

## Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae*, with Implications for Tropical Tree Diversity<sup>1</sup>

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### ABSTRACT

We examined the interaction between a palm and two bruchid beetles along with several mammal species to explore how poachers and habitat fragmentation may indirectly alter the spatial pattern of seed dispersal, seed predation, and seedling recruitment in central Panama. The large, stony endocarps of *Attalea butyraceae* decay slowly and bear distinctive scars when opened by rodents or beetles. We determined the final distance between endocarps and reproductive trees (which we call an ecologically effective dispersal distance), the predation status of each endocarp, and the distance between seedlings and reproductive trees. The 68 focal trees were divided among 14 sites and four levels of anthropogenic disturbance. Levels of disturbance included full protection from poachers, light and heavy pressure from poachers, and small island habitat fragments. Ecologically effective seed dispersal distances were greatest for protected sites, intermediate for lightly poached sites, and shortest for heavily poached sites and habitat fragments. Seed predation by rodents increased with distance to the nearest reproductive *Attalea* and was greatest for fully protected sites, intermediate for lightly poached sites, and least for heavily poached sites and habitat fragments. Seed predation by beetles reversed the patterns described for seed predation by rodents. Total seed predation by beetles and rodents combined was independent of distance, greatest for fully protected sites, and lower for poached sites and habitat fragments. Seedling densities were always greatest close to reproductive trees; however, the increase in seedling densities close to reproductive trees was minimal for fully protected sites, clearly evident for poached sites, and pronounced for habitat fragments. Increased seedling recruitment near conspecific trees may in time reduce tree diversity where humans disrupt mammal communities.

*Key words:* *Attalea butyraceae*; Barro Colorado Island; *Bruchidae*; *Dasyprocta punctata*; *habitat fragmentation*; *Janzen–Connell hypothesis*; *palm*; *Panama*.

POACHERS AND HABITAT FRAGMENTATION ALTER MAMMAL COMMUNITIES, which may in turn change the spatial pattern of plant regeneration and possibly alter plant diversity. Hunters kill or maim 60 million animals each year in Neotropical forests (Redford 1992). In the Neotropics, preferred game species include monkeys, peccaries, tapir, deer, and the larger caviomorph rodents (Redford & Robinson 1987). These herbivores disperse seeds, eat seeds, and/or browse seedlings. Many of the same species are also highly susceptible to habitat fragmentation and are quickly lost from remnant forest patches wherever humans open forested landscapes. Their loss may directly alter seed dispersal distances and seed and seedling survival. Their loss may have additional indirect effects on plant regeneration if competitive release favors other herbivores. Squirrels, other small rodents, and nocturnal, arboreal mammals are rarely hunted in the Neotropics (Redford & Robinson 1987). Several of these spe-

cies are also less affected by habitat fragmentation. These species also disperse and eat seeds, and their numbers may increase after anthropogenic removal of other mammal species. Insects and microbes that attack seeds and seedlings may also multiply if seed and seedling densities increase. In sum, a range of direct and indirect effects may alter the spatial pattern of plant regeneration when humans disrupt mammal communities.

The spatial pattern of plant regeneration is thought to be a critical factor maintaining tree diversity in tropical forests (Janzen 1970, Connell 1971). Many plant pests are host-specific and congregate near large adult hosts or at dense aggregations of juvenile hosts. If such pests killed virtually every seed near parent trees, then only seeds dispersed some minimum distance from the nearest adult conspecific would be able to survive. This could prevent single-species dominance and maintain space for the regeneration and coexistence of additional tree species (Becker *et al.* 1985, Armstrong 1989). If anthropogenic disturbance of mammal communities changed the spatial pattern of plant regeneration, this could in turn alter plant diversity.

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Janzen (1970) modeled the spatial pattern of plant recruitment as the product of seed density and survival probability. We used his model to explore possible consequences when humans disrupted populations of seed dispersal agents and seed predators (Fig. 1). For simplicity, seed density (I) and survival probability (P) were assumed to be exponential functions of distance to the nearest conspecific tree. The population recruitment curve (PRC), or density of seedling recruits, is the product of P and I and is also an exponential function of distance. Seed density invariably declines with distance to seed-bearing trees (Howe & Smallwood 1982). Survival probabilities often increase with distance, although there are exceptions (McCanny 1985, McCanny & Cavers 1987, Hammond & Brown 1998). For illustrative purposes, we used relative functions for P, I, and PRC suggested by a recent analysis of seed survival for 53 tropical trees (Harms *et al.* 2000). Seed density tended to vary by about three orders of magnitude, seed survival was invariably negatively density dependent, and seed survival tended to vary by about two orders of magnitude so that the density of seedling recruits tended to increase with seed density. Seed density and distance to the nearest reproductive tree are tightly correlated (Howe & Smallwood 1982), and distance was substituted for density in Figure 1A to represent the spatial pattern of plant regeneration for a community with minimal anthropogenic disturbance. When humans reduce seed dispersal agents, seed dispersal distances will decline, making the seed density–distance relationship (I) steeper. All else equal, the steeper seed density–distance relationship will cause a steeper population recruitment curve (Fig. 1B vs. 1A). When humans reduce populations of mammalian seed predators, the survival–distance relationship (P) is expected to shift upwards. A change in slope is not expected because mammals tend to be polyphagous and forage over large areas so that seed and seedling survival is reduced by similar amounts everywhere (Hammond & Brown 1998). All else equal, an upward shift in the survival–distance relationship will cause an upward shift in the population recruitment curve (Fig. 1C vs. 1B). Both changes in the spatial pattern of plant regeneration anticipated when humans disrupt mammal communities increase seedling recruitment near conspecific trees. To the extent that low recruitment near conspecifics facilitates the coexistence of plant species, a decline in plant diversity can be anticipated.

Here, we used the interaction between a palm

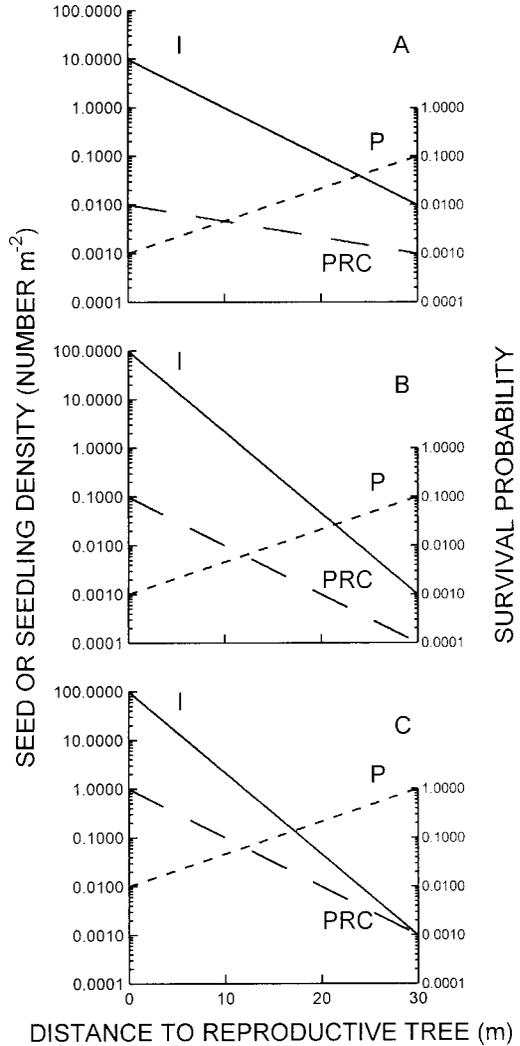


FIGURE 1. Predicted spatial patterns of plant regeneration for a fully protected forest (panel A), a disturbed forest with reduced seed dispersal (panel B), and a disturbed forest with reduced seed dispersal and increased seed and seedling survival (panel C). Following Janzen (1970) as modified by Hubbell (1980), seed density (I, solid line) declines, survival probability (P, short dashed line) increases, and seedling density (PRC, long dashed line) declines with distance to the nearest reproductive conspecific. A recent analysis of seed survival for 53 tropical species suggested the functions for I, P, and PRC in panel A (see text). Changed values in panels B and C represent qualitative predictions.

and two bruchid beetles along with a wide range of mammal species to explore how poachers and habitat fragmentation alter the spatial pattern of seed dispersal, seed predation by beetles and rodents, and seedling recruitment. We tested the pre-

ditions that poachers and habitat fragmentation (1) reduce seed dispersal distances, (2) increase seed survival, (3) increase overall seedling recruitment, and (4) increase seedling recruitment disproportionately near reproductive adults. We also explored secondary effects of poachers and habitat fragmentation on the spatial pattern of seedling recruitment. These secondary effects included seed predation by beetles and additional seed and seedling mortality caused by unknown agents.

## MATERIALS AND METHODS

**STUDY SPECIES.**—The palm *Attalea butyraceae* (Mutis ex. L.f.) Wess. Boer (formerly *Scheelea zonensis*) is abundant in central Panama. The monoecious trees are 30 m tall and produce one to three (rarely four) infructescences each year (DeSteven *et al.* 1987). The number of fruit per infructescence ranges from 100 to 600 (Wright 1990). Fruit mature and seeds disperse between April and October (De Steven 1987, Wright 1990, Forget *et al.* 1994). Each fruit contains a single endocarp with a single seed (rarely two or three seeds) (Bradford & Smith 1977). The stony endocarps are large (3–5 cm long), easy to locate on the forest floor, and persist for several years before decomposing (Wright 1983, 1990; Harms & Dalling 1995). These traits permit quantification of seed dispersal and seed fate (Wright *et al.* 2000). The first two to four (rarely five) leaves produced by seedlings are simple. Older seedlings produce compound leaves and develop into a basal rosette of fronds, which may persist for more than 20 years before trunk growth begins (SJW, pers. obs.).

Several mammals disperse *Attalea* seeds, including white-faced monkeys (*Cebus capucinus*), spider monkeys (*Ateles geoffroyi*), howler monkeys (*Alouatta palliata*), kinkajous (*Potos flavus*), coatis (*Nasua narica*), red-tailed squirrels (*Sciurus granatensis*), agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), and spiny rats (*Proechimys semispinosus*; Enders 1935, Smythe *et al.* 1982, Giacalone-Madden *et al.* 1990, Gompper 1996, Kays 1999). Several species of opossum, olingos (*Bassaricyon gabbii*), tayras (*Eira barbara*), armored rats (*Hoplomys gymnurus*), collared peccaries (*Tayassu tajacu*), and tapir (*Tapirus bairdii*) may also disperse the seeds (Charles-Dominique *et al.* 1981, Kiltie 1981, Fragoso 1997). Red-tailed squirrels and agoutis scatter hoard endocarps, which are rarely buried below 3 cm depth (SJW, pers. obs.). Neither bats nor birds disperse *Attalea* seeds (E. Kalko and C. O. Handley, pers. comm.; SJW, pers. obs.).

Three rodent species and two beetle species eat *Attalea* seeds. Red-tailed squirrels, agoutis, and spiny rats gnaw through the stony endocarps to eat the seed within (Smythe *et al.* 1982, Giacalone-Madden *et al.* 1990, Adler 1995, Hoch & Adler 1997). This leaves persistent and unmistakable tooth scars on the endocarp. Bruchid beetles (*Speonomeris giganteus* [Chevrolat] and *Pachymerus carido* [Fahraeus]) are the only other seed predators (Wright 1990, Johnson *et al.* 1995). The larger *S. giganteus* is overwhelmingly more abundant in Panama (Wright 1990). Adults of both species leave persistent and unmistakable emergence holes.

**STUDY SITES.**—We selected study sites with four distinct levels of anthropogenic influence. The most severely affected were small islands (<2 ha) in Gatun Lake, which was flooded between 1912 and 1914 to complete the Panama Canal. Today the only terrestrial mammals found on these small islands are spiny rats and common opossums (*Didelphis marsupialis*) (Adler & Seamon 1991). We studied Ormosia Island, Annie Island, and unnamed islands numbered 44, 48, and 49 (see maps in Adler & Seamon 1991, Leigh *et al.* 1993). We will refer to the five small islands as habitat fragments.

The remaining study sites fell along a gradient of protection from poachers. Three replicate sites were studied for each of three levels of protection. Wright *et al.* (2000) evaluated levels of protection, levels of poaching, and abundance of game species for each site. Briefly, levels of protection were lowest and poaching was most severe within the eastern margin of the contiguous Parques Nacionales Soberanía and Camino de Cruces near rapidly growing towns. Physical evidence left by poachers was readily apparent at these sites, and the abundance of howler monkeys, white-faced monkeys, collared peccaries, deer, and agouti was very low (see density estimates in Wright *et al.* 2000). Levels of protection were considerably better and poaching occurred at lower levels in remote parts of the Parque Nacional Soberanía and on mainland peninsulas within the Barro Colorado Nature Monument (BCNM). Physical evidence left by poachers was relatively rare at these sites, and the abundance of game species was intermediate. Protection is believed to be complete on Barro Colorado Island (BCI), where there was no physical evidence of poachers and game species were substantially more abundant. We studied heavily poached sites at Plantation Road, Sendero Las Cruces, and Carretera C25 within the eastern portion of the national

parks; lightly poached sites on the Bohio, Peña Blanca, and Gigante Peninsulas within the BCNM; and fully protected sites near the eastern, southern, and western margins of BCI (see map in Wright *et al.* 2000).

The level of protection changed for sites in the national parks and on the mainland of the BCNM in 1979 when the Canal Zone Government ended. Before 1979, hunters from Panama were largely excluded while hunters from the Canal Zone were encouraged. Protection was extended to mainland portions of the BCNM and to the Parques Nacionales Soberanía and Camino de Cruces in 1979, 1979, and 1985, respectively. Poaching began immediately. Many adult palms and older juveniles established under the unknown pre-1979 hunting regime. For this reason, we will only evaluate the performance of seeds and recent seedlings (plants with simple leaves only), which integrate conditions over perhaps three years.

The study sites all support secondary evergreen forests with 20 to 30 m tall canopies (10–20 m on the small islands). Annual rainfall averages 2188 mm at sites to the southeast near the eastern margin of the national parks and 2612 mm to the northwest on BCI (Windsor 1990). This gradient reflects heavier wet season rainfall to the northwest and has little effect on the vegetation. The entire area would be classified as lowland rain forest in a wet climate under Walsh's (1996) scheme. Tree species composition is strikingly similar at all sites except on the small islands (R. Condit, pers. comm.; Leigh *et al.* 1993).

**CENSUSES OF ENDOCARPS AND SEEDLINGS.**—Endocarp and seedling censuses were conducted between January and June 2000 for reproductive trees. Reproductive trees supported an infructescence in their crown or had fallen spathes or pedicels on the ground beneath. A 30° wedge-shaped transect was extended 30 m from the base of potential census trees. Transects were discarded if a second reproductive tree fell within 30 m of the transect. Trees were discarded if no possible transect met this criterion. We censused one tree for two small islands; two trees for three small islands; and five, six, and seven trees for Plantation Road, Carretera C25, and the seven remaining mainland and BCI sites, respectively. One transect was censused for each tree. Seedlings were defined to include all *Attalea* lacking compound leaves (simple leaves only) and were tallied exhaustively within each transect, noting distance to the focal tree.

The large, durable endocarps of *Attalea* made

it possible to locate dispersed seeds. We collected endocarps from the leaf litter and the upper 3 cm of soil from 0.25 m<sup>2</sup> plots. Old decomposing endocarps, which could be crushed by hand (HCD), were excluded because decomposition may have obliterated scars left by bruchids and rodents. Recent endocarps dispersed in 2000 were readily distinguished by the presence of fibrous mesocarp and were also excluded because they first appeared part-way through the census. Endocarp plots were located at the following distances from each census tree: 2, 5, 8, 11, 14, 17, 20, 23, 26, and 29 m. The number of plots at each distance was 3, 3, 3, 4, 5, 6, 7, 8, 9, and 10, respectively. Plots were placed at 1 m intervals perpendicular to transect midlines and were displaced to avoid large rocks and tree boles. The absolute number of seeds and seedlings at each distance was estimated by multiplying mean density by the area of a 1 m wide annulus at the appropriate distance from the central reproductive tree. Henceforth, distance will refer to distance to the nearest reproductive tree.

**SEED PREDATION.**—Endocarps were placed in one of the following categories: opened by bruchids, opened by rodents, or unopened. Emergence holes and tooth scars identified endocarps opened by bruchids and rodents, respectively. A small number of endocarps had both types of scars. These mostly multi-seeded endocarps were considered opened by both bruchids and rodents. The “unopened” category included a small number of viable endocarps and large numbers of empty endocarps. We discount the possibility that a seed failed to develop within an empty endocarp because several thousand recently mature fruit have been opened without encountering an empty endocarp (Wright 1983, 1990). Microbes may have killed the seeds from empty endocarps (Janzen 1971); however, this has rarely been observed in central Panama (Wright 1983, 1990). Most empty endocarps probably germinated and then died as seedlings. To maintain sample size, proportions of endocarps opened by bruchids and rodents were calculated after pooling the following census distances: 2 m; 5 and 8 m; 11, 14, and 17 m; and 20, 23, 26, and 29 m.

Rodents eat the great majority of *Attalea* seeds in forests protected from poachers in central Panama (Wright *et al.* 2000). Seedling recruitment would increase dramatically in areas where humans reduced rodent abundance unless other mortality agents compensated. To quantify compensatory mortality caused by bruchids, the relationship be-

tween the proportion of endocarps opened by bruchids and the proportion of endocarps opened by rodents was evaluated. Bruchids will have precisely compensated if this relationship is linear with a slope equal to  $-1$ .

**SEEDLING-TO-ENDOCARP RATIOS.**—The ratio of seedling density to endocarp density provides an index of survivorship that integrates all sources of mortality. The interpretation of seedling-to-endocarp ratios is, however, complicated by unknown differences in endocarp and seedling longevity. A simple example illustrates the complication. If every endocarp decomposed after  $e$  years and every surviving seedling produced its first compound leaf and left the seedling cohort after  $s$  years, the ratio would incorporate  $e$  and  $s$  years of reproductive effort for endocarps and seedlings, respectively. Mean values of  $e$  and  $s$  are probably between two and three years (SJW, pers. obs.). Nonetheless, seedling-to-endocarp ratios must be interpreted cautiously until distributions of  $e$  and  $s$  are determined. In the meantime, relative values of seedling-to-endocarp ratios should be valid for comparisons when the distributions of  $e$  and  $s$  are similar. The understory microenvironment largely controls rates of endocarp decay and seedling growth, and hence, distributions of  $e$  and  $s$ . Understory microenvironments were indistinguishable across the poaching gradient but were lighter and drier on the small islands (Asquith 1998). For this reason, we only compared seedling-to-endocarp ratios for sites within the poaching gradient and for distances within each type of site. The ratio was not compared for small islands versus other sites. To maintain sample sizes, seedling-to-endocarp ratios were calculated after pooling the following census distances: 2 m; 5 and 8 m; 11, 14, and 17 m; and 20, 23, 26, and 29 m.

**ANALYSES.**—Seed and seedling densities; proportions of endocarps opened by beetles, by rodents, and by beetles and rodents combined; and seedling-to-endocarp ratios were analyzed by repeated measures analyses of variance (ANOVA). For each analysis, the grouping factor was the level of protection from poachers, and the repeated measures factor was distance to the nearest reproductive *Attalea*. For the analysis of seed density, trees were replicates and sites were nested within levels of protection. The nested site factors were insignificant ( $F_{6,51} = 1.19$  for Site[Protection];  $F_{34,455} = 0.089$  for Site[Protection]  $\times$  Distance). For the remaining analyses, sparse data at the level of individual trees

precluded treating trees as replicates. Instead, trees were pooled within sites, and sites served as replicates. Angular transformation of proportions and ratios and logarithmic transformation of densities largely satisfied the compound symmetry assumption of repeated measures ANOVA (see Results). To transform zero density at appropriate scales, seed and seedling density were transformed as  $\ln(\text{density} + 1)$  and  $\ln(\text{density} + 0.001)$ , respectively.

The small island habitat fragments were excluded from the ANOVA analyses to isolate the effects of poaching and because there were just one or two census trees per island. Data from the small islands are presented in Figures for visual comparison.

Linear regression was performed to evaluate the relationship between proportions of endocarps opened by bruchids versus rodents. The proportion opened by rodents was treated as the independent variable because rodents preempt bruchids (Wright *et al.* 2000). To maintain sample size, proportions were calculated after pooling island fragments and the following census distances: 2 m; 5 and 8 m; 11, 14, and 17 m; and 20, 23, 26, and 29 m.

All analyses were performed with SYSTAT 8.0 (SPSS 1998).

## RESULTS

**SEED DISPERSAL.**—We collected 4929 endocarps (Table 1). Just 177 were viable.

Distances between endocarps and the nearest reproductive tree represent ecologically effective dispersal distances. True dispersal distances are unknown because source trees are unknown and dispersal may place an endocarp closer to an unrelated tree than to its source tree. The measured distances are ecologically effective dispersal distances with respect to intraspecific interactions and with respect to herbivores and pathogens that concentrate near reproductive trees. The measured distances represent final effective dispersal distances for endocarps that had germinated or died. Further secondary dispersal of viable endocarps is unlikely because the mesocarp that attracts dispersal agents decays within one month of fruitfall (Forget *et al.* 1994) and our censuses began four months after the fruiting season ended. Henceforth, ecologically effective dispersal distance will refer to the spatial pattern of endocarps with respect to the nearest reproductive *Attalea*.

Endocarp density declined faster than exponentially with distance (Fig. 2A). The rate of decline

TABLE 1. Sample effort and numbers of endocarps and seedlings encountered.

Type of site	No. of sites	Trees/site	No. of endocarp plots	No. of endocarps <sup>a</sup>	No. of seedling transects	No. of seedlings <sup>b</sup>
Fully protected	3	7	1218	1036	21	136
Lightly poached	3	7	1218	2332	21	545
Intensely poached	3	5, 6, 7	1160	1267	18	217
Small islands	5	1, 1, 2, 2, 2	464	294	8	39

<sup>a</sup> Excludes decomposing endocarps that could be crushed by hand and recently matured endocarps that had fresh mesocarp.

<sup>b</sup> Seedlings with entire leaves only. Excludes juveniles with compound leaves.

varied with the level of protection (significant distance–protection interaction in Table 2). Endocarp density fell with distance by roughly one, two, and three orders of magnitude at fully protected, lightly poached, and heavily poached sites, respectively (Fig. 2A). Absolute numbers of endocarps were independent of distance for fully protected sites and declined with distance for poached sites (Fig. 2B). Ecologically effective dispersal distances were very similar for small islands and heavily poached sites (Fig. 2).

SEEDLINGS.—We sampled 937 seedlings (Table 1). Seedling density declined with distance (Fig. 3A). Once again, the rate of decline varied with the level of protection (significant distance–protection interaction in Table 2). Seedling density fell minimally at fully protected sites and by less than one order of magnitude at both lightly and heavily poached

sites (Fig. 3A). In contrast, absolute numbers of seedlings increased with distance for fully protected sites, first increased then decreased with distance for lightly poached sites, and declined with distance for heavily poached sites (Fig. 3B).

The distribution of seedlings with respect to the nearest reproductive tree was distinctive on small islands (Fig. 3). The decline in seedling density with distance was much steeper on small islands than at any other site (Fig. 3A). Absolute numbers of seedlings were unusually low beyond 10 m from the nearest reproductive tree (Fig. 3B).

SEED PREDATION.—Bruchids rarely opened more than 50 percent of endocarps (Fig. 4A). The proportion of endocarps opened by bruchids decreased with distance at all sites (Table 2). Levels of bruchid infestation also tended to differ, with the level of protection being greatest at heavily poached sites

TABLE 2. Repeated measures analyses of variance for endocarp density (Fig. 2A); seedling density (Fig. 3A); the proportion of endocarps opened by bruchids (Fig. 4A), by rodents (Fig. 4B), and by bruchids and rodents combined (Fig. 4C); and seedling-to-endocarp ratios (Fig. 6). Entries are F-values and, in the final row, Huynh-Feldt epsilon values. The grouping factor is the level of protection from poachers. Repeated measures are on distance to the nearest reproductive *Attalea butyraceae*. Logarithmic transformations of densities and angular transformations of proportions and ratios largely satisfied the compound symmetry assumption (Huynh-Feldt epsilon approaches 1). Within-subjects significance levels reflect the Huynh-Feldt correction.

Source	Endocarp density	Seedling density	Dependent variable			
			Bruchid opened endocarps	Rodent opened endocarps	Total opened endocarps	Seedling: endocarp
Between-subjects						
Protection	8.87***	5.69*	4.45†	6.68*	17.4**	26.1**
Within-subjects						
Distance	142.0***	4.71**	3.95*	6.15**	1.91	7.07*
Distance*Protection	6.70***	2.63*	1.73	1.43	0.656	1.64
Huynh-Feldt epsilon	0.99	0.70	0.73	0.88	0.97	0.55

†  $P = 0.0653$ .

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

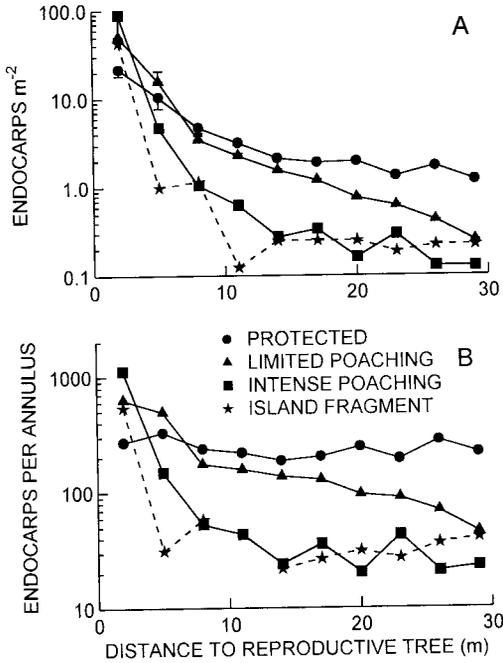


FIGURE 2. Post-dispersal density (panel A) and absolute number (panel B) of endocarps of *Attalea butyraceae*. The horizontal axis represents distance to the nearest reproductive *A. butyraceae*. Endocarp density declines faster than exponentially with distance (panel A). This decline was least for fully protected sites, intermediate for lightly poached sites, and greatest for severely poached sites and for small island fragments (dashed line). Absolute numbers of endocarps in 1 m wide annuli were unaffected by distance at protected sites and declined with distance at other sites (panel B). Means ( $\pm 1$  SEM in panel A) are plotted. Error bars are unidirectional to minimize overlap. Error bars were smaller than plotting symbols for severely poached sites and island fragments (except at 2 m distance when 1 SEM equaled 29 and 16, respectively).

and least at fully protected sites (marginally significant in Table 2).

Rodents opened up to 97.8 percent of endocarps and frequently opened more than 50 percent of endocarps (Fig. 4B). Seed predation by rodents reversed the trends observed for bruchids. Seed predation by rodents increased with distance and differed with the level of protection, being greatest for fully protected sites and least for heavily poached sites (Table 2).

Together bruchids and rodents opened between 67 and 98 percent of endocarps (Fig. 4C). There was a linear relationship between proportions of endocarps opened by bruchids and rodents (Fig. 5,  $R^2 = 0.86$ ). The slope of this relationship ( $-0.73 \pm 0.048$  [95% ci]) was significantly less than zero

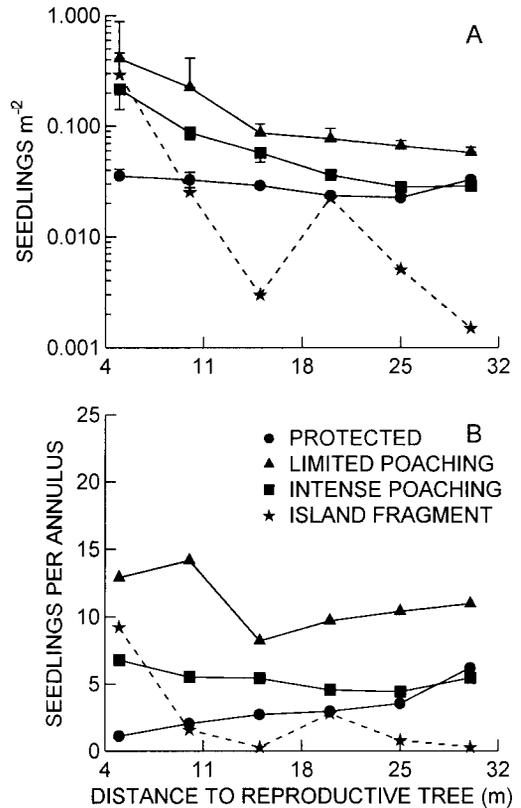


FIGURE 3. The density (panel A) and absolute number (panel B) of seedlings of *Attalea butyraceae*. The horizontal axis represents distance to the nearest reproductive *A. butyraceae*. Seedling densities were nearly independent of distance for fully protected sites, declined with distance for lightly and severely poached sites, and declined most rapidly with distance for small island fragments (panel A). Absolute numbers of seedlings in 1 m wide annuli increased with distance at protected sites, peaked at intermediate distance for lightly poached sites, declined with distance at severely poached sites, and declined rapidly with distance in small habitat fragments (panel B). Means ( $\pm 1$  SEM in panel A) are plotted. Error bars are unidirectional to minimize overlap.

and greater than  $-1$  ( $t = -15.2$  and  $t = -5.71$ , respectively;  $df = 38$ ,  $P < 0.001$ ). Thus, bruchids partially compensated for differences in seed predation by rodents and emerged from an average of 73 percent of the endocarps that escaped rodents. Total seed predation by bruchids and rodents differed significantly among sites, with higher predation at fully protected sites (Table 2). Total seed predation was unaffected by distance (Table 2).

Levels of bruchid infestation were unusually severe near reproductive trees on small islands (Fig. 4A). Seed predation by rodents was similar for

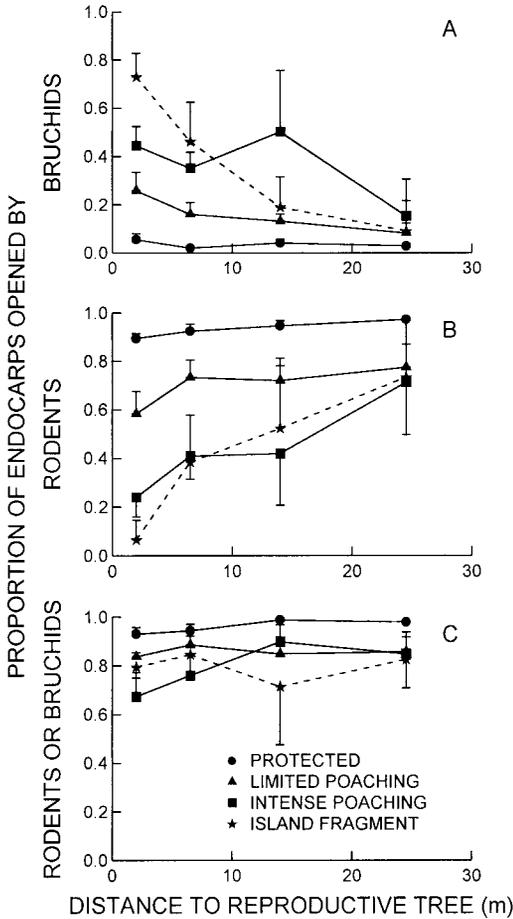


FIGURE 4. Predation on endocarps of *Attalea butyraceae* by bruchid beetles (panel A), by rodents (panel B), and by bruchids and rodents summed together (panel C). The horizontal axis represents distance to the nearest reproductive *A. butyraceae*. Bruchids and rodents had opposing effects. Bruchids destroyed a greater proportion of endocarps near reproductive palms, on small habitat fragments, and where protection from poachers was most limited. Rodents destroyed a greater proportion of endocarps away from reproductive palms, on large landmasses, and where protection from poachers was greatest. Means ( $\pm 1$  SEM) are plotted. Error bars are unidirectional to minimize overlap.

small islands and heavily poached sites (Fig. 4B). Total seed predation by bruchids and rodents combined was similar for small islands and poached sites (Fig. 4C).

SEEDLING-TO-ENDOCARP RATIOS.—The ratio of seedling density to endocarp density varied among levels of protection, being greater when poachers were active (Fig. 6; Table 2). This difference was similar

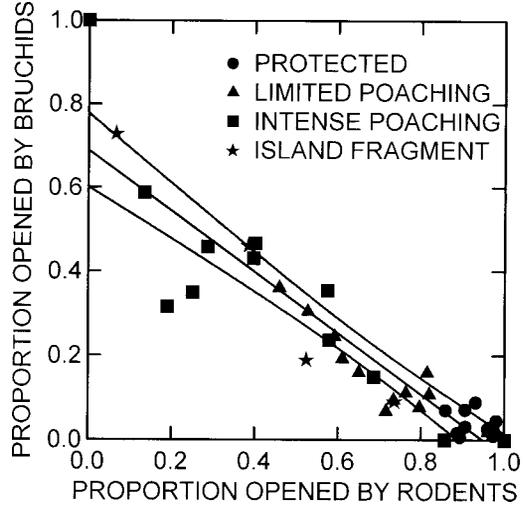


FIGURE 5. The relationship between the proportions of endocarps of *Attalea butyraceae* opened by bruchid beetles and by rodents. Solid lines represent the least squares linear regression and its 95 percent confidence limits. The slope ( $-0.73 \pm 0.048$  [ $\pm 95\%$  confidence limits]) indicates that bruchids only partially compensated when seed predation by rodents fell to low levels. Each symbol represents a site–distance combination, with distances pooled as in Figures 4 and 6 and sites pooled for island fragments only.

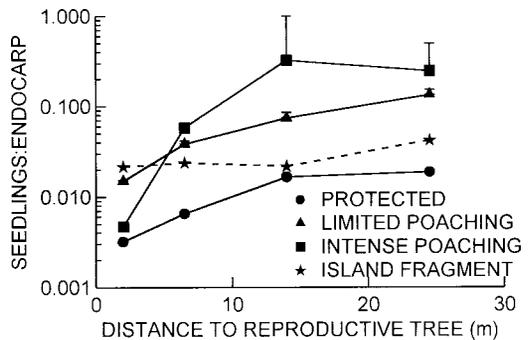


FIGURE 6. Recruitment success of *Attalea butyraceae* as estimated by the ratio of seedling density to endocarp density. This ratio integrates all agents of mortality over the earliest stages of *Attalea* regeneration. The horizontal axis represents distance to the nearest reproductive *A. butyraceae*. Seedling-to-endocarp ratios were greater where poachers were active and increased with distance across the poaching gradient but not on small islands. Means ( $\pm 1$  SEM) are plotted. Error bars are unidirectional to minimize overlap. Sparse data beyond 5 m distance precluded calculation of standard errors for small islands.

in magnitude to the difference in seed predation by rodents and bruchids combined (compare the complement of values in Fig. 4C with values in Fig. 6). Seedling-to-endocarp ratios increased with distance for all levels of protection (Fig. 6; Table 2). In contrast, total seed predation by rodents and bruchids combined was independent of distance (Fig. 4C; Table 2); thus, unknown agents of mortality must have introduced the distance dependence evident for seedling-to-endocarp ratios. We believe most of this additional mortality occurs after germination as seedlings succumb to shade, pathogens, herbivores, and falling debris. Debris falling from the nearest reproductive *Attalea* can be discounted as a factor contributing to distance dependence for two reasons. First, falling debris rarely extends 2 m from the source tree (Wright *et al.* 2000); second, all trees produce similar debris and yet the distance dependence was absent on small islands (Fig. 6). We conclude that unknown pathogens and seedling herbivores caused disproportionate increases in mortality near reproductive trees across the poaching gradient, but not on small islands.

## DISCUSSION

Our initial four predictions were supported. Ecologically effective seed dispersal distances were greatest at fully protected sites, intermediate at lightly poached sites, and lowest at heavily poached sites and on habitat fragments (Fig. 2). Seed survival and seedling recruitment were lowest at fully protected sites and greater with anthropogenic disturbance (Figs. 3, 4C, and 6). Most importantly, the increase in seedling recruitment with anthropogenic disturbance was disproportionately large near reproductive trees (Fig. 3). An earlier study of *Attalea* regeneration contrasted areas within 2 m of seed-bearing trees versus areas away from seed-bearing trees (Wright *et al.* 2000). Poaching was associated with lower proportions of seeds dispersed away, lower levels of rodent predation on dispersed seeds, higher levels of beetle predation on dispersed seeds, and higher seedling recruitment. The present study extends these earlier results to small island habitat fragments and to distances beyond 2 m from the nearest seed-bearing tree.

We believe the relationships among poaching intensity, habitat fragmentation, seed dispersal, seed predation, and seedling recruitment are causal. Habitat fragmentation and poaching altered mammal communities. The fully protected site supports 17 mammal species likely to disperse *Attalea* seeds

and 3 rodent species that eat *Attalea* seeds (see Study Species). Two potential dispersal agents are absent from all other sites (spider monkeys and tapir), and 13 additional dispersal agents and 2 rodent seed predators are absent from the small islands. Moreover, the abundance of several dispersal agents and 2 rodent seed predators are greatest at the fully protected site and progressively lower at more heavily poached sites (Wright *et al.* 2000). Anthropogenic disturbance lowered the abundance and diversity of seed dispersal agents and rodent seed predators. This in turn lowered effective seed dispersal distances and levels of seed predation by rodents. Bruchids were only able to compensate partially for the lower levels of rodent seed predation, consuming 73 percent of the seeds that escaped rodents (Fig. 5). To summarize, anthropogenic disturbance indirectly reduced seed dispersal and seed predation. This concentrated seeds near reproductive trees and enhanced seed survival. As a consequence, seedling recruitment increased with the intensity of anthropogenic disturbance, with disproportionate increases near seed-bearing trees.

**ANTHROPOGENIC EFFECTS ON HIGHER TROPHIC LEVELS.**—Poachers and habitat fragmentation also remove felids and large raptors that prey on herbivorous mammals. Terborgh (1992) hypothesized that felids control the abundance of many herbivorous mammals in pristine Neotropical forests. This hypothesis is relevant here because it is widely believed that felids are absent from our fully protected sites on BCI and that several herbivorous mammals are unusually abundant as a result (Redford 1992, Terborgh 1992). If the BCI mammal community were unusual, our interpretation of poaching effects would require modification. We will therefore review recent studies of BCI mammals.

A recent survey evaluated all published abundance estimates for Neotropical forest mammals (bats and primates restricted to South America excluded; Wright *et al.* 1994). The status of felids was determined from the original publication or by contacting the authors. The presence or absence of puma (*Felis concolor*) and jaguar (*Panthera onca*) had no effect on the abundance of 14 herbivorous taxa (ecologically similar congeners were pooled). Moreover, BCI abundance estimates were above the median for 7 taxa and below the median for 7 taxa. The abundance data do not suggest that the mammal community of BCI is atypical. Nonetheless, it is widely believed that the agouti, in particular, is

superabundant on BCI (Redford 1992, Terborgh 1992). We therefore emphasize agouti below.

Ongoing observations indicate that the three largest Neotropical felids are present on BCI. The ocelot (*Felis pardalis*) has always been resident and surprisingly abundant on BCI (Enders 1935, 1939; Glanz 1982; Wright *et al.* 1994) despite published assertions to the contrary (Redford 1992). Agouti remains were found in 22 percent of 60 ocelot scats recently collected on BCI (R. Moreno, pers. comm.). Trip cameras operated on BCI recorded up to four different puma in a single dry season in the 1920s (Enders 1935). Poachers became active on BCI in the 1930s and puma sign declined (Enders 1939). The first systematic survey of mammal sign conducted away from permanent trails on BCI since the 1930s detected puma tracks in 1997 and 1998 (SJW, pers. obs.). The first trip cameras operated systematically on BCI since the 1920s photographed two different puma in 1999 and three different puma in 2000 (J. Giacalone, pers. comm.). The status of puma on BCI between the 1930s and 1997 may never be known. Agouti remains were found in 31 percent of 42 puma scats recently collected on BCI (R. Moreno, pers. comm.). Jaguar were never resident after BCI became an island; however, jaguar swim freely to BCI (Enders 1935). Reliable observers sighted jaguar on BCI in 1983, 1988, 1993, 1994, and 1998 (G. Willis, C. Handley, B. DeLeon, J. Dalling, and A. Dircz, pers. comm.), and repeated sightings of tracks suggest a kitten was raised successfully in 1993. To summarize, ocelot are resident on BCI, puma have been resident since at least 1997, and jaguar are irregular visitors. The presumption that BCI lacks large felids is incorrect. Moreover, both ocelots and puma prey upon the agouti, which is most frequently cited as the superabundant mammal on BCI. We conclude that the available evidence is inconsistent with the hypothesis that an absence of felids has permitted herbivorous mammals to attain unusual abundance levels on BCI.

**DISTANCE-DEPENDENT RECRUITMENT.**—Seed predation may increase or decrease with distance to seed-bearing trees depending on the numerical and functional responses of herbivores (McCanny 1985). Many insects have a strong numerical response and congregate near seed-bearing trees so that seed mortality decreases with distance (Janzen 1970, Hammond & Brown 1998). Bruchids congregate at seed-bearing *Attalea* (Janzen 1971, Wright 1990), and the proportion of endocarps opened by bruchids decreased with distance (Fig.

4A; Table 2). In contrast, vertebrates often have relatively weak numerical responses and may be satiated near seed-bearing trees so that seed mortality is unaffected by distance or actually increases with distance to the nearest seed-bearing tree (McCanny 1985, McCanny & Cavers 1987, Hammond & Brown 1998). The social systems of the three rodent seed predators potentially limit their numerical response (Smythe 1978, Glanz *et al.* 1982, Adler *et al.* 1997, Seamon & Adler 1999), and the proportion of endocarps opened by rodents increased with distance (Fig. 4B; Table 2). Negative distance dependence characterized seed predation by bruchids, and positive distance dependence characterized seed predation by rodents. Total seed predation by bruchids and rodents combined integrates these offsetting trends and was independent of distance (Fig. 4C; Table 2). Total seed predation did not contribute to the distance dependence of seedling recruitment.

The spatial pattern of seedling recruitment reflected limited seed dispersal and distance-dependent mortality caused by agents other than seed predators. Seed density declined with distance (Fig. 2), an index of seed plus early seedling survival increased with distance (Fig. 6), the density decline was always stronger than the survival increase, and seedling density decreased with distance for all levels of anthropogenic disturbance (Fig. 3). In terms of Janzen's (1970) model of plant regeneration, the seedling recruitment curve always peaked near reproductive trees.

**DIVERSITY AND SPECIES COMPOSITION OF PLANT COMMUNITIES.**—Anthropogenic disruption of mammal communities had two effects on *Attalea* regeneration, with implications for the structure and diversity of plant communities. First, poaching was associated with decreased seed predation by rodents and a concomitant increase in overall seed survival for all distances from 2 to 29 m from reproductive trees (Figs. 4B and 6; Table 2). All else equal, increased seed survival will increase *Attalea* abundance, altering plant species composition. More generally, the anthropogenic disruption of mammal communities has widespread potential to change plant species composition given the wide range of strengths of interaction between particular plant species and particular mammal species (Dirzo & Miranda 1991, Redford 1992, Terborgh 1992, Wright *et al.* 2000). Such changes in species composition could increase or decrease plant diversity, depending upon the relative abundance of species

avored or hindered by the disruption of mammal communities.

The second effect, with direct implications for plant diversity, concerns the spatial pattern of *Attalea* regeneration. Widespread failure to regenerate near conspecific adults could prevent single-species dominance and maintain space for the regeneration and coexistence of additional tree species (Janzen 1970, Connell 1971). We have already seen that *Attalea* seedling densities were always greatest near conspecific adults (Fig. 3A); however, the distance dependence of seedling density varied with anthropogenic disturbance so that absolute numbers or frequencies of seedlings were greatest far from adults at fully protected sites, peaked at intermediate distances for lightly poached sites, and were greatest near adults for heavily poached sites and for small islands (Fig. 3B). Becker *et al.* (1985) demonstrated that adult-to-adult recruitment distances will reflect seedling frequency, and not seedling density, when successful regeneration requires a randomly distributed microhabitat (*e.g.*, treefall gaps). Changes in the spatial pattern of early regeneration associated with humans may have set the stage for increased adult recruitment near existing adults and for a decline in plant diversity.

Plant diversity may decline when anthropogenic disturbance reduces seed dispersal and increases seed survival. Recruitment distant from reproductive conspecifics will be buffered if lower seed dispersal is offset by higher seed survival. Recruitment near reproductive conspecifics will be greatly enhanced if the concentration of poorly dispersed seeds is reinforced by higher seed survival. This appears to describe the response of *Attalea* regeneration to poaching. Seedling density far from adults was similar for poached and fully protected sites because the lower seed density at poached sites was offset by higher seed survival (Figs. 2, 3, and 6). Seedling density near adults was much greater at poached sites than at fully protected sites because the much greater seed density was reinforced by greater seed survival (Figs. 2, 3, and 6). Seedling recruitment far from adults was unaffected by poaching, and seedling recruitment near adults was increased by poaching. This could reduce plant diversity by allowing *Attalea* to regenerate in monospecific stands.

The small Gatun Lake islands were isolated 86 years ago and offered an opportunity to evaluate the effects of habitat fragmentation on tree diversity (Leigh *et al.* 1993). Tree diversity was lower on the small islands than for mainland plots of similar size. Tree species composition was also remarkably similar across the small islands, largely because *Attalea* and two other species with relatively large seeds, *Protium panamense* and *Swartzia simplex*, were codominants on many islands. Leigh *et al.* (1993) inferred that tree diversity had collapsed and tree species composition had converged after the small islands were isolated. Drought associated with the 1997–1998 El Niño lowered the level of Gatun Lake by 7 m and offered an opportunity to validate this inference by examining the forest drowned in 1914 and preserved by the anaerobic conditions of Gatun Lake. The distinctive trunk of *Attalea* was rare in the drowned forest, even immediately adjacent to small islands on which *Attalea* today dominates the canopy layer (SJW, pers. obs.). This confirms the inference that *Attalea* abundance increased markedly in the past 86 years. On small islands, seed survival was unaffected by distance to the nearest reproductive adult (Fig. 6) and seedling densities near adults were among the largest observed (Fig. 3A). This suggests a connection between enhanced recruitment near adults and low tree diversity.

Monospecific carpets of seedlings are commonplace beneath conspecific trees at Las Tuxtlas, Mexico, where poachers and habitat fragmentation have severely altered the mammal community (Dirzo & Miranda 1991). Monospecific carpets of seedlings have also developed in large fenced plots that exclude mammals in Panama (W. Carson, pers. comm.). The widespread disruption of mammal communities by humans may have profound effects on plant diversity in tropical forests.

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