

Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages

Marcondes A. Oliveira, Alexandre S. Grillo and Marcelo Tabarelli

Abstract In this study we surveyed all trees ≥ 10 cm diameter at breast height within 20 0.1 ha plots in a 3,500 ha forest fragment, surrounded by sugar cane fields, of the Brazilian Atlantic forest to compare tree species assemblages at the forest edge (0–100 m into forest) vs forest interior (> 200 m). Plots were perpendicular to the margin. The mean number of tree species was significantly higher in the forest interior ($35.4 \pm \text{SD } 7.1$ vs $18.4 \pm \text{SD } 4.4$). In addition, forest edge differed from interior in the proportion of shade-tolerant, emergent, large/very large-fruited species, and large-seeded

tree species. Among the 134 tree species recorded, 24% were exclusive to the forest edge and 57% to the forest interior. Our results suggest that both the current system of protected areas and archipelagos of small fragments (1) tend to retain only a subset of the original flora, (2) will converge in terms of floristic and ecological composition (biotic simplification and homogenization), and (3) will lose rare and threatened tree species.

Keywords Atlantic forest, Brazil, fragmentation, fruits, seeds, species loss, species richness.

Introduction

Tropical rain forests are facing alarming rates of habitat fragmentation, and some of them are already archipelagos of small fragments (Gascon *et al.*, 2000). Even large and still inaccessible continuous tracts of tropical forests, such as those of Central Amazonia, will probably suffer fragmentation in the near future (Peres, 2001). Forest fragmentation drives populations to subdivision and isolation, increases human pressure, causes microclimatic changes and enhances forest invasion by exotic species (Zuidema *et al.*, 1996). As a result, several groups of organisms, notably mammals, birds, amphibians and trees, are suffering drastic changes in their local abundance and regional distribution in the fragmented portions of tropical forests (Turner, 1996; Bierregaard *et al.*, 2001).

Studies in the Amazonian and the Brazilian Atlantic forests (Viana *et al.*, 1997; Laurance *et al.*, 1998, 2000) have demonstrated the negative impacts of habitat fragmentation on particular tree species. The major source of the impacts is edge effects: the diverse physical and biotic changes associated with the abrupt and artificial margins of forest fragments (Bierregaard *et al.*, 2001). Edge effects (1) reduce plant recruitment due to habitat desiccation and seedling damage caused by litterfall and treefall near

forest edges, (2) increase sapling mortality by competition with lianas, vines and ruderal species, and (3) increase adult mortality by elevated rates of uprooting and breakage near forest edges (Laurance, 2001; Tabarelli *et al.*, 2004).

Because of these and other edge-related processes, several shade-tolerant, emergent and large-seeded tree species are regarded as edge-sensitive species and their abundances are expected to decrease at local (i.e. forest fragment) and regional (a pool of forest fragments) levels (Tabarelli *et al.*, 2004). In contrast, short-lived pioneer trees appear to benefit from habitat fragmentation and their abundance increases in archipelagos of small fragments (Mesquita *et al.*, 1999; Tabarelli *et al.*, 1999). Thus, it is reasonable to expect that tree species assemblages in small fragments and forest edges will differ markedly from those in continuous forests in terms of species richness and diversity, and ecological and taxonomic composition (Fox *et al.*, 1997). More specifically, if forest edges lose tree species within particular groups, archipelagos of small fragments will tend to support only an impoverished subset of trees from the original biota (Laurance, 2001).

The Atlantic forest of north-east Brazil, 56,400 km² in original extent (IBGE, 1985), is one of the most distinctive centres of endemism in South America. The biological uniqueness of this area has been recognized by biogeographic studies of the forest's plants, birds and butterflies (Whitmore & Prance, 1987). Unfortunately, only 5.6% of this forest still remained by 1990, and the remaining has been reduced to an archipelago of small forest fragments in a matrix of sugar cane fields (Silva &

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Tabarelli, 2000). Most fragments are now <50 ha and only a few are >1,000 ha (Ranta *et al.*, 1998). Level of habitat fragmentation is so great that only 6% of the remaining forest (i.e. 192 km²) can be considered forest-interior habitat if edge effects reach 300 m into forest fragments (Ranta *et al.*, 1998).

In this study we surveyed plots in the Atlantic forest of north-east Brazil in order to compare tree species assemblage in forest edge vs forest interior. Our main goal was to analyse to what extent forest edge differs from forest interior in terms of tree species richness and diversity, ecological composition and taxonomic composition. This paper (1) provides comparative measures of tree species richness and diversity, (2) quantifies the proportion of species within categories of regeneration strategy, forest stratification, seed dispersal mode, fruit type, fruit and seed size, and (3) tests the occurrence of particular tree species assemblages in each of these habitats. We discuss the role of protected areas and archipelagos of small fragments in retaining representative portions of the biodiversity of the Atlantic forest.

Study site

This study was carried out at Usina Serra Grande, a 200 km² private property located in the State of Alagoas,

north-east Brazil (Fig. 1). The study site is located on the low altitude plateaus (500–600 m), where prevailing soils are latosols and podzols (IBGE, 1985). The climate is tropical, with a 3-month dry season (<60 mm per month). Annual rainfall is c. 2,000 mm, with the wettest period in April–August. The vegetation is classified as lower montane rain forest, and Leguminosae, Lauraceae and Sapotaceae are the richest families in terms of tree species in this forest (Tavares *et al.*, 1971).

Methods

To characterize species richness and diversity in both forest edge and forest interior habitats we established 10 0.1 ha plots (10 × 100 m) in each of these habitats in Coimbra forest, a fragment of c. 3,500 ha. Coimbra is the largest fragment in the Atlantic forest of north-east Brazil, completely surrounded by sugar-cane fields. Pairs of plots were set randomly along the 39.9 km perimeter of Coimbra forest according to the following design: edge plots started in the first metre of forest vegetation, perpendicular to the margin of the fragment, and penetrated 100 m into the fragment. Interior plots started at 200 m distant from the fragment margin. This design was determined by the fact that edge effects are expected to penetrate at least 100 m into fragments (Laurance *et al.*,

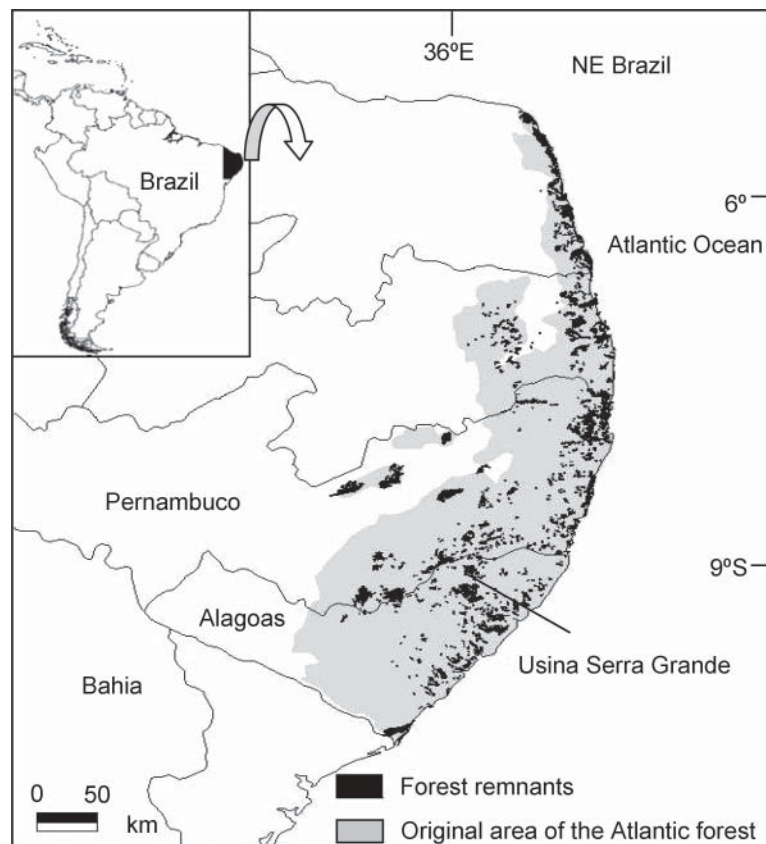


Fig. 1 The location of the study site at Usina Serra Grande in the Atlantic forest of north-east Brazil.

1998). We considered each pair of plots (edge and forest interior) to be an independent sample. The study was carried out between March 2001 and February 2003.

Within plots all trees > 10 cm DBH (diameter at breast height, 1.5 m) were recorded to determine the number of tree species and for the calculation of species diversity, using the Shannon-Wiener function (H') to the base \log_2 (Krebs, 1989), for each plot. We also quantified the number of tree species within each plot based on a random sample of 43 individuals (the lowest number of individuals recorded within a plot). Plant voucher specimens were lodged at Herbarium UFP of the Universidade Federal de Pernambuco, Brazil (voucher nos 34.445 to 36.120).

All tree species recorded within plots were classified according to categories of regeneration strategy, forest stratification, and seed-dispersal mode by checking (1) the relevant literature (Reitz, 1965; Roosmalen, 1985; Lorenzi, 1998; Barroso *et al.*, 1999; Spironello, 1999, Silva & Tabarelli, 2000; Smith *et al.*, 2004; and several issues of *Flora Neotropica*), (2) plant specimens stored at eight regional herbaria, and (3) a fruit and seed collection (172 samples) stored at Herbarium UFP. We also used our personal knowledge of the species' life-history traits (Tabarelli *et al.*, 1999; Silva & Tabarelli, 2000; Tabarelli & Peres, 2002).

The categories used were as follows. *Regeneration strategy*: (1) shade-tolerant species, capable of regenerating in the shaded understorey of old growth forests, and (2) pioneer species requiring high light environments provided by treefall gaps and forest edges (Hartshorn, 1978). *Forest stratification*: (1) understorey species consisting of small trees and shrubs occurring in the lower forest stratum (below 10 m), (2) species occurring in the forest canopy, and (3) emergent species occurring in the highest stratum of the forest (Wilson, 1989). *Seed dispersal*: (1) vertebrate-dispersed species producing diaspores attached to a fleshy pulp, aril, or other features typically associated with vertebrate dispersal agents, and (2) abiotically-dispersed species with winged seeds, plumes or other wind-dispersal devices that slow the rate of seed fall, or those dispersed entirely by free fall or propelled explosively by a fruit that opens suddenly or by a trip lever (Pijl, 1982).

Fruits of vertebrate-dispersed species were classified as drupe, berry, pod, capsule and others (pseudo-fruit, pyxidium and monocarp) according to Roosmalen (1985). These fruits were also classified within size categories: (1) small, <0.6 cm in length, (2) medium, 0.6–1.5 cm, (3) large, 1.6–3.0 cm, and (4) very large, >3.0 cm. Seeds of vertebrate-dispersed species were classified as small (<1.5 cm in length) or large (>1.5 cm).

Paired-sample *t* tests were used to analyse differences in species richness and diversity between the forest edge

and interior. Data were first tested for normality using Lilliefors tests. Differences in the proportion of species within ecological groups were analysed using *G*-tests (Sokal & Rohlf, 1995).

Results

Altogether 134 tree species belonging to 40 families were recorded; 58 species at the forest edge (601 individuals) and 102 species in the forest interior (885 individuals). Mean species richness was $18.4 \pm \text{SD } 4.4$ per 0.1 ha at the forest edge and $35.4 \pm \text{SD } 7.1$ in the forest interior ($t = 6.35$, $df = 18$, $P < 0.0001$). Similarly, mean species richness based on a random sample of 43 trees was $16.2 \pm \text{SD } 3.5$ at the forest edge and $23.3 \pm \text{SD } 3.2$ in the forest interior ($t = 4.69$, $df = 18$, $P < 0.001$). Mean species diversity was $H' = 3.4 \pm \text{SD } 0.64$ at the forest edge and $4.4 \pm \text{SD } 0.47$ in the forest interior ($t = 3.96$, $df = 18$, $P = 0.001$).

Forest edge and interior differed significantly in the proportion of pioneer tree species ($G = 32.8$, $df = 1$, $P < 0.0001$), and in the proportion of emergent tree species ($G = 8.6$, $df = 1$, $P = 0.013$). Forest edge had twice as many pioneer species as forest interior (83 vs 37%), and only one third of the emergent species found in forest interior (Fig. 2). Vertebrate-dispersed species were predominant, and the proportion of species in this group was similar in both habitats.

Within vertebrate-dispersed species drupe- and berry-fruited species were >50% of all tree species recorded in forest edge and interior, and no significant differences were found between the proportion of species within categories of fruit type between these habitats (Fig. 3a). In contrast to seed-dispersal mode and fruit type, forest edge and interior differed significantly in the proportion of species within categories of fruit size ($G = 10.5$, $df = 3$, $P = 0.015$). Tree species with large and very large fruits accounted for 45% of all species recorded at the forest edge, whereas these groups of species accounted for 73% of species in the forest interior (Fig. 3b). The proportion of large-seeded species was also significantly lower at the forest edge (15%) than in the interior (44%) ($G = 11.04$, $df = 2$, $P = 0.001$).

Among the 134 species recorded in both habitats, 32 (24% of all species found) were exclusive to the forest edge, 76 (57%) were exclusive to the forest interior, and 26 (19%) were common to both habitats. The proportion of species exclusive to one habitat was significantly higher in interior forest (75%) than at the forest edge (55.1%; $G = 12.6$, $df = 1$, $P < 0.001$). Proportions of shade-tolerant, emergent, large/very large-fruited species, and large seeded tree species within the set of exclusive species were significantly higher in the forest interior (Table 1).

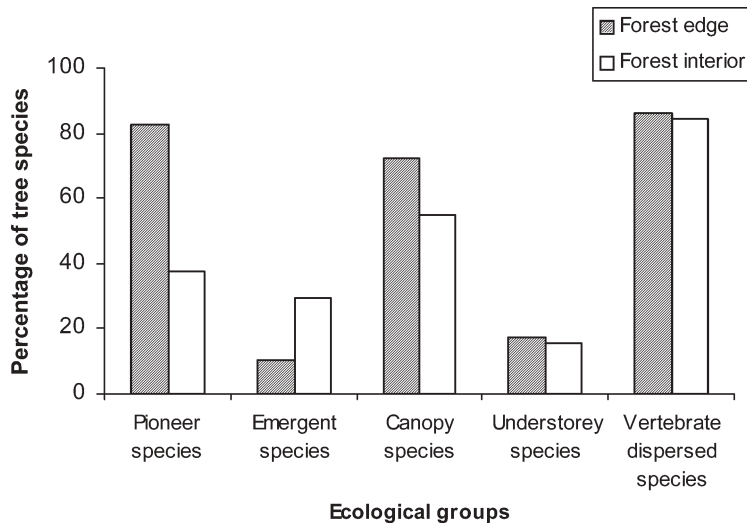


Fig. 2 Percentage of tree species (total number = 134) within five ecological groups (see text for details) at the forest edge and in the forest interior at Usina Serra Grande.

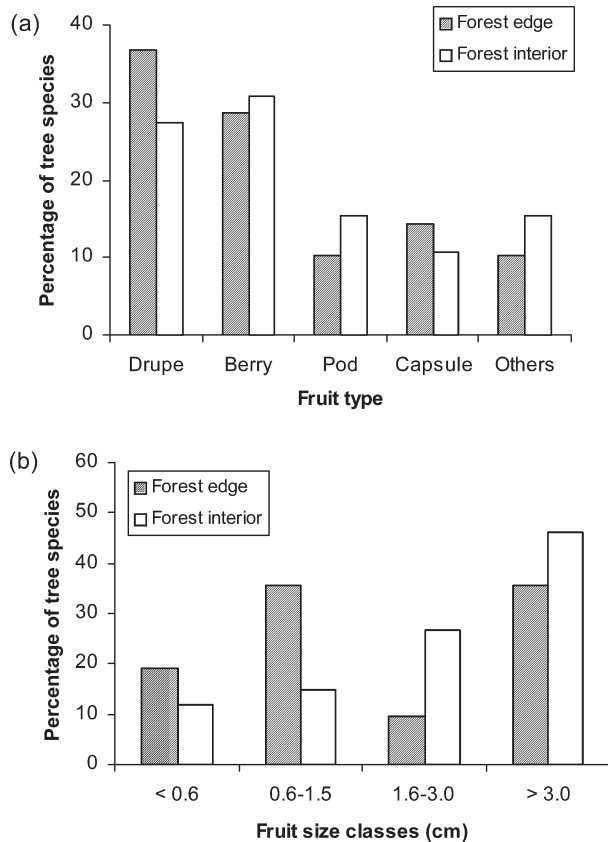


Fig. 3 Percentage of tree species within classes of (a) fruit type, and (b) fruit size at the forest edge and in the forest interior at Usina Serra Grande.

Discussion

Our results indicate that forest edge and forest interior are contrasting habitats in terms of tree species richness,

Table 1 Ecological grouping of tree species, with the number and percentage of species exclusive to the forest edge or interior, and species common to both.

Ecological groups	Exclusive species		Common species
	% of species (N) at forest edge	% of species (N) in forest interior	
Pioneer species	93.7 (30)	26.3 (19)	69.2 (18)
Shade-tolerant species	6.3 (2) ^a	73.6 (53) ^b	30.7 (8) ^c
Emergent species	3.1 (1) ^a	33.3 (24) ^b	19.2 (5) ^{ab}
Canopy species	84.3 (27) ^a	52.7 (38) ^b	57.6 (15) ^{ab}
Understorey species	12.5 (4)	13.8 (10)	23.1 (6)
Large- and very large-fruited species	34.3 (11) ^a	56.9 (41) ^b	30.7 (8) ^{ab}
Large-seeded species	9.3 (3) ^a	33.3 (24) ^b	19.2 (5) ^{ab}
Pioneer emergent species	3.1 (1) ^a	12.5 (9) ^a	19.2 (5) ^a

*Numbers in the same line followed by different superscripted letters are significantly different (pairwise *G*-tests, $P \leq 0.05$).

species diversity, ecological composition and taxonomic composition. This pattern emerged despite the fact that interior plots were only 200 m distant from the fragment's margin. It means that if edge effects penetrated 300 m into fragments, as proposed by Laurance (1991), we probably underestimated the differences in tree species assemblages between forest edge and those portions of forest not affected by edge effects, the forest interior or core area *sensu* Laurance *et al.* (1998).

A number of processes related to edge effects may explain the pattern found in this study, such as reduction in seedling recruitment due to habitat desiccation, and higher rates of adult mortality due to uprooting and breakage caused by wind turbulence (Tabarelli *et al.*, 2004). However, Melo (2004) accumulated evidence at

the study site suggesting that alterations in allochthonous seed rain (i.e. seeds from other habitats) may reduce the frequency and abundance of large-seeded tree species at the forest edge and thus drastically alter tree species composition in this habitat. Melo (2004) also concluded that seeds from several large-seeded species of Sapotaceae have not reached the forest edge even though they are common in the interior forest. In the neotropical lowland forests, species of Sapotaceae are usually shade-tolerant trees (Pennington, 1990; Jesus, 2001) with seeds dispersed by arboreal mammals, scatter-hoarding rodents and occasionally by bats and large birds (Spironello, 1999).

Coimbra forest contains at least 10 canopy or emergent shade-tolerant species of Sapotaceae in the genera *Pouteria*, *Chrysophyllum*, *Micropholis*, *Pradosia* and *Manilkara*. Nine of the species are completely restricted to well-preserved portions of forest interior and were recorded in this study. In contrast, only *Chrysophyllum viride* has been recorded at the forest edge, reinforcing the categorization of Sapotaceae as an old-growth family (Laurance, 2001). During 9 months (October 2002 to June 2003) 517 large seeds were trapped within 100 1 m² seed traps in the Coimbra forest interior (2.3% of all seeds recorded in this habitat), including seeds from at least five Sapotaceae species. On the other hand, only 250 large seeds (0.65%) were recorded in the forest edge, none of them from species of Sapotaceae (F.P. Melo & M. Tabarelli, unpubl. data). This indicates that the forest edge has not received seeds from a number of large-seeded Sapotaceae species. Reduction of allochthonous seed-rain does not explain why large adults have disappeared from the forest edge but it does account for the lack of recruitment of species of Sapotaceae.

In this context a large proportion of Sapotaceae species that occur in the Amazonian and Atlantic forests have narrow geographic distributions and have been described as both locally and regionally rare (Pennington, 1990; Walter & Gillett, 1998). This is exemplified by *Manilkara dardanoi*, which is known from only two localities in the Atlantic forest of north-east Brazil (Pennington, 1990). Because of this natural rarity >50 species of Sapotaceae found in these forests are considered threatened with extinction (Walter & Gillett, 1998; Hilton-Taylor, 2000; IUCN, 2003). In forest edge habitat, however, >80% of species were pioneer trees, which are now widely distributed in the Brazilian Atlantic forest and abundant in human-disturbed forests; examples are *Tapirira guianensis* (Anacardiaceae) and *Schefflera morototoni* (Araliaceae) (Lorenzi, 1998).

In summary, our study provides evidence that forest fragmentation leads to the establishment of two assemblages of tree species. The forest interior holds a rich assemblage of tree species consisting mostly of

shade-tolerant canopy and emergent species, among them some exclusive large-seeded tree species that appear to be naturally rare at local and regional levels. On the other hand, the forest edge has an impoverished assemblage of tree species in which species adapted to disturbance prevail. In the Atlantic forest of north-east Brazil >90% of protected areas are <500 ha and most of the remaining forest on private land consists of archipelagos of small fragments composed of forest edge habitat. If our results describe a general pattern we hypothesize that both the current system of protected areas and archipelagos of fragments (1) tend to retain only a subset of the original flora, (2) will converge in terms of floristic and ecological composition (biotic simplification and homogenization), and (3) will lose rare and threatened tree species.

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Biographical sketches

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