



Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments

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ABSTRACT

Habitat loss and fragmentation promote relatively predictable shifts in the functional signature of tropical forest tree assemblages, but the full extent of cascading effects to biodiversity persistence remains poorly understood. Here we test the hypotheses that habitat fragmentation (a) alters the relative contribution of tree species exhibiting different reproductive traits; (b) reduces the diversity of pollination systems; and (c) facilitates the functional convergence of reproductive traits between edge-affected and early-secondary forest habitats (5–32 years old). This study was carried out in a severely fragmented 670-km² forest landscape of the Atlantic forest of northeastern Brazil. We assigned 35 categories of reproductive traits to 3552 trees (DBH \geq 10 cm) belonging to 179 species, which described their pollination system, floral biology, and sexual system. Trait abundance was calculated for 55 plots of 0.1 ha across four habitats: forest edges, small forest fragments (3.4–83.6 ha), second-growth patches, and core tracts of forest interior within the largest available primary forest fragment (3500 ha) in the region. Edge-affected and secondary habitats showed a species-poor assemblage of trees exhibiting particular pollination systems, a reduced diversity of pollination systems, a higher abundance of reproductive traits associated with pollination by generalist diurnal vectors, and an elevated abundance of hermaphroditic trees. As expected, the reproductive signature of tree assemblages in forest edges and small fragments (edge-affected habitats), which was very similar to that of early second-growth patches, was greatly affected by both habitat type and plot distance to the nearest forest edge. In hyper-fragmented Atlantic forest landscapes, we predict that narrow forest corridors and small fragments will become increasingly dominated by edge-affected habitats that can no longer retain the full complement of tree life-history diversity and its attendant mutualists.

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1. Introduction

Habitat loss and fragmentation promote rapid, drastic, and persistent changes in the functional signature of tropical tree assemblages as forest edges and small forest fragments (edge-affected habitats) tend to retain but a small, non-random subset of species bearing particular life-history traits (Laurance, 2001; Laurance et al., 2006a). For example, edge-affected habitats may face a sharp reduction in the total number of tree species (Oliveira et al., 2004; Santos et al., 2008) and show decreased species richness of canopy and emergent trees (Laurance et al., 2000), understorey trees (Tabarelli et al., 1999), heavy-wooded, slow-growing trees

(Michalski et al., 2007), large-seeded trees dispersed by medium to large-bodied frugivores (Cordeiro and Howe, 2001; Melo et al., 2006; Terborgh and Nuñez-Iturri, 2006), and shade-tolerant, edge-sensitive trees (Laurance, 2001). Collectively, lower species richness within these functional groups and hyper-proliferation of pioneer trees gradually shift the functional signature of tree assemblages in edge-affected habitats into those typically observed in early-secondary forest patches following slash-and-burn agriculture (Santos et al., 2008). Such a functional and taxonomic convergence means that forest remnant archipelagos in old deforestation frontiers that are overwhelmingly dominated by small forest patches may be comprised of no more than a collection of early- to mid-successional secondary forest stands in terms of tree species richness and life-history traits (Santos et al., 2008).

Decreased richness within some functional groups of trees (i.e. functional depauperation) probably results from a myriad of biotic and abiotic processes in edge-affected habitats that can either

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favour the establishment and spread of pioneer species, or suppress the recruitment of shade-tolerant and mature forest species (Tabarelli et al., 2004). Population collapses of shade-tolerant species may be due to (1) reduced seed arrival (Melo et al., 2006), (2) increased seedling mortality caused by litterfall suppression, pathogens, increased herbivory and treefall damage near forest edges (Benítez-Malvido, 1998; Didham and Lawton, 1999; Benítez-Malvido and Lemus-Albor, 2005; Wirth et al., 2008), (3) increased sapling/adult mortality resulting from competition with lianas, vines, and ruderal species (Viana et al., 1997; Pérez-Salícru, 2001), and (4) increased adult mortality caused by physiological stress from desiccation and wind turbulence, resulting in elevated rates of both uprooting and breakage (Laurance et al., 2000; D'Angelo et al., 2004).

However, changes in the functional profile of tropical tree assemblages in edge-affected habitats need not to be restricted to their regeneration strategy, seed size, and life-form (Santos et al., 2008). A recent study by Girão et al. (2007) has also documented decreased richness and abundance of tree species bearing particular reproductive traits (e.g. pollination by vertebrates, self-incompatibility), which resulted in reduced functional diversity in small forest fragments. Community-wide changes in plant breeding systems and reproductive characteristics likely have pervasive consequences to tropical forest foodwebs because the vast majority of tropical forest plant species are animal-pollinated (see Machado and Lopes, 2004 for a review). Additionally, plant–animal mutualistic interactions in this ecosystem consist of intricate networks (Jordano, 1987; Memmott, 1999) in which the number of interactions increases with overall network complexity and nestedness (Bascompte et al., 2003). Unfortunately, the role played by complex and strongly structured mutualistic networks in ecosystem functioning remains poorly understood (Memmott et al., 2004; Fontaine et al., 2006; Jordano et al., 2006), but biodiversity persistence relies on the integrity of these networks (Bascompte and Jordano, 2006, 2007; Jordano et al., 2006), such as those involving tropical trees and their animal pollinators (see Rathcke and Jules, 1993; Murcia, 1996; Harris and Johnson, 2004; Aguilar et al., 2006). By altering the balance between shade-tolerant and pioneer trees and the frequency of tree species bearing particular reproductive traits, habitat fragmentation ultimately promotes shifts in the patterns of plant resource availability for primary consumers, which in turn may disrupt interaction networks and trigger cascades of extinctions in fragmented landscapes (e.g. Terborgh et al., 2001; Terborgh and Feeley, 2008). By altering the balance between shade-tolerant and pioneer trees, as well as the balance of interactions, habitat fragmentation is also expected to drive edge-affected habitats towards early-secondary forest patches in terms of tree reproductive traits, and lead to functional convergence as proposed by Santos et al. (2008).

Here we investigate to which extent habitat fragmentation alters the reproductive signature of tree assemblages in an aging, hyper-fragmented landscape of the Atlantic forest of northeastern Brazil. We test the hypotheses that habitat fragmentation (a) alters the relative contribution of tree species within different categories of reproductive traits; (b) reduces the diversity of pollination systems; and (c) drives plant communities in edge-affected habitats to much greater similarity with those in early-secondary forests (5–32 years old) compared to primary forest interior areas. First, we present data on the proportion of tree species and individuals within 35 categories of reproductive traits (belonging to three major classes: pollination system, floral biology, and sexual system) across four habitats: forest edges, second-growth patches, small forest fragments, and core forest interior areas. Second, we compare scores of functional diversity across-habitats using the number of species and individuals within different pollination

systems. Finally, we discuss the processes driving reproductive depauperation of tree assemblages and address the potential consequences of reduced functional diversity for biodiversity persistence in hyper-fragmented tropical forest landscapes. We also question the application of biodiversity corridors to restore landscape connectivity, the most important paradigm currently shaping conservation efforts in the Brazilian Atlantic forest.

2. Methods

2.1. Study landscape

This study was carried out at Usina Serra Grande, a large private sugar-cane landholding in the State of Alagoas, northeastern Brazil (8°30'S, 35°50'W; Fig. 1) within the most threatened region of the Brazilian Atlantic forest (Silva and Tabarelli, 2000). This landscape still retains ~9000 ha of forest of the Pernambuco Centre of Endemism (*sensu* Prance, 1982), a unique biogeographic region of the Atlantic forest and a global biodiversity hotspot (Myers et al., 2000). The Serra Grande landscape has been the focus of several fragmentation-related studies (see Oliveira et al., 2004; Melo et al., 2006; Girão et al., 2007; Santos et al., 2008). Pôrto et al. (2006) provide a comprehensive multitaxa checklist of plant and vertebrate species occurring in the region.

We selected a large, hyper-fragmented landscape (667 km²; 9.2% of forest cover), containing dozens of forest fragments (range in size = 1.67–3500 ha) surrounded by a uniform, stable and inhospitable matrix of sugar-cane monoculture. The study landscape is located on a low-altitude plateau (300–400 m a.s.l.), that includes two similar classes of dystrophic soils with high clay fractions: yellow-red latosols and yellow-red podzols (*sensu* IBGE, 1985). Annual rainfall is ~2000 mm, with a 3-month dry season (<60 mm/month) from November to January (Oliveira et al., 2004). The forest physiognomy consists of lowland *terra firme* forest (<400 m a.s.l.), and the families Leguminosae, Lauraceae, Sapotaceae, Chrysobalanaceae, and Lecythidaceae account for most tree species (Grillo, 2005; Grillo et al., 2006).

Sugar-cane cultivation in this landscape dates back to the early 18th century (see Coimbra-Filho and Câmara, 1996) and provided the strongest incentive for clearing large tracts of pristine old-growth forests. The remaining forest has been protected against wildfires and logging to ensure watershed protection and water supply for sugar-cane irrigation (Santos et al., 2008). This has ensured the positional stability of forest fragment borders and the subsequent establishment of reproductive pioneer and shade-tolerant trees along post-closure forest edges (Melo et al., 2006). The remaining forest in this landscape includes the 3500-ha Coimbra Forest – the largest and best preserved private forest patch in northeast Brazil (Oliveira et al., 2004; Santos et al., 2008). This exceptionally large forest patch still retains a full complement of ecological groups occurring in vast undisturbed tracts of Atlantic forest, such as large-seeded trees and medium-sized frugivorous vertebrates (see Pimentel and Tabarelli, 2004; Melo et al., 2006; Santos et al., 2008).

2.2. Tree surveys and habitat classification

Trees ≥ 10 cm in diameter at breast height (DBH) were inventoried in four habitat types as described elsewhere (Santos et al., 2008): (1) forest edges: peripheral areas within 100 m of the border of the largest fragment (Coimbra Forest); (2) core forest areas: old-growth forest interior areas of the Coimbra Forest beyond 200 m of the border, showing no detectable edge influence. Forest edges and core areas were defined on the basis of Laurance et al. (2002), who showed that most edge effects penetrate <200 m into



Fig. 1. (A) map of northeastern Brazil, showing (B) the distribution of the Atlantic forest in the Pernambuco Centre of Endemism region; the original and current distributions of forest cover are indicated by grey and black areas, respectively. Study landscape (white rectangle, and (C) showing the 55 floristic plots located along forest edges, small forest fragments, second-growth patches, and core forest interior (dark grey polygons), including the 3500 ha Coimbra Forest (lower right). Light grey and white areas represent unsampled forest fragments and sugar-cane monoculture, respectively.

Amazonian forest fragments; (3) forest gaps: small (<2 ha) regenerating patches of early-secondary forests of known age located within the Coimbra Forest. Secondary forest patches consisted of a 5–32 years old chronosequence created by the abandonment of slash-and-burn plots following 5–10 years of subsistence agriculture (maize, cassava, beans). The age (years) of secondary stands were determined to within a 6-month error by comprehensive interviews with long-term residents and company employees who had long been in charge of subsistence agriculture at these sites; and (4) small forest fragments: 20 forest fragments ranging between 3.4 and 83.6 ha in size, which are at least 60 years old (see Oliveira et al., 2004; Grillo, 2005) and remain entirely surrounded by sugar-cane fields. Location of all sites was recorded using a hand-held GPS.

Botanical surveys were conducted in a total of 55 plots of 0.1 ha (10 × 100 m) distributed across the four habitats: (1) 10 forest edge plots placed randomly along the 39.9-km perimeter of the Coimbra Forest, starting at the forest edge, and penetrating perpendicularly 100 m into the fragment; (2) 10 core area or forest interior plots within the Coimbra Forest, which were randomly placed at >200 m from the nearest edge; (3) 15 secondary forest plots placed within 15 independent secondary forest patches located within the Coimbra Forest (one plot per gap; Fig. 1); and (4) one plot located at the geometric centre of each of the 20 small forest fragments. Between-plot distance across the four habitats ranged from 218 m to 30,433 m, and the average distance between all 55 plots exceeded 1000 m. The distance between tree plots and the nearest forest edge was 0–100 m for forest edge plots, 200–1013 m for forest interior plots, 31.8–681 m for second-growth plots, and 60.5–392 m for plots in small forest fragments. All plant vouchers were deposited at the Federal University of Pernambuco

(UFP) Herbarium, Brazil (Serra Grande vouchers No. 34,445–36,120; partly available at www.cepan.org.br).

We are aware that the study design was limited by the landscape configuration available to us; the Coimbra Forest does not fully represent a ‘continuous forest’ and consists of a single, unreplicated tract of forest at the landscape and regional scales. However, this is the best available contemporary scenario to assess the long-term effects of habitat fragmentation on the structure of Atlantic forest tree assemblages, particularly because tree assemblages in “old” fragments may be approaching near-equilibrium conditions (Santos et al., 2008).

2.3. Reproductive traits of tree species

A total of 179 tree species and 3552 individuals (48 families and 120 genera) were recorded in the 55 plots sampled here (Supplementary Material A: Species abundance per plot). All tree species were assigned into three major classes of reproductive traits: (1) pollination systems, (2) floral biology, and (3) sexual systems (Table 1). These classes follow Girão et al. (2007) and species assignments were based on (1) a comprehensive review of floras and botanical monographs (e.g. Ribeiro et al., 1999; Lorenzi, 2002a, b; Backes and Irgang, 2004), including several issues of *Flora Neotropica*; (2) web searches including published and referenced data; (3) field observations and a survey of specimens from the UFP and IPA Herbaria, including the plant vouchers from the Serra Grande collection; and (4) our personal knowledge and other published observations (see Machado and Lopes, 2004 for a review).

We thereby obtained for each tree plot across the four habitats the proportion of tree species and individuals within the 35 categories belonging to the three major classes of reproductive traits

Table 1

Major classes of tree reproductive traits adopted in this study (modified from Girão et al., 2007).

Reproductive traits	Categories ^a
1. Pollination system ^a	1. Bats; 2. bees; 3. birds; 4. diverse small insects (DSI); 5. Sphingids (hawkmoths); 6. non-flying mammals; 7. others insects [beetles, butterflies, flies, moths (excluding hawkmoths), wasps]; and 8. wind
2. Floral biology Size ^b	1. Inconspicuous (≤ 4 mm); 2. small ($>4 \leq 10$ mm); 3. medium ($>10 \leq 20$ mm); 4. large ($>20 \leq 30$ mm); and 5. very large (>30 mm)
Resource ^a	1. Nectar; 2. oil; 3. pollen; 4. nectar/pollen; and 5. others [brood or mating places/floral tissues (BMFT), resin, without resource (other than deceit flowers)]
Type ^c	1. Brush; 2. flag; 3. inconspicuous (attributed to very small flowers, ≤ 4 mm); 4. open/dish; 5. tube; and 6. others (bell/funnel, camera, gullet)
Anthesis period ^a	1. Diurnal and 2. nocturnal
3. Sexual system ^d (morphological expression)	1. Dioecious (including all subtypes); 2. hermaphrodites (including heterostylous hermaphrodites); and 3. monoecious (including all subtypes)

^a Following Faegri and Pijl (1979), Endress (1994) and Proctor et al. (1996).

^b Following Machado and Lopes (2004).

^c Adapted from Faegri and Pijl (1979).

^d Following Richards (1997).

* In addition to these 29 categories, we also grouped some categories into six new ones as: (1) small + inconspicuous flowers; (2) medium + large + very large flowers; (3) open/dish + inconspicuous flowers (=flowers with easily accessible resource *sensu* Faegri and Pijl, 1979); (4) floral types other than open or inconspicuous (=flowers with concealed resource *sensu* Faegri and Pijl, 1979); (5) bird- + bat- + non-flying mammal-pollinated flowers (=vertebrate pollination), and (6) non-hermaphrodite sexual systems.

(Table 1). In order to detect broader changes in the reproductive profile of tree assemblages, we also grouped some species into more general biologically meaningful categories (all of which referred to by Faegri and Pijl (1979) or Kang and Bawa (2003)), as following: (1) pollination by generalist pollen vectors (*sensu* Kang and Bawa, 2003), including small bees, butterflies, diverse small insects (DSI), flies, moths, wasps, and wind; (2) pollination by specialist pollen vectors (*sensu* Kang and Bawa, 2003), including bats, medium to large-bodied bees, beetles, birds, hawkmoths (Sphingids), and non-flying mammals; (3) small and inconspicuous flowers (≤ 10 mm); (4) medium, large, and very large flowers (>10 mm); (5) open/dish, inconspicuous flowers [=flowers with easily accessible resources (*sensu* Faegri and Pijl, 1979)]; (6) floral types other than open or inconspicuous flowers [=with concealed resources (*sensu* Faegri and Pijl, 1979)]; (7) bird-, bat-, and non-flying mammal-pollinated flowers (=vertebrate pollination); and (8) non-hermaphrodite sexual systems (monoecious and dioecious, including their subtypes). Although a few tree species were incompletely assigned to all reproductive categories (see Section 3), this was unlikely to have introduced systematic biases to the across-habitat comparisons as habitats were compared in terms of the proportion of species and individuals within categories, which defined the reproductive signature of tree assemblages.

2.4. Functional diversity of pollination systems

We operationally define a functional group as a set of tree species within the same category of reproductive traits, i.e. a set of species sharing a life-history trait as previously adopted elsewhere (see Mayfield et al., 2005; Girão et al., 2007). Evenness-based indices for estimating functional diversity has been frequently recommended (see Petchey and Gaston, 2002; Petchey et al., 2004; Ricotta, 2005). The functional diversity of pollination systems in

forest edges, second-growth patches, small forest fragments, and forest interior areas was therefore calculated on the basis of Shannon's (\log_2) and Simpson's indices (Krebs, 1989), following Girão et al. (2007). We used these two metrics to evaluate the contribution of richness and evenness to the diversity scores. We calculated these indices twice for each of the 55 plots: first by using pollination categories as species analogues and the number of tree species within each category; and second by using categories as species analogues and the number of stems assigned to each category (see Girão et al., 2007).

2.5. Explanatory variables

Several patch and landscape-scale environmental variables are expected to affect the structure of tree assemblages in tropical forests (Laurance et al., 2006b; ter Steege et al., 2006). Previous studies at Serra Grande considering the same set of plots examined here were unable to detect any significant effect of soil and vegetation type on tree species composition (see Girão et al., 2007; Santos et al., 2008). We therefore discarded these baseline variables, but explicitly considered habitat type (forest edge, second-growth patches, forest fragments, and forest interior) and plot distance to the nearest forest edge as explanatory variables for the proportion of species and individuals occurring within different categories of reproductive traits in the tree assemblages. Distances to edges were obtained using a digital map (Santos et al., 2008). Additionally, we performed a Mantel test (Primer package) with weighted Spearman rank correlations to address the effect of forest plot spatial location on levels of taxonomic similarity as previously adopted by Girão et al. (2007) and Santos et al. (2008). Straight-line distances between plots were ln-transformed, as suggested by Condit et al. (2002) and Jones et al. (2006). The Mantel test was carried out considering a group of 20 fragments and 55 0.1-ha plots from which information on tree species composition was available (Oliveira et al., 2004; Grillo, 2005).

The functional structure of tropical tree assemblages may reflect phylogenetic composition (Chazdon et al., 2003; Sodhi et al., 2008), however, due to clear taxonomic evidence, we did not statistically address phylogenetic effects as most reproductive traits were independent of taxonomy. For example, (1) species pollinated by vertebrates belonged to five families in four orders and four superordinal clades (*sensu* APG II, 2003), (2) species pollinated by "diverse small insects (DSI)" belonged to 19 families in 13 orders and eight superordinal clades, and (3) species with inconspicuous/open flowers belonged to 25 families in 14 orders and 10 superordinal clades. In addition, none of these families were exclusive of any given type habitat, and the vast majority (76%) of the 120 tree genera recorded were monotypic (15.83% were represented by two species) which further reinforces the small relevance of phylogenetic analyses. In sum, the patterns documented in our landscape cannot be explained by trait-based phylogenetic clustering as argued by Girão et al. (2007).

2.6. Data analysis

The variation in the proportion of species and individuals within different reproductive trait categories, and in the functional diversity of pollination systems were examined using the following complementary approaches. First, between-habitat differences were tested using one-way ANOVAs followed by Tukey post-hoc comparisons. Second, general linear models (GLMs) were used to confirm the effects of habitat type and examine the additional effect of plot distance to the nearest edge considering all 55 plots across the four habitats. Prior to these analyses, percentages of species and individuals (dependent variables) were arcsine-transformed in order to stabilize variance, improve normality, and

consequently increase the explanatory power of models; distance to forest edges was \log_{10} -transformed. Normality of all response variables were verified using Lilliefors tests and analyses were carried out using the Statistica package.

To test the hypothesis that tree assemblages in forest edge and small fragment plots were functionally more similar to those of second-growth patches than those in the forest interior of the largest fragment, we performed non-metric multidimensional scaling (NMDS) ordinations of all 55 plots using an Euclidean similarity matrix of trait composition (Krebs, 1989). Two ordination plots were performed (Primer package) based on either the proportion of individuals or of species within reproductive trait categories.

3. Results

3.1. Reproductive signature of tree assemblages

In general, the distribution of reproductive traits differed widely across tree assemblages in different habitats, with four main patterns emerging. First, tree assemblages in forest edges, second-growth patches, and small forest fragments (hereafter, altered habitats) were markedly different from those in forest interior plots; significant differences were evident in 31–57% of the 35 categories of reproductive traits examined, considering the number of both species and individuals (Table 2; Figs. 2–4). Second, altered habitats were very similar to one another since forest edges did not differ from second-growth patches in terms of the proportion of species within trait categories and second-growth patches differed from forest fragments in only 5.7% of the

traits (two categories, Table 2). Third, forest edge and forest interior plots were most dissimilar to one another, despite the fact that these two habitats were embedded within the same large fragment (Coimbra Forest) and separated by relatively short distances. Fourth, across-habitat differences were far more evident in terms of numbers of individuals within reproductive trait categories (habitats differed in 46–57% of the 35 categories considered; Figs. 2B, 3 and 4) than in terms of numbers of species (31–40%).

Considering reproductive traits individually, altered habitats and forest interior areas differed in nearly half of all pollination system categories (Fig. 2). In terms of species, the most conspicuous differences can be summarized in four points: (1) altered habitats exhibited an increase of up to 60% in the proportion of tree species pollinated by diverse small insects (DSI) in comparison with forest interior areas; (2) plants pollinated by non-flying mammals were conspicuously absent from forest edges, and only occurred in the other altered habitats at frequencies 2–30 fold lower than in forest interior areas; (3) altered habitats also showed significantly lower frequencies of bird-pollinated trees; and (4) pollination by vertebrates as a whole (birds, bats, and non-flying mammals) decreased dramatically in all altered habitats (Fig. 2A). The proportion of individuals within different categories of pollination systems exhibited similar trends (Fig. 2B), but by pooling all pollination categories into two broader categories of pollen vectors, the proportion of individuals pollinated by generalist vectors in forest edges ($51.71 \pm 6.85\%$), second-growth patches ($61.08 \pm 6.51\%$), and small forest fragments ($73.05 \pm 2.46\%$) was higher than in forest interior areas ($45.82 \pm 2.89\%$; $F = 4.67$; $P = 0.006$).

Table 2
Percentage of tree species (mean \pm SE) within major classes of reproductive traits (except for pollination systems in Fig. 2A) in 55 0.1-ha plots located along forest edges, and in small forest fragments, second-growth patches, and core forest interior areas at Usina Serra Grande, northeastern Brazil (data on the reproductive traits for the species are available upon request).

Reproductive traits (% species)	Forest edges	Second-growth	Forest fragments	Forest interior	ANOVA	
	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	F	P
<i>Floral sizes (N = 110)</i>						
Inconspicuous	46.96 \pm 2.62	48.25 \pm 4.31	40.84 \pm 2.82	37.26 \pm 3.20	1.94	0.134
Small	18.90 \pm 3.50	18.57 \pm 2.77	23.84 \pm 1.52	24.60 \pm 3.36	1.93	0.136
Medium	24.17 \pm 1.55a	16.96 \pm 3.32ab	15.01 \pm 2.15ab	10.45 \pm 1.52b	2.93	0.042
Large	1.14 \pm 0.76a	5.75 \pm 2.06ab	1.77 \pm .066a	6.33 \pm 1.46b	5.036	0.004
Very large	8.83 \pm 2.24a	10.47 \pm 2.43a	18.54 \pm 1.89bc	21.37 \pm 1.38c	6.59	0.001
Inconspicuous + small	65.86 \pm 2.95	66.82 \pm 3.53	64.68 \pm 2.99	61.86 \pm 1.45	0.46	0.707
Medium + Large + Very large	34.14 \pm 2.95	33.18 \pm 3.53	35.32 \pm 2.99	38.14 \pm 1.45	0.46	0.707
<i>Floral resources (N = 127)</i>						
Nectar	49.88 \pm 2.42ab	40.45 \pm 4.46a	66.04 \pm 1.90c	64.97 \pm 2.20bc	13.93	< 0.0001
Pollen	24.14 \pm 2.97a	23.70 \pm 3.44ab	12.39 \pm 1.13b	16.89 \pm 2.56ab	3.13	0.033
Oil	10.62 \pm 1.39	7.32 \pm 1.43	6.04 \pm 0.64	7.36 \pm 3.24	1.7	0.161
Nectar/pollen	12.68 \pm 2.15a	14.54 \pm 2.78a	9.56 \pm 1.14a	3.16 \pm 1.04b	5.14	0.003
Others	2.69 \pm 1.15	13.98 \pm 6.96	5.97 \pm 1.27	7.61 \pm 1.28	1.48	0.231
<i>Floral types (N = 119)</i>						
Inconspicuous	34.14 \pm 3.16	42.13 \pm 4.69	39.33 \pm 3.46	30.10 \pm 2.76	1.54	0.213
Open/dish	25.11 \pm 1.58a	26.12 \pm 3.51ab	20.21 \pm 1.73ab	13.75 \pm 1.58b	2.71	0.055
Flag	3.91 \pm 1.33a	3.65 \pm 1.11a	5.11 \pm 1.18ab	10.99 \pm 1.82b	3.55	0.021
Brush	12.50 \pm 2.83ab	8.91 \pm 2.06a	10.28 \pm 1.74a	21.80 \pm 2.51b	4.12	0.011
Tube	7.46 \pm 1.59ab	5.72 \pm 3.26a	5.48 \pm 0.90ab	11.18 \pm 1.90b	2.7	0.05
Others	16.87 \pm 2.10	13.47 \pm 2.68	19.59 \pm 2.00	12.18 \pm 1.28	1.99	0.127
Inconspicuous + open	59.26 \pm 2.33ab	68.25 \pm 4.04a	59.54 \pm 2.80a	43.85 \pm 2.12b	7.34	< 0.0001
All non-inconspicuous/open	40.74 \pm 2.33ab	31.75 \pm 4.04a	40.46 \pm 2.80a	56.15 \pm 2.12b	7.34	< 0.0001
<i>Anthesis (N = 140)</i>						
Diurnal	95.63 \pm 1.94a	92.35 \pm 2.39a	92.31 \pm 1.29a	81.86 \pm 2.07b	6.38	0.001
Nocturnal	4.37 \pm 1.94a	7.65 \pm 2.39a	7.69 \pm 1.29a	18.14 \pm 2.07b	6.38	0.001
<i>Sexual systems (N = 141)</i>						
Hermaphrodites	72.14 \pm 4.35	59.43 \pm 5.15	67.59 \pm 2.34	60.31 \pm 2.19	2.36	0.084
Monoecious	8.81 \pm 1.71	8.85 \pm 2.36	6.61 \pm 1.35	6.89 \pm 1.14	0.647	0.598
Dioecious	19.05 \pm 3.17	31.72 \pm 5.30	25.80 \pm 1.61	32.80 \pm 1.80	2.66	0.058
All non-hermaphrodites	27.86 \pm 4.35	40.57 \pm 5.15	32.41 \pm 2.34	39.69 \pm 2.19	2.34	0.084

Significant differences in Tukey post-hoc comparisons between-habitat types are indicated by different letters in the same row.

The proportion of tree species within different floral size categories was, in general, similar across the habitats, despite a clear trend of reduced proportion of large and very large flowered species in altered habitats (Table 2). The same trend emerged in terms of individual-based abundances (Fig. 3A). This becomes even more apparent when we collapsed the five flower size categories into two [i.e. inconspicuous/small, and medium/large/very large]. Individuals with inconspicuous/small flowers predominated in altered habitats, whereas medium/large/very large flowered individuals predominated in forest interior areas ($F = 5.63$; $P = 0.002$; Fig. 3A). In relation to floral resources, the most prominent result was the elevated abundance of both species and individuals (Fig. 3B; $F = 4.736$; $P = 0.005$; Table 2) bearing nectar/pollen flowers, which were at least three times more common in altered habitats.

Marked differences were also found in terms of floral types (Table 2; Fig. 3C). The most prominent trend was the reduced proportion of stems bearing flag, brush, or tube flowers in altered habitats (Fig. 3C). Collapsing the six categories of floral types into only two classes of resource accessibility [(1) easily accessible resources, including inconspicuous and open/dish flowers and (2) concealed resources, including all other floral types] a clear pattern emerged: inconspicuous/open flowers predominated in terms

of both species (Table 2) and individuals (Fig. 3C; $F = 8.226$; $P < 0.0001$) in altered habitats, whereas the concealed strategy was far more common in forest interior plots. In addition, although all habitats were dominated by tree species bearing diurnal anthesis, nocturnal anthesis was more frequent in forest interior plots (Table 2). Differences were even more marked for individuals bearing nocturnal anthesis: $3.35 \pm 1.82\%$ in forest edges; $9.14 \pm 4.85\%$ in second-growth plots, and $5.75 \pm 1.57\%$ in small fragments (no significant differences among altered habitats), but reached $35.39 \pm 4.18\%$ in forest interior areas ($F = 17.057$; $P < 0.0001$). In sum, altered habitats, particularly forest edges, were clearly dominated by species and individuals bearing reproductive traits associated with pollination by generalist vectors (e.g. inconspicuous/open flowers, offering pollen/nectar resources that are easily accessible to visitors), and generalist pollination systems (e.g. diverse small insects, *sensu* Kang and Bawa, 2003). In contrast, forest interior plots were dominated by trees bearing more specialized reproductive traits (e.g. floral types other than inconspicuous/open flowers, offering resources that were at least partly concealed) and pollinated by specialist pollen vectors (e.g. flying and non-flying vertebrates, *sensu* Kang and Bawa, 2003).

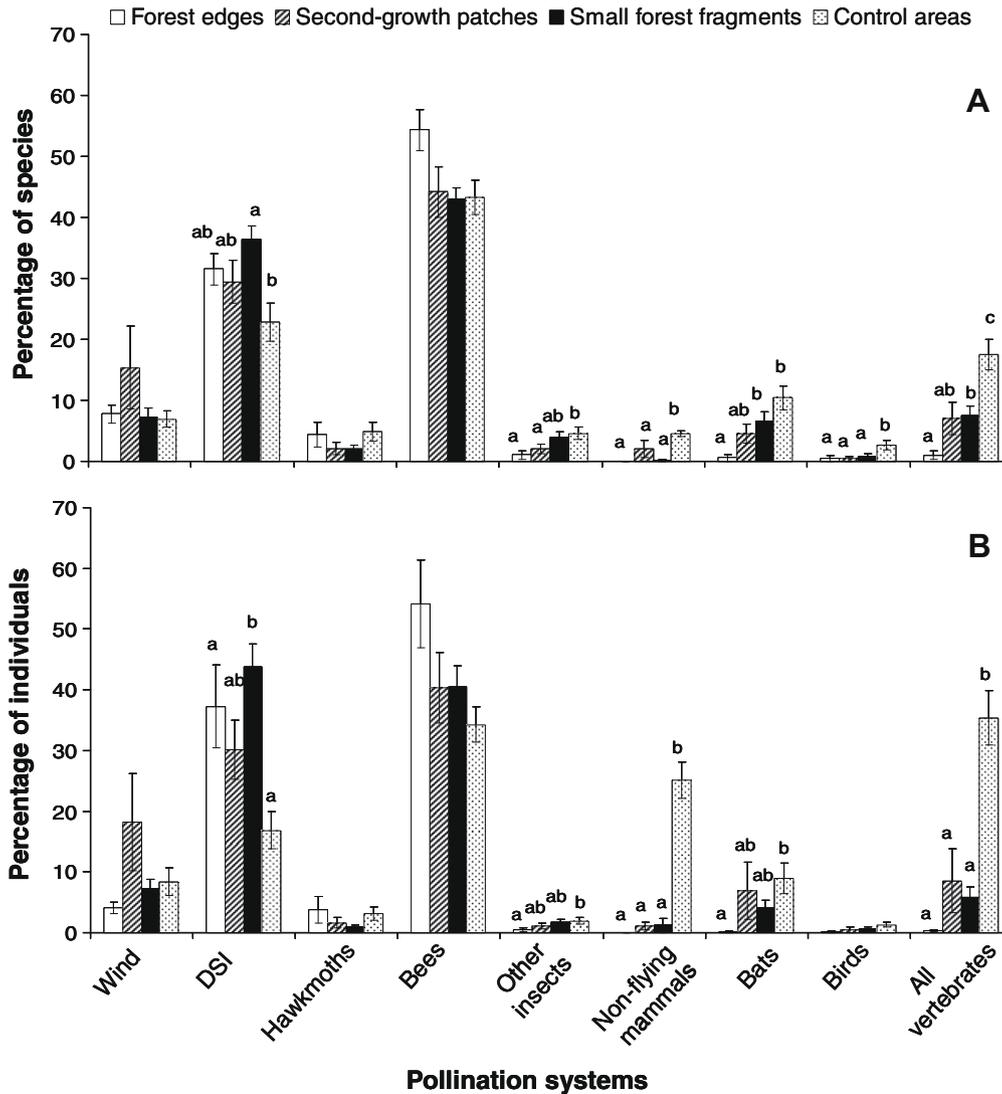


Fig. 2. Percentage (mean \pm SE) of tree species (A; $N = 138$ species) and individuals (B) within categories of pollination systems within 55 plots located along forest edges, and in second-growth patches, small forest fragments, and core forest interior at Usina Serra Grande, northeastern Brazil. Frequencies for each habitat type are represented by bars. Tukey post-hoc comparisons (following ANOVAs), testing for between-habitat differences, are indicated by letters above the bars.

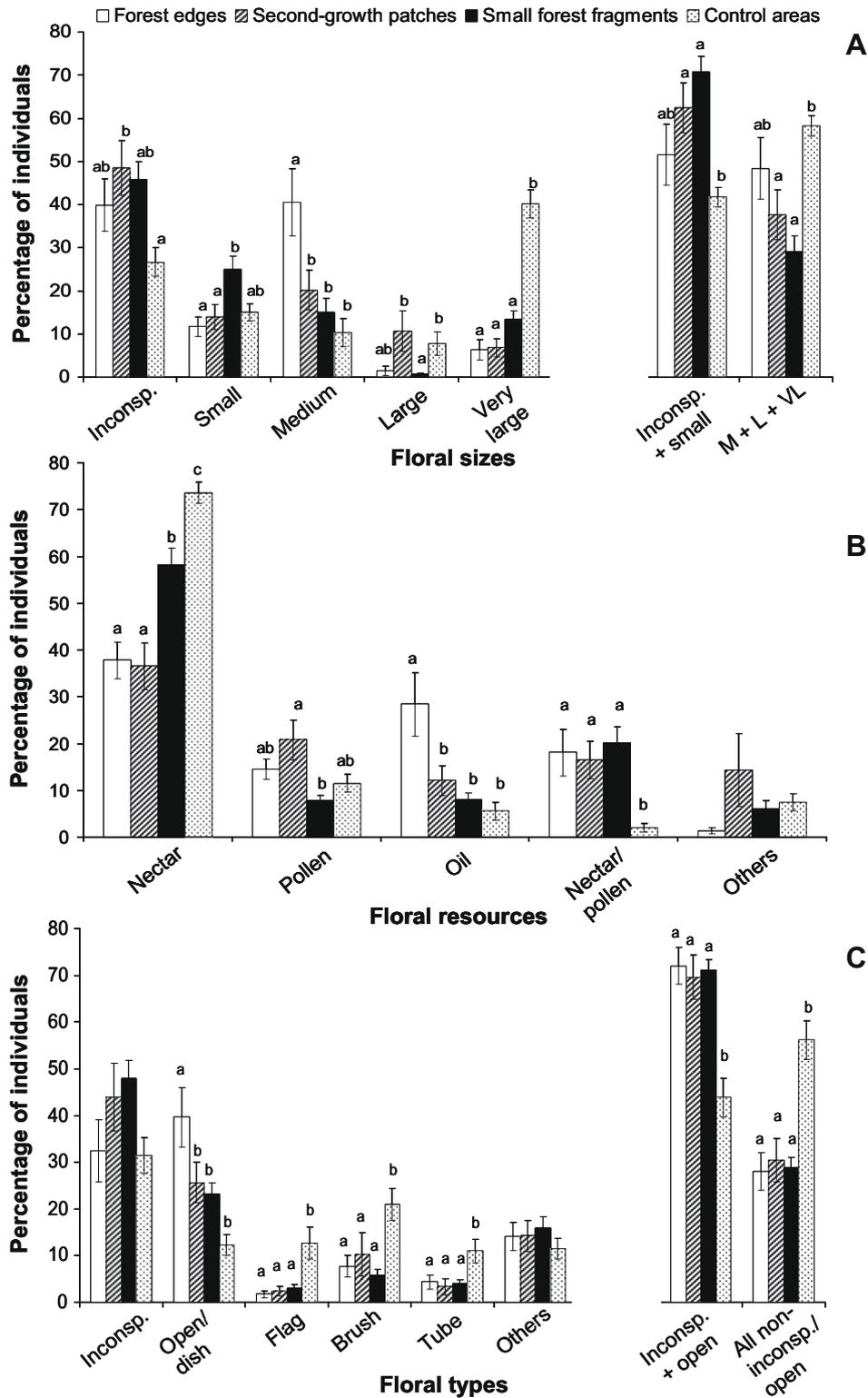


Fig. 3. Percentage of individual trees (mean \pm SE) within categories of floral sizes (A; $N = 110$ species), floral resources (B; $N = 127$ species), floral types (C; $N = 119$ species), and sexual systems (D, $N = 141$ species) in 0.1-ha plots ($N = 55$ plots) located along forest edges, and in second-growth patches, small forest fragments and core forest interior, at Usina Serra Grande, northeastern Brazil. Frequencies for each habitat type are represented by bars. Tukey post-hoc comparisons (following ANOVAs), testing for between-habitat differences, are indicated by letters above the bars.

Hermaphroditism was the most frequent sexual system among tree species and prevailed in all habitat types (Table 2). However, reproductive trait distribution based on individuals showed that non-hermaphrodite systems were prevalent in core areas of forest interior which differed greatly from altered habitats ($F = 4.84$;

$P = 0.005$), in which hermaphroditic individuals accounted for up to 75% of all stems (Fig. 3D). Accordingly, GLMs clearly identified habitat type and distance to forest edges as the most important explanatory variables driving the reproductive signature of tree assemblages. Collectively, these variables explained between

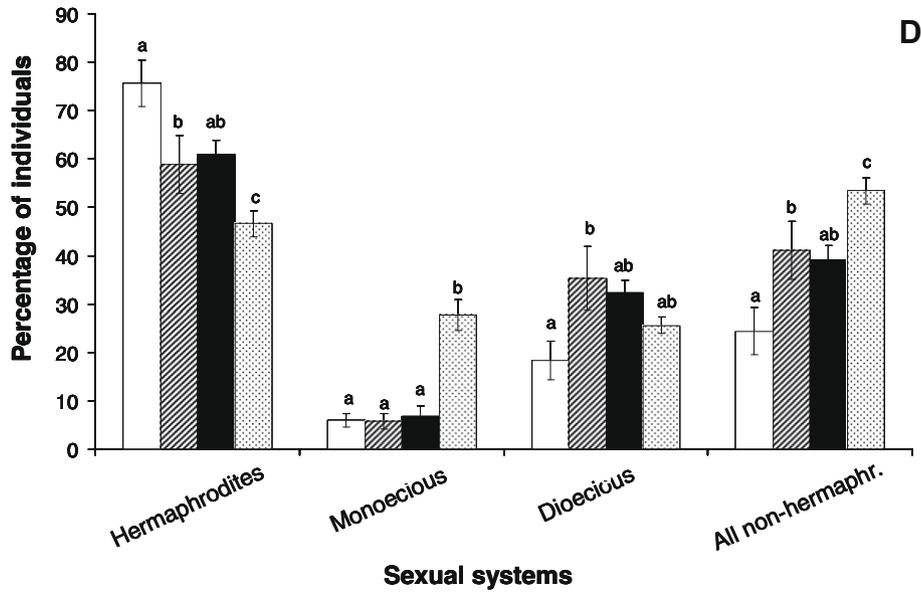


Fig 3. (continued)

18.6% and 81.2% of the variation in the proportion of individuals within 86.4% of the reproductive categories examined ($P < 0.05$ for the whole model and explanatory variables). Considering species occurrences, these variables explained 17.5–48.6% of the variation in 78.3% of categories. In particular, we noted that even tree assemblages located >300 m from the nearest forest edge can exhibit a distorted distribution of reproductive traits in forest fragments. Additionally, a Mantel test failed to uncover any spatial effects on the taxonomic similarity among plots ($Rho = -0.157$; $P = 0.85$). Finally, NMDS ordination of tree plots based on functional similarity (i.e. proportion of traits) resulted in two consistent and clearly segregated clusters: one formed by the 10 forest interior plots, and another formed by the plots in forest edges, small fragments, and second-growth patches (Fig. 4). This pattern emerged for both individuals and species, and plot ordination was well supported by low stress levels of 0.1 and 0.12 (Fig. 4).

3.2. Functional diversity of pollination systems

Regardless of the metric used here, functional diversity of pollination systems gradually decreased from forest interior to forest edge plots (Fig. 5). Using a Shannon metric based on the number of tree species within pollination system categories, functional diversity declined by up to one third (Fig. 5A). On the basis of individuals, altered forest habitats were even less functionally diverse than forest interior plots – pollination systems in small forest fragments and along forest edges were, respectively, up to 31.9% and 46.7% less diverse than those of core forest plots (Fig. 5B). The Simpson’s metrics detected essentially the same trends, although the reduction in functional diversity, which was up to one third along forest edges, was in general less pronounced than that detected by the Shannon metric (Fig. 5C and D).

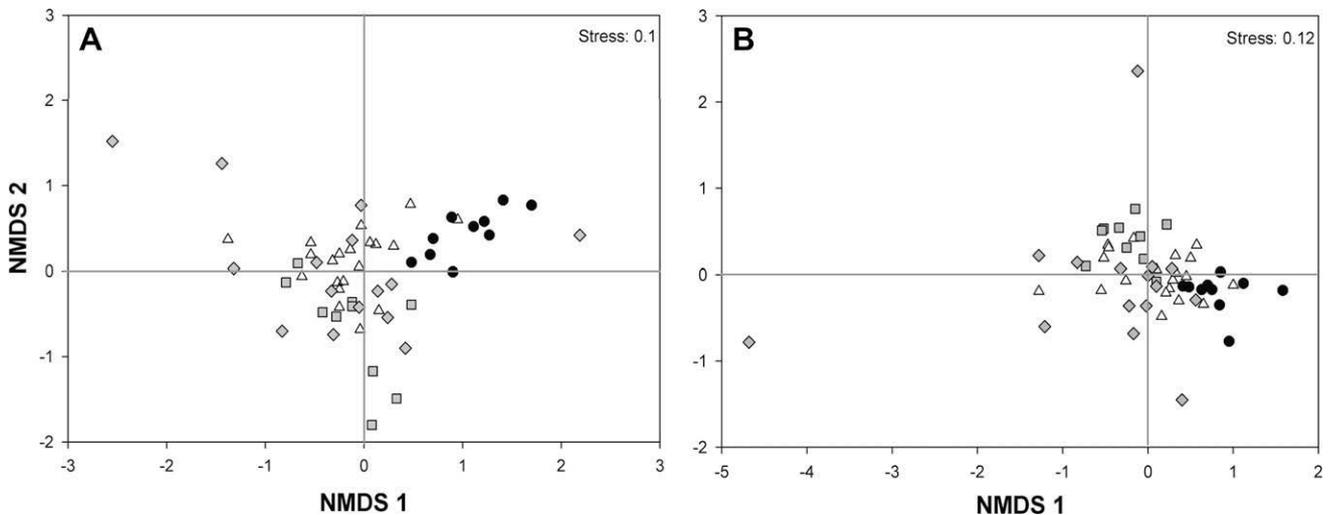


Fig. 4. NMDS ordination of 55 plots based on their similarity in reproductive traits in terms of either (A) individuals or (B) species, at Usina Serra Grande, northeastern Brazil. Open triangles, grey squares, grey diamonds and black circles represent plots in small fragments ($N = 20$), forest edges ($N = 10$), second-growth patches ($N = 15$), and core areas of forest interior ($N = 10$), respectively.

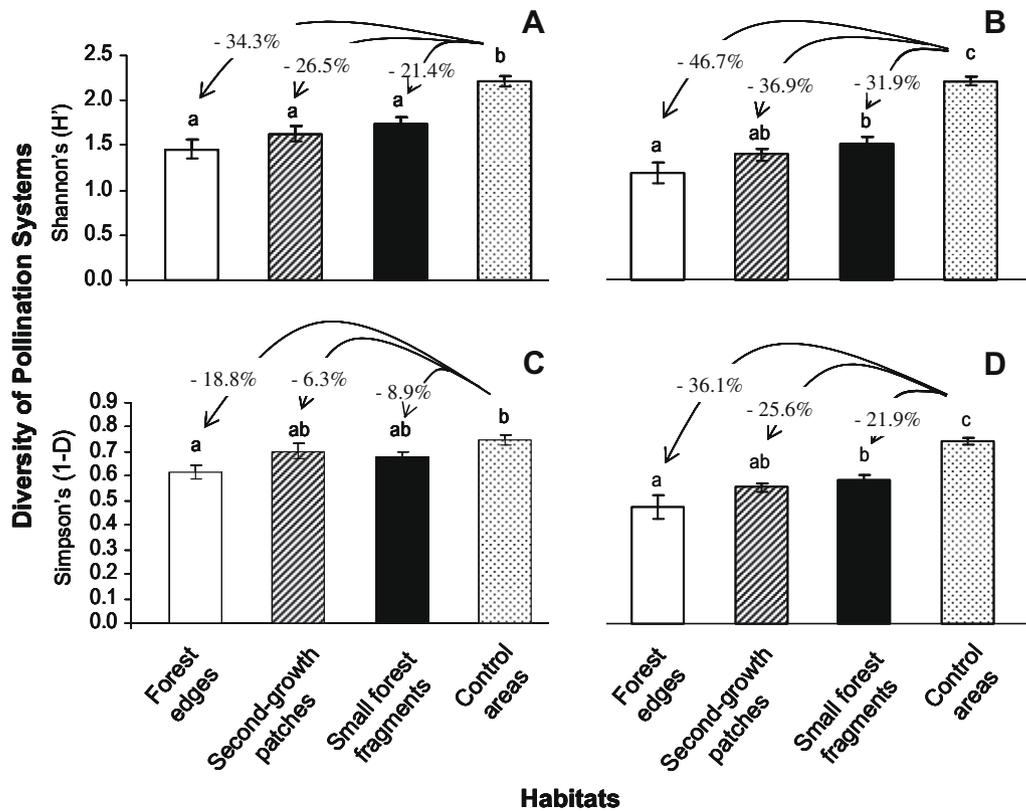


Fig. 5. Functional diversity (mean \pm SE) of pollination systems in tree assemblages within the 55 plots located along forest edges, and in second-growth patches, small forest fragments, and core forest interior, at Usina Serra Grande, northeastern Brazil. Diversity was calculated based on species within categories (A,C) and individuals within categories (B,D). Arrows indicate reductions in diversity by comparing core forest interior vs. altered habitats. Between-habitat differences, tested by Tukey post-hoc comparisons (following ANOVAs), are indicated by letters above the bars ($P < 0.0001$ in A, B, and D; $P = 0.008$ in C).

4. Discussion

4.1. Patterns and underlying mechanisms

Our results reveal a marked shift in the spectrum of reproductive strategies of tree assemblages in edge-dominated small forest fragments that have been embedded in a stable hyper-fragmented landscape of the Brazilian Atlantic forest for as long as 200 years. These shifts were clearly observed at the level of both individual and species occurrences, and tree assemblages in small fragments and along the edges of a large forest remnant were much more similar to those in early-secondary forest stands (5–32 years old) than to core forest interior areas showing no detectable edge influence. Such altered habitats were considerably impoverished in terms of tree species bearing certain pollination systems (e.g. pollination by vertebrates); exhibited a distorted profile of tree species bearing reproductive traits associated with easily accessible floral resources presented to diurnal, generalist vectors (*sensu* Kang and Bawa, 2003); and an increased abundance of hermaphroditic trees. This depauperated and distorted distribution of tree guilds resulted in reduced functional diversity of pollination systems, although altered habitats still retained all traits observed in core forest interior tree assemblages. Habitat type and plot distance to the nearest edge consistently emerged as the most important explanatory variables for the relative abundance of tree reproductive traits. This provides clear evidence that creation of forest edge drives the shifts documented here in the reproductive signature of tree assemblages in our aging, hyper-fragmented landscape.

Overall, our findings largely confirm the patterns recently documented in the Serra Grande landscape (see Girão et al., 2007),

which reported reduced diversity of pollination systems in small fragments and misrepresentation of reproductive traits associated with pollination mediated by specialist pollen vectors. However, we extend the ecological generality of these patterns by documenting similar (and more drastic) changes along the edges of the Coimbra Forest, and the magnitude of this community-wide functional depauperation process in terms of trait convergence among forest edges, small forest fragments and early-secondary forest patches (see also Chazdon et al., 2003). Moreover, we offer empirical evidence supporting the general notion that plant–pollinator interactions are largely vulnerable in fragmented forest landscapes (Rathcke and Jules, 1993; Aizen and Feinsinger, 1994; Murcia, 1996; Kearns et al., 1998; Renner, 1998; Harris and Johnson, 2004; Aguilar et al., 2006; Sodhi et al., 2008) by revealing, for example, that vertebrate-pollinated tree species are virtually extirpated over many decades in edge-affected habitats.

Furthermore, our findings further support the recent hypothesis of “fragmentation-induced degeneration of tree assemblages” (*sensu* Santos et al., 2008), which postulates a forest degeneration process or a retrogressive succession triggered by the creation of forest edges. Over time, tree assemblages are expected to retain gradually fewer species, life-history traits and lower biomass, resulting in assemblages that are functionally analogous to those of early-secondary forests. This degeneration hypothesis was proposed by documenting a reduced species richness of large-seeded, emergent and shade-tolerant trees; and a hyper-abundance of short-lived pioneers in the same altered habitats examined in this study. In this context, our results suggest that plant assemblages in forest edges and small forest fragments are depauperated in terms of key reproductive traits and face reduced functional diversity (see also Laurance et al. (2006a) and Girão et al. (2007)). In fact,

the fragmentation-induced degeneration process (*sensu* Santos et al., 2008) may represent a much more predictable and pervasive simplification of tropical tree assemblages.

Proliferation of pioneer species, a sharp decrease of shade-tolerant trees, and reduced reproductive fitness due to pollination limitation in forest edges and small fragments remain the best candidates to explain the marked shifts in the abundance of reproductive traits in these habitats (Aguilar et al., 2006; Girão et al., 2007). Pioneer proliferation and collapse of shade-tolerant trees in fragmented landscapes is now a well documented pattern in several neotropical forests (Tabarelli et al., 1999, 2008; Laurance et al., 2006a, b; Michalski et al., 2007). In our landscape, short- and long-lived pioneer species represent a multitaxa functional group [16 orders and eight supraordinal clades *sensu* APG II (2003)], accounting for over 70% of all tree species and individuals occurring in altered habitats, but fewer than 30% in core areas of the Coimbra Forest (Oliveira et al., 2004; Grillo, 2005; Santos et al., 2008). Although a robust analysis is unfeasible due to the relatively small number of tree species in our dataset, simple pairwise comparisons between pioneer and shade-tolerant species revealed a lower incidence of pollination by vertebrates, nocturnal anthesis, and hidden-resource flowers among pioneers (A.V. Lopes et al., unpublished data). Additionally, some pollination systems, such as pollination by beetles, hawkmoths, and non-flying mammals, were missing entirely from the pioneer species addressed in this study. This provides weak but informative evidence that reproductive traits are not equally distributed among pioneers, regardless of whether this reflects either adaptive or phylogenetic constraints (see Turner, 2001; Tabarelli et al., 2008). Local extirpation of shade-tolerant trees and a concomitant proliferation of pioneers may therefore result in detectable shifts in the relative abundance of life-history traits, and consequently severely alter the guild structure of tree assemblages in edge-dominated fragmented habitats. However, this does not rule out the possibility of a negative feed-back process between limited floral resource availability for pollinators and loss of tree reproductive fitness due to pollination limitation, leading to the functional impoverishment of tree assemblages.

4.2. Consequences for biodiversity persistence in fragmented landscapes

Translating the implications of our findings to conservation on the ground can follow several pathways. As many as 98–99% of the flowering plant species in tropical forests (and 97.5% of the trees) rely on animals for pollination (Bawa et al., 1985; Bawa, 1990). This implies that a substantial fraction of the biodiversity in these ecosystems benefits from floral resources via plant–pollinator interaction networks, which have been found to be highly structured (Jordano et al., 2006). Given a lower diversity of pollination systems and a distorted trait distribution favouring tree species and individuals pollinated by diverse small insects, edge-affected habitats are expected to sustain a narrower range of flower-mediated resources. As a consequence, we should expect a bottom-up cascade of population co-declines and co-extinctions among specialized plant consumers (e.g. large insects and vertebrates acting as pollinators, floral robbers/thieves, nocturnal pollinators), and the ensuing simplification of flower-mediated interaction networks (as observed by Fontaine et al., 2006 in simple experimental communities). This could compromise long-distance pollen transfer and gene flow at the expense of self-incompatible plant species.

Protected areas remain a crucial tool for biodiversity conservation, but their limited coverage has led to a growing interest in the conservation value of anthropogenic landscapes (e.g. Barlow et al., 2007). Studies in several fragmented landscapes have documented congruent patterns of biodiversity erosion marked by local-

and landscape-level extirpation of tree species within particular functional groups: large-seeded species (Santos et al., 2008), emergent and large canopy trees (Laurance et al., 2000), shade-tolerant (Tabarelli et al., 1999) and heavy-wooded trees (Michalski et al., 2007), epiphytic species (Sodhi et al., 2008), species pollinated by specialist pollen vectors such as mammals (Girão et al., 2007; Sodhi et al., 2008), and self-incompatible trees (Laurance et al., 2006a; Girão et al., 2007). Collectively, this rather predictable erosion of tree diversity (see Tabarelli et al., 2004) and the profound shifts in the functional signature of tree assemblages, raise serious doubts over the effectiveness of conservation services provided by edge-dominated habitats, which account for the vast majority of both relic and restoration forest habitat in hyper-fragmented landscapes (Tabarelli and Gascon, 2005). This is particularly the case of the Atlantic forest since most of its original distribution (1.5 million km²) has been converted into archipelagos of small forest remnants (Silva and Casteleti, 2003). By retaining only edge-affected habitats, severely fragmented landscapes face a severe threat in terms of biodiversity loss, which clearly impairs their eligibility as future conservation targets and degrade their potential value in terms of ecosystem services and economic opportunities (*sensu* Zarin, 2004). With low net revenues flowing from edge-affected habitats, opportunity costs for forest protection will tend to increase, thereby weakening the justification to avoid further deforestation in already severely fragmented Atlantic forest landscapes.

Conservation biologists have repeatedly called for regional networks of protected areas that are well connected via narrow forest corridors and immersed in benign matrix to avoid massive species loss. Indeed, the biodiversity corridor concept (Sanderson et al., 2003) is one of the most appealing conservation approaches in tropical forest regions. This is particularly the case of the Atlantic forest, where several regions already lack large core forest areas and remaining forest fragmented are fairly isolated (Ribeiro et al., 2009). However, corridors consisting largely or entirely of edge-affected habitat cannot retain a full complement of life-history traits in plant communities and consequently the plant–animal interaction webs they support. Large blocks of core primary forest habitat therefore remain an irreplaceable target for achieving biodiversity conservation in tropical forests, and every effort should be made to prevent rather than repair the ravaging effects of hyper-fragmented landscapes.

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Appendix A. Supplementary Material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2009.01.007](https://doi.org/10.1016/j.biocon.2009.01.007).

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