexes (H', in nats/ind.), equitability (J'), and floristic similarities among the three areas (Sørensen) were calculated using Mata Nativa 2 software (Souza et al., 2006).

Mortality, recruitment rates, and annual growth (in diameter) for both canopy and understory species were calculated using the algebraic formulas described by Sheil et al. (1995) and the data arc-tangent transformed for the statistical analyses of each plot 10 × 10 m.

Comparisons of the structural characteristics of the vegetation in each plot (plots 10 × 10 m) between the two surveys (2005 and 2008) were performed using a paired sample *t* test (unilateral). Comparisons of the structures and dynamics of the areas (outer and inner edge, and interior of fragment) were submitted to one criterion ANOVA that was complemented by the Tukey test when ANOVA indicted significant differences between the environments ($p = 0.05$), if the data showed a normal distribution according to the Kolmogorov-Smirnov test. Data that did not fit normality were analyzed by the nonparametric Kruskal-Wallis test and complemented by Dunn's test. The tests were performed using Bioestat 5.0 software (Ayres et al., 2007).

Results

In 2005, the canopies in the two edge areas (Table 1) had higher densities (2020 and 2280 plants ha^{-1}) than the canopy in the forest interior (1110 plants ha^{-1}) while the understory (Table 1) in outer edge had a lower density (5200 plants ha^{-1}) than the forest interior (9960 plants ha^{-1}). Recruitment rates from 2005 to 2008 were higher than mortality rates in all areas and in both the canopy and understory (Table 1). Thus, densities increased in both strata and in all areas but the general differences between them remained the same.

Both recruitment (2.0 to 5.4 % $year^{-1}$; 150 to 250 plants ha^{-1}) and mortality (0.6 to 1.2 % $year^{-1}$; 20 to 80 plants ha^{-1}) were relatively low in the canopy, without significant differences between the two areas (Table 1). The number of recruits (2200 plants ha^{-1}) in the understory of the outer edge was only half that of the other areas (4240 and 4280 plants ha^{-1}), but as the initial density there was also lower, recruitment rates were similar (12 to 15% $year^{-1}$). Mortality in the outer edge (6.65 % $year^{-1}$; 1080 plants ha^{-1}) was almost double that of the inner edge (3.99% $year^{-1}$; 800 plants ha^{-1}), while mortality in the forest interior was even lower (1.44% $year^{-1}$; 440 plants ha^{-1}). The low number of recruits in the understory of the outer edge combined with the large number of deaths resulted in the smallest increase in density in that area. Thus, the outer edge not only had the lowest density but the differences between it and the two other areas were still increasing. The opposite occurred in the canopy, with density differences between the areas decreasing (although with only small magnitude, considering the absolute plant numbers).

In 2005, average stem diameters were similar among the three areas (Tables 1) in terms of both canopy (10.1 to 13.4 cm) and understory plants (1.8 to 1.9 cm). From 2005 to 2008, the stem growth rate (Table 1) of canopy plants in the outer edge was negative (-0.02 cm $year^{-1}$), contrasting with positive rates in the other two areas (0.08 cm $year^{-1}$ in the inner edge and 0.18 cm $year^{-1}$ in the forest interior). This negative rate reflected reductions of about 40% in the stem diameters of all canopy plants, especially those branched below the measuring height (1.3 m). The stem growth rates of understory plants were all positive and similar among the areas (0.04 to 0.09 cm $year^{-1}$), and were of the same magnitude as the canopy plants.

Basal areas increased in both strata and in all areas, reflecting increases in densities and stem diameters - except in the canopy of the outer edge, where the density increase was offset by decreases in stem diameters. Thus, all of the areas were apparently still accumulating biomass.

The canopy had higher species richness in the edge areas than in the forest interior in both 2005 and 2008 (Figure 1), while the opposite was observed with the understory (Table 1). The two edge areas were floristically more similar to each other than to the forest interior (Figure 1).

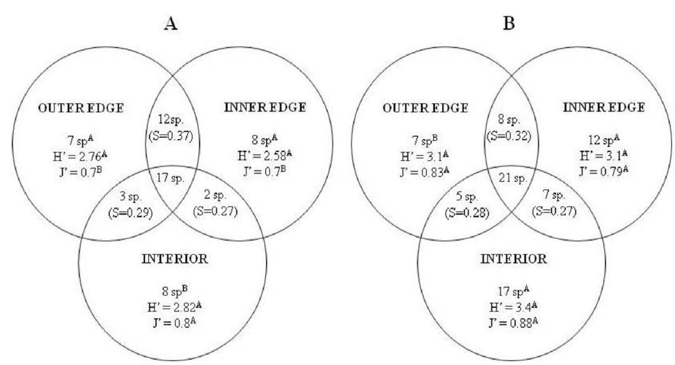

Figure 1. Venn diagrams demonstrating richness, diversity, equitability, and the Sørensen similarity indexes of the canopy (A) and understory (B) vegetation in outer edge, inner edge, and forest interior areas in Igarassu, PE, Brazil. Letters indicate statistically significant differences ($p \le 0.05$, Tukey test) between the environments

Table 1. Physiognomic parameters and plant dynamics in the canopy and understory of outer edge, inner edge, and forest interior areas in Igarassu, PE, Brazil. Upper case letters represent significant differences ($p \le 0.05$) between 2005 and 2008 (t test), while lower case letters indicate significiant differences between areas (Tukey test and Dunn's test)

	Canopy						**Understory**					
	Outer edge		**Inner edge**		**Interior**		**Outer edge**		**Inner edge**		**Interior**	
	2005	**2008**	**2005**	**2008**	**2005**	**2008**	**2005**	**2008**	**2005**	**2008**	**2005**	**2008**
Physiognomy												
Density (plants ha^{-1})	2020^{Ba}	2190^{Aa}	2280^{a}	2390^{a}	1110^{Bb}	1280^{Ab}	5200^{b}	6320^{b}	7640^{B}	11080^{Aa}	9960^{Ba}	13800^{Aa}
Basal area (m^2 ha^{-1})	27.6	27.4	24.1^{B}	25.6^{A}	22.1	23.8	2.7^{Bb}	4.9^{Ab}	1.6^{B}	2.8^{Aa}	2.8^{Ba}	5.2^{Aa}
Mean diameter (cm)	11.4^{A}	10.8^{B}	10.1	10.1	13.4^{A}	12.6^{B}	1.8	1.9	1.9	2.1	1.9	2.0
Maximum diameter (cm)	50.5	45.2	42.9	48.3	50.7	49.6	4.5	5.9	4.7	6.7	4.6	7.0
Dynamics												
Surviving (number of individuals)	-	194	-	224	-	109	-	103	-	171	-	238
Deaths (number of individuals)	-	8	-	4	-	2	-	27	-	20	-	11
Recruits (number of individuals)	-	25	-	15	-	19	-	55^{B}	-	106^{A}	-	107^{A}
Recruitment (% yr^{-1})	-	4.14	-	2.01	-	5.41	-	12.15	-	15.98	-	12.26
Mortality (%yr^{-1})	-	1.17	-	0.74	-	0.60	-	6.65^{A}	-	3.99^{B}	-	1.44^{B}
Growth (cm yr^{-1})	-	-0.02	-	0.08	-	0.18	-	0.04	-	0.09	-	0.04

Discussion

The canopy of the 40-year old edge areas had densities (2190 to 2390 plants ha^{-1}) higher than those of the forest interior (1280 plants ha^{-1}); their densities were also higher than those reported in other surveys conducted in northeastern Brazil with the same plant inclusion criteria (ranging from 1553 to 1657 plants ha^{-1}) (Nascimento & Rodal, 2008; Rocha et al., 2008). These results indicate that the border plant density quickly reaches that of the interior, and then overshoots it - and only after a good deal of time does it return to values typical of the forest interior. As such, the observed border density was probably in a phase in which it had already exceeded the interior density and presumably would begin to decrease - indicating that full recuperation in the structure had not yet occurred.

Basal areas were similar among the different areas (24 to 27 m^2 ha^{-1}) and at the lower limit of the ranges previously reported in similar surveys in the region (Alves-Júnior et al., 2006). The total basal area of the forest border more slowly approached the value observed for the interior than did density, as that parameter could only compensate the smaller mean diameters during the phase of greater plant density. After attaining values equivalent to the forest interior, however, the basal area could no longer differ greatly, as plant deaths would compensate increases in the mean diameters - maintaining the total basal area more or less stable. As such, total basal area is not an accurate indicator of final phase recuperation, while density would be. As such, the basal area parameter likewise indicated that this forest fragment had not fully recuperated, or at least that the border structure still differed from that of the interior.

Density in the understory of the outer edge area was lower than in the forest interior (6,320 versus 13,800 plants ha^{-1} respectively), a pattern similar to that reported by Silva et al. (2008) in a 357 ha fragment (4,371 and 9,314 plants ha^{-1} respectively) and by Gomes et al. (2009) in a 91 ha fragment (13,040 and 32,200 plants ha^{-1} respectively). The fact that the border environments had lower plant densities and greater mortalities (even while recruitment was similar to that seen in the interior) indicated that it had not stabilized and would require still more time to reach the values observed in the interior.

In addition to the differences seen between canopy and understory densities along the gradient, the fact that the species richness of the canopy was higher in the edge areas, while the opposite was true in the understory, indicates that these strata have different recovery times after disturbance (Metzger, 1998). It has been observed that some species can rapidly respond to changes resulting from fragmentation, while other species have slower response times (Hanski & Ovaskainen, 2002). As an example of this lag in response time, Metzger (1998) reported that the species richness of the understory in an area of Atlantic Forest in southeastern Brazil was more sensitive to changes in environment structure than the canopy (which took more time to demonstrate changes in richness and diversity). According to Metzger et al. (2009), the mechanisms controlling differences in response times are still poorly known as their examination would require measuring the evolution of the landscape structure, while individual responses appear to be species dependent.

The dynamics of mature forests have been reasonably well studied and can be compared with our data for the forest interior. The mortality rate in the canopy in the study fragment (0.6% $year^{-1}$) was lower than the lowest value (0.86 to 2.02 % $year^{-1}$) reported in a review by Lewis et al. (2004) of forest fragments ranging in size from 9.5 to 50 ha. Canopy recruitment (5.41% $year^{-1}$), on the other hand, was higher than the values (1.65 and 2.87 % $year^{-1}$) cited by Condit et al. (1999) for 1500 and 2000 ha fragments respectively.

Conclusions about canopy dynamics were limited by the small numbers of recruited and dead plants. The decrease in understory mortality from the fragment edge to the interior indicates that forest borders represent less stable environments.

Conclusions

The complexity of forest successional processes has been cited by a number of authors, and there is still no consensus on basic questions such as the recovery times of different parameters after disturbance. Studies of these processes clearly need to be undertaken in an integrated manner, as the analysis of isolated parameters may lead to divergent conclusions.

Although an edge effect was detected in the present study, many of the hypotheses put forward were not corroborated, as we expected the canopy of the edge environment to have a lower density and a lower basal area than the interior environment, as well as higher rates of mortality and recruitment. These results may reflect the fact that 40 years was not sufficient to observe expected mortality effects on most canopy trees. It is also probable that the death of some of the trees allowed greater development of other individuals, increasing plant density in the environments closest to the forest border. This increase was sufficient to compensate reductions of basal areas through tree mortality, so that basal area did not in fact vary along the border to interior gradient.

Additionally, we expected the understory border environment to have higher density, lower evenness, and higher species richness than the interior understory, which was not in fact observed. We did observe that the border and interior environments were similar in terms of their understories, but distinct in terms of their canopies, which indicates differences in response times between the canopy and the understory.

The results of the present study indicate that neither the canopy or the understory of the forest fragment examined had fully recovered in terms of most of the parameters examined, as differences were observed between the forest edge and interior - indicating that large forest fragments are not homogeneous (sensu Tabarelli et al., 2008) and that some areas of the forest fragment investigated may still be well conserved.

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