Rainforest fragmentation and the demography of the economically important palm *Oenocarpus bacaba* in central Amazonia

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Abstract We summarize a long-term study of the effects of edge creation on establishment of the economically important arboreal palm *Oenocarpus bacaba* in an experimentally fragmented landscape in central Amazonia. Recruitment and mortality of large individuals (≥10 cm diameter-at-breast-height) were recorded within 21 1-ha plots in fragmented and intact forests for periods of up to 22 years. In addition, 12 small (0.7 × 14 m) sub-plots within each 1-ha plot were used to enumerate the abundance of seedlings and saplings (5–400 cm tall). On average, the recruitment of large trees was over two times faster near forest edges, leading to a sharp (90%) increase in the mean population density of large individuals near forest edges, whereas the density of larger trees remained constant in the forest interior. Overall seedling and sapling density was significantly lower in edge than interior plots, but edge plots had a much higher proportion of larger (>100 cm tall) saplings. Our findings demonstrate that forest edges can have complex effects on tree demography and that one must consider all tree life stages in order to effectively assess their effects on plant populations.

Keywords Arecaceae · Edge effects · Population dynamics · Tree seedlings

Introduction

Forest fragmentation is a grave threat to biological diversity and causes three distinctive changes to ecosystems: reduced forest area, increased isolation of forest fragments, and a dramatic increase in the amount of artificial forest edge. Collectively, these changes can depress population sizes of fragmentation-sensitive species and dramatically increase their local extinction risk (Tilman et al. 1994).

Fragment area and edge effects can strongly affect the demography of tropical trees. As the size of fragments decreases with a concomitant increase in edge effects, the proportion of large, old-growth tree species typically declines from elevated tree mortality, whereas the recruitment of light-demanding, gap-dependent successional trees increases (Laurance et al. 1998a, b, 2006a, b; Tabarelli et al. 1999; Hill and Curran 2001; Oliveira et al. 2004). For old-growth tropical trees, the deleterious effects of fragmentation may be amplified because most species

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are locally rare and patchily distributed and therefore have very small population sizes in fragments (e.g., Turner et al. 1996; da Silva and Tabarelli 2000).

Forest fragmentation can also affect the reproduction of tropical trees via changes in biotic processes, such as pollination, seed production (Cascante et al. 2002), seed dispersal (Wright et al. 2000; Cordeiro and Howe 2001, 2003; Galetti et al. 2006), seed predation (Curran and Webb 2000; Chacoff et al. 2004), and seedling herbivory (Benitez-Malvido et al. 1999). As a result, biotic changes in fragments can have a substantial influence on tree reproduction and persistence (Benitez-Malvido 1998; Scariot 1999; Benitez-Malvido and Martinez-Ramos 2003).

As a consequence of interacting area and edge effects and biotic changes, habitat fragmentation can have complex effects on plant demography. In some species, for instance, fragmentation might reduce reproduction via disruption of pollination or seed dispersal, but once established its seedlings might survive and grow faster in fragments and hence be likely to reach reproductive maturity. In other species, however, reproductive success and seed predation might be unaffected by fragmentation, but rates of germination, seedling recruitment, and growth can be reduced in fragments (e.g. Bruna 1999, 2002; Bruna and Kress 2002). Thus, understanding the effects of fragmentation on a long-lived tree species requires one to consider its entire demographic structure, from seedling to adult stages.

Most studies of the impacts of forest fragmentation on tree structure and dynamics have focused on larger individuals [$\geq$10 cm diameter-at-breast-height (dbh)] (e.g., Laurance et al. 1998a, b, 2006b; Hill and Curran 2001). In this study, however, we tested how both larger trees ($\geq$10 cm dbh) and seedling and sapling stages (5–400 cm tall) of the economically important Amazonian arboreal palm *Oenocarpus bacaba* respond to edge creation. By combining a two-decade dataset on the demography of larger individuals in fragmented and intact forest with intensive surveys of seedlings and saplings, we were able to address two fundamental questions: (1) Do the recruitment, mortality, and population density of larger trees differ between fragment edge and interior habitats? (2) Does the density of naturally established seedlings and saplings differ between edge and interior habitats? Our findings reveal that both datasets are needed to understand the responses of

this important Amazonian tree species to forest fragmentation.

Methods

Study site

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), the world's largest and longest-running experimental study of habitat fragmentation (Laurance et al. 2002). Located 80 km north of Manaus, Brazil (2°30′ S, 60° W), the BDFFP is comprised of replicated forest fragments of 1, 10, and 100 ha that were isolated in the early to mid-1980s by clearing and burning the intervening forest to create cattle pastures. Reserves ranging from 1 to 1,000 ha in area were delineated in nearby continuous forest to serve as experimental controls (Lovejoy et al. 1986). The BDFFP consists of non-flooded, tropical lowland rainforest from 50 to 150 m in elevation. The forest has a complex canopy architecture from 30 to 40 m tall (Rankin-de-Merona et al. 1992), a high density of smaller-diameter trees and relatively few large ($\geq$60 cm dbh) trees (Nascimento and Laurance 2002), and remarkably high alpha diversity of trees (averaging 280 species ha^{-1} of $\geq$10 cm dbh; Oliveira and Mori 1999). Rainfall ranges from 1,900 to 3,500 mm annually with a pronounced dry season from June to October.

Study species

Oenocarpus bacaba (Arecaceae, Matius) is an arboreal subcanopy palm widely distributed throughout the northern Amazon rainforest (Balick 1986). *O. bacaba* reaches up to 25 m in height and 30 cm in stem diameter and is the most common arboreal palm species in our study area ($X \pm SD = 6.1 \pm 4.0$ trees of $\geq$10 cm dbh ha^{-1}) . The species is monoecious and pollinated by beetles that feed on its pollen (Küchmeister et al. 1998). It produces more fruits than any other palm in central Amazonia, averaging $2,530 \pm 2,260$ fruits per bunch (Lepsch-Cunha 2003), which are consumed by a variety of birds and mammals (Zaminelli 2006). The fruits are 2–2.5×1.3–2 cm in size and dark red to dark blue in color. The tree is economically important; after the fruit is cooked, the pulp provides a nutritious juice

that is much sought after by local people in the Amazon.

Field sampling

Since the early 1980s, a long-term study of tree-community dynamics and composition (individuals ≥ 10 cm dbh) has been conducted in fragmented and continuous forests in the BDFFP study area, based on a network of permanent 1-ha study plots. For this study, we sampled 21 plots located arrayed across four 1-ha fragments and three 10-ha fragments (each sampled with one edge plot), two 100-ha fragments (each with two forest-interior plots and two edge plots), and two continuous-forest sites (each with three forest-interior plots). Edge plots were centered <100 m from the nearest edge, whereas interior plots were >400 m from the nearest edge. All plots were initially censused between January 1980 and January 1987, then recensused four to seven times, with the most recent recensus completed in February 2004. During the initial census, before the fragments were isolated, all trees (including all *O. bacaba*) in each plot were marked with numbered aluminum tags and mapped. During recensuses, all new trees and palms were mapped and marked, and all dead or severely damaged trees (with broken crowns or snapped boles) were recorded.

In 2005, we placed 12 small (0.7 × 14 m) sub-plots within each of the 21 1-ha plots. Each 1-ha plot was evenly divided using six transects, with two sub-plots established along each transect separated by a distance of 20 m. In each sub-plot, all *O. bacaba* seedling and saplings (individuals 5–400 cm tall) were counted and divided into four height classes (5–30, 31–60, 61–100, and >100 cm).

Data analysis

Due to the nature of our sampling design in which most of our 10- and 100-ha forest fragment plots are located in edge environments, to test the effects of fragmentation on *O. bacaba* establishment, we combined the edge plots from the fragment sizes into a single class, 'edge' ($N = 11$) and compared them to unfragmented, forest interior plots ($N = 10$). Statistical comparisons between edges and forest interiors for recruitment, mortality, and density of seedlings and saplings were conducted using non-parametric

Mann–Whitney U-tests in SAS 8.01 (SAS Institute Inc. 1999) with a significance level of 0.05. Prior to these statistical analyses, data were tested for normality (Kolmogorov–Smirnov test statistics), but for all cases non-normal distributions persisted. To avoid pseudoreplication, all the sub-plots were scaled up to the 1-ha level.

Results

Mean recruitment and mortality rates of larger (≥ 10 cm dbh) *O. bacaba* individuals were highly variable among plots, ranging from 0 to 1.06 and 0 to 0.79 trees year^{-1} near forest edges and from 0 to 0.53 and 0.06 to 0.63 trees year^{-1} in forest interiors, respectively. Because of this high variability, there was no significant difference in recruitment rates between edge and interior plots ($P = 0.09$, Mann–Whitney U-test), despite the fact that mean recruitment was over twice as high in edge than interior plots (mean ± SD = 0.43 ± 0.35 vs. 0.19 ± 0.17 trees ha^{-1} year^{-1}). *O. bacaba* mortality, however, was quite similar between edges and interiors, averaging 0.17 ± 0.23 and 0.24 ± 0.20 deaths ha^{-1} year^{-1} in the edge and interior, respectively (Fig. 1a). As a result, the net change in population size in edge plots (+0.26 trees ha^{-1} year^{-1}) was much greater than in interior plots (−0.05 trees ha^{-1} year^{-1}). Overall, the mean density of *O. bacaba* increased in edge plots during our two-decade study, from 4.69 to 9.38 trees ha^{-1} (an increase of nearly 90%), whereas the density of trees in interior plots remained nearly constant (Fig. 1b).

Unlike larger trees, however, the density of seedling and juveniles was significantly lower in edge than interior plots ($P = 0.027$, Mann–Whitney U-test), averaging 1,538 ± 1,769 and 2,755 ± 1,450 stems ha^{-1} in edge and interior habitats, respectively (Fig. 2). This difference was even more evident if a single edge plot with abundant seedlings is removed, with edges then averaging just 1,080 ± 953 stems ha^{-1}. Edge and interior plots differed significantly in the proportion of individuals among the four height classes ($P = 0.0017$, d.f. = 3, $\chi^2 = 15.14$; Chi-square test), with edge plots having a higher proportion of plants in the >100-cm height class than did interior plots (10.6% vs. 2.4%). Most plants in the interior plots were in the smaller size classes (Fig. 3).
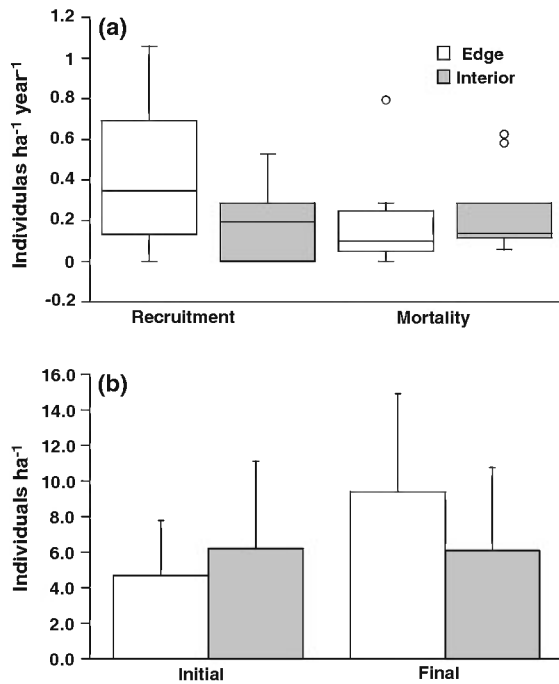
Fig. 1 (a) Comparisons of the medians between edge and interior habitats of the recruitment and mortality of *O. bacaba* and (b) mean (±SD) density of individuals ≥10 cm DBH in the initial (before edge creation) and final (18–22 years after forest fragmentation) census
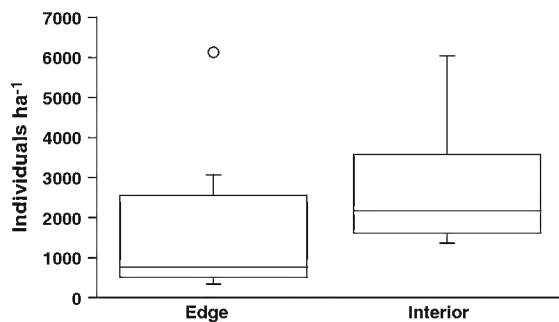
Fig. 2 Comparison of the medians between edge and interior habitats of the density of *O. bacaba* seedlings and juveniles (5–400 cm tall). The graphic shows the quartile-like data dispersion measure. The point above the error bar represents an outlier

Discussion

Our findings suggest that edge creation can have surprisingly varied effects on different life stages of tropical trees. Our fragments are only two-decade old and because many tropical trees are long-lived
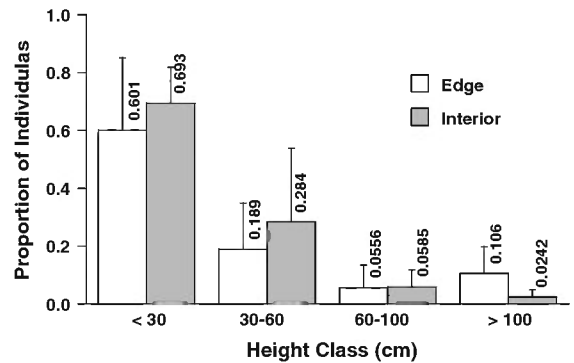
Fig. 3 Proportion of individuals (mean ± SD) of seedlings and juveniles in each of four height size classes for edge and interior habitats. Numbers above bars indicate exact mean proportions

(Laurance et al. 2004), we can assume that all *O. bacaba* individuals that recruited into the ≥10-cm dbh class were established prior to forest fragmentation. The increasing abundance of these larger individuals in edge plots over time suggests that larger *O. bacaba* are favored by forest fragmentation. This evidently arises because of elevated growth of established individuals in edge habitats, where key resources such as light may be less limiting (see below). However, the reduced density in edge plots of smaller seedlings and saplings, which would likely have germinated and become established after fragmentation, paints a very different picture; at least for these early life-stages, forest fragmentation appears to have a negative impact on *O. bacaba* recruitment.

The reduction of seedlings and saplings near forest edges could be a consequence of several processes. In our same study area, Lepsch-Cunha (2003) showed that although adult *O. bacaba* trees are more fecund along forest edges and other degraded habitats than in continuous forest, trees in edge habitats produce abortive seeds at much greater rates. Such habitat-specific differences in reproduction could potentially be caused by pollen limitation and higher rates of biparental inbreeding, leading to inbreeding depression (Cunningham 2000; Cascante et al. 2002). This could in turn affect rates of seed abortion and seedling fitness, with consequences for long-term population recruitment and persistence.

Shifts in animal assemblages in fragment and edge habitats can be important for plant communities. Seed-dispersal agents are especially important for plant

species that are vulnerable to density-dependent seed or seedling mortality (Howe and Smallwood 1982; Clark et al. 2001; Howe and Miriti 2004), such as many palm species (e.g., Cintra and Horna 1997; Silva and Tabarelli 2001; Pimentel and Tabarelli 2004; Galetti et al. 2006). For example, forest fragmentation in Tanzania reduced dispersal agents for the tree *Leptonychia usambarensis* and, as a consequence, caused a decline of juvenile-tree density (Cordeiro and Howe 2003). Similarly, small defaunated forest fragments in the Atlantic forest of Brazil reduced seed consumption and removal of the palm *Astrocaryum aculeatissimum* by rodents and low densities of seedlings and juveniles (Galetti et al. 2006). *O. bacaba* is a large-seeded species that is highly dependent on animals, especially large-bodied rodents and birds, for dispersal (Zaminelli 2006). Scatter-hoarding rodents, such as agoutis and pacas, can have a large effect on seedling recruitment of palm species because seeds buried by these animals exhibit much higher germination rates and seedling survival as a result of protection against predation (Wright et al. 2000; Silva and Tabarelli 2001; Galetti et al. 2006). Zaminelli (2006) reported that fruit removal of *O. bacaba* by rodents is lower in fragments than forest interiors, although some potential avian seed dispersers (such as birds in the Ramphastidae and Cracidae families) could be occasional visitors to fragments. Palms are recognized as being highly prone to pre- and post-dispersal seed predation by rodents and beetles (e.g., Janzen 1971; Forget 1991). In degraded areas, such as young secondary forests (Uhl 1987; Hammond 1995), and in forest fragments (Silva and Tabarelli 2001; Galetti et al. 2006), seed mortality associated with predation was the major cause of mortality. Moreover, because seed resource availability along forest edges is biased in favor of smaller seeds (e.g., Melo et al. 2006) and such seeds are more likely to attract small rodents than large scatterhoarding species, changes in seed resource availability and rodent communities may have cascading effects on plant–rodent interactions in edge habitats and post-dispersal seed predation processes.

In our study area, previous studies have shown that the elevated tree mortality and proliferation of canopy gaps promoting higher light availability are key processes altering tree-community composition near forest edges (Laurance et al. 1998b, 2006a, b). Such microenvironmental alterations (Lovejoy et al. 1986; Kapos 1989) might be responsible for elevated recruitment of *O. bacaba* into the larger ($\geq$10 cm dbh) size class observed in this study and might also explain the high relative abundances of larger (>100 cm tall) saplings observed near forest edges. In fact, in a transplantation experiment, *O. bacaba* growth was over twice as high in secondary forests than in the dark environment of forest interiors (N. Lepsch-Cunha personal communication). As a result, *O. bacaba* individuals along forest edges and in regrowth are shorter and thicker, with a higher diameter:height ratio than individuals growing in forest interiors (Lepsch-Cunha 2003).

Our findings suggest that previously established larger individuals of *O. bacaba* are generally favored in forest fragments, but that the seedlings and saplings of this species are declining in abundance. This finding reveals that different life-history stages of plants may respond very differently to forest fragmentation and edges. Moreover, because most studies of tropical trees focus on larger individuals only, researchers may sometimes be developing a biased view of the winners and losers in fragmented landscapes. Mature *O. bacaba* individuals might appear to be thriving in fragments, but they appear to have limited success in regenerating effectively in situ. Some tree species may even be considered "living-dead" (Janzen 1986) because they can persist as adults but are reproductively non-functional in fragmented habitats. Given both *O. bacaba*'s broad ecological role in Amazonian forests and its economic value motivate researches to improve its conservation, management, and possible silviculture. Because seedling recruitment in the forest interiors in our study was different to that at the edge, we conclude that the conservation of *O. bacaba* and the processes of tree regeneration in fragmented Amazonian forests depend on the management of edges. The largest forest fragments should be a conservation priority, and further fragmentation of existing forests should be avoided, as well as the established and closed forest edge surrounded by well-developed matrix should be maintained.

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