

Habitat fragmentation and the future structure of tree assemblages in a fragmented Atlantic forest landscape

Edgar E. Santo-Silva · Wanessa R. Almeida ·
Marcelo Tabarelli · Carlos A. Peres

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Abstract The biodiversity value of human-modified landscapes has become a central question in the tropical forest conservation biology, yet the degree to which plant populations and communities are restructured in response to environmental change remains unclear. Here, we address tree species density in a fragmented Atlantic forest landscape to test the hypothesis that tree assemblages inhabiting edge-dominated forest habitats approach typical conditions of early successional systems. Seedlings and adults from 141 tree species were sampled across 39 0.1-ha plots: 19 in small fragments (<100 ha) and 20 in mature forest stands within the interior of the largest forest remnant of the study landscape (3500 ha). A total of 5448 seedlings and adults were recorded, with

>55 % of all tree species exhibiting higher densities in small fragments than in mature forest, particularly pioneers (>60 % of all species). Seedlings and adults of these proliferating species differed from species exhibiting population declines in terms of wood density and seed size, respectively. Additionally, pioneers were more abundant than shade-tolerant species, as were hardwood species in the case of seedlings. Tree species showing highest population increases consisted largely of long-lived, light-demanding canopy species bearing soft or hardwood and small-to-medium-sized seeds. Tree assemblage structure also differed in terms of forest habitats with small forest fragments supporting few rare species, whereas the most rapidly proliferating species were much more widespread and abundant in fragments. However, 60 % of all adult pioneer species recorded in small fragments were not recorded as seedlings in this habitat type, although both seedling and adult assemblages were dominated by pioneer species. Edge-

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E. E. Santo-Silva · M. Tabarelli (✉)
Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego, S/N, Cidade Universitária, Recife, PE 50670-901, Brazil
e-mail: mtrelli@ufpe.br

E. E. Santo-Silva
Unidade Acadêmica de Serra Talhada, Universidade Federal Rural de Pernambuco, Av. Gregório Ferraz Nogueira, S/N, José Tomé de Souza Ramos, Serra Talhada, PE 56909-535, Brazil

W. R. Almeida
Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG 38400-901, Brazil

C. A. Peres
School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR47TJ, UK

dominated tree assemblages are likely to experience long-term shifts toward greater dominance of long-lived, pioneer canopy species.

Keywords Extinction debt · Forest fragmentation · Pioneer species · Population density · Seed size · Tree assemblages · Tropical forest · Wood density

Introduction

Tropical forests represent the world's most diverse biome, accounting for the provision of key ecosystem services such as carbon storage and climate regulation (Avisar and Werth 2005; FAO 2010). However, mounting human population pressure driven by greater demand for forest commodities and agricultural land is expected to threaten the largest remaining tracts of old-growth forests globally (FAO 2011; Laurance et al. 2014). In particular, habitat loss and fragmentation are major threat processes to tropical biodiversity, driving species extinction at multiple scales (Sala et al. 2000). Accordingly, it has been argued that large tropical forest reserves represent an irreplaceable biodiversity conservation strategy and a core element of any effective conservation initiative aiming to safeguard representative portions of regional biodiversity (Laurance 2005; Peres 2005).

However, large forest remnants are either dwindling or missing in many regions, including biodiversity hotspots and centers of species endemism (Ribeiro et al. 2009). Therefore, human-modified landscapes have attracted increasing interest from conservation biologists, particularly as complementary landscape elements such as biodiversity corridors or biodiversity-friendly matrices (Melo et al. 2013). In this context, recent research efforts have identified (1) several ecological or functional groups sensitive to human disturbances, most of which referred to as forest-dependent species (Girão et al. 2007; Lopes et al. 2009; Melo et al. 2010; Santos et al. 2008; Tabarelli et al. 2010a) and (2) the presence of altered but rather impoverished communities in taxonomic, ecological, and phylogenetic terms along edge-affected habitats (Santo-Silva et al. 2013; Santos et al. 2008, 2010). Population declines, species extinctions, shifts in community structure, and collapse in forest structure proceed rapidly as soon as forest edges are created. Although species losses are expected to reach

a relaxation point over time, the ultimate nature/composition of tree assemblages in human-modified landscapes remains an open question (see Arroyo-Rodriguez et al. 2009, 2012; Santos et al. 2008, 2010).

The Brazilian Atlantic forest biome has a long history of human disturbances and over 80 % of all forest remnants are smaller than 50 ha (Ribeiro et al. 2009). Tree assemblages inhabiting forest edges and small forest fragments (i.e., edge-affected habitats) have provided key evidence on the potential effects imposed by habitat loss and fragmentation, particularly the establishment of forest edges immersed into open-habitat matrices (see syntheses in Joly et al. 2014; Tabarelli et al. 2010b). Impoverished tree assemblages are dominated by some pioneer species, which tend to proliferate from local to regional scales (Lôbo et al. 2011; Tabarelli et al. 2010a). Proliferation of pioneer and light-demanding species (successional species *sensu* Laurance et al. 2006b) parallels population collapses and extirpations of species in several ecological groups belonging to the old-growth flora, such as large-seeded (Santos et al. 2008) and emergent species (Oliveira et al. 2008), and those with specialized floral biology (Girão et al. 2007; Lopes et al. 2009). Collectively, these shifts have been interpreted as a successional trajectory triggered by habitat fragmentation, transforming edge-affected habitats into early successional systems (Tabarelli et al. 2008). However, it remains unclear whether shifts in plant assemblage composition have already reached a saturation point even after centuries of forest conversion.

Here, we address the population density of 141 tree species as both seedlings and adults in a fragmented Atlantic forest landscape with a long history of sugarcane production. We tested the hypothesis that tree assemblages inhabiting edge-dominated forest habitats with no record of clear-cutting approach typical conditions of early successional systems; this change is more permanent rather than transitory (Tabarelli et al. 2008). Briefly, we document population density and the structure of tree assemblages in adult and seedling stages to project the magnitude of fragmentation-related effects and the future of these assemblages in small forest fragments. We identify which species seems to be favored and disadvantaged in small forest fragments based on their density ratio (density in small forest fragments over their density in mature areas of a large forest remnant), considering

both age classes. Density ratio is examined across functional groups relative to regeneration strategy, seed size, and wood density. Finally, we discuss the implications of our findings in the light of current knowledge on tree assemblage responses to habitat fragmentation and the conservation value of human-modified landscapes.

Materials and methods

Study area

This study was carried out in a severely fragmented landscape of the Brazilian northeastern Atlantic forest, located within the 66,700-ha Usina Serra Grande landholding (8°58'50"S, 36°04'30"W; Fig. 1; Table S1). The area is comprised largely of sugarcane monoculture surrounding 109 forest fragments ranging in size between 1.6 and 3500 ha. The region presents a tropical climate, with a mean annual rainfall of ~2000 mm, and temperatures between 22 and 24 °C, with a dry season lasting 3 months (November–January). At a regional scale, the evergreen or semideciduous forest remnants (Veloso et al. 1991) are largely dominated by Lauraceae, Sapotaceae, Moraceae, and Fabaceae tree species (Grillo et al. 2005).

Serra Grande represents a long-standing fragmented forest landscape, given that sugarcane plantations date back to the nineteenth century (Santos et al. 2008). In addition, the size and shape of forest fragments have remained stable to ensure water supply for sugarcane irrigation. The Serra Grande landscape also holds the 3500-ha Coimbra Forest, the largest and best preserved forest patch in the region, which still retains large areas of mature forest with typical elements of undisturbed primary forest, such as large-seeded tree species and large frugivorous birds (Oliveira et al. 2004; Santos et al. 2008).

Seedling and adult tree surveys

Surveys of adult and seedling trees were carried out only in the dry seasons. Adult trees were surveyed from 2003 to 2005, while seedling inventory was carried out from 2007 to 2009. Tree assemblages were sampled in 39 plots of 0.1-ha (10 × 100 m) within two habitat types: (1) mature forest—20 plots in old-

growth forest stands located inside the Coimbra Forest and at least 200 m from the nearest edge and (2) small forest fragments—19 plots in 19 forest fragments (one plot placed at the geometric center of each fragment) ranging in size from 3.4 to 91.2 ha (mean = 40.9 ha; median = 31.7 ha). This set of forest fragments was selected because (1) the remaining Atlantic forest is vastly dominated by patches smaller than 100 ha (Ribeiro et al. 2009); (2) they have not been exposed to clear-cutting; and (3) they are isolated from continuous forest for more than a century (Santos et al. 2008). As previously stated (Santos et al. 2008), we acknowledge that the Coimbra Forest consists of a single and unreplicated tract of forest and thereby it does not truly represent a 'continuous forest.' However, Coimbra is the best available contemporary scenario and its undisturbed areas of forest interior have been successfully adopted as 'control' sites to assess the long-term effects of habitat fragmentation on the structure of the plant assemblages (see for example Girão et al. 2007; Lopes et al. 2009; Santo-Silva et al. 2013; Santos et al. 2008; Tabarelli et al. 2010a).

For adult tree assemblages, we surveyed all stems ≥ 10 cm DBH (diameter at breast height). During seedling surveys, we randomly selected 100 seedlings (10–50 cm in total height) in 0.1-ha plots. In particular, we set 200 random points within each plot and sampled the nearest seedling to each point. We subsequently discarded all seedlings that did not belong to the tree species, and then randomly selected a subset of 100 seedlings. We decided to use this methodology to avoid sampling monospecific seedling aggregations and to ensure an equal sample size across all sites. These overlapping adult and seedling tree assemblages have yet to be examined together, mainly in functional terms, but previous studies have considered them separately [Santos et al. (2008) and Santo-Silva et al. (2013), respectively]. The spatial distribution of plots is necessarily limited because all mature forest areas are restricted to the same large fragment (Coimbra Forest). However, the overall distribution of the tree flora in the Serra Grande landscape is not affected by large-scale spatial effects (Santos et al. 2008).

Regeneration niche, seed size, and wood density

To identify likely ecological attributes driving changes in population density, we assigned each

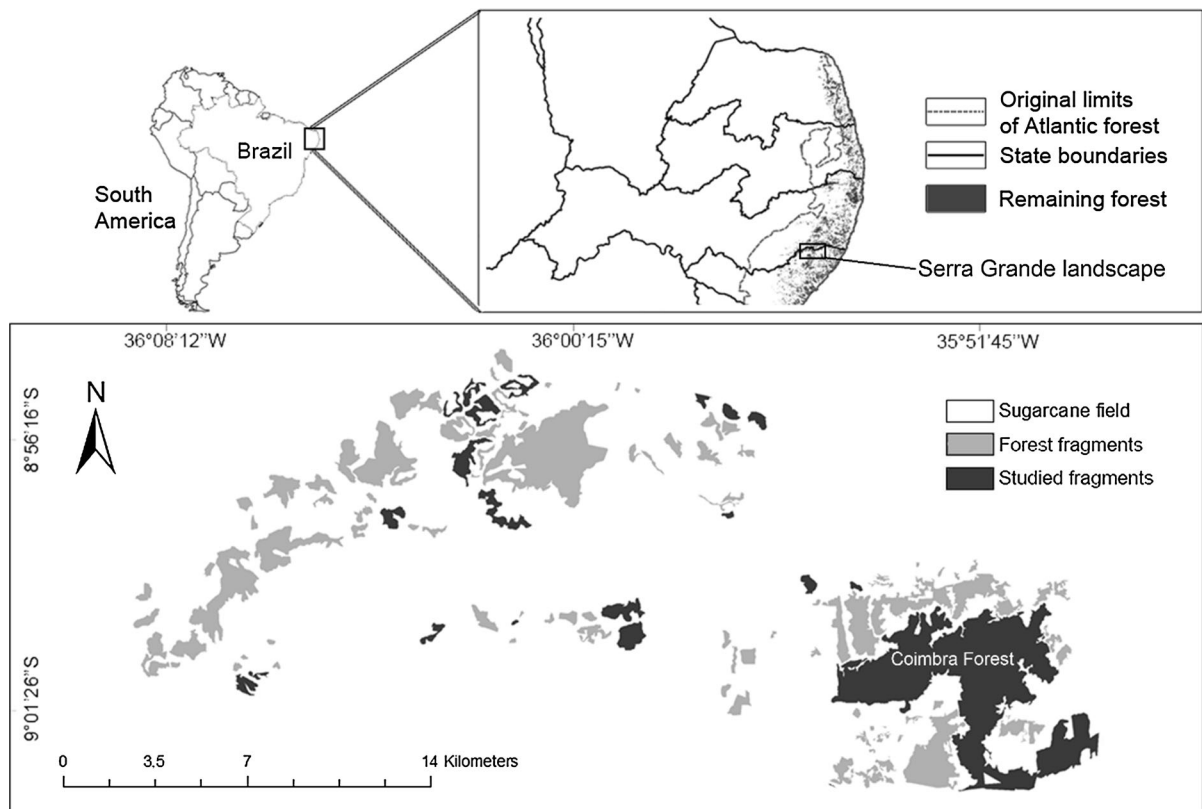


Fig. 1 Map of the Serra Grande landscape and the distribution of forest fragments investigated

species into functional groups according to their regeneration niche, seed size, and wood density, which is a good correlate of individual growth rate (Enquist et al. 1999). In terms of regeneration niche, all stems were assigned into either (1) pioneer or (2) shade-tolerant species (Hartshorn 1978). For seed size, species were assigned into four groups: (1) small (<6 mm in length), (2) medium-sized (6–15 mm), (3) large (>15–30 mm), and (4) very large (>30 mm). For wood density, we assigned each species into two major groups: (1) softwood (wood density <0.7 g/cm³) or (2) hardwood (>0.7 g/cm³). These criteria for assigning species into functional groupings had been adopted previously (Michalski et al. 2007; Oliveira et al. 2004; Santo-Silva et al. 2013; Santos et al. 2008). Information on regeneration niche and seed size were obtained from a comprehensive literature review, including floras and checklists (e.g., Lorenzi 1992; Oliveira 2007; van Roosmalen 1985), and complemented by our own personal knowledge following over two decades of research on the Atlantic forest tree species (e.g., Melo et al. 2006; Oliveira et al. 2004;

Santo-Silva et al. 2013; Silva and Tabarelli 2000; Tabarelli et al. 1999; Tabarelli and Peres 2002). Data of wood density were obtained from Zanne et al. (2009), and we used average values for genera or families if species-specific data were unavailable.

Data analysis

For each ontogenetic stage (seedlings and adults) and habitat type (small forest fragments and mature forest), we calculated the average population density of each species (i.e., total abundance divided by the number of 0.1-ha plots). To infer on either positive or negative changes in population densities in small fragments, we calculated separately for adults and seedlings the ratio between the density in small fragments and the density in mature forest for each species (hereafter, SF/MF ratio). In the lack of long-term demography data (which are logistically and financially unfeasible in most circumstances), this ratio is a very simple metric indicating potential cross-habitat changes in species abundance or even presence

(i.e., SF/MF ratios >1 and <1 indicate species that were either more abundant or less abundant in small fragments than in mature forest areas, respectively). However, this metric must be interpreted with caution. Since some species were only found in either small fragments or mature forest, we arbitrarily added one individual for all species in each habitat type in order to enable estimates of the SF/MF ratio.

Using only those species that had been assigned into a functional group in terms of regeneration niche, seed size, and wood density, we first performed χ^2 tests to evaluate if species with SF/MF ratio >1 and SF/MF ratio <1 (hereafter proliferating and declining species, respectively) differed in terms of functional composition. Second, we performed GLMs (family = Gaussian; link = identity) adopting the regeneration niche, seed size, and wood density as factors and the ln-transformed SF/MF ratio as a continuous-response variable. χ^2 tests and Linear Models were performed separately for adults and seedlings. Finally, we provide species rank curves on the basis of both species abundance and distribution (number of plots) for each habitat (Magurran 1988), considering both adult and seedling assemblages. To obtain species rank curves, all species recorded as adult and seedling were considered, even those not assigned into functional groups. All analyses were performed in Statistica 7 and in R (R Core Team 2015).

Results

We recorded a total of 2778 adult trees representing 103 species (Table S2), 58 (56.3 %) of which were assigned to proliferating species. Consistent with the pattern recorded for seedlings, this group consisted predominantly of pioneers (62.1 %) and softwood species (70.7 %) bearing medium-sized (60.3 %) and small seeds (24.1 %). Considering the whole adult flora recorded at both habitats, there were no differences between proliferating and declining species in relation to regeneration niche ($\chi^2 = 0.19$, $df = 1$, $P = 0.659$; Fig. 2a) and wood density ($\chi^2 = 1.29$, $df = 1$, $P = 0.256$; Fig. 2c). However, large- and very large-seeded adult trees were more frequent among declining species than those that were proliferating ($\chi^2 = 8.23$, $df = 3$, $P = 0.041$; Fig. 2b).

Considering the seedling flora, a total of 2640 individuals representing 76 tree species were recorded

across both mature forest and small fragments (Table S2), with 48 species (63.2 %) exhibiting higher abundances in small fragments (SF/MF ratios >1). Most of these proliferating species had been classed as pioneers (72.9 %), hard-wooded (54.2 %), and bearing either medium-sized (50 %) or small seeds (27.1 %). Furthermore, proliferating and declining species in seedling assemblages did not differ in terms of regeneration niche ($\chi^2 = 1.21$, $df = 1$, $P = 0.27$; Fig. 2d) and seed size ($\chi^2 = 5.76$, $df = 3$, $P = 0.124$; Fig. 2e), but the percentage of softwood species was one-third lower in proliferating species ($\chi^2 = 6.12$, $df = 1$, $P = 0.013$; Fig. 2f).

The SF/MF ratios were highly variable ranging from 0.004 to 81.1 in seedling assemblages and from 0.003 to 77.9 in adult assemblages. Among all functional groups, pioneers had higher SF/MF ratios than shade-tolerant species (Adults, $F = 4.82$, $P = 0.031$; Seedlings, $F = 5.21$, $P = 0.025$; Fig. 3a, b), whereas hardwood species had higher SF/MF ratios than softwood species in seedlings ($F = 10.44$, $P = 0.002$). Although pioneer species on average exhibited higher SF/MF ratios than shade-tolerant species in both ontogenetic stages, this elevated density was more pronounced in seedlings than in adults. When we compared population densities between adult and seedling assemblages, almost all shade-tolerant species exhibited a reduced density at the seedling stage in both habitat types (Fig. 4a), whereas pioneer species were much more evenly split between those exhibiting either lower or greater densities at the seedling stage (Fig. 4b). Considering both adult and seedling assemblages, hyperdominant species in small fragments exhibiting the highest SF/MF ratios were predominantly long-lived, canopy gap-demanding species bearing small-to-medium-sized seeds (Table 1).

Finally, adult and seedling assemblages differed markedly in terms of community structure across habitat types since only a small number of rare seedling species were recorded in small fragments (Fig. 5), whereby the number of species represented by only one or two individuals in small fragment plots was 81 % lower compared to those in mature forest areas. Among the ten top ranking proliferating species (highest SF/MF ratios), only three were recorded as both adults and seedlings in mature forest, where they were typically rare. In contrast, most of these top ten species were very abundant in small fragments as both

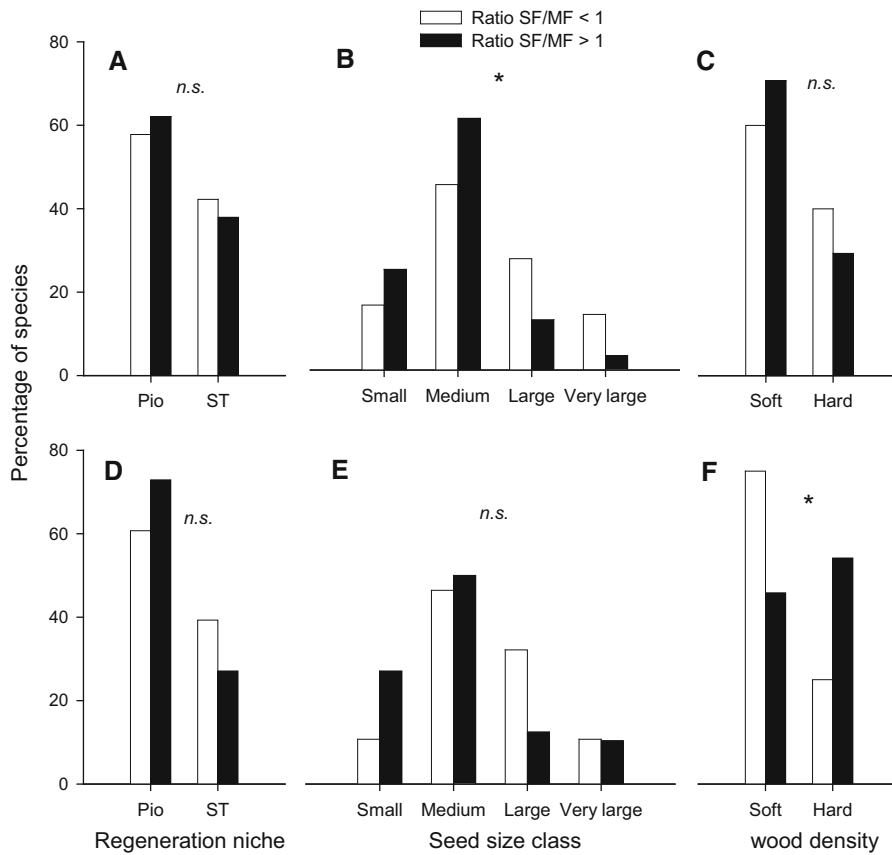


Fig. 2 Percentage of species assigned into functional groups in terms of regeneration niche, seed size, and wood density at the Serra Grande-fragmented landscape. **a–c** indicate the percentages of species in adult assemblages, whereas **d–f** indicate the

percentages of species in seedling assemblages. *Open bars* represent the percentage of species with SF/MF ratios <1, whereas *black bars* represent those with a SF/MF >1. *Pio* pioneer, *ST* shade-tolerant, *n.s.* nonsignificant, **P* < 0.05

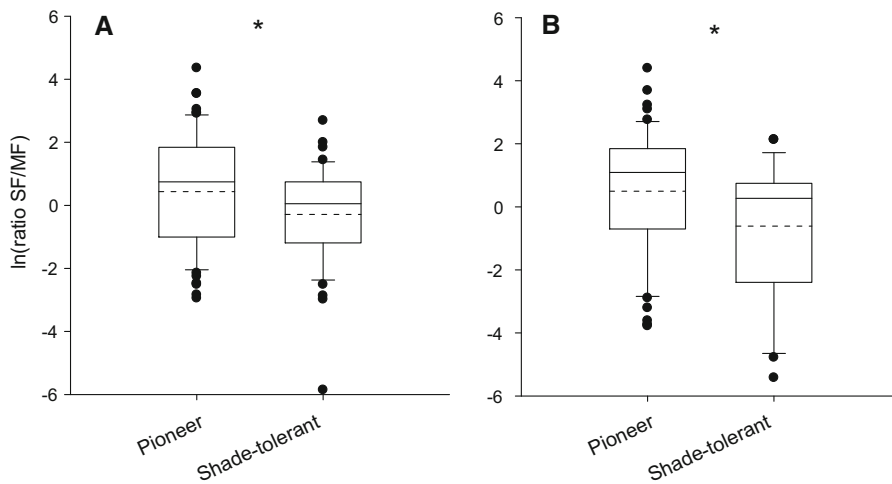


Fig. 3 Relationship between SF/MF ratios and the regeneration niche of **a** adults and **b** seedlings. *Boxes* indicate the 25th and 75th percentiles, *error bars* represent the 10th and 90th

percentiles, and the points are the outliers. *Solid and dashed lines* indicate the median and mean, respectively. **P* < 0.05

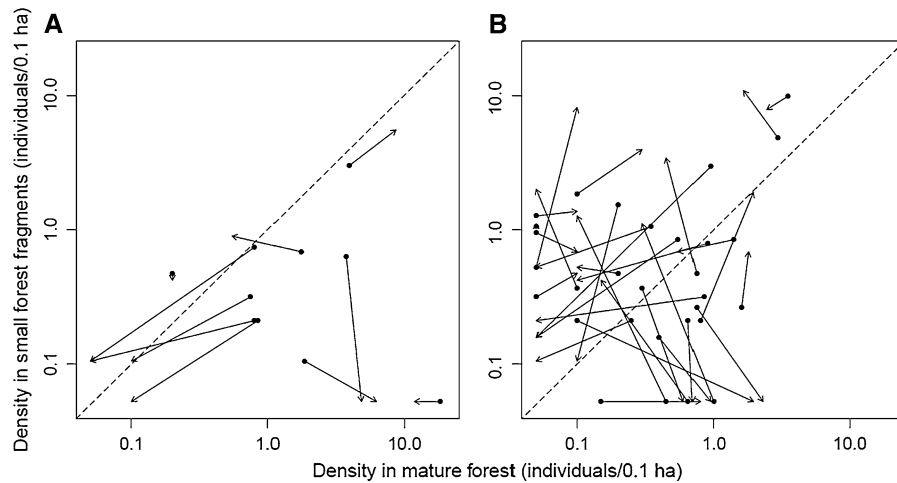


Fig. 4 Relationship between population density in adult and seedling tree assemblages for **a** shade-tolerant and **b** pioneer species, considering only those species that were found in both ontogenetic stages. Each *arrow* represents one species and the

end of the *arrow* (black dots) indicates density in adult assemblages, while the *arrow heads* indicate the density in seedling assemblages in mature forest areas and small forest fragments

seedling and adults, including the pioneers *B. sericea*, *B. virgilioides*, *C. oblongifolia*, and *C. racemosa* (see Table 1). A similar pattern was observed considering species occupancy across plots (Fig. 6). Compared to mature forest, seedling assemblages in small forest fragments exhibited a reduction of two-thirds in the number of species recorded in only one or two plots. Additionally, the three top ten species in mature forest patches were only recorded in 1–3 plots. In small fragments, however, the top ten species were relatively ubiquitous, occurring as adults in 2–17 plots and as seedlings in 2–18 plots. *B. virgilioides* was the most frequent species in adult assemblages (17 plots), while *C. oblongifolia* was the most frequent in seedling assemblages (18 plots). Despite the high relative abundance and occupancy exhibited by some pioneer species and a marked reduction in rare species, over 60 % of all pioneer species recorded as adults in small fragments failed to be recorded as seedlings in this habitat type.

Discussion

Tropical forest dynamics cannot be properly addressed without long-term demographic surveys, but for obvious reasons this approach is rarely feasible. We adopted simple measures of population density in seedling and adult tree assemblages to infer on the

nature of future floristic transitions and the magnitude of fragmentation-related effects. Our results suggest that a large proportion of tree species are still experiencing altered abundances as seedlings and adults in small forest fragments, even two centuries after primary forest fragmentation and patch isolation. Several tree species are apparently declining while others are proliferating in small forest fragments. Both negative and positive shifts in abundance, rather than occurring randomly, were observed in particular tree functional groups related to regeneration strategy, seed size, and wood density. In general, shade-tolerant representatives of the old-growth flora have declined, while pioneers could respond in both directions. However, most top-ranking species that proliferated as seedlings included both hard and softwood pioneers, and long-lived species inhabiting the forest canopy. Several proliferating taxa that are becoming hyperabundant in small forest fragments present low abundances in mature forest areas of the Coimbra forest, suggesting a release in abundance in edge-dominated forest habitats. These differential responses across several trait-based functional groups largely result in severely altered plant assemblages in small fragments, which are becoming impoverished in both taxonomic and functional terms. Finally, if we accept taxonomic and ecological differences between seedling and adult assemblages in small fragments as a prognosis of future floristic transitions, the future adult

Table 1 The ten top ranking proliferating tree species in small forest fragments at the Serra Grande landscape, northeast Brazil, considering both adult and seedling stages

Species	Family	Regeneration niche	Life span	Seed size	Wood density	Forest stratification	SF/MF ratio
Adults							
<i>Bowdichia virgilioides</i>	Fabaceae	Pioneer	Long	Medium	Hard	Canopy	77.9
<i>Byrsonima sericea</i>	Malpighiaceae	Pioneer	Short	Medium	Hard	Canopy	34.7
<i>Cupania impressinervia</i>	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	34.7
<i>Artocarpus heterophyllus</i>	Moraceae	Pioneer	Long	Very large	Soft	Canopy	21.1
<i>Miconia prasina</i>	Melastomataceae	pioneer	Short	Small	Hard	Canopy	18.9
<i>Cupania racemosa</i>	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	18.4
<i>Cupania</i> sp. 2	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	15.8
<i>Cupania</i> sp.	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	15.3
<i>Swartzia macrostachya</i>	Fabaceae	Shade-tolerant	Long	Medium	Hard	Canopy	14.7
<i>Cupania oblongifolia</i>	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	10.5
Seedlings							
<i>Cupania oblongifolia</i>	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	81.1
<i>Guazuma ulmifolia</i>	Malvaceae	Pioneer	Short	Small	Soft	Canopy	40
<i>Eugenia</i> sp. 3	Myrtaceae	Pioneer	Short	Medium	Hard	Canopy	25.3
<i>Artocarpus heterophyllus</i>	Moraceae	Pioneer	Long	Very large	Soft	Canopy	22.1
<i>Alseis floribunda</i>	Rubiaceae	Pioneer	Short	Small	Hard	Canopy	15.8
<i>Cupania racemosa</i>	Sapindaceae	Pioneer	Long	Medium	Soft	Canopy	13.2
<i>Eugenia</i> sp. 4	Myrtaceae	Pioneer	Short	Medium	Hard	Canopy	12.6
<i>Guapira opposita</i>	Nyctaginaceae	Pioneer	Long	Medium	Hard	Canopy	12.6
<i>Brosimum guianense</i>	Moraceae	Pioneer	Long	Medium	Hard	Canopy	10.5
<i>Eschweilera</i> sp. 2	Araliaceae	Shade-tolerant	Long	Large	Hard	Canopy	8.4

SF/MF ratios are defined as the density of a given species in small fragments over the density of the same species in mature forest areas in a large forest remnant. Species classified into short- and long-lived pioneers have a life span shorter and longer than 25 years, respectively. Information on regeneration niche, seed size, life span, and forest stratification was obtained by literature review and complemented by our own knowledge (see “Materials and methods” section)

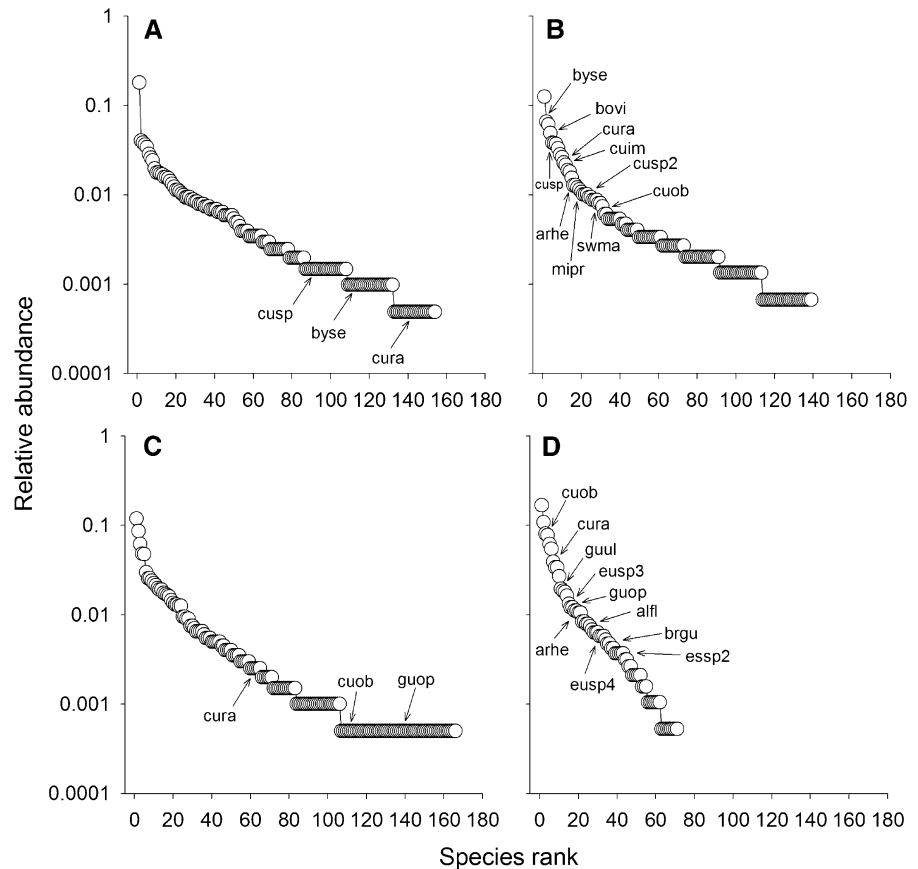
tree flora of the ancient Serra Grande forest landscape will likely be radically different from the one today.

Our findings reinforce key notions about fragmentation-related effects on tropical tree species assemblages, several of which are supported by the empirical evidence from Amazonian and other studies in the Atlantic forests. In particular, (1) edge-affected habitats tend to support distorted tree species assemblages in both taxonomic and functional terms (Laurance et al. 2006a, b; Tabarelli et al. 2008), which can be observed also in seedling assemblages (Santo-Silva et al. 2013); (2) small forest fragments are becoming increasingly dominated by pioneer species (Pütz et al. 2011; Tabarelli et al. 2008); and (3) some native pioneer species are proliferating at multiple spatial scales (Tabarelli et al. 2012), particularly *B. sericea*,

B. virgilioides, *C. oblongifolia* and *C. racemosa*. Although it has been shown that tree assemblages in small forest fragments are predominantly composed of small-seeded species (Melo et al. 2010; Santo-Silva et al. 2013; Santos et al. 2008), our results suggest that production of large numbers of small seeds in itself does not necessarily confer the ability to proliferate in small fragments.

Finally, we offer new evidence for the establishment of adult tree assemblages dominated by a mix of short- and long-lived successional canopy species that are light-demanding pioneers, which represent only a small fraction of species in undisturbed tropical forest (Laurance et al. 2006b). This more detailed description of the floristic drift experienced by edge-affected habitats support other key working hypotheses: (1)

Fig. 5 Rank-abundance curves for different tree species based on the relative abundance of adults (**a**, **b**) and seedlings (**c**, **d**) at the Serra Grande landscape. **a** and **c** represent stands within the Coimbra mature forest, whereas **b** and **d** represent small forest fragments. Key to the top ten proliferating species (i.e., highest SF/MF ratios) for each ontogenetic stage as follows: alfl, *Alseis floribunda*; arhe, *A. heterophyllus*; bovi, *B. virgilioides*; brgu, *B. guianense*; byse, *B. sericea*; cuob, *C. oblongifolia*; cura, *C. racemosa*; cuim, *C. impressinervia*; cusp, *Cupania* sp.; cusp2, *Cupania* sp. 2; essp2, *Eschweilera* sp. 2; eusp3, *Eugenia* sp. 3; eusp4, *Eugenia* sp. 4; guop, *G. opposita*; guul, *G. ulmifolia*; mipr, *M. prasina*; swma, *S. macrostachya*



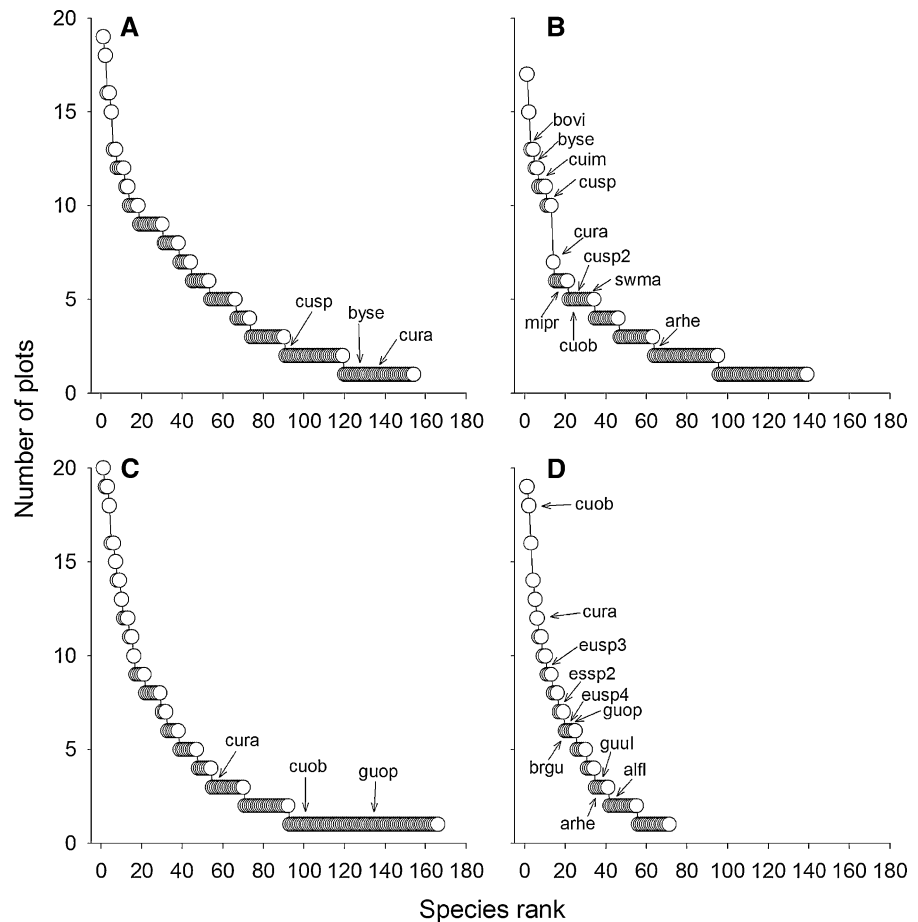
assemblage-wide compositional shifts tend to persist for however long forest environments remain exposed to the open-habitat matrix, suggesting that these shifts are more permanent rather than transitory and (2) edge-dominated forest habitats approach typical conditions of early successional systems, even without clear-cut (Tabarelli et al. 2008).

Although we did not explicitly examine causal mechanisms for the patterns we uncovered in this study, they have been generally considered to be caused by edge effects and seed-dispersal failure. In particular, mechanistic explanations of nonrandom compositional drift are likely related to reduced dispersal movement of large seeds at multiple spatial scales (Cramer et al. 2007; Melo et al. 2006, 2010; Peres and Palacios 2007; Silva and Tabarelli 2000), persistently low seedling recruitment of shade-tolerant old-growth tree species (Santo-Silva et al. 2013), increased mortality of large trees due to uprooting and physiological stress (Laurance et al. 2000), and

hyperproliferation of light-demanding species facilitated by high propagule pressure and increased light availability (Tabarelli et al. 2008). These mechanisms are likely to account for the prevalence of canopy, rather than emergent, hard-wooded pioneer tree species among the ten top-ranking SF/MF ratios, such as those from the genus *Cupania*.

Tree assemblage response to habitat loss and fragmentation, and particularly forest edge creation, in Amazonian forests is consistent with the patterns described here and in other studies for the Atlantic forest. For example, the collapse of the old-growth tree flora and the proliferation of pioneers, particularly short-lived species, have been well documented in Amazonian forest landscapes dominated by both cattle pastures and young secondary forests (Laurance et al. 2006b) and open water (Benchimol and Peres 2015). Based on the patterns found here, we also expect that recently fragmented Amazonian forest landscapes will eventually experience a proliferation of long-lived,

Fig. 6 Rank-occupancy curves for different tree species based on the number plots where adults (**a, b**) and seedlings (**c, d**) were recorded at the Serra Grande landscape. **a** and **c** represent stands within the Coimbra mature forest, whereas **b** and **d** represent small forest fragments. Arrows indicate the ten highest SF/MF ratios. Key to the top ten proliferating species (i.e., highest SF/MF ratios) for each ontogenetic stage as follows: alfi, *A. floribunda*; arhe, *A. heterophyllus*; bovi, *B. virgilioides*; brgu, *B. guianense*; byse, *B. sericea*; cuob, *C. oblongifolia*; cura, *C. racemosa*; cuim, *C. impressinervia*; cusp, *Cupania* sp.; cusp2, *Cupania* sp. 2; essp2, *Eschweilera* sp. 2; eusp3, *Eugenia* sp. 3; eusp4, *Eugenia* sp. 4; guop, *G. opposita*; guul, *G. ulmifolia*; mipr, *M. prasina*; swma, *S. macrostachya*



canopy pioneers, including hard-wooded species. In other words, patterns documented for ‘old’ and ‘newly’ fragmented landscapes represent different stages of a long continuum of floristic drift experienced by edge-dominated habitats.

On the other hand, these apparently general and widespread patterns are in marked contrast to those documented in other neotropical biotas, such as Lacandona in Mexico, where forest fragments smaller than 100 ha exhibit tree assemblages with species diversity, structure, and relative abundance of pioneer similar to those in continuous forest (Hernandez-Ruedas et al. 2014). Given our rationale, this puzzling contrast may result from a different disturbance history and configuration of these Mesoamerican landscapes. Nevertheless, Amazonian and the Atlantic forests present analogous responses regardless of landscape configuration, time elapsed since forest

fragmentation and isolation, and abundance of large-bodied vertebrate seed dispersers (Laurance et al. 2006a, b; Michalski et al. 2007; Santos et al. 2008). We call attention to the evolutionary biogeography of different regions as underlying forces shaping the intensity with which, rather than the direction, different tropical forest settings respond to habitat loss fragmentation. With an evolutionary time exposure to catastrophic natural disturbance events such as hurricanes, plus a long history of human disturbance from pre-Colombian populations, Mexican tropical forest floras may “naturally support” a higher proportion of disturbance-adapted species, thereby exhibiting less pronounced responses to contemporary conversion to nonforest land uses.

Although marked responses of tree assemblages to habitat fragmentation have already been documented, the floristic and functional trajectories experienced by

these assemblages over longer isolation time lags remain poorly understood. Tree assemblages inhabiting edge-affected habitats probably experience long-term shifts toward greater dominance of long-lived, pioneer canopy species (Tabarelli et al. 2008). In terms of conservation implications, pioneers and light-demanding species represent only a small fraction of tropical forest floras (Laurance et al. 2006b), although their relative contribution is likely to vary across biotas. This has clear implications to contemporary forest diversity even if only a modest fraction of this ecological group can become hyperabundant in edge-dominated habitats as advocated here. Pioneer-dominated tree assemblages, including those at Serra Grande, have reduced floristic and functional diversity (Santos et al. 2008), reduced size structure (Oliveira et al. 2008), reduced low levels of carbon retention (Paula et al. 2011), reduced diversity of floral attributes (Girão et al. 2007; Lopes et al. 2009), and reduced phylogenetic diversity (Santos et al. 2010). Moreover, pioneer-dominated assemblages have an altered pattern of fruit phenology and much lower relative abundance of trees bearing large fruits (Tabarelli et al. 2010a), which can reduce habitat quality for many frugivorous vertebrates (*sensu lato*) that play important roles in forest regeneration as seed dispersers and seed predators. Finally, tropical forest ecosystems experiencing high levels of recurrent disturbance tend to provide reduced levels of ecosystem services, including carbon retention and water cycling (Melo et al. 2013). This reinforces the notion that landscapes consisting of small fragments far from large tracts of old-growth forest and surrounded by a cropland matrix represent low conservation value (Melo et al. 2013; Tabarelli et al. 2010b). However, exactly what functional traits ensures species persistence in fragmented landscapes such as Serra Grande are still required, as this question is far from completely elucidated.

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