

Edge Effects and Seedling Bank Depletion: The Role Played by the Early Successional Palm *Attalea oleifera* (Arecaceae) in the Atlantic Forest

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ABSTRACT

In this study, we examined the impacts of *Attalea oleifera* on the structure of seedling bank and discuss potential mechanisms of palm influence. Seed rain, seedling bank, and palm leaf fall were assessed beneath the canopy and in the vicinity of 16 adult palms across the edges of a large fragment (3500 ha) of the Atlantic forest. Moreover, we examined *A. oleifera* impacts on seed germination and seedling mortality by experimentally submitting seeds and seedlings to prolonged palm-leaf covering. As expected, seedling bank beneath the adults exhibited reduced abundance and species richness at local and habitat scale. Small to large seeds (3.1–30 mm) were underrepresented in the seed rain below adults palms, while experimental leaf covering drastically reduced both seed germination and seedling survivorship. *A. oleifera* leaf fall occurred over the whole year (3.6 ± 2.7 leaves/individual/yr), which resulted in deep leaf litter mounds (10.7 ± 9.2 cm). Finally, adult palm density (21.6 ± 11.9 individuals/ha) correlated negatively with seedling density across *Attalea* clusters. Our results suggest that *A. oleifera* exerts negative effects on the seedling bank by reducing seedling abundance and richness as a consequence of two complementary mechanisms: impoverished and size-biased seed rain plus reduced seed germination and increased seedling mortality due to prolonged covering by fallen leaves.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: Brazil; canopy litter fall; forest regeneration; seedling mortality; seed rain.

TROPICAL FOREST REGENERATION and the long-term persistence of many tropical tree species rely on the occurrence of seedlings that remain suppressed in forest understory (Swaine 1996). This seedling bank influences the structure of future tree assemblages, as well as demographic attributes of tree species populations, especially of shade-tolerant tree species with recalcitrant seeds (Alvarez-Buylla *et al.* 1996, Loiselle *et al.* 1996, Peña-Claros & De Boo 2002). Because of this crucial ecological role, much attention has been focused on the processes that drive the structure of the seedling bank, such as seed rain, seed germination, and seedling mortality (Swaine 1996). Although the contributions of each one of these factors on the seedling community have been examined, how seedling recruitment varies spatially still represents a relevant question to understand the regeneration of tropical tree species.

Habitat fragmentation and the creation of artificial forest edges have the potential to deplete the seedling bank of tropical forests by reducing plant recruitment due to failures in seed germination and seedling desiccation near forest edges (Benítez-Malvido 1998, Bruna 1999, Laurance *et al.* 2001, Melo *et al.* 2007). Moreover, extirpation of large primary forest trees by elevated rates of uprooting and breakage near forest edges (Laurance *et al.* 2000, Oliveira *et al.* 2008) may depress seed diversity or alter the composition of autochthonous seed rain across forest edges (Melo *et al.*

2006). Finally, habitat loss and fragmentation, usually associated with hunting, may deplete the abundance of vertebrate seed dispersers and consequently the patterns of seed movement and delivery (Cordeiro & Howe 2001, Wright & Duber 2001, Cordeiro & Howe 2003, Melo & Tabarelli 2003). Indeed, forest edges and small forest remnants have been reported to support impoverished seedling banks (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003a, Melo *et al.* 2007).

Despite these landmark findings, the whole suite of forces driving the structure of seedling banks and the successional trajectory of edge-affected habitats has not been fully described (Tabarelli *et al.* 2008). For instance, hyper-proliferation of pioneer trees and the persistence of early successional-dominated assemblages along forest edges may impose additional changes on the seedling banks and act as an ecological filter for some groups of tree species. Several arborescent palm species, such as *Astrocaryum acaule*, *Attalea humilis*, *Bactris maraja*, and *Lepidocaryum tenue*, are known to increase their densities in disturbed habitats, including small forest fragments and forest edges (Scariot 1999, Souza & Martins 2003, Pimentel & Tabarelli 2004). Increased recruitment rates in response to increased light availability (Souza & Martins 2003) and changes in dispersal-predation dynamics are two of the mechanisms that lead these palm species to enhance their densities following forest fragmentation (Wright *et al.* 2000, Pimentel & Tabarelli 2004). Furthermore, increased palm density across human-disturbed habitats may increase seedling and sapling mortality due to the intense fall of debris and microclimatic modifications beneath their canopies (Denslow *et al.* 1991, Farris-Lopez *et al.* 2004, Peters *et al.* 2004, Wang & Augspurger 2006). Thereby, an

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increased density of palm canopies has the potential to disrupt seedling banks and shift the regeneration trajectory of plant communities over large spatial scales as already locally demonstrated for human-undisturbed tracts of tropical forests (Farris-Lopez *et al.* 2004, Peters *et al.* 2004).

The Atlantic forest of northeast Brazil is one of the most striking examples of large-scale ecosystem conversion to anthropogenic/hyper-fragmented landscapes. With its current distribution reduced to < 6 percent of its original pre-Columbian extent, the Atlantic forest has been disturbed since the 16th century (Galindo-Leal & Câmara 2003, Tabarelli *et al.* 2005). Habitat loss and fragmentation in the northeast have been so striking that almost half of the remaining fragments are < 10 ha and currently dominated by pioneer species (Ranta *et al.* 1998; Oliveira *et al.* 2004, 2008). This scenario, marked by a long-term disturbance history, offers an excellent opportunity to investigate cascade effects triggered by proliferation of pioneer/early-successional plant species in edge-affected habitats. Here we ask whether the early successional palm *Attalea oleifera* Barb. Rodr. can effectively impact the seedling bank along the forest edges of a 3500 ha fragment of Atlantic forest. In particular, we examine the hypothesis that *A. oleifera* reduces seedling density and species richness by altering local seed rain and by reducing both seed germination and seedling survivorship via intense leaf fall and subsequent seed/seedling covering by fallen leaves. First, we describe patterns of seed rain and the structure of seedling bank beneath and away from adult palm canopies. Second, we report rates of seed germination and recruitment/survivorship of seedlings experimentally submitted to prolonged palm leaf covering. Finally, we address some of the impacts produced by palm species on the seedling bank and discuss the processes driving the nature of seedling assemblages in dense aggregations of *Attalea* palms, as well as their implications for forest successional trajectory across the edge-affected habitats of Atlantic forest.

METHODS

STUDY SITE.—This study was carried out in the Coimbra Forest—the largest and best preserved Atlantic forest fragment in northeast Brazil (Grillo *et al.* 2006)—located at Usina Serra Grande ($8^{\circ}30' S$, $35^{\circ}50' W$), a private sugar-cane landholding in the state of Alagoas. The 3500 ha Coimbra forest retains a full complement of plant and vertebrate groups typical of undisturbed tracts of Atlantic forest, including large-seeded trees, large frugivorous birds, and populations of valuable timber trees such as the softwood *Urucuba* (*Virola gardneri*) and the hardwoods *Sapucaia* (*Lecythis pisonis*) and *Jatoba* (*Hymenaea courbaril*). Coimbra is covered by an evergreen lowland forest (*sensu* Whitmore 1998), in which Leguminosae, Lauraceae, Sapotaceae, Moraceae, Chrysobalanaceae, and Euphorbiaceae account for more than half of tree species richness (Grillo *et al.* 2006; and see Pôrto *et al.* 2006 for a comprehensive multitalia checklist of plant and vertebrate species inhabiting the Serra Grande landscape). Mean annual temperature and rainfall are $23^{\circ}C$ and 2100 mm, respectively. The climate is Aw, according to Köppen classification, with 3 mo of dry season (November, December, and January; average rainfalls < 60 mm/mo; IBGE 1985). Dystrophic

soils with high clay fractions prevail in the area; *i.e.*, yellow-red latosols and podsols in the Brazilian soil taxonomy system, and oxisols according to the U.S. system of soil taxonomy (USDA 1999, Santos *et al.* 2003).

Sugar-cane cultivation in this landscape dates back at least to the 19th century, and the remaining forest, including the Coimbra fragment, has been protected against wildfires and logging to provide 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 postclosure forest edges (Melo *et al.* 2006).

ATTALEA OLEIFERA.—*A. oleifera* is a broad-leaved arborescent palm species, with adults reaching > 50 cm dbh and 25 m tall (Lorenzi *et al.* 2004, Pimentel & Tabarelli 2004). As an early successional species, *A. oleifera* achieves high abundance in open/disturbed habitats of the Brazilian Atlantic forest, such as early secondary forests, forest edges, small forest fragments, and open forests covering the top of low-altitude hills (Lorenzi *et al.* 2004, Pimentel & Tabarelli 2004). The ability to colonize open areas or disturbed forests is common among *Attalea* species (*e.g.*, *A. butyracea*, *A. dubia*, *A. funilifera*, *A. mariipa*, and *A. speciosa*; Henderson *et al.* 1995, Lorenzi *et al.* 2004) and within the subtribe Attaleinae (the *Babaçu* subtribe), such as *Orbygnia phalerata* (Kahn & Granville 1992). This ability to colonize disturbed areas results from *Attalea* life history strategies, such as short- and long-distance seed dispersal mediated by several vertebrate species, high-energetic-content seeds that can be retained in the soil seed bank for long time periods, resprouting ability of seedlings and saplings (Henderson 2002), low sensitivity to density-dependent mechanisms of seed/seedling mortality (Wright *et al.* 2000, Wright & Duber 2001), and increased growth rates in light habitats (Henderson 2002, Lorenzi *et al.* 2004). In the Coimbra forest, *A. oleifera* has developed dense and spatially independent aggregations or discrete clusters that can reach 21.6 ± 11.9 adult individuals/ha across forest edges (A. Aguiar & M. Tabarelli, unpubl. data). At these clusters *A. oleifera* is the dominant species, but other species that are frequent on forest edges in the study area are also common within the clusters. These palm aggregations are not restricted to the Coimbra forest, rather it has been observed in small forest fragments and other forest edges across the Serra Grande landscape. Throughout edge-affected habitats in several forest fragments there is a frequent layer of thick, dead *Attalea* leaves (up to 4 m length), which decay slowly on the ground, generating deep leaf litter mounds.

ATTALEA ADULTS AND THE SEEDLING BANK.—To examine possible influences of *A. oleifera* on the structure of the seedling banks across the edges of Coimbra forest (34 km perimeter), we randomly selected and tagged 16 focal adults of *Attalea* within 16 spatially independent palm clusters (one focal adult per cluster, with clusters at least 90 m apart). To ensure spatial independence, focal individuals were at considerable distances from each other (minimum distance: 151 m, average distance: 2655 m). All clusters were located no farther than 100 m from the nearest forest edge. These 16 spatially independent adults had their umbrella-like crowns projected on the

ground (a crown projection refers to the ellipse area formed by the two main perpendicular crown diameters). These projections were assigned as our palm plots. Within plots, all seedlings were manually harvested (*i.e.*, physically eliminated from plots by uprooting), morphotyped and quantified twice—in the dry seasons of 2003 and 2004. This procedure permitted us to assess the standing seedling bank richness and abundance, its regeneration performance in both habitats, and allowed us correct seedling identification based on comparisons with herbarium specimens. Seedlings were defined as individuals < 50 cm tall, including shrub, tree, liana, and palm species. Individuals with evidence of resprouting or subterraneanous stems (stolons) were disregarded. Assignment of seedlings into morphotypes was possible with the help of a local parataxonomist and via comparisons with specimens deposited in the UFP Herbarium (vouchers no. 34,445–51,604 for the study site) and in the Serra Grande seedling and fruit/seed collection stored at the Plant Ecology Laboratory of the Universidade Federal de Pernambuco, Brazil, as previously adopted by Melo *et al.* (2006). As a control, we set a paired sample by replicating the exact palm plot area outside the *Attalea* crown, but no farther than 10 m distant from the treatment plot. To determine this nonpalm plot location, we selected the closest forest floor patch that was not beneath any *A. oleifera* crown, either from the focal palm or from its neighbors. Both, palm plot and nonpalm plot, were embedded at the same physical and biotic environment and this pair-wise design allowed us to quantitatively compare the seedling bank structure beneath the palm and in its vicinity, with negligible variation on other factors affecting the seedling bank structure rather than the *A. oleifera* influence.

SEED RAIN ASSESSMENT.—Similarly, we adopted a paired experimental design to assess the seed rain beneath each palm and in its vicinity. We mounted seed traps beneath a new set of 20 adult palms (within the 16 clusters mentioned earlier) and the same number of nonpalm seed traps not farther than 10 m away from the palm trap. Four clusters received two pairs of seed traps (palm and nonpalm) but these pairs were set at least 50 m apart. The seed traps consisted of a green nylon screen measuring 1 m² (1 × 1 m, 1 mm aperture) framed by 3-mm-thick stainless-steel wire and fixed to the stems of understory plants at about 1 m height. This method has been previously adopted for seed rain assessment in the Coimbra forest (Melo *et al.* 2006). Seed rain traps were checked every month during a 13-mo period (April 2004 to April 2005). All seeds collected were morphotyped and counted, with the exception of very small seeds (< 3 mm length). For these small seeds, we assigned the value of 300 seeds each time one of these species was sampled because this value reasonably describes the magnitude and relative representation of very small seeds in the seed rain across the edges of Coimbra forest as adopted by Melo *et al.* (2006). To compare the size–seed distribution between habitats (*i.e.*, beneath the palm and in its vicinity), we assigned seeds within mutually exclusive categories: (1) very small seeds (1–3 mm in length); (2) small (3.1–6 mm); (3) medium (6.1–15 mm); (4) large (15.1–30 mm); and (5) very large (> 30 mm). Similar seed-size categories have been adopted for the

Atlantic forest woody flora (Tabarelli & Peres 2002, Melo *et al.* 2006).

SEED GERMINATION, SEEDLING MORTALITY, AND THE AREA IMPACTED BY *A. OLEIFERA*.—To evaluate the impacts of *Attalea* fallen leaves on seed germination and seedling recruitment, we haphazardly established 15 pairs of 1-m² plots, one pair per palm cluster. These plots were established no farther than 50 m from the nearest forest edge in Coimbra, within areas without risk of palm leaf falling. We counted and tagged all the seedlings inside these plots and then randomly assigned one of the plots within each pair to receive a recently fallen *Attalea* leaf (*i.e.*, the covered plots), which covered the standing seedling bank. We checked these plots monthly for seed germination and seedling mortality during a 13-mo period (November 2003 to November 2004). During the same period, the depth of leaf litter (*i.e.*, litter mounds) was measured beneath our 16 focal adults and in their nonpalm plots. Four measurements were made at circumferences with a radius of 1.5 m: one centered at the palm stem and another at the center of the nonpalm plot. The quadrants (each one of the four points was separated by 90°) had the same orientation for the treatment and nonpalm plots.

Finally, to obtain a rough estimate of the understory area impacted by *Attalea* adults within the clusters, we multiplied the average area of adult palm crown by their density within the 16 clusters assessed in the Coimbra forest. The average area of the *A. oleifera* crown was measured for the seedling bank experiment and the *A. oleifera* density was estimated by counting all the adult individuals within a radius of 30 m from the focal adult stem.

DATA ANALYSIS.—Wilcoxon or paired *t*-tests were used to examine differences between palm and nonpalm plots in terms of seedling density, species richness and diversity, and depth of the litter layer. The choice of statistical tests was based on data normality checked by Lilliefors tests. We also estimated total species richness per habitat (*i.e.*, community level analysis) by obtaining mean species-area accumulation curves for three nonparametric estimators: the incidence-based coverage estimator, Chao-2, and Jackknife-2 (see Colwell & Coddington 1994), all of them provided by EstimateS 8.0 (Colwell 2006). These estimators are based on the incidence of species and have been described in the literature as the best estimators of seedling richness in tropical forests (Chazdon *et al.* 1998, Benítez-Malvido & Martínez-Ramos 2003a). To generate the species accumulation curves we performed 300 randomizations of both palm and nonpalm plots, and the estimators were expressed per 1235 m² as it represented the total area sampled per habitat. To obtain the nonparametric estimators, we set the EstimateS patchiness parameter at 0. Patchiness 0 means that each seedling was haphazardly sorted to a sample within species, while the distribution of seedlings among species and the number of samples were maintained as the observed seedling community. We adopted this procedure to eliminate any bias resulting from high levels of species patchiness as adopted by Benítez-Malvido and Martínez-Ramos (2003a) and Melo *et al.* (2007).

Differences in seed rain were examined via *G* tests, and the same approach was adopted to check for differences in seed

germination and seedling mortality. To examine possible relationships between seedling richness and the abundance of adult palms within clusters, we used Spearman or Pearson correlation coefficients. All the statistical procedures adopted here are described in Sokal and Rohlf (1995). We performed them in the Statistica 6.0 software (StatSoft 2001), except for the mean species-area accumulation curves for three nonparametric estimators, for which we used EstimateS 8.0 (Colwell 2006).

RESULTS

A total of 8511 seedlings belonging to 117 plant morphospecies were recorded; most of them were pioneer species within families such as Anacardiaceae, Rubiaceae, and Melastomataceae. Two-thirds of the seedlings (5655) were recorded in the nonpalm plots, and thereby average seedling density in this habitat was twice as high as in palm plots in both surveys/dry seasons ($Z=2.58$, $N=16$, $P=0.01$; $t=3.08$, $df=15$, $P=0.007$; Fig. A and 1B). This robust difference emerged despite the high abundance of palm seedlings beneath their parents: *Attalea* seedlings accounted for 16.7 percent (482) of the seedlings in the palm plots, but they represented only 2.1 percent (117) in the nonpalm plots. A similar pattern emerged regarding average seedling richness as it was 23 and 48 percent higher in the nonpalm plots in the first and the second surveys, respectively ($t=3.44$, $df=15$, $P=0.0036$; $Z=3.51$, $P<0.001$; Fig. 2A and B). At the community level, species-area accumulation curves showed that seedling assemblages were not completely recorded in both habitats irrespective of survey (Figs. 2C and D). However, as previously documented for average species richness, the total number of seedling species was significantly different between habitats as suggested by the confidence intervals. In the first survey, species richness ranged from 79 ± 6.4 species (S_{obs} , mean \pm SD) to 103 ± 5.6 species (Jackknife-2) palm plots, whereas it ranged from 99 ± 9.6 species (S_{obs}) to 145.7 ± 5.0

species (Jackknife-2) in the nonpalm plots (Table 1). A similar trend was observed in the second survey. Despite the differences of seedling density and richness at local scale, seedling diversity, estimated by Simpson's indexes (1D), was similar among habitats as it varied between 3.18 ± 0.74 (first survey) and 0.813 ± 0.134 (second survey) in the palm plots vs. 3.1 ± 0.74 and 0.82 ± 0.13 in the nonpalm plots.

A total of 10,210 seeds from 39 morphospecies were collected and seed rain was highly variable during the 13-mo period. Considering both habitats, average seed rain varied between 0 and 1.18 seed species/ m^2/mo (Fig. 3A), and 0 and 75 seed species/ m^2/mo (Fig. 3B), but no differences were found between palm and nonpalm plots. On the other hand, the total number of seeds accumulated in the control plots was *ca* 25 percent higher than in palm plots after the 13-mo period ($\chi^2=47.6$, $df=1$, $P<0.05$)—5451 seeds belonging to 34 seed species vs. 4755 within 22 species. Seed rain also differed between habitats in terms of seed size (Fig. 3C) as seeds ranging from 3.1 to 30 mm (intermediate size classes) were underrepresented beneath palms ($\chi^2=126$, $df=4$, $P<0.001$).

Seed germination and seedling mortality experiments revealed an impressive impact of leaf covering—76.6 percent ($N=36$) of all germinated seeds appeared in the nonpalm plots, while just 11 new seedlings were registered for the covered plots ($\chi^2=13.3$, $df=1$, $P<0.001$). In addition, more seedlings died in covered plots—49.4 vs. 16.3 percent ($N=319$ seedlings monitored, $\chi^2=132$, $df=1$, $P<0.001$). We replaced the leaves used at the smothering experiment only once, in order to ensure complete covering for seeds and seedlings throughout the 13-mo period. This evidences the high durability of fallen leaves on the ground and their potential for providing prolonged cover. These results also implied that our experiment reproduced a natural situation. As expected, *A. oleifera* discarded and dropped senescent and almost entire leaves (≤ 5 m distant from adult stems) over the whole year with an average of 3.6 ± 2.7 leaves individual/yr. This supported huge and permanent mounds of decomposing leaves, which reached 10.7 ± 9.2 cm in depth beneath palm canopies in contrast to only 3.5 ± 2.0 cm of leaf litter in the nonpalm plots, a significant difference of nearly 300 percent ($Z=5.5$, $N=16$, $P<0.001$).

Within clusters, adult palm density reached 21.6 ± 11.9 individuals/ha with an average crown area of 77.2 ± 16.1 m^2 , thereby *ca* 16 percent of forest understory area was covered by *Attalea* adults and exposed to their direct impacts. We did not find significant correlations between adult palm density within clusters and the attributes of seedling bank beneath palms (habitat scale analysis). However, seedling density in nonpalm plots correlated negatively with adult palm density ($r_s=-0.58$, $N=16$, $P=0.0179$) in the first survey (*i.e.*, the standing seedling bank). This implies that denser clusters supported more depauperated seedling banks.

DISCUSSION

In this study, we addressed the impacts of adult *Attalea* palms on the structure of the seedling banks across the edges of a large fragment of the Atlantic forest. Our results clearly suggest that

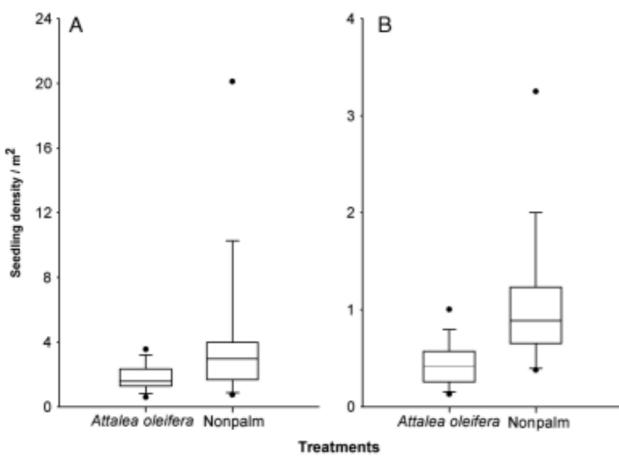


FIGURE 1. Seedling density beneath the canopy of *Attalea oleifera* adults and nonpalm plots in the dry season of 2003 (A) and 2004 (B) in the Coimbra forest, Brazil. The box indicates the 25th and 75th percentile, and the line within the box marks the median. Error bars indicate the 90th and 10th percentiles, and the black points the outlying plots.

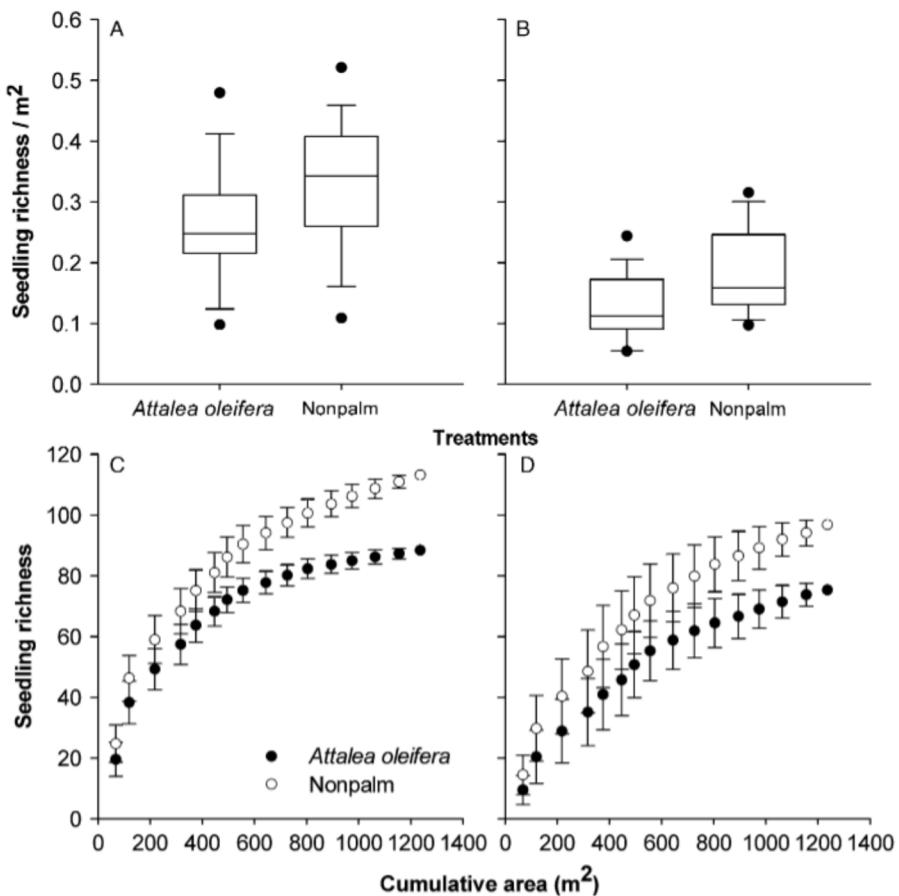


FIGURE 2. Seedling richness beneath the canopy of *Attalea oleifera* adults and nonpalm plots in the dry season of 2003 (A) and 2004 (B). The box indicates the 25th and 75th percentile, and the line within the box marks the median. Error bars indicate the 90th and 10th percentiles, and the black points the outlying plots; seedling species-area accumulation curves for the first (C) and second (D) survey (open dots: nonpalm plots; black dots: palm plots) in the Coimbra forest, Brazil. Error bars are the 95% CI generated from 300 randomizations.

A. oleifera adults exert a negative effect on the local structure of the seedling bank by reducing its abundance and richness by a half at local scale (*i.e.*, beneath palms). Moreover, the seedling bank contains a reduced number of species at habitat scale (*i.e.*, reduced beta-diversity across *Attalea* clusters). This impoverished bank results

TABLE 1. Average total number of seedlings species (mean \pm SD) according to three estimators (ICE, Chao-2, Jackknife-2) plus the number of observed species (Sobs) beneath the canopy of *Attalea oleifera* adults and nonpalm plots in the first and second surveys in the Coimbra forest, Brazil.

Estimators	1st survey		2nd survey	
	Attalea	Nonpalm plots	Attalea	Nonpalm plots
Sobs	79 \pm 3.3	99 \pm 4.9	63 \pm 4.4	82 \pm 4.5
ICE	93.5	131	104	125
Chao-2	92.3 \pm 7.8	133 \pm 15.7	93.0 \pm 14.8	111 \pm 13
Jackknife-2	103	146	104	127

from two complementary mechanisms: (1) reduced, impoverished, and size-biased seed rain reaching the adult palms, which is followed by (2) reduced seedling recruitment/survivorship due to seed/seedling covering by fallen leaves. Additionally, because of its outstanding adult density within clusters (up to 45 individuals/ha) and an increased frequency of clusters, *A. oleifera* may affect the seedling bank over large areas across the edges of Coimbra forests, as well as in other edge-affected habitats, such as small fragments, as *Attalea* clusters are a common feature of many forest remnants in our study region.

It has already been demonstrated that the presence of arboreal palms can influence the seedling/sapling banks on tropical forests in terms of plant stature and density, species richness, and taxonomic composition (Farris-Lopez *et al.* 2004, Peters *et al.* 2004, Wang & Augspurger 2006). Although multiple mechanisms may cause these community-wide alterations, increased seedling/sapling damage by fall of coarse debris from the canopy has been frequently proposed as the main driving force behind these palm-mediated disturbances (Wang & Augspurger 2006). Evidence of physical damage on saplings imposed by debris fall was 40–

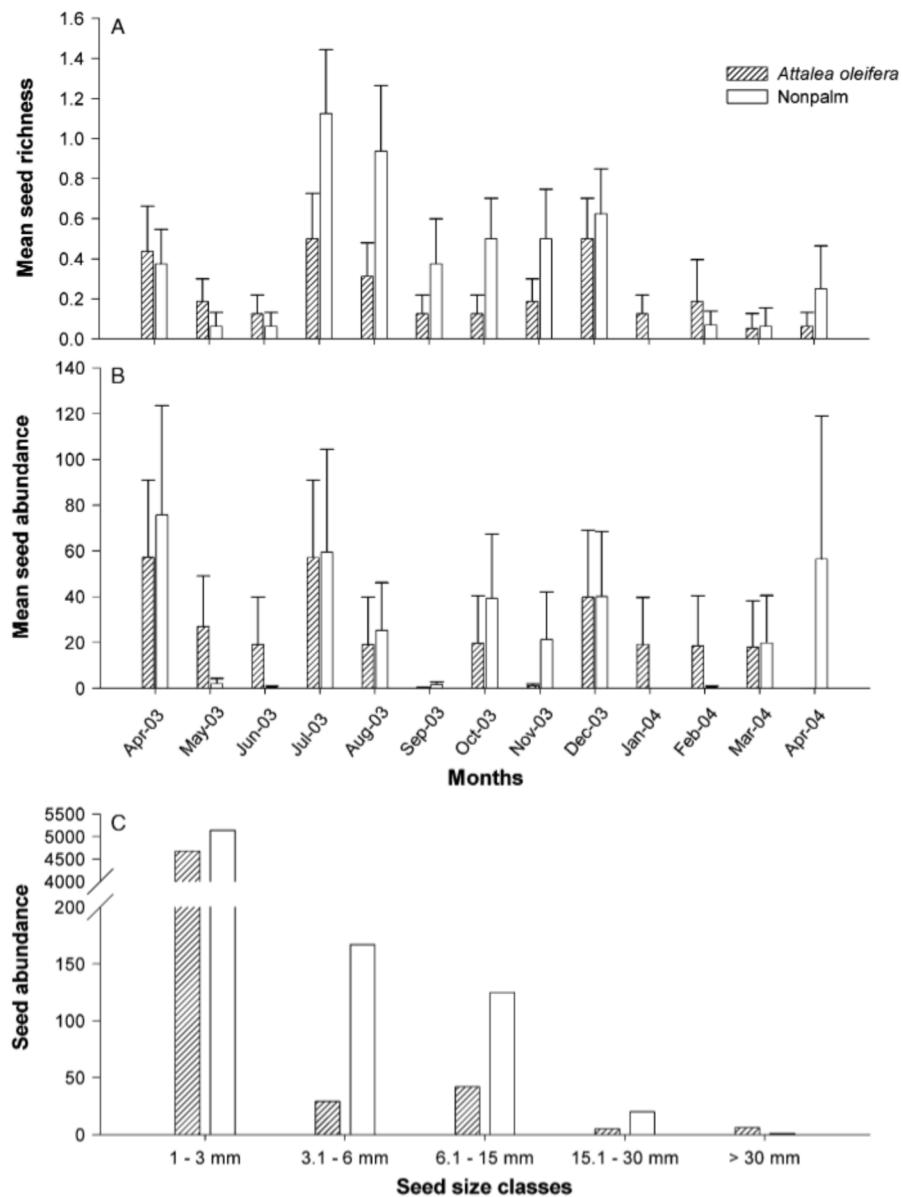


FIGURE 3. Time course of seed rain showing the mean richness (A) and abundance (B) *per sample unit (mean \pm SE)* in 16 m^2 . Dashed bars stands for the mean richness/abundance beneath *Attalea oleifera* and white bars stands for the nonpalm traps. Seed number by classes of seed size beneath the canopy of *A. oleifera* adults and nonpalm traps (C) in the Coimbra forest, Brazil.

125 percent more common in the vicinities of *Iriartea deltoidea* adults (Peters *et al.* 2004). Indeed, our smothering experiment offered empirical evidence that fall of coarse debris from palm canopies impoverishes the seedling bank beneath them.

A. oleifera produces large-seeded and hard pyrenes that in the Coimbra forest are exclusively dispersed by terrestrial mammals via synzoochory (Pimentel & Tabarelli 2004). Although in undisturbed forest tracts palm fruits are an important food resource for several vertebrate species (Henderson 2002), in forest fragments where hunting and poaching occurs this resource is likely to exceed the demand as a consequence of low densities of frugivorous populations (Wright & Duber 2001). By attracting few frugivorous

vertebrates that respond for gut-dispersal of medium to large seeds (e.g., birds and primates dispersing medium-sized seeds), adults of *A. oleifera* are likely to (1) impose a barrier for seed arrival and (2) receive a seed rain biased toward small seeds that are dispersed either abiotically or by generalist vertebrates. In the Atlantic forest of northeast Brazil and consequently in the Coimbra forest, medium-sized seed species represent 76.8 percent of the entire woody flora (Silva & Tabarelli 2000).

Additionally, the seedlings occurring beneath the palm experience a higher chance of being covered or damaged by fallen and long-lasting dead leaves. This physical suppression is likely to last as long as the adult palm lives due to continuous leaf fall, a common

feature among *Attalea* species (Voeks 2002). This prolonged covering may be particularly detrimental for small seeds, which are deposited more frequently beneath palm adults. Forest sites exposed to intensive debris fall and litter accumulation have been recognized as offering ecological filters by hindering both seed germination (Vazquez-Yanes *et al.* 1990) and seedling/sapling growth (Clark & Clark 1991, Peters *et al.* 2004), particularly due to seed covering and seedling physical damage (Vazquez-Yanes *et al.* 1990; Gillman & Ogden 2001, 2003; Gillman *et al.* 2004). By regular and intense leaf fall, *Attalea* adults are expected to impose restrictions and create a harsh and unsuitable habitat for the establishment of plant species beneath and around their crowns. However, the impact caused by palm presence is not similar for all plant species as seedlings and saplings greatly vary in their ability to recover from physical damage (Wang & Augspurger 2006, Alvarez-Clare & Kitajima 2009). Those seedling species with attributes that provide better resistance to physical damage and replacement of lost aboveground biomass (*e.g.*, storage cotyledons and resprouting capacity) probably experience higher chances of successful recruitment whether or not they are exposed to increased abundance of adult palms (Farris-Lopez *et al.* 2004). Conversely, those plant species bearing recalcitrant seeds and seedlings sensitive to physical damage or growth suppression promoted by prolonged leaf covering (*e.g.*, small-seeded, tiny seedlings) are expected to face reduced chances of establishment within *Attalea* clusters. The magnitude of this filtering mechanism may be mediated by density of adult palms as it correlated negatively with seedling density within the 16 clusters we assessed along the edges of Coimbra forest.

In Neotropical forests, as soon as forest edges are created as a consequence of habitat fragmentation, small fragments and forest edges tend to experience a rapid, hyper-proliferation of short-lived pioneer trees (Laurance *et al.* 2006). Concomitantly, several groups of shade-tolerant/old growth tree species (*e.g.*, large-seeded, long-lived emergent, hardwood tree species) are disfavored, and these species gradually become rare and eventually may be driven to extinction at the landscape scale (Laurance *et al.* 2000, Cramer *et al.* 2007, Michalski *et al.* 2007). Collectively, pioneer proliferation and reorganization of the old growth flora result in a detectable floristic convergence across the landscape (Oliveira *et al.* 2004, Michalski *et al.* 2007). This is likely to reduce both alpha (within fragment) and beta (among fragments) diversity, and render tree assemblages more impoverished in terms of species composition, life-history traits, and functional diversity (Girão *et al.* 2007). The Coimbra forest edges, for instance, retain just a half of the tree species richness found in their core interior areas and are largely dominated by early successional species, from seedling bank to adult tree assemblages (Oliveira *et al.* 2004, Melo *et al.* 2007, Santos *et al.* 2008). By proliferating and altering the nature of the seedling banks, *Attalea* probably exerts some influence on the forest successional trajectory across edge-affected habitats. More precisely, we propose that by filtering some ecological groups, *Attalea* clusters impose an additional source for the impoverishment of edge-affected habitats. This sort of higher-order effect of habitat fragmentation might explain why edge-affected habitats, including the edges of Coimbra forest, retain impoverished seedling banks and plant assemblages (Benítez-

Malvido 1998; Benítez-Malvido & Martínez-Ramos 2003a, b; Laurance *et al.* 2006; Melo *et al.* 2007).

In synthesis, arborescent palm species and their debris have long been recognized as imposing small-scale disturbances to the understory of tropical forests (Farris-Lopez *et al.* 2004, Peters *et al.* 2004). This paper outlines shifts in the seedling bank mediated by the presence of *Attalea* adults, which appear to disfavor the local arrival of medium to large seeds and filter those seeds/seedlings species that are not able to stand physical suppression imposed by prolonged leaf covering. These two complementary forces promoting reductions on seedling recruitment may be specific of some synzoochoric palm species with vegetative phenology marked by constant and intense fall of entire senescent leaves. This sort of *Attalea*-mediated small-scaled disturbance has never described and reinforces the notion that pioneer species proliferation in response to habitat fragmentation may have subtle effects on the biological dynamics of fragmented landscapes, particularly on the functional signature and regeneration of tree assemblages across edge-affected habitats. We hope this paper will instigate a more comprehensive assessment of the role played by palm species on the successional trajectory on tropical forests, including the hyper-fragmented landscapes and their poorly investigated biological dynamics.

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