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The Effect of Internal and External Edges on Vegetation Physiognomy and Structure in a Remnant of Atlantic Lowland Rainforest in Brazil

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ABSTRACT

This study was carried out in a remnant (305.78 ha) of the Atlantic Rainforest in Northeastern Brazil, and investigated the effects on vegetation of two edge conditions: external with sugarcane fields (EE) and internal along a road (IE). Three 10 × 100 m transects perpendicular to the each edge were established for sampling trees (10 × 10 m plots) and understory (5 × 5 m plots). We confirmed weaker edge effects on forest physiognomy at IE, where the tree assemblage is denser, taller, with higher diversity. At this edge, 1,693 trees ha^{-1} were recorded, the first 70 m being distinctive only for density, and 4,200 understory $ind.ha^{-1}$; with differences on heights and diameters in the first 40 m. At EE, 1016 trees ha^{-1} were recorded, with differences in physiognomy up to 40-60 m for height and density; 6,093 $ind.ha^{-1}$ were found in the understory, the first 60 m showing greater diameters. The two edge types were different regarding canopy density, basal area and height, all greater along IE, whereas understory density was greater at EE. Regarding forest composition, the similarity (Sorensen coefficient) was of 0.72 between edge conditions. Cluster analysis showed the structure of two distinct groups (IE and EE), followed by sub-clusters individualizing the first 30 m at each edge. Forty-five families and 154 species were recorded in total, with a low percentage of indicator species in the overall community. Sapotaceae and Myrtaceae (at IE), Anacardiaceae/ Mimosaceae and Euphorbiaceae (at EE) had the greatest tree and understory densities, respectively. Our results indicate that a 40-60 m-wide belt along fragment perimeter is strongly influenced by external or internal edge, although less markedly in the latter. However, this effect is actually narrower than often thought, pointing towards a more optimistic prognosis of the sustainability of the fragmented Atlantic Rainforest.

Keywords: edge effect, forest fragment, fragmentation, internal clearing, road

INTRODUCTION

The fragmentation of terrestrial ecosystems exposes organisms on the newly-created boundaries to conditions quite distinct from intact habitats, and these have been denominated as edge effects (Saunders *et al*. 1991; Murcia 1995) or edge influences (*sensu* Harper *et al*. 2005). Edges are omnipresent in nature, representing zones of transition, contact or separation between two distinct elements (Cadenasso *et al*. 2003b), ranging from cell membranes, to the soil-air interface, and to the abrupt margins of forest remnants resulting from ecosystem fragmentation (Laurance *et al*. 2001). Edge zones or ecotones are presumed to have negative consequences for wildlife (Saunders *et al*. 1991) and have been studied in boreal, temperate, and tropical ecosystems (Harper *et al*. 2005). Industrialization and the replacement of natural tropical ecosystems by extensive agriculture have led to a rapid environmental degradation over the last decades in areas of tropical moist forests (Myers 1988), where fragmentation seems to have greater negative effects than in temperate systems (Fahrig 2003).

Although many studies have focused on edge effects in tropical ecosystems, few firm generalizations are possible due to the lack of standardization of variables and sampling designs (Murcia 1995). An important theoretical synthesis was formulated by Cadenasso *et al*. (2003a), whose model is based on fluxes of organisms, matter, energy, and information between elements in a mosaic, and is applicable to all types of boundaries. Ries *et al*. (2004) reviewed the mechanisms that cause edge responses and examined a model showing that such responses, for plants, are predictable and consistent. Harper *et al*. (2005) synthesized the literature available concerning edge effects on plant communities and demonstrated that, after the initial isolation phase, an area of influence is defined in each remnant that tends to expand with time, defining a zone where modifications of vegetation structure and floristic composition are expected.

Edge effects in forest ecosystems, quantified as variations in microclimate and vegetation physiognomy and structure, are usually detectable up to about 50 m of width (Williams-Linera 1990; Matlak 1993; Young and Mitchel 1994; Oosterhoorn and Kappelle 2000) or less (Fox *et al*. 1997). In Australian forests, exotic herbs were recorded penetrating up to 500 m from the edges (Laurance 2000). Based on a 20-year dataset in the Amazon forest, a pronounced increase on tree damages and mortality was recorded within the first 60-100 m from the edge, and smaller changes could be detected at distances up to 300 m (Laurance *et al*. 1998a), reducing fecundity, influencing arboreal structure, facilitating the proliferation of pioneer species, and altering biogeochemical cycles (Laurance *et al*. 2001). These results influenced the view of 300 m as being the edge width in Amazonian fragments (Nascimento and Laurance 2006), and, in the absence of data assessing distance of edge influence or edge depth for the coastal forests, the adoption of a 100 m-deep edge for the Atlantic Rainforest in southeastern (Paciência and Prado 2004) and northeastern Brazil (Oliveira *et al*. 2004). Nevertheless, the examination of biotic and abiotic data and their interactions in forest edges is an area of ongoing research (Cadenasso *et al*. 1997; Nagaike 2003).

After many economical cycles along the Brazilian At-

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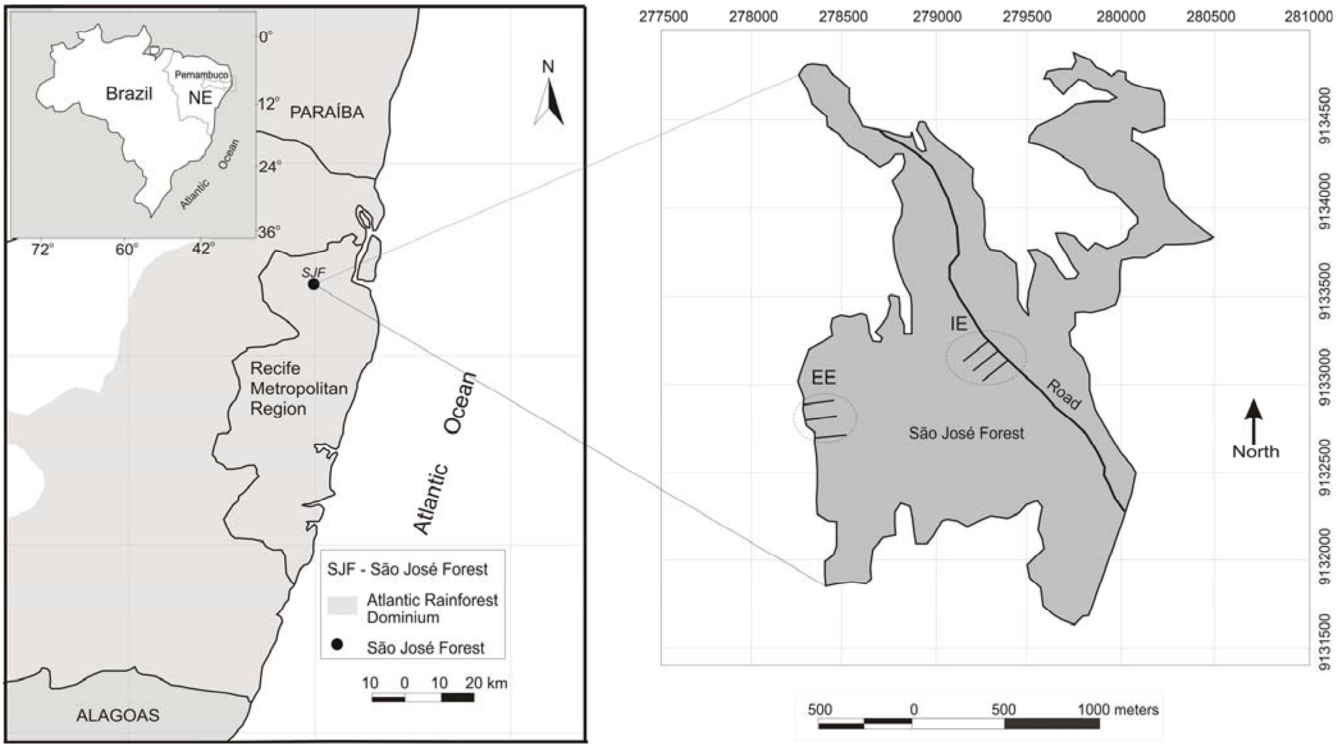

Fig. 1 Map of study area and location of data collection transects, São José Forest, Igarassu, Pernambuco, Northeastern Brazil. IE, Internal edge; EE, external edge.

lantic coast, less than 10% of the original tropical forest remains, with scattered remnants forming a mosaic landscape (Morellato and Haddad 2000; Galindo-Leal and Câmara 2003). This forest occurs in a coastal band stretching from Northeastern to Southeastern Brazil in a region where 80% of all the country's consumed crops are produced and where 70% of its population lives (Pinto and Brito 2003). Therefore, the Atlantic rainforest is a priority for conservation because of its high fragmentation, high species richness and species endemism. It is considered one of the world's 25 conservation hotspots, where 44% of all of the world's vascular plants are found on just 1.4% of earth's surface (Myers *et al.* 2000).

In the most eastern region of Brazil, a high percentage of mature forest was destroyed over the last three decades (Trindade *et al.* this volume, pp 5-13), resulting in small and closely spaced forest remnants, surrounded by sugarcane fields (Ranta *et al* 1998). Large fragments are often cut by roads, power lines, or gas lines, defining a net of "internal fragmentation" characteristic of modern landscape and representing one of the greatest human influences on natural environments outside of urban areas (Goosem 1997). The environmental consequences of opening of roads have been discussed for the Amazon (Anderson 1990; Laurance *et al*. 2001), and for montane forests (Young 1994), and studies have demonstrated that opening roads can affect slope stability, cause local extinctions of specialist species, and create edge effects influencing vegetation in much the same way as forest gaps do, although with significantly higher magnitude (Nagaike 2003). Although these internal lines are a common feature in the fragmented forest along the Brazilian northeastern coast, no studies have examined their impact on the natural environment, especially the conversion of internal areas into new edges (Reed *et al*. 1996).

In this study, we investigated edge effects on the vegetation in a fragment of Atlantic Rainforest in Pernambuco, northeastern Brazil. We hypothesize that these influences will be distinguishable when the edges are bordered by farmed fields or by roads that cross the fragment, the latter determining weaker effects. Our objectives were to describe the quantitative attributes of the physiognomy and structure of the canopy trees and understory vegetation, and to compare these two edge conditions, in order to establish the effective edge depth and gain a better understating of the magnitude of edge influences in a forest remnant.

MATERIALS AND METHODS

Study site

The "São José Forest" fragment (7° 49′ 12.66″ to 7° 50′ 55.43″ S and 35° 0′ 35.92″ to 34° 59′ 21.29″ W), also known as Piedade Forest, is a protected area in the municipality of Igarassu, Pernambuco, Brazil, occupying 305.78 ha (**Fig. 1**). The forest is owned by, and is located next to, the Usina São José S.A., a sugar mill. The forest area lies within the Botafogo River Basin, and protects springs, slopes, and soil resources in the region. The site represents a narrow valley within the plio-pleistocenic Barreiras Sedimentary Group (CPRH 2003), with steep slopes (more than 30% inclination), and altitudes varying from 30 m to 113 m. The local climate is classified as Köppen As' (hot and humid), with an average rainfall of 1687 mm, with a moderate summer water deficit, and mean temperature of 24.9°C (meteorological data collected at the Usina São José Station, from 1998 to 2006).

The fragment is a well preserved remnant of Moist Dense Lowland Forest (IBGE 1992), with a small percentage of secondary forests and little signs of any use of its natural resources (Santos *et al*. 2001). There are aerial photographs (1975) available for the area at a scale of 1:30.000, and 2005 Ikonos II satellite images (4 × 4 m pixel) (Trindade *et al*. this volume, pp 5-13). This cartographic material made it possible to determine that the edges examined were formed at least 30 years ago, and are now consolidated and in a mature phase, i.e. they are older edges with structural and compositional vegetation changes (Harper *et al*. 2005).

Forest limits were defined in this study as the line that delimits the road or the first few meters of an agriculture field, which has only bare soil or low herbaceous cover. As such, part of the canopy could extend beyond the edge boundary, or the first tree trunks could actually be found at some distance from the technically defined boundary.

Sample design

After analyzing the cartographic material, topographic conditions, and existent physiognomical classification (Santos *et al*. 2001) for the studied remnant, two edge conditions were found: 1) internal edge (IE), and 2) external edge (EE).

The internal edge (IE) is limited by an 8-10 m wide road crossing the fragment, with slopes of 10% and a maximum altitude of 111 m. The road is used for low-intensity vehicle movement all year round, and sugarcane trucks during harvest period (August-December). The external edge (EE) is limited by sugarcane fields with a declivity of 15%, at altitudes between 100 and 114 m. This edge is separated from farmed fields by a 5 m wide track kept with bare soil. Three transects (100 m long by 10 m wide) were established parallel to each other and perpendicular to each edge type (**Fig. 1**).

Sampling design was modified from Oosterhoorn and Kappelle (2000). Survey plots were established along all transects every 10 m, forming 10 contiguous 10 × 10 m quadrats and designated from the edge to the end as 1-10 consecutively; in inner corners of these quadrats other 5 × 5 m sub quadrants were established for sampling understory plants. All woody individuals were counted, marked, identified by local name, measured (circumference at breast height - CBH and height), and subsequently placed into two distinct size categories: (1) Canopy - trees and lianas with CBH $\geq$ 15 cm in the 10 × 10 m quadrats, and (2) Understory - small trees, saplings and shrubs with CBH > 3 cm and < 15 cm in the 5 × 5 sub-quadrats.

Specimens recorded were collected and identified using specialized literature (taxonomic monographs), plant morphology, the assistance of specialists, and comparisons with the plant collections from the Usina São José Forest fragments at the Herbarium Professor Vasconcelos-Sobrinho (PEUFR) at the Universidade Federal Rural de Pernambuco (UFRPE). All plants were vouchered and stored at the PEUFR herbarium. Lianas were not identified, but rather grouped together for an estimation of their importance. The resulting floristic list followed the classification system of Cronquist (1981).

Data analyses

For each sample plot, the following absolute physiognomic variables were calculated: density (stems/area), dominance (basal area), mean height and diameter. Variables were tested for normality using the Shapiro-Wilk test prior to a one-way analysis of variance (ANOVA) or its non-parametric equivalent (Kruskal Wallis) for comparisons between the two edge conditions and edge distances (10 distances, three replicates in each condition), using the SAS Statistical Package (1998). When ANOVA showed significant differences between edge distances, Tukey test was carried out to detect differences. Means of physiognomic variables in each edge distance were calculated for trees and for the understory. Additionally, t-tests or Mann-Whitney test for comparisons of means were run between groups of edge distances; for example, group 1 (plots from 0 to 20 m) x group 2 (plots from 20 to 100 m), group 1 (plots from 0 to 40 m) x group 2 (plots from 40 to 100 m), and so on, in order to assess whether an increase or decrease of the recorded values influenced the group averages. We used a significant statistical level of P = 0.05 in all analyses. Considering the difficulty in estimating heights for lianas, these were not included in the mean height data, but considered when calculating density and basal area, because of their importance to forest physiognomy.

Relative parameters of density, frequency, and dominance were calculated for each recorded species and family (Brower and Zar 1984), and their sum total composed the importance value (IV) for each edge category, using the FITOPAC software package (Shepherd 1995). Plant species diversity was calculated for each edge condition, and for each size category, using three indices: species richness, the Shannon-Weaver diversity index H' and the Simpson evenness D (Magurran 2003). The floristic similarities between edge conditions and positions were calculated using the Sørensen coefficient. Additionally, cluster analysis was carried out with the aim to assess the existence of structural groups using species as descriptors, using the Bray-Curtis coefficient of distance (abundance) and UPGMA technique (group average) (Kent and Coker 1994). A single contingency matrix was used with 20 objects (samples) and all species with more than 5 individuals, adding together relative densities of trees and understory plants in each object. Plots in each distance were grouped into a single sample per position; dead standing individuals and lianas were not included. Indicator species analysis (ISA) was also performed assigning a category according to edge condition and/or structural group previously formed, for size category and the total sample. Each species received an indicator value (INDVAL), which combines species relative abundance and its frequency of occurrence in the sites of a particular group, followed by a random reallocation procedure (1000 permutations) of sites among site groups to test the significance of INDVAL, returning a probability of a random distribution (Dufrêne and Legendre 1997). Indicator species are the most characteristic species of each group, found mostly in a single group and present in the majority of the sites belonging to that group. For these multivariate analyses, software PC-ORD for Windows 4.0 was used (McCune and Melford 1999).

RESULTS

Edge effects on vegetation physiognomy

An estimated 1,693 ind.ha^{-1} were growing in the canopy along the internal edge (IE), with a mean height of 11.23 m (**Table 1**), the tallest individuals reaching 26 m. Mean diameter was 12.5 cm, with a maximum of 200.22 cm. IE contained 78% of all lianas and 70% of all dead standing trees. The estimated understory plant density was 4,200 ind.ha^{-1} at this edge, basal area was 1.515 m^2.ha^{-1}, and mean heights varied from 1.30 m to 10 m (mean 2.59 m). At this edge, while no significant differences in basal area, height, or diameter for tree and understory were observed between plots at various distances from forest boundary, tree densities were significantly different at different positions (p=0.048; F=2,416), especially between position 1, up to 10 m (mean =10.33 ind/quadrant) and 10, between 90 and 100 m (mean =23.33 ind/quadrant). When groups of positions were compared (plots between 0–70 m *vs.* 70 to 100 m), tree density was found to be significantly greater at further distances from forest boundary (p=0.05; t=1,617) (**Fig. 2**). For the understory, differences of pooled plots were found at shorter distances from the edge (0 to 40 m *vs.* 40 to 100 m) for mean heights (p=0.007; n_1=12; n_2=18) and for average stem diameters (p=0.029), both variables significantly greater in positions more distant from the edge (**Fig. 2**).

Along the external edge (EE), an estimated 1,016 ind. ha^{-1} were found in the canopy, with a basal area of 20.56 m^2 ha^{-1}, heights ranging from 2 to 19 m, and average diameter of 12.66 cm (maximum 60.48 cm) (**Table 1**). EE understory had 6,093 ind.ha^{-1}, mean heights varied from 0.8 to 9.5 m, and the mean diameter was 1.85 cm. Although physiognomic characteristics did not significantly differ between individual edge positions, groups of positions demonstrated sig-

Table 1 Values for plant diversity variables (Shannon diversity index, equitability index and species richness) and physiognomic variables (density, basal area, mean height and mean diameter) at the São José Forest, Igarassu, Pernambuco, Brazil.

Plant size Edge condition	Diversity index[1]	Equitability index	Species richness	Density (ind./ ha)	Basal area (m^2/ ha)	Mean height (m)	Mean diameter (cm)
Trees							
Internal edge	4.101	0.914	89	1693	55.02	11.23	12.50
External edge	3.615	0.851	70	1016	20.56	8.99	12.66
Understory							
Internal edge	3.798	0.882	74	4200	1.515	2.59	1.89
External edge	3.827	0.848	91	6093	1.948	2.60	1.85

1. Shannon-Weaver, H', Log$_n$

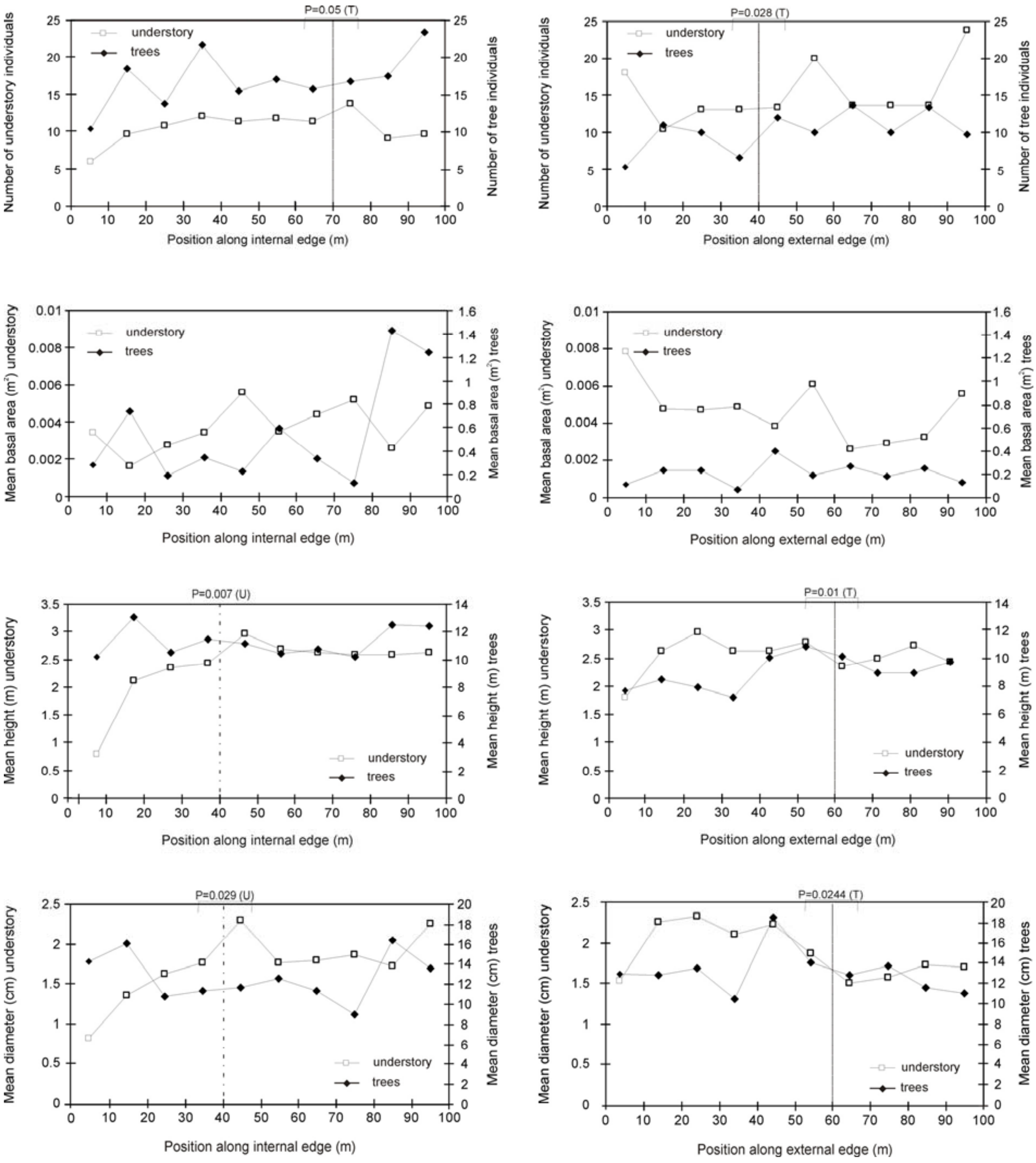

Fig. 2 Physiognomical parameters along transects at internal edge (on the left) and external edge (on the right) of São José Forest, Igarassu, Brazil. Vertical lines mark edge influence width according to variables tested, probabilities of significance (p) are given for t-tests (T) or Mann-Whitney (U) between groups of positions.

nificant differences in terms of: tree density for distances 0-40 m *vs.* 40-100 m (p=0.028; t=1.9364), increasing at greater positions from forest boundary; tree height, for distances 0-60 m *vs.* 60-100 m (p=0.01; t=2.3035), the average height increasing from 7.2 to 10.07 m at greater distances from the edge; and understory diameter, the first 60 m with greater mean diameter (p=0.0244; t=2.0598), showing a concentration of thin understory individuals from the mid-distance plots inward (**Fig. 2**).

The two edge conditions were different in terms of canopy density ($p \leq 0.001$; t=5.3303), 60% greater at IE, and understory density, significantly lower at IE (p=0.0069; F=7.8632). Mean canopy height ($p \leq 0.001$; t=5.2233) and canopy basal area (p=0.036; Z(U)=2.4099) were also significantly greater at IE, due to the presence of large trees at this edge, especially between distances from 90 to 100 m (**Fig. 2**). Understory mean heights and diameters were similar in both edge conditions.

Composition and structure of vegetation

Richness and diversity showed different tendencies under the two edge conditions, decreasing for trees and increasing for understory from IE to EE (**Table 1**). Thus, greater species richness and diversity were observed in IE canopy and EE understory, whereas EE canopy was the least diverse and least species rich, among a total of 154 plant species (**Table 2**). There was an overall floristic similarity of 0.72 (Sørensen coefficient) between the two edge conditions, decreasing for 0.61 when comparing only trees and 0.64 for understory. Lower similarities were found when comparing species compositions of trees and understory within the same edge type (0.59 for IE, and 0.45 for EE). Despite the high similarity of species, cluster analysis demonstrated a strong distinction between IE and EE (**Fig. 3**). IE cluster is divided into sub-clusters according to distances from forest boundary: the first 10 m separated first, followed by distances 20-30 m, and then an inner cluster composed of all re-

Table 2 List of species and families recorded at two edge conditions (internal and external) at São José Forest in Igarassu, Pernambuco, Northeastern Brazil. D_e = estimated density of each species population (ind. ha^{-1}) at each condition, for one hectare, adding together trees and understory estimates. Capital letters in brackets indicate the plant size category sampled: T=trees, U=understory in each edge condition. Species are organized according to their presence in both conditions to one condition, and alphabetically within each group. Species followed by * are indicators of an edge condition at $P \leq 0.05$ and by ** at $P \leq 0.01$.

Species	Family	Internal Edge		External Edge	
		D_e		**D_e**	
Alseis pickelii Pilger & Schmale *^{IE}	Rubiaceae	207	(T, U)	80	(U)
Anaxagorea dolichocarpa Sprague & Sandwith	Annonaceae	13	(U)	27	(U)
Aspidosperma discolor A. DC.	Apocynaceae	313	(T, U)	187	(T, U)
Aspidosperma spruceanum Benth. ex Müll. Arg.	Apocynaceae	30	(T, U)	137	(T, U)
Bactris ferruginea Burret	Arecaceae	103	(T, U)	17	(T, U)
Bocoa sp.	Fabaceae	27	(U)	40	(U)
Bowdichia virgilioides Kunth	Fabaceae	13	(U)	30	(T, U)
Brosimum guianense (Aubl.) Huber	Moraceae	180	(T, U)	267	(U)
Brosimum rubescens Taub. **^{IE}	Moraceae	90	(T, U)	13	(U)
Brosimum sp.	Moraceae	13	(U)	27	(T, U)
Byrsonima sericea DC.	Malpighiaceae	27	(T)	30	(T, U)
Calyptranthes brasiliensis Spreng.	Myrtaceae	273	(T, U)	160	(U)
Casearia arborea (Rich.) Urb.	Flacourtiaceae	7	(T)	7	(T)
Casearia javitensis Kunth *^{EE}	Flacourtiaceae	7	(T)	97	(T, U)
Cecropia pachystachya Trécul	Cecropiaceae	10	(T)	17	(T)
Chaetocarpus myrsinites Baill.	Euphorbiaceae	3	(T)	3	(T)
Chamaecrista ensiformis (Vell.) H.S. Irwin & Barneby *^{IE}	Caesalpiniaceae	53	(T)	3	(T)
Chrysophyllum splendens Spreng.	Sapotaceae	3	(T)	3	(T)
Clarisia racemosa Ruiz & Pav.	Moraceae	20	(T)	3	(T)
Cordia superba Cham.	Boraginaceae	30	(T, U)	70	(T, U)
Dialium guianense (Aubl.) Sandwith	Caesalpiniaceae	27	(U)	93	(U)
Diploon cuspidatum (Hoehne) Cronquist	Sapotaceae	63	(T, U)	40	(U)
Eriotheca crenulaticalyx A. Robyns*^{IE}	Bombacaceae	90	(T, U)	10	(T)
Erythroxylum squamatum Sw.	Erythroxylaceae	17	(T, U)	3	(T)
Eschweilera ovata (Cambess.) Miers	Lecythidaceae	317	(T, U)	673	(T, U)
Fabaceae 1	Fabaceae	13	(U)	13	(U)
Guapira laxa (Netto) Furlan	Nyctaginaceae	23	(T, U)	20	(T, U)
Guapira opposita (Vell) Reitz	Nyctaginaceae	110	(T, U)	67	(T, U)
Guatteria schomburgkiana Mart.	Annonaceae	107	(U)	40	(U)
Helicostylis tomentosa (Poepp. & Endl.) Rusby**^{EE}	Moraceae	37	(T)	383	(T, U)
Himatanthus phagedaenicus (Mart.) Woodson	Apocynaceae	107	(T, U)	70	(T, U)
Hortia arborea Engl.	Rutaceae	97	(T, U)	80	(U)
Hymenolobium janeirense Kuhlm.	Fabaceae	3	(T)	3	(T)
Inga capitata Desv. *^{EE}	Mimosaceae	13	(U)	100	(T, U)
Inga striata Benth.	Mimosaceae	27	(U)	13	(U)
Inga thibaudiana DC. *^{EE}	Mimosaceae	7	(T)	107	(T, U)
Lecythis pisonis Cambess.	Lecythidaceae	27	(U)	107	(U)
Licania kunthiana Hook. f.	Chrysobalanaceae	3	(T)	13	(U)
Manilkara salzmannii (A. DC.) H.J. Lam	Sapotaceae	23	(T, U)	13	(U)
Manilkara sp1	Sapotaceae	13	(U)	13	(U)
Maytenus distichophylla Mart.	Celastraceae	77	(T, U)	97	(T, U)
Miconia calvescens DC.	Melastomataceae	10	(T)	3	(T)
Miconia prasina (Sw.) DC.	Melastomataceae	3	(T)	43	(T, U)
Miconia pyrifolia Naudin.	Melastomataceae	17	(T)	27	(U)
Myrcia fallax (Rich.) DC.	Myrtaceae	77	(T, U)	3	(T)
Myrcia sp1	Myrtaceae	63	(T, U)	7	(T)
Myrcia sp2	Myrtaceae	67	(U)	13	(U)
Myrcia sylvatica (G. Mey.) DC.	Myrtaceae	30	(T, U)	107	(U)
Ocotea gardneri (Meisn.) Mez	Lauraceae	53	(T, U)	113	(T, U)
Ocotea glomerata (Nees) Mez	Lauraceae	47	(T, U)	10	(T)
Ocotea limae Vattimo	Lauraceae	40	(T, U)	60	(T, U)
Ouratea castaneifolia (DC.) Engl.	Ochnaceae	17	(T, U)	3	(T)
Ouratea hexasperma (A. St.-Hil.) Baill.	Ochnaceae	70	(T, U)	80	(U)
Parkia pendula (Willd.) Benth. ex Walp.	Mimosaceae	103	(T, U)	87	(T, U)
Paullinia trigonia Vell.	Sapindaceae	67	(U)	57	(T, U)
Paypayrola blanchetiana Tul.	Violaceae	70	(T, U)	160	(U)
Piper arboreum Aubl.	Piperaceae	33	(T, U)	47	(T, U)
Plathymenia reticulata Benth.	Mimosaceae	20	(T, U)	17	(T, U)
Pogonophora schomburgkiana Miers ex Benth.	Euphorbiaceae	333	(T, U)	623	(T, U)
Pouteria bangii (Rusby) T.D. Penn.	Sapotaceae	47	(T, U)	73	(T, U)
Pouteria grandiflora (A. DC.) Baehni	Sapotaceae	53	(U)	67	(U)
Pouteria gardneri (Mart. & Miq.) Baehni	Sapotaceae	133	(T, U)	167	(T, U)
Pouteria sp. **^{IE}	Sapotaceae	67	(T, U)	13	(U)
Pradosia glycyphloea (Casar.) Liais	Sapotaceae	3	(T)	3	(T)
Pradosia lactescens (Vell.) Radlk.	Sapotaceae	3	(T)	7	(T)
Protium aracouchini (Aubl.) Marchand	Burseraceae	63	(T, U)	3	(T)
Protium giganteum Engl.	Burseraceae	153	(T, U)	123	(T, U)

Table 2 (Cont.)

Species	**Family**	**Internal Edge**		**External Edge**	
		D_e		**D_e**	
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	93	(T, U)	60	(T, U)
Psychotria carthaginensis Jacq.	Rubiaceae	20	(T, U)	13	(U)
Psychotria racemosa (Aubl.) Raeusch.	Rubiaceae	13	(U)	13	(U)
Psychotria sp.	Rubiaceae	13	(U)	3	(T)
Sapotaceae sp1	Sapotaceae	10	(T)	17	(T, U)
Sclerolobium densiflorum Benth. *^{IE}	Caesalpiniaceae	57	(T, U)	13	(T)
Senefeldera multiflora Mart.	Euphorbiaceae	10	(T)	3	(T)
Sloanea guianensis (Aubl.) Benth.	Elaeocarpaceae	53	(U)	13	(U)
Sorocea hilarii Gaudich.	Moraceae	7	(T)	13	(U)
Strychnos sp.	Loganiaceae	17	(T, U)	27	(U)
Tabebuia sp. *^{IE}	Bignoniaceae	57	(T, U)	13	(U)
Tabernaemontana flavicans Willd. *ex* Roem. & Schult.	Apocynaceae	13	(U)	3	(T)
Tabernaemontana salzmannii A. DC.	Apocynaceae	23	(T, U)	93	(T, U)
Tapirira guianensis Aubl. *^{EE}	Anacardiaceae	50	(T)	130	(T, U)
Tetragastris catuaba Soares da Cunha **^{IE}	Burseraceae	63	(T, U)	17	(T, U)
Thyrsodium spruceanum Benth.	Anacardiaceae	60	(T)	183	(T, U)
Tovomita brevistaminea Engl. *^{IE}	Clusiaceae	170	(T, U)	30	(T, U)
Trichilia ramalhoi Rizzini	Meliaceae	13	(U)	13	(U)
Virola gardneri (A. DC.) Warb.	Myristicaceae	37	(T)	50	(T, U)
Albizia pedicellaris (DC.) L. Rico	Mimosaceae	3	(T)		
Annona coriacea Mart.	Annonaceae	7	(T)		
Apeiba tibourbou Aubl.	Tiliaceae	7	(T)		
Artocarpus heterophyllus Lam.	Moraceae	7	(T)		
Coussarea sp.	Rubiaceae	7	(T)		
Fabaceae 3	Fabaceae	27	(U)		
Ficus trigonata L.	Moraceae	7	(T)		
Henriettea succosa (Aubl.) DC.	Melastomataceae	20	(T, U)		
Hyeronina sp.	Euphorbiaceae	3	(T)		
Lauraceae 1	Lauraceae	3	(T)		
Lauraceae 2	Lauraceae	7	(T)		
Luehea ochrophylla Mart. *^{IE}	Tiliaceae	70	(T, U)		
Luehea paniculata Mart.	Tiliaceae	13	(T)		
Mangifera indica L.	Anacardiaceae	3	(T)		
Manilkara sp2	Sapotaceae	27	(U)		
Meliaceae 1	Meliaceae	13	(U)		
Miconia francavillana Cong. *^{IE}	Melastomataceae	57	(T, U)		
Micropholis sp.	Sapotaceae	3	(T)		
Pradosia sp.	Sapotaceae	13	(U)		
Sacoglottis mattogrossensis Malme	Humiriaceae	13	(U)		
Sapotaceae 2	Sapotaceae	3	(T)		
Sloanea sp.	Elaeocarpaceae	3	(T)		
Solanum gemellum Sendtn.	Solanaceae	27	(U)		
Trichilia lepidota Mart. *^{IE}	Meliaceae	27	(T, U)		
Xylopia frutescens Aubl.	Annonaceae	7	(T)		
Andira fraxinifolia Benth.	Fabaceae			7	(T)
Annonaceae 1	Annonaceae			13	(U)
Apeiba tibourbou Aubl.	Tiliaceae			13	(T)
Carica papaya L.	Caricaceae			3	(T)
Chrysobalanaceae 1	Chrysobalanaceae			3	(T)
Clusia nemorosa G. Mey.	Clusiaceae			27	(U)
Coccoloba confusa R.A. Howard	Polygonaceae			13	(U)
Coccoloba laevis Casar.	Polygonaceae			13	(U)
Coccoloba sp.	Polygonaceae			7	(T)
Coccoloba sp.	Polygonaceae			13	(U)
Connaraceae 1	Connaraceae			13	(U)
Copaifera cearensis Huber *ex* Ducke	Caesalpiniaceae			107	(U)
Coussarea sp.	Rubiaceae			13	(U)
Cupania racemosa (Vell.) Radlk.	Sapindaceae			3	(T)
Diplotropis purpurea (Rich.) Amshoff	Fabaceae			3	(T)
Erythroxylum cuspidifolium Mart.	Erythroxylaceae			13	(U)
Gomidesia sp.	Myrtaceae			27	(U)
Hortia sp.	Rutaceae			27	(U)
Hymenaea rubriflora Ducke	Caesalpiniaceae			23	(T, U)
Ilex sapotifolia Reissek	Aquifoliaceae			13	(U)
Inga blanchetiana Benth.	Mimosaceae			3	(T)
Margaritaria nobilis L.f. **^{EE}	Euphorbiaceae			360	(U)
Myrcia rostrata DC.	Myrtaceae			13	(U)
Myrcia sp3	Myrtaceae			27	(U)
Myrtaceae 2	Myrtaceae			40	(U)
Myrtaceae 6	Myrtaceae			27	(U)
Psychotria bracteocardia (DC.) Müll.Arg.	Rubiaceae			13	(U)

Table 2 (Cont.)

Species	**Family**	**Internal Edge**		**External Edge**	
		D_e		**D_e**	
Psychotria erecta (Aubl.) Standl. & Steyerm.	Rubiaceae			13	(U)
Psychotria platypoda A.DC.	Rubiaceae			13	(U)
Rubiaceae 1	Rubiaceae			13	(U)
Rutaceae 1	Rutaceae			13	(U)
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae			17	(T)
Sparattanthelium botocudorum Mart.	Hernandiaceae			3	(T)
Swartzia pickelii Killip *ex* Ducke	Fabaceae			3	(T)
Talisia elephantipes Sandwith *ex* Tutin ^{**EE}	Sapindaceae			80	(U)
Trema micrantha (L.) Blume	Ulmaceae			3	(T)
Vismia guianensis (Aubl.) Choisy	Clusiaceae			13	(U)
Dead standing individuals		233	(T, U)	180	(T, U)
Lianas		140	(T)	40	(T, U)
Undetermined A		63	(T, U)	53	(U)
Undetermined B		3	(T)		
Undetermined C		13	(T)		
Undetermined D		13	(U)		
Undetermined E				7	(T)
Undetermined F				13	(U)
Cut stems (not collected)		3	(T)		
Estimated total density/ ha		5893		7110	

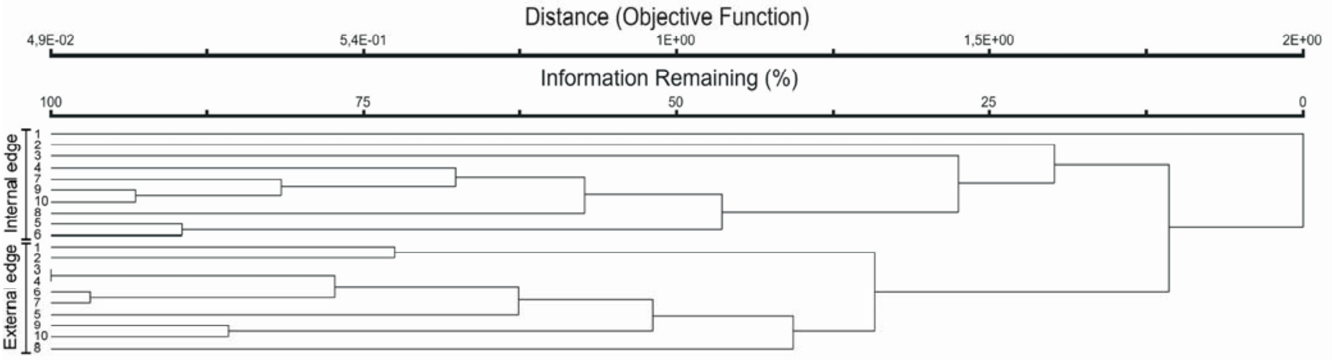

Fig. 3 Cluster diagram of sampled positions (1-10) along transects at internal (IE) and external (EE) edges, using species abundance as descriptors, Bray-Curtis distance and UPGMA linking method. São José Forest, Igarassu, Brazil.

maining distances. At EE, a sub-cluster distinguished the first 20 m from an interior group composed of distances from 20 to 100m (position 8 more distinguishable).

Eighty-eight species occurred under both edge conditions, although their individual importance for community structure varied greatly. There were 28 species exclusive at IE, and 38 exclusive to EE. There were 30 species common to both edge conditions which were present in only one size category in either edge type. For example, the important canopy species *Chamaecrista ensiformis* in IE was absent in the understory, while *Guatteria schomburgkiana* and *Lecythis pisonis* were recorded only in the understory and were absent in the canopy. Amongst the five main canopy species, *Parkia pendula*, *Sclerolobium densiflorum*, *Tapirira guianensis* and *Pogonophora schomburgkiana* were important under both edge conditions (Importance Value, IV). *Maytenus distichophylla*, *Luehea ochrophylla*, *Eriotheca crenulaticalyx* and *Eschweilera ovata* were also important canopy species in IE, whereas *Protium giganteum*, *Ocotea limae*, *Inga thibaudiana* and *Thyrsodium spruceanum* showed a high canopy IV at EE. Tree species such as *E. ovata* and *P. schomburgkiana* were important in the understory under both edge conditions, and represented the regeneration of the arboreal layer. Other plants important in understory, such as *Calyptranthes brasiliensis* in both edge conditions, *Alseis pickelii* (in IE), and *Paypayrola blanchetiana* (in EE), had low importance or were not present in the canopy layer. Forty-five species occurred only in the understory, with a greater number at EE, including some typical sub-canopy shrub species (*Psychotria bracteocardia*, *P. erecta*, *P. platypoda*, *P. racemosa*, *Solanum gemelum*, *Vismia guianensis* and many Myrtaceaes). The others, even though only recorded in the sub-canopy, are species that can reach the canopy, such as *Dialium guianense*. Within the community as a whole, Sapotaceae and Myrtaceae (at IE), Anacardiaceae/Mimosaceae and Euphorbiaceae (at EE) had the greatest tree and understory densities, respectively. Fifteen species belonged to Sapotaceae, the most species-rich family, with many individuals in the genus *Pouteria*.

The indicator species method revealed only a low percentage of indicator species in the overall community (12% with INDVAL ≥ 50 and significance ≤ 0.05), with twelve species for IE and seven for EE (**Table 2**). When the data was computed separately for each of the two size categories and considering the typology resulting from cluster analysis (two subgroups at each edge), *Brosimum rubescens*, *Eriotheca crenulaticalyx*, *Tetragastris catuaba*, *Pouteria* sp., *Chamaecrista ensiformis* and *Trichilia lepidota* were confirmed as indicators of IE, with high INDVAL for canopy, the last three mainly at inner distances. *Luehea ochrophylla* was indicator of IE for understory, mainly in the first 20 m. At EE, *Helicostylis tomentosa*, *Margaritaria nobilis*, *Inga capitata* and *Talisia elephantipes* were indicators of understory, whereas *Tapirira guianensis* and *Inga thibaudiana* were indicator for trees.

DISCUSSION

The edge influence on forest fragments has been previously examined for edges limited by adjacent sugarcane fields (Ranta *et al.* 1998; Oliveira *et al.* 2004) and pasture (Fox *et al.* 1997; Oosterhoorn and Kappelle 2000), and it is known that such edges experience lower levels of humidity, greater radiation flux, and higher temperatures, resulting in strong edge effects, mainly within the first 50 to 60 m. Roads have also been reported to induce edge effects on adjacent forests (Young 1994; McGurk and Fong 1995; Reed *et al.* 1996; Nagaike 2003). However, it is possible that road openings do not induce effects at the same magnitude as an external matrix, but rather function as "linear clearings" (Goosen 1997). In the present study, analyses on physiognomy and structure along the edge-interior gradient showed that differences on the first 40-60 m occur at internal and external edges, similar to the frequently found edge depth mentioned by Murcia (1995). However, our results confirmed more modest effects along internal edges. Overall, the tree assemblage at IE site is denser, taller, with higher diversity and evenness, as opposite to external edges.

Along anthropic edges, a long-term reduction in the density of individuals due to higher mortality is frequently observed (Tabanez *et al.* 1997; Laurance *et al.* 1998a, 1998b; Oliveira *et al.* 2004; Tabarelli *et al.* 2004). The lower overall density of canopy individuals at EE, and also closer to forest limits under both edge conditions, reaffirm this observed pattern. However, understory density was greater at EE, indicating that density responses vary according to plant size category or habit. Certainly, EE experiences a greater penetration of light that facilitates plant regeneration (Harper *et al.* 2005).

Two other commonly reported edge effects on forest physiognomy were also observed: changes in plant heights and liana abundance. There was a reduction of tree heights at EE, mainly along the first 60 m from forest boundary, which can be attributed to wind effects, the falling of large trees, breakage due to drying, or falls due to root exposure (Laurance 1991; Laurance *et al.* 2000; Oosterhoorn and Kappelle 2000; Harper and Macdonald 2002). The presence of lianas is often related to edge effects due to the ability of this life form in competing for light, water and nutrients (Delamônica *et al.* 2001). Based on that, we would have expected a higher number of lianas at the more disturbed EE, but 78% of all lianas occurred at IE. According to Schnitzer and Bongers (2002), liana abundance varies with several key biotic and abiotic factors, including soil fertility, tree biomass and disturbance, which were found to significantly predict liana abundance in some forests. However, there are still many questions to be answered about the role of lianas on the plant community (Schnitzer and Bongers 2002) and our findings reveal that the relation between disturbed edges and lianas is not always positive. In the same sense, the fact that only 30% of all standing dead trees were recorded at EE, the most disturbed site, differed from most survey observations (e.g. Laurance *et al.* 1998b), since edge-induced mortality may persist long after fragment formation (Tabanez *et al.* 1997). Nevertheless, our study does not assess mortality rates, which require long-term studies on mortality factors such as natural death, desiccation, or treefall (Laurance *et al.* 1998b; Tabarelli and Mantovani 1999; Laurance *et al.* 2000). During the present study, treefall was observed only at EE. Possibly, there is a higher mortality of emergent trees at EE, with subsequent treefalls attributable to edge effects (Laurance *et al.* 2000), resulting in lower tree density and greater density of understory plants at EE. Differently, at IE, dead trees remain standing for longer periods.

The two edge conditions examined had distinct structural patterns, with opposite trends in diversity according to plant size category, and changes on species IVs in the plant assemblages. Indeed, plant edge communities usually demonstrate changes in species composition and structure over time, sometimes becoming dominated by early successional plants (Young and Mitchell 1994). Oliveira *et al.* (2004) suggested that fragmentation would lead to distinct plant assemblages, and a general pattern of homogeneity and simplification along the edges accompanied by long-term species losses. Generally, edge formation provokes differential patterns of recruitment and mortality among understory plants, with species composition being more affected than diversity (Harper *et al.* 2005). In the present study, the understory at EE appeared as an important low stratum, with great richness and diversity including arboreal species not sampled as trees. It is possible that, in the long term, species assemblage will become more distinct from IE, and more simplified due to the fact that many species could not mature into canopy individuals due to edge effects on recruitment and growth (Benítez-Malvido 1998). Some species or families are apparently more sensitive to edge proximity, showing decline in abundance, whereas others can be favored by it. Pioneer or early-secondary species are usually more abundant at forest edges (Young and Mitchel 1994; Oosterhoorn and Kappelle 2000). *Cecropia* ssp. and *Vismia* ssp. play an important role in edge "sealing" in Amazonian forests (Didham and Lawton 1999), and other species have been identified with similar roles exclusively at forest edges in New Zealand (Young and Mitchel 1994). *Tapirira guianensis*, *Sclerolobium densiflorum*, *Eschweilera ovata* and *Pogonophora schomburgkiana* appear to have this function at the studied edges. These species are often found in secondary forests (Montagnini *et al.* 1995; Siqueira *et al.* 2001), and frequently becomes established in disturbed environments. On the other hand, *Parkia pendula*, a large emergent and late secondary tree that is an important food resource for animals (Peres 2000), with allelopathic characteristics (Souza Filho *et al.* 2005), usually occurs in low density populations with high dominance values. Arboreal species such as *P. pendula* were probably present before forest isolation but are not regenerating well at the edges at present.

Amongst the 12 indicator species found at IE and seven found at EE, only four were exclusive of an edge condition, two at each: *Luehea ochrophylla* and *Miconia francavillana* at IE, *Margaritaria nobilis* and *Talisia elephantipes* at EE. These species came the closest to being a perfect indicator species (Dufrêne and Legendre 1997) as they were exclusive and recorded with high densities, especially *M. nobilis*. Amongst families recorded, Sapotaceae is considered to be sensitive to edge effects, together with many other canopy and emergent species (Tabarelli *et al.* 2004), often demonstrating low densities, or even absence in small forest fragments (Tabarelli *et al.* 1999). Oliveira *et al.* (2004) noted that this family was restricted to well preserved portions of forest interior and reinforced its categorization as an old-growth family. However, our data show that this is not a general rule, since Sapotaceae was the species-richest family at EE, occurring along the entire 100 m edge-interior gradient, and was recorded with the highest densities at IE. Therefore, in the absence of consensus about the performance of this family along edges, we suggest prudence on the use of Sapotaceae as an indicator of less disturbed conditions.

In the absence of data about edge depth or studies about edge effects along linear clearings, predictions about how much is left of interior habitats in remnants of coastal forests in Northeastern Brazil have led to bad scenarios for the conservation of this biome, considering a strong effect on forest structure to penetrate up to 100 or 300 m (Ranta *et al.* 1998; Oliveira *et al.* 2004). Our study demonstrated that a 40-60 m wide belt along fragment perimeter is strongly influenced by external edges, and to a lesser extent by a road that cuts the fragment, where diversity are still kept at high numbers. Nevertheless, edge influences on vegetation structure may be more restricted than commonly thought, offering a better prognosis of the sustainability of the fragmented Brazilian Atlantic Rainforest.

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