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Research Article

Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro, Brazil.

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Abstract

This study investigates the changes of tree species composition and diversity along the gradient from fragment edge to interior, and between edge and interior habitats, on a regional scale, in nine Atlantic forest fragments (6–120 ha), in southeastern Brazil. A total of 1980 trees (dbh ≥ 5 cm) comprising 252 species, 156 genera and 57 families were surveyed using the point-centered quarter method. From the fragment edge towards the interior the proportion of shade-tolerant trees increased continuously. The majority of all trees within the first 100 m from the edge belonged to the pioneer-guild. Floristic dissimilarity was found to be higher among interior habitats of different fragments than among the corresponding edge areas or among different small fragments. Species diversity increased along the edge-interior gradient 1.5 times within the first 250 m. Our results support previous findings that the establishment of edge-affected habitats leads to tree species impoverishment and homogenization via the dominance and proliferation of pioneer species in the forest edges of severely fragmented tropical landscapes. We argue that conservation strategies which include the creation of buffer zones between forest edges and the matrix will be more efficient than the establishment of narrow corridors to connect fragments and protected areas.

Keywords: Atlantic forest; biotic homogenization; pioneer species; forest fragmentation; edge effects

Resumo

O estudo investiga as mudanças na composição e diversidade das espécies arbóreas ao longo do gradiente borda-interior e entre habitats na borda e no interior a escala regional em nove fragmentos florestais da Mata Atlântica (6–120 ha) no sudeste do Brasil. Um total de 1980 árvores (dap ≥ 5 cm) pertencentes a 252 espécies, 156 gêneros e 57 famílias foram investigadas utilizando-se o método de ponto-quadrante. A proporção de árvores tolerantes à sombra aumenta continuamente ao longo do gradiente borda-interior. Dentro dos primeiros 100 metros a partir da borda florestal, a maioria das árvores pertence à guilda das pioneiras. A dissimilaridade florística foi maior entre as áreas do interior de diferentes fragmentos que entre as áreas de borda correspondentes ou entre diferentes fragmentos pequenos. Nos primeiros 250 metros, ao longo gradiente borda-interior, a diversidade de espécies aumentou 1.5 vezes. Nossos resultados sustentam conclusões prévias de que o estabelecimento de habitats afetados pelos efeitos de borda leva ao empobrecimento e homogeneização das espécies arbóreas através da dominância e proliferação das espécies pioneiras nas bordas florestais de paisagens tropicais severamente fragmentadas. Concluímos que estratégias de conservação que incluam o estabelecimento de zonas de amortecimento entre bordas florestais e a matriz poderiam ser mais eficientes do que o estabelecimento de corredores estreitos para conectar fragmentos e áreas protegidas.

Palavras chaves: Mata Atlântica; homogeneização biótica, espécies pioneiras, fragmentação florestal, efeito de borda

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Introduction

The vanishing Brazilian Atlantic rainforest (Mata Atlântica), which once covered an area of about 1.1 million km^2, is among the most species rich and most threatened tropical forests in the world [1, 2]. The Mata Atlântica is believed to harbor 5% of the world's plant diversity [3]. Nowadays only about 12% of its original extent is still forested and what is left is severely fragmented [4, 5], scattered throughout a landscape dominated by agriculture. Most fragments are less than 50 ha in size and are extremely isolated [6]. Deforestation and fragmentation are still ongoing. For example, in the state of Rio de Janeiro 1039 ha of Atlantic rainforest was lost between 2005 and 2009 [1]. This continuous anthropogenic threat in the most populous region of Brazil, coupled with the forest's rich biodiversity, is making the Brazilian Atlantic rainforest one of the 'hottest hotspots' of biodiversity in the world [7, 8].

Fragmentation of habitats in anthropogenically modified landscapes is one of the main forces driving biodiversity loss [9–11]. In addition to area reduction and patch isolation, the formation of edge habitats is one of the most problematic processes of forest fragmentation [12–14] and a main driver of tree species loss in tropical forest fragments [15]. Core habitats become exposed to the conditions of the surrounding ecosystem [16] and this leads to the elimination of sensitive old-growth forest species while early-successional and non-forest species thrive. [13, 17, 18]. This results in the transition of tree communities near forest edges to early-successional stages [19, 20]. This biotic reassembly can be described as a 'few winners, many losers' scenario, as McKinney and Lockwood suggest [21]. In this global pattern of community transition, the 'losers' are often described as native and endemic species and the 'winners' portrayed as exotic ruderal species [22, 23]. Tabarelli et al. [24] extended this paradigm beyond the perspective of invasion biology and included the replacement of native biotas by robust indigenous r-strategists rather than alien species. Current publications indicate that this shift in species composition, where a species-rich pool of old-growth trees is replaced by a small number of early-successional species, leads, in the long term, not only to poorer communities but also to a general biotic homogenization along forest edges [24, 25]. More specifically, the proliferation of early-succession species, together with the decline of old-growth forest species, can result in a reduction of species richness [26], and the diminishment of functional diversity [27] as well as functional and taxonomic convergence across edge-affected habitats [28].

Because of severe fragmentation and extensive edge effects, we expect most of the forest remnants in the Atlantic rainforest will be affected by biotic homogenization. This has dramatic consequences for conservation programs aimed at retaining representative portions of tree species diversity in the region.

Against this background, the major aim of our study was to investigate how species composition and diversity varied from fragment edge to interior, and between edge and interior habitats, at a regional scale in the Guapiaçú River Basin. We hypothesized a domination of pioneer-species in very small forest fragments and along the edges of bigger fragments, a decreased β-diversity of these habitats and an increasing α-diversity from edges to interior areas. More specifically, this study addresses the following questions:

- Are tree communities dominated by pioneer species in fragments of the Atlantic forest in the Guapiaçú River Basin in Rio de Janeiro and, if so, what is the threshold distance from a fragment's edge?
- Do the edge communities represent a more similar assemblage than interior communities throughout the landscape?
- In what ways are these patterns reflected in species diversity?

Our study area, in the Guapiaçú River Basin, forms part of the Guapi-Macacu Watershed, which is considered an important natural region within the state of Rio de Janeiro [29]. Most of the forest fragments in the lowlands between 20 m and 200 m above sea level are less than 10 ha and very few are bigger than 50 ha [30]. In comparison to the upper altitudinal levels of the region, forest cover in these elevational zones is much more reduced and fragmented and under much more pressure from anthropogenic activities [29, 31, 32]. Consequently, forest fragments play an important role in the conservation of biodiversity at these altitudinal levels [33–37]. Yet, despite their strategic importance for the conservation management within the Central Fluminense Atlantic Forest Mosaic, fragments in the Guapiaçú River Basin are floristically poorly studied. Our study is one of the first surveys addressing the forest fragments in this important region.

Methods

Study area

The upper Guapiaçú River Basin is located in the Municipality of Cachoeiras de Macacu. Streams provide drinking water for the nearby metropolitan area of Rio de Janeiro and the basin is part of the Central Fluminense Atlantic Forest Mosaic, which conjoins a large number of protected areas and is one of the four protected areas networks within the Serra do Mar Corridor [38]. The watershed contains major areas of continuous forest on the slope of the Serra dos Órgãos, which are part of two fully protected nature reserves: the Paraíso Ecological Station and the Três Picos State Park, the largest protected forest area in the state. Important elements of the tree flora are species of *Myrtaceae, Sapotaceae, Arecaceae, Rutaceae, Meliaceae, Rubiaceae, Euphorbiaceae, Fabaceae, Melastomataceae* and *Araliaceae* [39].

The lowlands consist almost entirely of pasture and cropland. Forest fragments of different sizes occur primarily on slopes and on the hilltops inbetween. These are patches of the Atlantic forest on the lowland and the lower submontane levels [40–42].

The soils are mainly classified as Cambisols (on the slope of the mountain range), Ferrasols and Fluvisols (only near rivers) [43]. The climate is tropical (Af climate according to the KÖPPEN Classification) with an annual mean temperature of 23°C [39]. Annual mean precipitation varies from 1800 mm to 2600 mm, with higher rainfall closer to the Serra dos Órgãos mountain range [44]. The original land cover was mainly dense evergreen rainforest [45].

Sampling design

Our study comprised 9 forest fragments (A-I), ranging from 6 to 120 ha, within an area of approximately 35 km² (Fig. 1, Appendix 2). Selection of the fragments was mainly guided by accessibility and landowner permission. All fragments were surrounded by pasture.

Fig.1. Location of the study area in the State of Rio de Janeiro, south-eastern Brazil, showing the forest fragments in the upper Guapiaçú River Basin, the study sites (fragments A-I, dark grey) and adjacent continuous forest (grey).

Five 200 m long transects were placed in each forest fragment. Sampling points were established every 20 m along the transects resulting in a total of 55 sampling points per fragment, except for the very small fragments where sampling points were established every 12 m along 120 m long transects. This was necessary on order to generate data for the same number of individuals in each fragment. At each sampling point the slope, aspect and geographical position were recorded. Using the point-centered quarter method [46] the 4 nearest trees with a minimum diameter at breast height (dbh) of 5 cm, were recorded in each sampling point, yielding a total sample of 220 individuals per fragment.

Voucher specimens were collected from all species and individuals whose co-specificity to previously collected species could not be confirmed in the field. Identification was done at the herbarium of the Botanical Garden Rio de Janeiro (RB). Some specimens could not be identified to species level and so, in the analyses of species diversity and similarity, were given provisional names and treated as distinct species.

Species Classification

Species were assigned to successional groups (Appendix 1) based on a thorough review of local and regional floras, web searches for published and referenced data, monographs and checklists including several issues of *Flora Neotropica*. To reduce errors resulting from different classification systems and inconsistent classification in the literature, species were classified into broad classes of pioneer (P) (including the frequently used classes 'pioneer' and 'early secondary') and shade-tolerant (ST) (including 'late secondary' and 'climax species') species [47, 48].

Data Analysis

To investigate changes in the abundance of pioneer species along the gradient from fragment interior to edge, all sampling points from all fragments were pooled together and grouped in classes with a width of 20 m, according to their distance to the edge. The proportions of trees belonging to pioneer and shade-tolerant species were calculated for each class. Species with unclear or inconsistent classification were excluded from this analysis. To ensure a minimum of 5 points (20 trees) in each class, points with an edge distance of over 200 meters were omitted. The ratio of pioneer to shade-tolerant individuals was then regressed against distance to the fragment edge using a generalized linear model (GLM) with binomial error distribution and logistic link function. There was no significant overdispersion in the data (residual deviance = 9.3 on 8 df). To estimate the goodness of fit of the model, the ratio of null deviance and residual deviance was evaluated. By analogy with R^2 this is sometimes referred to as D^2 [49, 50].

The intersection of the predicted regressions (the proportion of P and ST against edge distance) was taken as the minimum threshold to separate edge and interior sampling points for the analysis of similarity. We use the term 'interior' for the area of the fragment beyond the threshold, and we emphasize that these interior areas should not be confused with true core areas which have not been affected by edge effects. We identified five fragments large enough to have interior patches according to this definition (fragments E, F, G, H, I; 17.6–135.5 ha; Fig. 1). We then classified the sampling points in each of the five fragments as edge or interior. The small fragments (A, B, C, D; 5.8–12.5 ha) were treated as a third group. Principal Coordinates Analysis (PCoA) with Chao´s Index of dissimilarity was used to investigate the similarity within each of the three groups (edge, interior and small). Chao´s Index is the only distance measure that takes unseen species into account, which is especially advantageous in species-rich communities where under-sampling is likely to occur. Moreover, it is robust against small and unequal sample sizes [51]. In addition to the graphical interpretation of the ordination, we examined the β-diversity within the three groups. We obtained distance-to-centroid values using the 'betadisper' function in the R vegan package [52] that defines β-diversity as the average distance from all individual points (samples) to their group centroid in the full dimensional space of the PCoA. A permutation test for the homogeneity of multivariate dispersions, with 9999 permutations, was used to evaluate the differences in β-diversity among the groups. This is an ANOVA-like permutation test which is performed on the dispersions within groups and provides pairwise comparisons between groups [53].

In order to investigate species diversity as a function of distance from the edge, the transects were bisected, resulting in 90 subsamples of 5 points (20 trees). Mean distance to the nearest edge, mean slope and mean aspect was calculated for every subsample. Aspect raw data were transformed into a continuous north-south gradient (northness) and an east-west gradient (eastness) by using the sine and cosine transformations, respectively. The effective number of species (ENS) of all subsamples was estimated following Jost's equation 11b [54]. The advantage of this 'diversity of order 1' [55] is that it corresponds most closely with an intuitive sense of diversity and thus is easily comparable between samples. Because of its linearity, this measure behaves as one would expect an index of diversity to behave [54, 56]. Dauby and Hardy [57] showed that 'diversity of order 1' might be biased but is nevertheless suitable to compare diversity between communities of constant sample size, as in our study.

A linear mixed effects model was applied with ENS as the response variable, and mean distance to the nearest edge as a fixed effect, using maximum likelihood estimation. To control for topographic and other confounding factors the fragment area, average slope and aspect, and interactions between the latter, were used as additional fixed effects, and fragment identity as a random effect in the full model. All fixed effects data were z-transformed (mean = 0, SD = 1) to aid model interpretation. Model simplification was done by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictor variables remained in the model ($p < 0.05$). The minimum adequate model was then re-run using restricted maximum-likelihood methods to estimate the parameter values. Model residuals did not show any violation of our modeling assumptions (i.e. normality and homogeneity of variances).

All data analyses were performed using the 'vegan' [52], 'vegetarian' [58] and 'nlme' [59] packages in the 'R' statistical and programming environment [60].

Results

Proportion of pioneer trees in distance classes

A total of 1980 individuals comprising 252 species, 156 genera and 57 families were recorded in the fragments. Approximately 37% of the species are endemic to the Atlantic forest. Consistent classification to pioneer (P) and shade-tolerant (ST) species was possible for 188 species (75%); 86 were classified as pioneer species and 102 as shade-tolerant species (Appendix 1). As nearly all abundant species could be classified these 188 species comprised nearly 86% of the inventoried individuals.

The proportion of individuals belonging to ST increased (and inherently the proportion of P decreased) with distance from the edge ($p < 0.001$, Fig. 2). The GLM explained 75% of the deviance ($D^2 = 0.746$). The predicted regressions intersected between classes 80–100 m and 100–120 m. This implies that the majority of trees within 100 m of the edge belonged to the pioneer-guild.

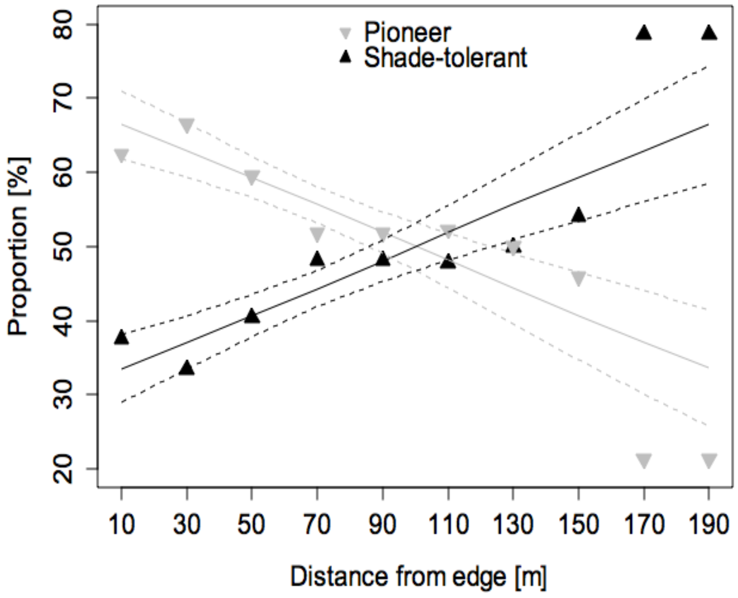

Fig. 2. Relationship between the proportion of pioneer and shade-tolerant tree species and distance to fragment edge. GLM model fits are represented by solid lines and the corresponding 95% confidence interval by dotted lines.

Similarity of edge and interior patches

The PCoA ordination of species composition and abundance of the three groups (edge habitat, interior habitat, and small fragments) showed no clear segregated clusters.

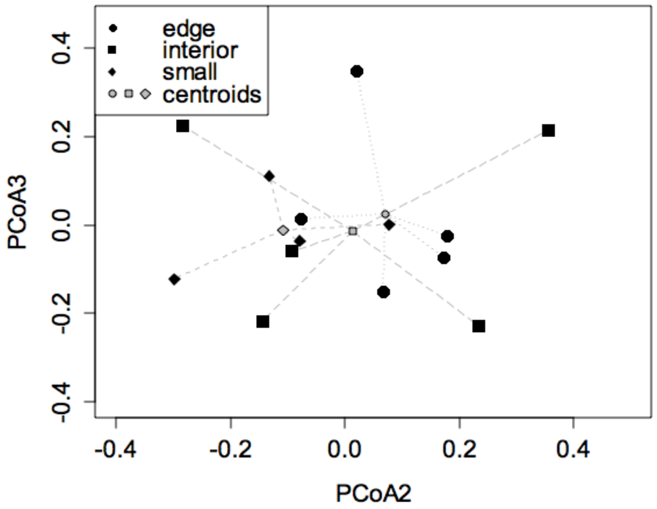

Fig. 3. Principal Coordinates Analysis of the small fragments and the edge and interior habitats of the large fragments based on Chao´s Index of dissimilarity with communities in black and respective group centroids in grey.

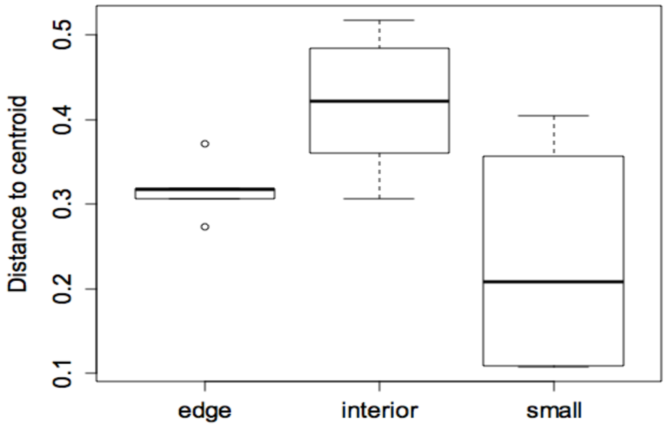

Fig. 4. The median (solid line), 25th and 75th percentiles (boundaries of boxes) the 5th and 95th percentiles (whiskers above and below) and the outliers of distances to the group centroids obtained from PCoA in Fig. 3.

However, the interior habitat sampling units were more dispersed in multivariate space than those of the edge areas and small fragments (Fig. 3). Average distance to the group centroid (Fig. 4) differed between interior and edge ($p = 0.039$*) and between interior and small fragments ($p = 0.046$*), but not between small fragments and edge habitats ($p = 0.257$), implying a higher β-diversity among interior habitats of different fragments than among the corresponding edge areas or small fragments.

Species diversity and edge distance

The mean effective number of species (ENS) increased from edge to interior 1.5 times in the first 250 m (Fig. 5). After model simplification, mean distance to the edge was the only significant fixed effect in the minimal adequate model (t-value = 2.605, $p < 0.05$, df = 80) predicting the ENS of the forest fragment tree assemblages (for results of the full model see Table 1).

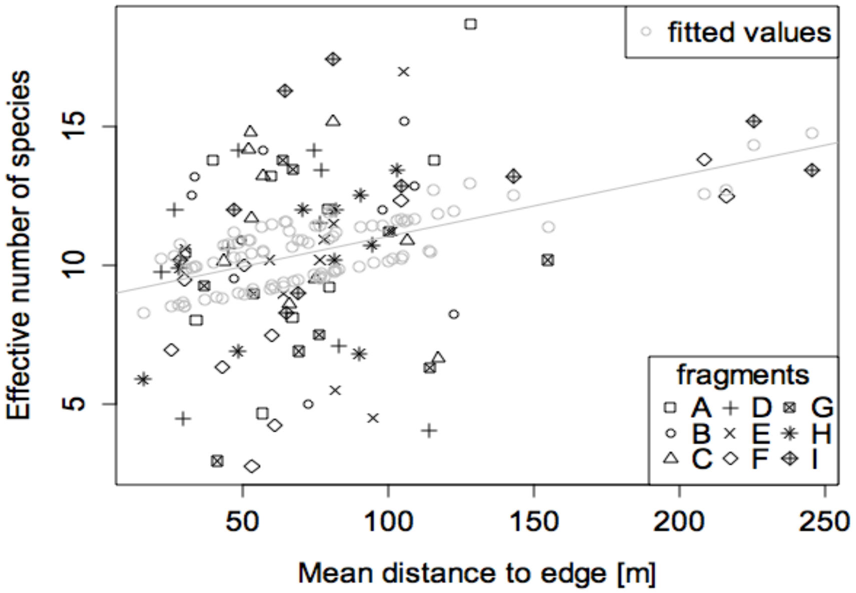

Fig. 5. Relationship between species diversity and mean distance to the fragment edge of the subsamples (explanation in text). Black characters indicate diversity values, grey circles and lines represent the fit of the minimal adequate linear mixed effects model.

Table 1. Effects influencing species diversity. Results of the full model including fragment identity as a random effect.

Fixed effects	F-value	p-Value
Distance to edge	6.726	0.0114*
Slope	1.758	0.1889
Slope × Northness	0.669	0.416
Northness	0.574	0.4509
Fragment area	0.600	0.4638
Eastness	0.382	0.5386
Slope × Eastness	0.018	0.895

Discussion

Patterns and underlying mechanisms

The abundance of successional species in forest edges is well documented in many neotropical studies of experimentally created fragments [26] and patches formed through land-use change [15, 19, 61–63]. Our study supports these findings, but also demonstrates a constant decrease in the pioneer to shade-tolerant ratio with increasing edge distance and the spatial extent of the pioneer-dominated edge habitats in the study region. Several studies have shown that the most important edge effects penetrate about 100 m inside forests [17, 64, 65] and scientists often use this threshold for defining edge and interior *a priori* [62]. This is consistent with our findings: up to 100 m from the forest edge the tree flora is dominated by pioneer species. However, it is known that the tree community studied here harbors a much greater fraction of pioneer species beyond this border than a nearby well-protected continuous forest (14% [Thier, unpubl.]). Finotti et al. [34] also found that communities from different sized forest fragments (ca. 15–160 ha) in the Guapiaçu River Basin have, in general, higher abundances of pioneer and/or early secondary species (the two classes are grouped together as pioneer species in our study). As by definition core areas are sites with no detectable edge effects, and areas where pioneer species represent about 50% of the individuals are probably suffering edge effects, we cannot describe the domain beyond 100 m as core habitat. The 100 m threshold should therefore be considered as a minimum distance for drastic shifts in the tree community. Small fragments (< 80 ha) of the Atlantic rainforest in particular have generally been found to have a higher number of pioneer species [62], and changes in functional trait distributions are known to occur at distances greater than 300 m into the interior [66].

Microclimatic conditions (e.g. air temperature, relative humidity and wind speed) differ between the forest edge and interior and may have significant impacts on vegetation structure [18, 67]. Increased wind turbulence along edges leads to elevated tree mortality rates which results in a greater number of tree-fall gaps. As most pioneer species are light demanding, the increased light penetration to the forest understorey is a key factor favoring such species. [17, 26, 68]. Additionally, sunlight and wind can penetrate laterally along a fragment´s margins increasing soil irradiance, humidity and temperature fluctuations [16, 69] which might trigger germination of pioneer species [70]. Elevated temperatures, reduced humidity and increased sunlight lead to depleted soil moisture and create stresses for drought-sensitive plants [71] while favoring more robust pioneer species. However, as most of the fragments in our study were on hilltops with their edges at the slope toe, which were particularly moist [72], this factor might be of minor importance in our study.

Forest edges may receive a greater seed rain from pioneer species that are proliferating outside in groves within the matrix [73]. Seeds of animal-dispersed and large-seeded shade-tolerant species may not reach the edge, even if they occur in the interior of the fragment [74, 75]. Additionally, increasing litter fall and debris from the canopy can damage seedlings and alter the species composition [76]. Aside from these factors, human activities, such as selective logging, pasture burning, and cattle entering fragments for shade can lead to additional disturbances in fragment edges [68, 77].

Our results showed that forest patches in the edges of different fragments are more similar to each other than the corresponding interior assemblages. This also applies analogously to small fragments, as they were also more similar to each other than the interior areas. This supports previous suggestions that small fragments and edge areas of large fragments may consist of no more than a small set of early- to mid-successional species and are almost indistinguishable from patches of young secondary forests (< 45-yr old) in terms of their tree species richness and species/functional composition, but remain very distinct from those in old-growth and core forest areas [20, 62, 78–80]. Normally such successional assemblages would be replaced by shade-tolerant late successional trees within decades. Liebsch et al. [81], for example, predicted 75% shade-tolerant species 75 years after strong disturbances in the Atlantic rainforest. In fragmented landscapes the edge-induced abiotic and biotic changes mentioned above maintain suitable conditions for pioneer recruitment, resulting in cycles of pioneer self-replacement [20]. As the extent of our fragments have been more or less stable for at least 40 years [historical areal images, unpubl.] our findings support the hypothesis that edge habitats represent a stagnant rather than a transient successional stage [20].

We found a constant increasing diversity with increasing distance from the edge. Moreover, distance to the edge was the only significant predictor explaining the species diversity of the surveyed communities, which is a strong indication of the floristic depauperization of tree communities in edge habitats. The main reason for this pattern might simply be that the guild of pioneers consists of fewer species than those of shade-tolerant trees in Neotropical forests. In addition, due to the similarity of the edge habitats, it is likely that only the best performing subset of pioneers will dominate the edge habitats throughout the landscape. Although some studies have found a higher diversity in edges than in the corresponding interior [82, 83] we believe, in view of the large number of recent studies and reviews [15, 28, 84–86] that support our findings, that the opposite might be the usual pattern in forest fragments, at least in tropical southeast Brazil. A higher diversity of edge habitats may exist shortly after edge creation, when some elements of the original tree flora are still present, although not reproducing, and pioneer species are beginning to proliferate [77, 87]. As Laurance et al. [85] highlighted, this time span is rather short, as marked changes in the composition of newly created edges are detectable after less than two decades.

Consequences

Assuming a minimum edge threshold of 100 m within the highly fragmented part of the upper Guapi-Macacu watershed on the foothills of the Serra do Órgãos, which includes our study area, the heavily edge-affected portion of the forest comprises about 81%, and only 14% of the 330 fragments contain one or more areas not dominated by pioneer-species [30]. In most fragments this area is less than five hectares. Furthermore, the interior areas are often discontinuous and therefore the mean size of a discrete interior area is even smaller (< 2.5 ha). The landscape in our study area must therefore be considered edge-dominated and to have limited habitats for forest dependent and old-growth forest species [20, 24, 28, 77, 80, 88–93]. Moreover, the forest patches within this part of the landscape will not contain the full set of mature forest species for the colonization of new secondary forest patches [77]. The continuous forest on the slopes of the mountains may provide the required diaspores, at least for the closest patches, but its importance as source of propagules will decrease with increasing distance.

Although the functional traits of these tree assemblages have not been analyzed in detail, we assume that the functional profile of the pioneer group will differ from those of the shade-tolerant species. The two groups are considered to be linked with a set of antithetical characteristics [48, 94]. In other parts of the Brazilian Atlantic Forest certain vegetative and reproductive traits have been found to have different frequency distributions among the guilds [27, 66, 86, 95] Consequently tree communities with contrasting pioneer to shade-tolerant ratios show considerable differences in their functional composition and diversity [27, 62, 66, 95]. Even if functional richness at fragment edges remain as high as in the interiors, functional evenness has been found to decrease markedly [86]. Based on these findings we believe that the lower floristic diversity of the forest edge tree communities in our study area will be associated with a lower functional diversity and thus a dramatic change in the distribution of life history traits and functional diversity at landscape level. The extent of this effect will depend on the trait diversity and ecological redundancy of the local pioneer flora [95].

Due to their functional depauperization, highly fragmented landscapes are expected to provide a more restricted spectrum of plant mediated resources, resulting in altered and simplified trophic interactions between plants and animals [96] characterized mainly by generalist-generalist mutualisms [27, 66, 95, 97–100]. These changes are thought to cause co-declines of populations and co-extirpation of species and therefore may exacerbate the negative fragmentation-related effects on species persistence. Thus, pioneer dominated landscapes, fragmented a long time ago, may continue to suffer biodiversity loss [27, 86, 95, 101]. The proliferation of fast growing, softwood pioneer species, and the decline of hardwood and emergent trees along forest edges, alters fundamentally the dynamics of biomass production and carbon storage capacity [19, 102–104].

Implications for conservation

Pioneer species form the major part of the tree communities in the fragments of the study region. Up to approximately 100 m from the edge, more than 50% of all trees belonged to such species. These assemblages are less diverse and more similar to each other than the interior patches. As pioneers are soft wooded and ecologically redundant in terms of pollination systems, phenology and dispersal strategies, this edge-induced taxonomic homogenization throughout the landscape is associated with an even more drastic simplification of functional diversity and species interactions that cascades to plant consumers and ecosystem services.

One of the most attractive and repeatedly advocated conservation approaches in tropical landscapes, particularly in the Atlantic rainforest, is the creation and maintenance of (riparian) forest corridors connecting remaining fragments and regional protected areas. Such a well-connected network could buffer the massive species loss through fragmentation-linked processes such as area reduction and isolation, and help to maintain biodiversity and coexistence with continued land use [105]. However, narrow corridors will consist entirely of edge habitats and, as we have shown, will not retain a full complement of species or traits and, consequently, the plant–animal interaction diversity will be impoverished. Corridor connectivity will fail to protect fragmented forest landscapes from drastic species loss if the remnant or recreated tracts of forests are not wide enough to harbor substantial amounts of core habitats [62]. This could be several hundreds of meters [65].

We believe a more reasonable conservation approach, alongside the protection of the last remaining continuous forests, would be the creation of buffer zones between the forest edges and the matrix with tree plantations, agro forestry systems or even spontaneous succession. This will soften the abiotic edge effects and human disturbances and could reduce the extent of edge-affected habitats [106]. Since most of the remaining forest fragments in the upper Guapi-Macacu watershed are located on the hilltops [30], the abandonment of unproductive, overgrazed, surrounding pastures on the steep slopes, allowing spontaneous regrowth, would be a big step forward. Certainly, every effort should be made to conserve the remaining continuous forests and large fragments. Given that almost half of the remaining Brazilian Atlantic rainforest is less than 100 m away from forest edges [6], small and mid-sized forest patches should also be included in conservation strategies.

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Appendix 1. Occurrence of detected species in the fragments (A-I) and their successional group (P = pioneer, ST = shade-tolerant, nc = not classified). Species endemic to the Brazilian Atlantic rainforest are marked with *. Taxonomy according to APG III.

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
ACHARIACEAE										
Carpotroche brasiliensis (Raddi) Endl.		x			x					ST
ANACARDIACEAE										
Astronium graveolens Jacq.								x		P
ANNONACEAE										
Anaxagorea dolichocarpa Sprague & Sandwith		x				x	x	x	x	ST
Annona emarginata (Schltdl.) H.Rainer					x					ST
Annona neolaurifolia H.Rainer *								x		P
Guatteria sellowiana Schltdl.		x	x	x	x	x	x	x	x	P
Oxandra martiana (Schltdl.) R.E.Fr. *					x				x	ST
Xylopia sericea A.St.-Hil.				x			x	x		P
APOCYNACEAE										
Himatanthus bracteatus (A.DC.) Woodson				x						ST
Malouetia cestroides (Nees ex Mart.) Müll.Arg. *	x	x							x	ST
Tabernaemontana laeta Mart.		x			x				x	P
ARALIACEAE										
Schefflera morototoni (Aubl.) Maguire et al.						x				P
ARECACEAE										
Astrocaryum aculeatissimum (Schott) Burret *	x	x	x	x	x	x	x	x	x	P
Bactris vulgaris Barb.Rodr. *				x						nc
Euterpe edulis Mart.		x					x		x	ST
Geonoma cf. *schottiana* Mart. *					x					ST
ASTERACEAE										
Eremanthus crotonoides (DC.) Sch.Bip.							x			nc
Moquiniastrum polymorphum (Less.) G.Sancho	x		x	x	x		x	x		P
Piptocarpha lundiana (Less.) Baker *					x					nc
*Piptocarpha macropoda (*DC.) Baker *	x				x					P
Stifftia chrysantha Baker						x				nc
Vernonanthura discolor (Spreng.) H.Rob.	x							x		P
BIGNONIACEAE										
Cybistax antisyphilitica (Mart.) Mart.	x									P
Handroanthus cf. *umbellatus* (Sond.) Mattos						x				P
Handroanthus serratifolius (Vahl) S.Grose		x							x	P
Jacaranda caroba (Vell.) DC.							x			nc
Jacaranda macrantha Cham.					x				x	P
Jacaranda micrantha Cham. *	x			x						P
Jacaranda puberula Cham. *	x									P
Sparattosperma leucanthum (Vell.) K.Schum.								x		P
BORAGINACEAE										
Cordia sellowiana Cham.	x		x	x		x		x		P
Cordia trichoclada DC. *	x				x		x			P
BURSERACEAE										
Protium cf. *kleinii* Cuatrec. *				x			x			ST
Protium glaziovii Swart *					x				x	nc
Protium warmingianum Marchand					x			x		ST

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
CALOPHYLLACEAE										
Kielmeyera insignis Saddi *									x	nc
CANNABACEAE										
Trema micrantha (L.) Blume									x	P
CARDIOPTERIDACEAE										
Citronella cf. *paniculata* (Mart.) R.A.Howard			x							ST
CARICACEAE										
Carica papaya L.					x					nc
Jacaratia spinosa (Aubl.) A.DC.		x						x		P
CELASTRACEAE										
Maytenus samydaeformis Reissek *						x			x	nc
CHRYSOBALANACEAE										
Hirtella angustifolia Schott ex Spreng.							x			nc
Hirtella hebeclada Moric. ex DC.			x			x				ST
Licania cf. *spicata* Hook.f. *						x				P
Licania kunthiana Hook.f.		x				x				ST
Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze						x				ST
Licania riedelii Prance *								x		ST
Parinari excelsa Sabine		x		x	x	x				ST
CLETHRACEAE										
Clethra scabra Pers. *	x	x	x	x	x		x	x	x	P
CLUSIACEAE										
Tovomitopsis paniculata (Spreng.) Planch. & Triana *	x									ST
COMBRETACEAE										
Buchenavia kleinii Exell *				x		x				ST
Terminalia januariensis DC. *									x	ST
CYATHEACEAE										
Cyathea corcovadensis (Raddi) Domin *						x				ST
ELAEOCARPACEAE										
Sloanea guianensis (Aubl.) Benth.						x			x	P
Sloanea hirsuta (Schott) Planch. ex Benth. *			x							ST
Sloanea retusa Uittien				x						nc
ERYTHROXYLACEAE										
Erythroxylum cuspidifolium Mart. *			x		x	x			x	ST
EUPHORBIACEAE										
Actinostemon klotzschii (Didr.) Pax									x	nc
Actinostemon verticillatus (Klotzsch) Baill. *		x			x				x	ST
Alchornea cf. *glandulosa* Poepp. & Endl.					x		x	x		P
Algernonia leandrii (Baill.) G.L.Webster *				x		x	x	x		nc
Aparisthmium cordatum (A.Juss.) Baill.	x	x		x			x		x	ST
Mabea piriri Aubl.			x		x	x	x	x	x	P
Manihot spec. 1		x								nc
Maprounea guianensis Aubl.						x			x	P
Senefeldera verticillata (Vell.) Croizat *					x			x		ST
Tetrorchidium rubrivenium Poepp.		x			x			x		P
FABACEAE										
Albizia pedicellaris (DC.) L.Rico	x		x	x		x	x	x		nc

					Fragment					
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
Albizia polycephala (Benth.) Killip ex Record									x	P
Andira fraxinifolia Benth.						x				P
Apuleia leiocarpa (Vogel) J.F.Macbr.	x	x	x	x	x	x	x			P
Bauhinia forficata Link *									x	P
Chamaecrista ensiformis (Vell.) H.S.Irwin & Barneby							x			P
Copaifera langsdorffii Desf.	x		x							ST
Copaifera lucens Dwyer *					x					ST
Copaifera trapezifolia Hayne		x								ST
Dahlstedtia pinnata (Benth.) Malme *									x	P
Dalbergia nigra (Vell.) Allemão ex Benth. *				x						P
Diplotropis incexis Rizzini & A.Mattos *				x						P
Inga cf. *flagelliformis* (Vell.) Mart.					x					ST
Inga platyptera Benth. *	x									nc
Inga striata Benth.					x			x		P
Machaerium brasiliense Vogel	x		x		x			x	x	ST
Machaerium nyctitans (Vell.) Benth.					x					P
Machaerium pedicellatum Vogel *									x	P
Myrocarpus frondosus Allemão		x			x			x	x	ST
Piptadenia gonoacantha (Mart.) J.F.Macbr.					x			x	x	P
Piptadenia paniculata Benth.					x					P
Plathymenia reticulata Benth.							x	x		ST
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima			x	x		x		x	x	P
Pseudopiptadenia inaequalis (Benth.) Rauschert *		x	x			x			x	ST
Pterocarpus rohrii Vahl		x			x			x	x	P
Schizolobium parahyba (Vell.) Blake *					x					P
Stryphnodendron dryaticum Scalon				x						ST
Swartzia apetala Raddi						x				ST
Swartzia simplex (Sw.) Spreng.							x		x	ST
Vatairea heteroptera (Allemão) Ducke ex de Assis Iglesias *			x							P
Zollernia ilicifolia (Brongn.) Vogel					x					nc
HYPERICACEAE										
Vismia cf. *martiana* Mart.			x							P
LACISTEMACEAE										
Lacistema pubescens Mart.	x		x	x		x	x	x	x	P
LAMIACEAE										
Aegiphila integrifolia (Jacq.) Moldenke	x			x			x	x		P
Aegiphila mediterranea Vell.					x					nc
Vitex megapotamica (Spreng.) Moldenke			x			x				P
Vitex polygama Cham.								x		nc
LAURACEAE										
Aiouea saligna Meisn.		x		x						ST
Aniba firmula (Nees & Mart.) Mez			x	x		x				ST
Beilschmiedia aff. *taubertiana* (Schwacke & Mez) Kosterm. *					x					nc
Cryptocarya aff. *moschata* Nees & Mart.									x	ST

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
Lauraceae spec. 15					x					nc
Licaria bahiana Kurz *	x	x	x	x	x	x	x	x		nc
Nectandra leucantha Nees & Mart. *									x	P
Nectandra membranacea (Sw.) Griseb.					x				x	nc
Nectandra oppositifolia Nees & Mart.	x							x		P
Nectandra psammophila Nees						x				P
Ocotea aff. *dispersa* (Nees) Mez *					x					ST
Ocotea aff. *elegans* Mez *						x				ST
Ocotea aff. *tenuiflora* (Nees) Mez *				x		x				ST
Ocotea brachybotrya (Meisn.) Mez *	x		x			x	x	x	x	ST
Ocotea diospyrifolia (Meisn.) Mez		x	x		x	x		x	x	ST
Ocotea elegans Mez *						x				ST
Ocotea glaziovii Mez				x		x			x	ST
Ocotea laxa (Nees) Mez *	x					x			x	ST
Ocotea odorifera (Vell.) Rohwer				x	x		x	x		ST
Ocotea puberula (Rich.) Nees									x	P
Ocotea silvestris Vattimo-Gil *		x								ST
Ocotea spec 1				x						nc
Ocotea spec 4				x		x	x			nc
Ocotea spec 5						x				nc
Ocotea vaccinioides (Meisn.) Mez *						x				ST
Rhodostemonodaphne macrocalyx (Meisn.) Rohwer ex Madriñán *		x			x					ST
Urbanodendron bahiense (Meisn.) Rohwer *							x			ST
LECYTHIDACEAE										
Cariniana estrellensis (Raddi) Kuntze			x							ST
Couratari pyramidata (Vell.) Kunth *					x					ST
Lecythis lanceolata Poir. *	x		x			x	x		x	ST
MAGNOLIACEAE										
Magnolia ovata (A.St.-Hil.) Spreng.							x			ST
MALPIGHIACEAE										
Bunchosia maritima (Vell.) J.F.Macbr. *									x	nc
Byrsonima oblanceolata Nied.			x	x						nc
Byrsonima spec.						x				nc
MALVACEAE										
Eriotheca pentaphylla (Vell. emend. K.Schum.) A.Robyns *					x		x			ST
Luehea cf. *divaricata* Mart. & Zucc.		x								P
Triumfetta grandiflora Vahl									x	nc
MELASTOMATACEAE										
Miconia albicans (Sw.) Triana	x			x			x			P
Miconia brasiliensis (Spreng.) Triana *						x				nc
Miconia calvescens DC.					x				x	P
Miconia cinnamomifolia (DC.) Naudin *	x						x		x	P
Miconia lepidota DC.	x		x	x	x	x				P
Miconia prasina (Sw.) DC.	x								x	nc
Tibouchina granulosa (Desr.) Cogn. *	x				x		x	x		P
MELIACEAE										
Cabralea canjerana (Vell.) Mart.		x	x			x		x	x	ST

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
Cedrela odorata L.	x	x	x		x		x		x	P
Guarea guidonia (L.) Sleumer		x	x		x		x	x	x	ST
Guarea macrophylla Vahl		x	x	x	x	x	x		x	ST
Trichilia lepidota Mart.									x	ST
Trichilia silvatica C.DC.		x			x	x		x	x	ST
MONIMIACEAE										
Mollinedia cf. *oligantha* Perkins *						x				ST
Mollinedia cf. *uleana* Perkins *		x	x						x	ST
Mollinedia gilgiana Perkins *			x							nc
MORACEAE										
Brosimum glaziovii Taub.		x			x					P
Brosimum guianense (Aubl.) Huber	x		x	x	x	x	x	x	x	ST
Ficus gomelleira Kunth & C.D.Bouché			x	x						P
Ficus mariae C.C.Berg, Emygdio & Carauta			x							nc
Helicostylis tomentosa (Poepp. & Endl.) Rusby	x	x	x	x	x	x	x	x	x	ST
Sorocea guilleminiana Gaudich.		x	x			x	x	x	x	nc
MYRISTICACEAE										
*Virola bicuh*yba (Schott ex Spreng.) Warb. *		x	x		x			x	x	ST
Virola gardneri (A.DC.) Warb. *									x	ST
MYRSINACEAE										
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	x									P
MYRTACEAE										
Calyptranthes lucida Mart. ex DC.							x			ST
Eugenia batingabranca Sobral *		x								nc
Eugenia candolleana DC.						x	x		x	ST
Eugenia cuprea (O.Berg) Nied. *	x	x	x	x	x	x	x	x	x	ST
Eugenia florida DC.									x	ST
Eugenia macahensis O.Berg *					x					nc
Eugenia oblongata O.Berg *							x			ST
Eugenia pisiformis Cambess. *		x		x	x				x	ST
Eugenia spec. 1				x						nc
Eugenia spec. 2							x			nc
Eugenia spec. 3					x			x		nc
Marlierea cf. *tomentosa* Cambess.							x			ST
Marlierea excoriata Mart. *			x							ST
Marlierea tomentosa Cambess.					x					ST
Myrcia crocea (Vell.) Kiaersk. *				x		x				nc
Myrcia laxiflora Cambess. *						x				ST
Myrcia spec. 1						x				nc
Myrcia spec. 2		x								nc
Myrcia spec. 3			x							nc
Myrcia splendens (Sw.) DC.	x	x		x			x			nc
Psidium myrtoides O.Berg									x	P
NYCTAGINCEAE										
Andradea floribunda Allemão *		x			x					P
Guapira aff. *nitida* (Mart. ex J.A.Schmidt) Lundell *							x			P
Guapira hirsuta (Choisy) Lundell			x			x		x		ST
Guapira opposita (Vell.) Reitz	x	x	x	x	x	x		x		P

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
OLACACEAE										
Heisteria silvianii Schwacke		x								ST
Tetrastylidium grandiflorum (Baill.) Sleumer *									x	ST
PERACEAE										
Pera heteranthera (Schrank) I.M. Johnst.	x						x		x	ST
PHYLLANTHACEAE										
Hieronyma alchorneoides Allemão		x							x	P
PHYTOLACCACEAE										
Seguieria langsdorffii Moq.		x			x					nc
PIPERACEAE										
Piper arboreum Aubl.					x				x	P
POLYGONACEAE										
Coccoloba cf. *fastigiata* Meisn. *							x			nc
Coccoloba declinata (Vell.) Mart.		x								nc
Ruprechtia lundii Meisn. *		x			x			x		P
RUBIACEAE										
Alseis floribunda Schott		x								ST
Amaioua intermedia Mart. ex Schult. & Schult.f.	x		x	x		x				P
Bathysa stipulata (Vell.) C.Presl *		x	x				x	x	x	ST
Bathysa sylvestrae Germano-Filho & M.Gomes *	x		x		x		x			nc
Coussarea accedens Müll.Arg. *		x							x	ST
Coussarea contracta (Walp.) Müll. Arg.				x						ST
Coussarea meridionalis (Vell.) Müll.Arg. *							x			ST
Coussarea nodosa (Benth.) Müll.Arg.								x		ST
Coussarea viridis Müll.Arg. *			x	x		x	x			nc
Coutarea hexandra (Jacq.) K.Schum.					x					ST
Posoqueria latifolia (Rudge) Schult.									x	nc
Psychotria appendiculata Müll.Arg. *						x		x		nc
Psychotria mapourioides DC.								x		ST
Psychotria nuda (Cham. & Schltdl.) Wawra *									x	ST
Psychotria subspathacea Müll.Arg. *					x				x	nc
Rudgea cf. *nobilis* Müll.Arg. *							x			nc
Rudgea recurva Müll.Arg. *					x					ST
Simira rubra (Mart.) Steyerm. *					x					nc
RUTACEAE										
Citrus spec. 1					x					nc
Hortia brasiliana Vand. ex DC.	x			x			x			nc
Zanthoxylum rhoifolium Lam.					x					P
SABIACEAE										
Meliosma sellowii Urb.							x			ST
SALICACEAE										
Casearia arborea (Rich.) Urb.					x					P
Casearia sylvestris Sw.		x	x	x		x	x	x	x	P
SAPINDACEAE										
Allophylus petiolulatus Radlk.								x		ST
Cupania cf. *racemosa* (Vell.) Radlk.	x		x	x		x	x	x	x	P
Cupania furfuracea Radlk.	x	x	x	x			x		x	nc
Cupania oblongifolia Mart.		x	x		x		x	x	x	nc

	Fragment									
Family / Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**SG**
Cupania racemosa (Vell.) Radlk.				x						P
Matayba cf. *guianensis* Aubl.									x	P
Matayba cf. *juglandifolia* (Cambess.) Radlk.						x	x			P
Matayba leucodictya Radlk. *		x								ST
Toulicia laevigata Radlk. *	x		x	x		x	x	x		P
Tripterodendron filicifolium Radlk. *									x	ST
SAPOTACEAE										
Chrysophyllum flexuosum Mart. *		x			x				x	ST
Ecclinusa ramiflora Mart.		x	x	x		x	x	x		ST
Pouteria cf. *bangii* (Rusby) T.D.Penn.								x		ST
Pouteria cf. *durlandii* (Standl.) Baehni									x	nc
Pouteria spec. 3						x				nc
Pouteria torta (Mart.) Radlk.							x		x	ST
Pradosia kuhlmannii Toledo *				x						ST
Sapotaceae spec. 8							x			nc
Sapotaceae spec. 9									x	nc
Sarcaulus brasiliensis (A.DC.) Eyma		x				x				nc
SIMAROUBACEAE										
Simarouba amara Aubl.							x		x	P
SIPARUNACEAE										
Siparuna guianensis Aubl.	x		x	x	x	x		x	x	P
Siparuna reginae (Tul.) A.DC.	x	x	x	x	x	x	x	x	x	ST
SOLANACEAE										
Cestrum cf. *intermedium* Sendtn.	x									P
Solanum leucodendron Sendtn. *					x					P
Solanum swartzianum Roem. & Schult.	x									P
URTICACEAE										
Cecropia glaziovii Snethl. *					x				x	P
Cecropia hololeuca Miq.	x		x	x	x	x				P
Pourouma guianensis Aubl.		x	x	x		x		x		P
VIOLACEAE										
Amphirrhox longifolia (A.St.-Hil.) Spreng.		x			x				x	ST
Rinorea guianensis Aubl.		x		x	x	x	x		x	ST

Appendix 2. Area of the surveyed fragments.

Fragment	Area [ha]
A	5.8
B	6.4
C	9.1
D	12.5
E	17.6
F	19.3
G	51
H	96.8
I	135.5