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Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest

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ABSTRACT

In this paper, we test the hypothesis that seed rain in forest edges differs from that in forest interior in terms of seed abundance, species richness, seed size, dispersal mode, and manipulation by vertebrates. The study was carried out in the Coimbra forest (3500 ha), the largest fragment currently found in the Atlantic forest of northeast Brazil. We assessed seed rain during a 1-year period by using a 1500-m long transect (with 100 sampling units) for each habitat. Seeds were categorized according to size, dispersal mode, and vertebrate manipulation. A total of 76,207 seeds belonging to 146 species were collected during the whole study and in average edge received more seeds and species per unit of area during particular periods of time. However, the analysis of all seeds and species recorded in both habitats during the 1-year period revealed that forest interior received a significant higher percentage of medium, large and very large seeds (21.8%) and species (82.6%) in comparison to edge (13.5% of seeds and 57.5% of species). The contribution of large and very large seed species dispersed by vertebrates was also lower in the edge forest as it represented 13.04% of all vertebrate-dispersed species recorded in this habitat vs. 31.5 % in the forest interior. Finally, seeds handled by vertebrates accounted for 5.9% of all seeds in forest edge, and reached 11% in the forest interior. The biased seed rain documented in the Coimbra forest raises the possibility that the creation of forest edges may alter some attributes of seed rain, particularly its content of large-seeded plants and of those dispersed by vertebrates.

1. Introduction

Habitat loss and fragmentation are omnipresent processes in tropical forests and represent the most serious threats to the biodiversity in these ecosystems (Laurance et al., 2002). In the case of mature forest tree species, threats to the long-term persistence of populations in fragmented landscapes result from direct processes, such as greater exposure to wind leading to higher tree mortality and damage (Laurance et al., 2000), as well as from more complex and indirect processes such as those resulting from disruptions of trophic-interactions. For example, Terborgh et al. (2001) showed that seedling density of canopy trees is reduced in forest fragments in response to a high abundance of both vertebrate herbivores and seed predators driven by the local extirpation of top predators. This is a higher-order effect of habitat fragmentation marked by the ecological release of herbivores and seed predators, i.e. relaxation of top-down controlling forces.

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Several threats to trees, operating at local and regional scales, result from the creation of forest edges and the consequent physical and biotic changes faced by fragments – the edge effects (*sensu* Bierregaard et al., 2001). Forest fragmentation and its edge effects (1) reduce plant recruitment due to desiccation and seedling damage caused by increased litterfall and treefall near forest edges (Benítez-Malvido, 1998; Bruna, 1999; Laurance, 2001); (2) increase sapling mortality due to competition with lianas, vines and ruderal species that become abundant in edges (Scariot, 2001); and (3) increase adult mortality due to physiological stress, and elevated rates of uprooting and breakage near forest edges (Laurance et al., 1998, 2000). Acting in concert, these processes are likely to promote local and regional extinction of tree species (Tabarelli et al., 2004), as well as the establishment of biased and impoverished plant assemblages in forest edges and small fragments (Laurance, 2001; Benítez-Malvido and Martínez-Ramos, 2003; Oliveira et al., 2004).

Some attention has been given to the impact of habitat fragmentation on seedling recruitment (see Benítez-Malvido and Martínez-Ramos, 2003) as seedling is the life stage most strongly affected by habitat desiccation promoted by the creation of forest edges, with detectable impacts on seedling abundance. However, depletion of seedling abundance may result from the scarcity of particular types of seeds due to disruptions in the seed dispersal process; i.e. changes in spatial patterns of seed delivery. For instance, extirpation of large primary forest trees by elevated rates of uprooting and breakage may depress or at least drastically alter both the taxonomic and ecological composition of autochthonous seed rain in forest edges. Even changes in allochthonous seed rain are possible in the case habitat loss and fragmentation, usually associated with hunting, deplete the abundance of vertebrate seed dispersers and consequently the rates of seed delivery (Cordeiro and Howe, 2001, 2003; Chapman et al., 2003; Melo and Tabarelli, 2003).

Therefore, forest edges and small fragments may become an inaccessible habitat for particular types of seeds and their emerging seedlings as fragments become older, dominated by small-seeded pioneers and lack frugivorous vertebrates. Reduction in seedling abundance driven by disruptions on seed rain receives support from the fact that allochthonous seed rain or actively dispersed seeds (i.e. seeds not simply dropped beneath the parent crown) can account for up to 68% of seedling recruitment of tree species (Webb and Peart, 2001). In fact, disruptions on seed rain may be particularly critical for large-seeded trees because their persistence at any spatial scale usually relies on prompt germination of actively dispersed seeds (Alvarez-Buylla et al., 1996; Loiselle et al., 1996; Peña-Carlos and de Boo, 2002).

At present, the Atlantic forest of northeast Brazil has reached a high level of degradation as its continuous tracts of habitat have been converted into human-dominated landscapes in which only archipelagos of small fragments persist (Tabarelli et al., 2003a). Based on the size and shape of the fragments, most of the remaining forest should be assigned as forest edge habitat even if we conservatively assume that edge effects penetrate only 50 m into forest fragments (Ranta et al., 1998). Furthermore, key vertebrate seed dispersers such as howler monkeys and guans are almost extinct in the entire region as a consequence of both habitat loss and hunting (Almeida et al., 1995; Silva and Tabarelli, 2000). This combination of human-driven disturbances makes reasonable to expect drastically changes in patterns of seed rain including changes in its taxonomic and ecological composition, such as the relative contribution of seeds within classes of size and dispersal mode.

In this paper we test the hypothesis that seed rain in forest edges differs from that in forest interior in a large fragment of the Brazilian Atlantic forest in terms of seed abundance, species richness and percentage of seeds within different categories of size, dispersal mode and manipulation by vertebrates. First, we describe seed rain for the whole fragment and the scores of seed abundance and species richness for each habitat throughout a 1-year period. Second, we document significant relationships between habitat and (1) abundance of large-seeded species; (2) dispersal mode; and (3) rates of seed handling by vertebrates. Finally, we address fragmentation-related processes which are expected to drive changes in the nature of seed rain.

2. Methods

2.1. *Study site*

The study was carried out at Usina Serra Grande (9°S,35°52′W), a 200 km^2 private property located in the State of Alagoas, northeast Brazil (Fig. 1A). The study site is located on low elevation plateaus (500–600 m a.s.l.), where predominant soils are latosols and podzols (IBGE, 1985). The climate is tropical, with a 3-month dry season (<60 mm per month). The annual rainfall is around 2000 mm, with the wettest period occurring between April and August. The vegetation can be classified as lower montane rain forest, one of the Brazilian Atlantic forest types that occur at 100–600 m altitude (Veloso et al., 1991). Regionally, Leguminosae, Lauraceae, Sapotaceae and Chrysobalanaceae are the most species-rich plant families in this type of forest (Tavares et al., 1971). The Usina Serra Grande retains some 9000 ha of forest comprised by dozens of fragments, ranging from 1 to 3500 ha in size, all of them completely surrounded by sugar-cane fields.

The seed rain assessment was carried out in the Coimbra forest – a 3500-ha fragment with 39 km of perimeter. We opted for this fragment due to the following reasons. First, Coimbra is one of the largest and well preserved forest remnants currently found in this region, and it supports several large-seeded tree species, which have almost disappeared in the entire region (Oliveira et al., 2004). Second, some vertebrates able to disperse large seeds, such as agoutis, pacas, toucans and guans, are still present in Coimbra (Pimentel and Tabarelli, 2004). Third, Coimbra is an old fragment (at least 60-years old), currently lacking any large-scale human disturbance. Its 39 km of borders are now sealed by dense second-growth vegetation what provides an interesting site for assessing some of the long-term effects resulting from creation of forest edges. Finally, several investigations focused on seed rain and seedling recruitment have been carried out in Coimbra (Melo, 2004; Oliveira, 2003; Pimentel and Tabarelli, 2004), which provided a good knowledge base about seed identity. Based on these studies we have: (1) identified 630

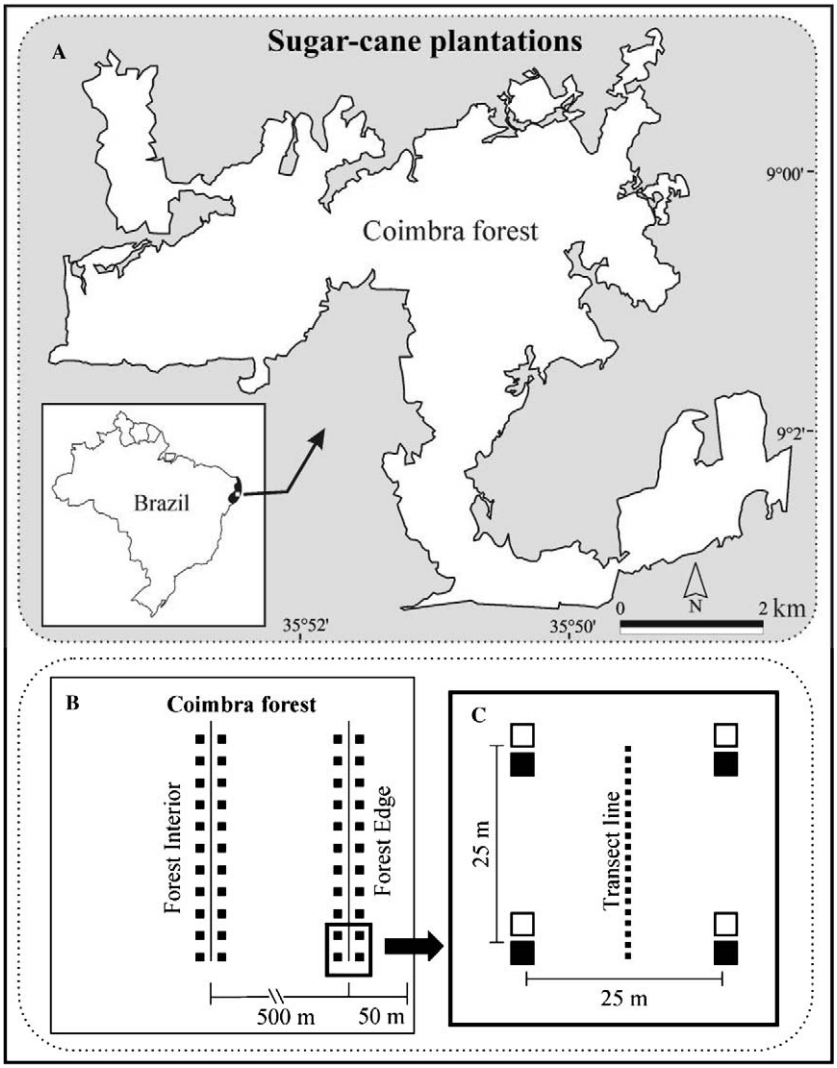

Fig. 1 – (A) Location of the study site Coimbra forest (3500 ha) at Usina Serra Grande, Brazil. (B) Schematic figure showing the experimental design used to assess the seed rain in the Coimbra forest. Both scale and shape of the fragment are illustrative as well as the location of transects within it. (C) Location of the sampling units within transects. In detail: shaded quadrants correspond to seed traps and empty quadrants to ground plots.

vascular plant species (including 218 trees and 58 lianas and climbers); (2) stored 1,180 vouchers at the Herbário da Universidade Federal de Pernambuco (UFP Herbarium – vouchers no. 34,445–38,904); and (3) established a fruit/seed collection with 172 samples and more than 400 digital photos (M.A. Oliveira, pers. comm.). Detailed information on forest structure and plant species composition of Coimbra forest is available in Oliveira et al. (2004).

2.2. *Seed rain assessment*

In order to assess the nature of the seed rain in forest edge and forest interior we used a 1500-m long transect for each habitat. One hundred sampling units were set within each transect and the sampling unit consisted of one 1-m^2 seed trap plus one 1-m^2 ground plot. Seed traps were made of 1×1 m plastic mesh net (1 mm aperture) with its border trussed by wire to maintain its shape. Traps were fixed to four neighbour stems at 1.2 m above the ground. Ground plots were set about two meters apart from each seed trap and demarcated by four wood stakes fixed at the corners of the plot. These ground plots were used exclusively to record large and very large seeds (>15-mm length) from shrubs smaller than 1.2-m height and those seeds discarded by terrestrial seed dispersers (e.g. scatterhoarding rodents). Because of this, we did not take into account very small, small and medium-sized seeds from ground plots. Along transects, sampling units were set 25-m apart: one unit on the right and another on the left side of the transect as showed in the Fig. 1B and C. As we avoided treefall gaps and inaccessible steep slopes, some sampling units were located more than 25 m apart. This procedure resulted in 100 sampling units (50 on the right and 50 on the left side of each transect), and a total sampling effort of 100 m^2 per habitat.

Transects were placed: one parallel to and 50 m distant from the fragment border (forest edge), and another >500 m distant from the fragment border (forest interior). Transect location was based on Laurance et al. (2002), who demonstrated that all 36 edge effects identified by the Biological Dynamics of Forest Fragments Project (BDFFP, Manaus, Brazil) penetrate less than 500 m into forest fragments and 50% of them penetrate up to 50 m. We considered a 1500-m long transect suitable to provide a rapid access to the sampling units and appropriate to capture any spatial heterogeneity on seed rain. Independence among sampling units within transects was confirmed by Mantel tests after 10,000 permutations, which did not detect any significant spatial autocorrelation of data in both forest interior ($r_{(A,B)}$ 0.025; $P = 0.538$) and forest edge ($r_{(A,B)} = 0.039$; $P = 0.094$). We used XLSTAT 7.5.3 trial version to execute this analysis.

Seed rain was checked every 15 days during a 1-year period – 24 surveys from October/2002 to September/2003. Seeds were processed according to five steps as follow. First, seeds of all species collected in each sampling unit (traps and ground plots pooled) were counted with exception of the very small seeds (1–3 mm length) found in seed traps, which frequently appeared by thousands within a single trap. As counting such large numbers of very small seeds proved to be impractical we considered a maximum of 300 seeds per trap per survey as previously adopted by Harms et al. (2000). This maximum of 300 seeds, although arbitrarily defined, represented almost 20 times the average seed number per sampling unit per survey – i.e. a 15-day interval. Because of this, such number reasonable described both the magnitude and the relative representation of very small seeded species in the seed rain. Moreover, a maximum of 300 turned our statistical analyses (frequency tests) conservative in detecting differences between habitats with respect to the relative contribution of seeds within categories of size.

Second, seeds were grouped into distinct morphospecies and classified to the finest possible taxonomic level with the help of a local parataxonomist and by comparing fruits/seeds to those available in the seed collection of the UFP Herbarium. Third, seed species were further classified within five classes of seed size: (1) very small 1–3 mm in length; (2) small 3.1–6 mm; (3) medium-sized 6.1–15 mm; (4) large 15.1–30 mm; and (5) very large >30 mm in length as proposed by Tabarelli and Peres (2002). For convenience, we simply refer to seeds within these increasingly larger size-classes as very small, small, medium-sized, large and very large.

Fourth, seed species were classified into two basic categories of primary dispersal mode: (1) vertebrate-dispersed species, or those producing diaspores adhered to a fleshy pulp, aril, or other features typically associated with vertebrate dispersal agents; and (2) species dispersed by abiotic means, or those presenting 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 suddenly bursts open (see van der Pijl, 1982). Classification of seed species into dispersal modes was based on: (1) our own knowledge of the flora recorded with respect to fruit and seed morphology (see Tabarelli and Peres, 2002; Tabarelli et al., 2003b; Oliveira et al., 2004); (2) detailed accounts of species life history traits available in the literature (e.g. Roosmalen, 1985; Lorenzi, 1998; Barroso et al., 1999); and (3) inspection of herbarium specimens and of the fruit/seed collection of the UFP Herbarium. Fifth, seeds from species classified as vertebrate-dispersed were further recognized as handled by vertebrates (i.e. potentially dispersed by mammals or birds) based on two situations: (1) medium-sized, large and very large seeds presenting vertebrate tooth or beak marks; and (2) seeds of any size found in fecal clumps as previously adopted by Hardesty and Parker (2002).

In summary, seed rain was assessed by setting 100 sampling units in forest edge and 100 in forest interior (which were checked via 24 surveys) and seeds were processed according to five steps. By these procedures we estimated parameters of seed rain at two levels. Sampling unit level – average number of seeds and species per sampling unit. Habitat level – total number of seeds and species per habitat within categories of size, dispersal mode, and manipulation by vertebrates. The reasons for adopting these two spatial levels are presented in the item 2.3. Finally, some limitations of our procedures must be informed: (1) we probably failed to identify a few seed species as we grouped together morphologically similar seeds; and (2) we were also unable to assign some seeds at any taxonomic level from species to family because Serra Grande houses more than 900 vascular plants (Pôrto et al., 2006). Although these sources of bias are expected to be similar for both habitats, the absolute numbers of seeds and species, particularly the case of very small seeds, must be interpreted with caution.

2.3. *Statistical analysis*

Sampling unit level – differences on the average number of seeds and species per sampling unit between habitats and among surveys (time-course) were analysed via generalized linear models (GLM sensu McCullagh and Nelder, 1999). Our GLM simulated factorial ANOVA with habitat and survey as the factors for the number of seeds and seed species recorded in the sampling units – i.e., individual sampling units as replicates. Models were constructed for Poisson error distribution with a log-link function and were also corrected for over-dispersion. GLM are an extension of the general linear models applied for data that fits any distribution of the exponential family (Agresti, 2001). We chose GLM rather than repeated measure ANOVA because our counts of seeds and species did not fit to a normal distribution. GLM have been largely used to analyse data consisting of seed/seedling counts (see Hardesty and Parker, 2002; Benítez-Malvido and Martínez-Ramos, 2003; Albert et al., 2005).

Habitat level – seeds and seed species within particular categories of size, dispersal mode and of manipulation by vertebrates were not adequately represented in the sampling units (i.e. too much zero counts) what turned these data inappropriate to be described and analysed using individual sampling units or even surveys as replicates. Thereby, we analysed the total frequency of seeds and species within these ecological categories at habitat level by considering all seeds and seed species recorded during the 24 surveys – i.e. by pooling all sampling units and surveys within each habitat. Comparisons of these totals permitted to reveal differences in

seed rain that did not appear by comparing average counts of seeds and species per sampling unit.

We used a χ^2 test (Sokal and Rohlf, 1995) to analyse the differences between forest edge and interior in the proportion of seeds within categories of size. Between-habitat differences in the proportion of seed species within categories of seed size and dispersal mode were tested through log-linear models (Sokal and Rohlf, 1995). The initial model consisted of a saturated or complete model with all main effects and interactions (habitat + dispersal mode + seed size + habitat * dispersal mode + habitat * seed size + dispersal mode * seed size + habitat * dispersal mode * seed size). The final model consisted of the minimal fitted model with only significant interactions as proposed by Sokal and Rohlf (1995). Low frequency cells were pooled for analyses in order to correct for Type I error and avoid loss of test power. Finally, G-tests were used to test for differences between habitats in the proportion of seeds and species handled by vertebrates. All analyses were performed by Systat 10.0 and Statistica 7.0.

3. Results

A total of 76,207 seeds belonging to 146 species were collected during the 12 months, what represented a seed input of some 1,905,175 seeds ha/year in the Coimbra forest. A large proportion was comprised of very small seeds (69%) and only a small fraction (1.1%) by large and very large seeds. Forest edge received 47,986 seeds (63%) from 73 species, whereas 28,221 seeds (37%) from 121 species were recorded in the forest interior.

Seed rain varied considerably through time (Fig. 2a), and average seed number per sampling unit differed among habitats and surveys (Table 1). In average, forest edge received more seeds per sampling unit than interior although these differences were not significant in many surveys. Moreover, the magnitude of the differences between habitats and among surveys was not constant for this variable. This was the reason for the significant interaction found between the factors "habitat" and "survey". A similar pattern was found regarding the average number of species per sampling unit (Table 1), but the magnitude of the differences between habitats and among surveys was much more expressive than in the case of the number of seeds (Fig. 2b). In synthesis, the average number of seeds and species arriving per unit of area in forest edge was higher than in forest interior during particular periods of time. We must highlight that the total number of species recorded in more than a half of the surveys (i.e. by pooling all sampling units within a survey) was higher in forest interior (see Fig. 2b).

At the habitat level, the analysis of all seeds recorded throughout the 24 surveys revealed a consistent difference between habitats in terms of seed size. The forest edge had significantly more small seeds and fewer medium, large and very large seeds than expected, whereas forest interior had fewer small seeds and more medium, large and very large seeds than expected (Table 2). The discrepancies between the observed and expected values of most of the individual cells in the contingency table were sufficiently high to constitute significant differences under the critical value of the overall χ^2 with 3 degrees of freedom with the exception of the cells corresponding to very small seeds.

The log-linear analysis for the distribution of seed species within habitats, dispersal modes and size classes showed a strong interaction between the explanatory variables "habitat" and "seed size" ($\chi^2 = 17.56$, df = 3, $P = 0.0002$; Fig. 3). This interaction evidenced a positive association between these variables in the forest interior for large and very large seed species, and a negative association for small and very small seed species. In contrast, in the forest edge this association was positive for small and very small seed species and negative for large and very large seed species. Differences between habitats with respect to the relative contribution of the group formed by large plus very large seed species was supported by the presence of 259 seeds of seven species (9.5% of all species) recorded in forest edge against 586 seeds of 33 species (27.2%) recorded in forest interior. A log-linear model also evidenced a marginally significant association between "habitat" and "dispersal mode" ($\chi^2 = 3.72$, df = 1, $P = 0.053$; Figs. 4a and b), in which the forest interior presented a positive association with vertebrate-dispersed species, and a negative association with abiotically-dispersed ones. In relative terms, vertebrate-dispersed species accounted for 63.1% of the species in the forest edge vs. 76.03% in the forest interior. Distribution of both abiotically- and vertebrate-dispersed species was not significantly correlated with categories of seed size.

Moreover, large and very large seed species were restricted to 27% of the sampling units in forest edge although they were present in 62% of the sampling units in forest interior, a significant difference in terms of frequency ($G = 18.1$, df = 1, $P < 0.0001$). Regarding habitat specificity, only one large seed species occurred exclusively in the forest edge (*Chrysophylum viride*). In contrast, 27 large and very large seed species (81.8% of all large and very large seed species recorded) were recorded only in the forest interior, including dominant mature-forest trees such as *Virola gardneri*, *Copaifera langsdorfii*, *Lecythis pisonis*, and several Sapotaceae species-all dispersed by vertebrates.

At least 5935 seeds presented any evidence of vertebrate handling (i.e. teeth/beak marks or fecal clumps with seeds), which represented 7.8% of all seeds recorded in the forest. However, in the forest edge this kind of evidence was observed in 5.9% of all seeds recorded, but it reached 11% in the forest interior ($G = 610.32$, df = 1, <0.0001). Almost all handled seeds recorded in both habitats were classified as very small seeds (92.2% in the edge and 91.6% in the forest interior), partially because the high number of seeds belonging to *Ficus* and *Miconia* species, which were deposited into sampling units through bat regurgitation and bird fecal clumps respectively. Finally, the summed percentage of large and very large seeds was ten-times lower in forest edge (0.07%) than in forest interior (0.7%, $G = 17.5$, df = 1, $P < 0.0001$) and, in terms of seed species, the percentage was almost threefold lower in the edge (12.5%) in comparison to forest interior (37.9%, Table 3).

4. Discussion

Seed rain can be described as the total amount of seeds received by any habitat during a certain period of time, and its magnitude and composition is driven by seeds that just

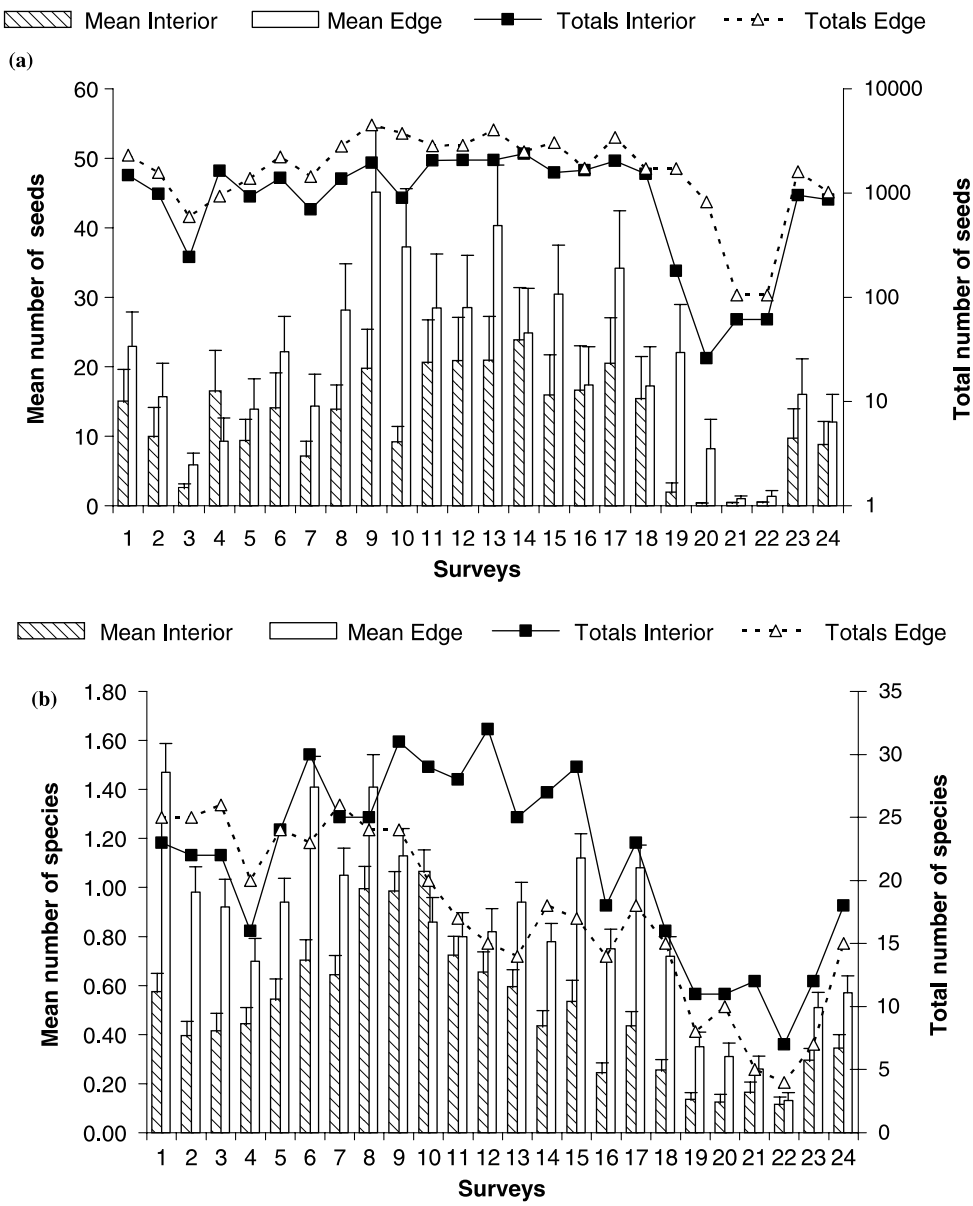

Fig. 2 – Time-course of seed rain showing the average number of seeds (a) and species (b) per sampling unit (mean ± SE), and the total number of seeds recorded in each survey in forest edge and forest interior at Serra Grande, Brazil. Surveys correspond to 15-day intervals, starting in Oct/2002 and finishing in Sep/2003. Here individual sampling units served as replicates (*n* = 100 sampling units per survey per habitat).

drop beneath parents as well as by seeds actively dispersed (Harper, 1977; Hardesty and Parker, 2002). Overall, our results suggest that both the interior and the old edge of Coimbra forest receive a large bulk of seeds, most of them being very small seeds dispersed via faeces from vertebrates such as bats and birds. They also suggest that in average this edge receives more seeds and species per unit of area during particular periods of time. At habitat level, however, seed rain in forest edge appears to be particularly impoverished in terms of: (1) large-seeded species (large plus very large seed species); (2) large-seeded species showing vertebrate seed-dispersal attributes; and (3) species handled by vertebrates. Such a biased seed rain was revealed despite of our relatively reduced sampling effort in terms of time and area covered by transects.

Habitat loss and fragmentation are believed to affect many of the crucial events taking part in the life cycle of tropical trees, such as pollination, seed dispersal, and seedling recruitment (see a synthesis in Laurance, 2001). Studies by J. Benítez-Malvido and collaborators, for instance (e.g. Benítez-Malvido, 1998; Benítez-Malvido and Martínez-Ramos, 2003), have clearly demonstrated that: (1) small fragments and forest edges house lower numbers of seedlings in comparison to continuous forests; (2) rare species in the continuous forest tend to be absent in small forest fragments; (3) dominant species in continuous forest tend to be rare as fragments become

Table 1 – Parameters of GLM fitted to number of seeds and species per sampling unit within 24 surveys and two habitats at Serra Grande, Brazil

Factor/dependent variable	df	Wald (χ^2)	P
Number of seeds			
Intercept	1	1455.258	0.000000
Habitat	1	34.759	0.000000
Survey	23	211.442	0.000000
Habitat*survey	23	51.138	0.000652
Number of species			
Intercept	1	724.4085	0.000000
Habitat	1	171.9018	0.000000
Survey	23	492.6129	0.000000
Habitat*survey	23	82.6102	0.000000

Models were constructed for a Poisson error distribution with a log-link function and were corrected for over-dispersion ($n = 100$ sampling units per survey per habitat; individual sampling units as replicates).

Table 2 – Observed values of seed abundance within classes of seed size in forest edge and forest interior at Serra Grande, Brazil

Categories of seed size	Number of seeds	
	Forest edge	Forest interior
Very small	33535 (+290)	19262 (−290)
Small	7949 (+1188)*	2789 (−1188)
Medium-sized	6243 (−1204)*	5584 (+1204)*
Large	259 (−269)*	580 (+269)*
Very large	0 (−4)*	6 (+4)*

Numbers in parenthesis show deviations from the expected values and their corresponding sign of the departures.
* Asterisks following parenthesis are significant contributions to the accumulative overall χ^2 values for number of seeds ($\chi^2 = 1474.28$; df = 3, $P < 0.0001$).

smaller; and (4) common species in forest fragments are rare in continuous forest. Decreased rates of seedling recruitment and survivorship due to creation of forest edges are likely to play an important role in these patterns. The biased seed rain documented in the Coimbra forest raises the possibility that the creation of forest edges may alter some attributes of seed rain close to fragment borders, particularly its content of large-seeded plants and of those dispersed by vertebrates. Unfortunately, we can not infer about the generality of this pattern as we did not have replicates for fragment.

In tropical forests, spatial heterogeneity in the seed rain results from a large suite of processes, including differences in precipitation and seasonality (Loiselle et al., 1996; Morellato and Leitão-Filho, 1996; Grombone-Guarantini and Rodrigues, 2002); spatial distribution of forest gaps (Hubbell et al., 1999); and phenology of "key" tree species, which are massively visited by frugivorous vertebrates during the fruiting period (Peres and Roosmalen, 2002). The discrepancy documented here between forest edge and forest interior in terms of seed rain cannot be attributed to these factors, as we sampled within a small spatial scale. Consequently, more local processes driving changes in seed rain must be operating. Extirpation of large and emergent trees in forest edge (Laurance, 2001), and consequent edge domination by small-seeded pioneer plants (Mesquita, 1995; Oliveira et al., 2004) may promote conspicuous changes in the attributes of seed rain, including species richness and ecological composition. At present, the old edge of Coimbra forest is dominated by reproductive small-seeded pioneers, such as *Miconia prasina* and *Cecropia pachystachya*, and this edge support less than 50% of the tree species richness observed in the forest interior (Oliveira et al., 2004). In fact, the edge of Coimbra forest houses twice as much pioneer tree species than forest interior (82.7% vs. 37.3%) and pioneers represent over 90% of the adult trees in this habitat (Oliveira et al., 2004; Grillo, 2005).

Because of this domination by pioneer trees, there is little surprise that both habitats strongly differ in terms of seed

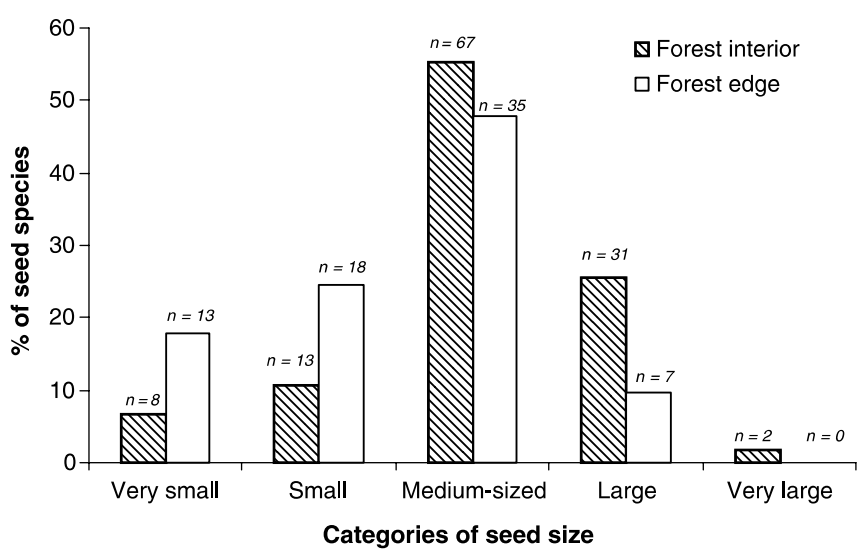

Fig. 3 – Percentage of seed species within categories of seed size in forest edge and forest interior at Serra Grande, Brazil. There was a significant log-linear association between habitat and seed size ($n = 73$ species from forest edge and 121 species from forest interior; individual seed species as replicates).

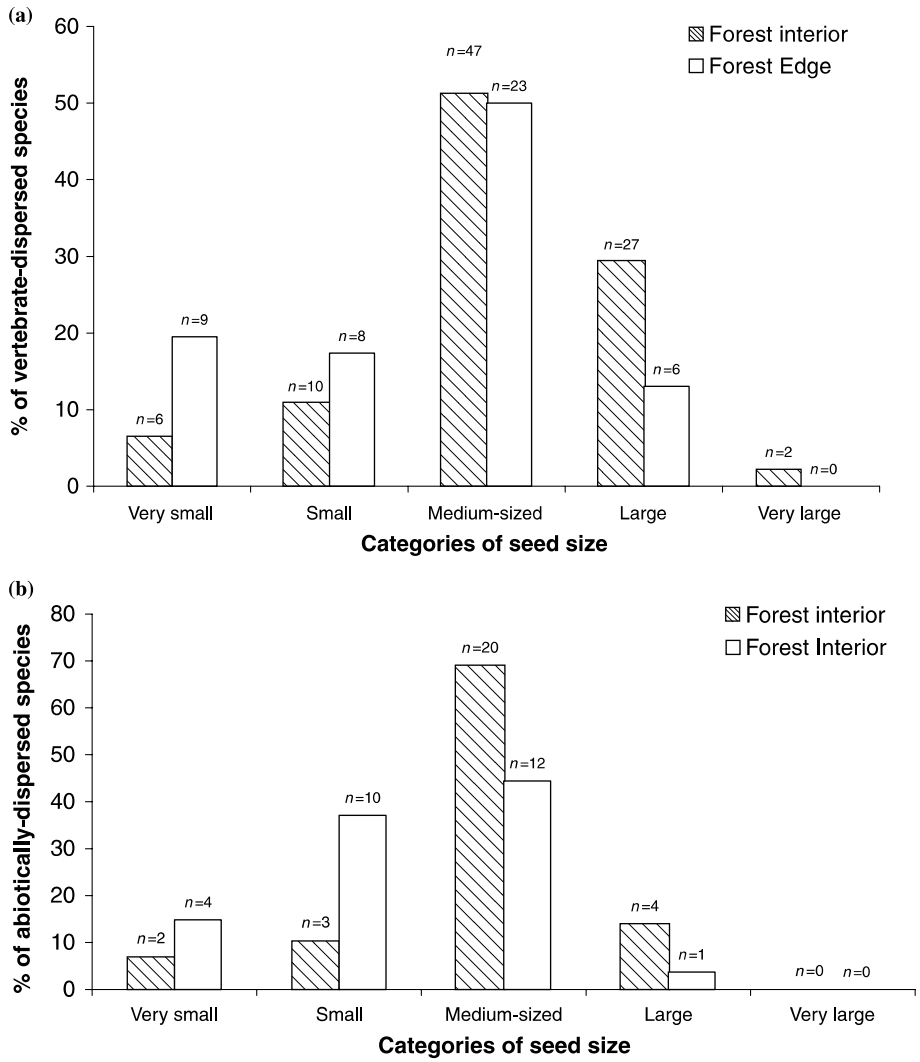

Fig. 4 – Percentage of seed species within categories of seed size and dispersal mode in forest edge and forest interior at Serra Grande, Brazil (*n* = 73 species in forest edge and 121 species in forest interior).

rain and that the edge of Coimbra forest receives an impoverished seed rain at habitat level. However, a complete lack of large and very large seeds from a myriad of abundant vertebrate-dispersed trees, as well as a lower proportion of vertebrate-handled seeds reaching the edge of this forest (only 5.9% of all seeds) suggest failure of active seed dispersal in the edge habitat. This rate of 5.9% contrasts, for instance, to that recorded in undisturbed tropical forests in which seed rain is largely composed of a rich array of actively dispersed species – i.e. transported by vertebrates from other forest patches (Webb and Peart, 2001; Hardesty and Parker, 2002). Our hypothesis is that large and very large seeds produced in the forest interior have composed the seed rain of this habitat by simply dropping from parents or via active dispersal by vertebrates, but they have not been able to reach the edge of Coimbra forest in similar rates due to a reduction on seed-delivery services provided by vertebrates. This disruption affects a dozen of large-seeded Sapotaceae species which

Table 3 – Percentage of vertebrate-handled seeds and seed species within classes of seed size in forest edge and forest interior at Serra Grande, Brazil

Classes of seed size	Percentage of seeds (no.)		Percentage of species (no.)	
	Forest edge	Forest interior	Forest edge	Forest interior
Very small	92.9 (2,638)	91.6 (2,837)	25 (4)	13.8 (4)
Small	1.6 (46)	0.67 (21)	18.7 (3)	13.8 (4)
Medium-sized	5.4 (153)	6.9 (216)	43.7 (7)	34.4 (10)
Large	0.07 (2)	0.64 (20)	12.5 (2)	31.0 (9)
Very large	0.0 (0)	0.064 (2)	0.0 (0)	6.9 (2)

currently have seeds, seedlings, saplings, and adults (>70 trees ha^{-1}) restricted to the interior of Coimbra forest (Melo, 2004; Oliveira et al., 2004).

Similar to Sapotaceae species, a plethora of large-seeded neotropical trees relies on large-gaped birds and medium- to large-bodied mammals for long-distance seed dispersal (Spironello, 1999; Feer and Forget, 2002; Peres and Roosmalen, 2002). Through a varied suit of mechanisms, including habitat loss and hunting, this irreplaceable guild of seed dispersers is expected to occur at low abundances or to be completely extirpated from fragmented forests (Malcolm, 1997; Chiarello, 1999; Peres, 2000; Gilbert and Setz, 2001). A large body of literature (e.g. Thébaud and Strasberg, 1997; Asquith et al., 1999; Silva and Tabarelli, 2000; Wright et al., 2000; Cordeiro and Howe, 2001; Laurance, 2001; Chapman et al., 2003) has emphasized that drastic changes in the abundance of this guild may promote direct, persistent and negative impacts on rates of seed removal around parents, seedling recruitment and, furthermore, on plant colonization ability based on events of long-distance seed dispersal.

At present, the Coimbra forest lacks its most important vertebrate seed disperser – the howler monkey (Almeida et al., 1995). Pacas, agoutis and large-gaped birds have achieved depleted populations as well (Silva and Tabarelli, 2000). Additionally, the use of forest edge by this remaining fauna may not be so intensive since large-seeded and large-fruited tree species are much more abundant and diversified in the interior of Coimbra forest (Oliveira et al., 2004; Grillo, 2005). Edge use by different groups of vertebrate species remains poorly documented. The results from fruit consumption by Galetti et al. (2003) suggest that frugivorous birds are more frequent in edges than in the forest interior, but less frequent in small in comparison to large fragments. In contrast, studies in the BDFFP have identified several edge avoiders, such as birds that forage in mixed-species flocks (see Laurance et al., 2002 for a synthesis). All these findings and possibilities make reasonable to hypothesise that reduction on seed-dispersal services provided by vertebrates may alter the interior-edge flux of large and very large seeds and consequently affect the nature of seed rain in the edge of Coimbra forest.

A variety of fragmentation-related threats to tropical trees have been identified (see Laurance, 2001; Tabarelli et al., 2004 for syntheses) and additional threats are expected to emerge as tropical forests are now facing escalating levels of human-related degradation (Corlett, 2000). Here we document a biased seed rain in the edge of the largest fragment of the Atlantic forest in northeast Brazil. As a future working hypothesis we propose that this bias results from edge dominance by small-seeded species, as well as from disruptions on seed-delivery services provided by vertebrates. In the case our results prove to be a widespread pattern, we should investigate in which extent disruptions on seed rain result in loss of potential habitats for plant colonization, decrease seedling recruitment, and consequently affect the long-term persistence of large-seeded trees in fragmented landscapes. This recommendation sounds reasonable as forest edges tend to be the prevalent habitat in human-dominated landscapes such as those currently found in the Atlantic forest of northeast Brazil.

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