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Forest Fragmentation Reduces Seed Dispersal of *Duckeodendron cestroides*, a Central Amazon Endemic

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ABSTRACT

Fragmentation that alters mutualistic relationships between plants and frugivorous animals may reduce the seed dispersal of trees. We examined the effects of forest fragmentation on the distributions of seeds and seedlings of a Central Amazon endemic tree, *Duckeodendron cestroides*. In the dry seasons of 2002–2004, seeds and first-year seedlings were counted within wedge-shaped transects centered around *Duckeodendron* adults in fragments and nearby continuous forests at the Biological Dynamics of Forest Fragmentation Project. Analyses showed that fragmentation reduced seed dispersal quantity and quality. The percent and distance of dispersed seeds were both twice as great in continuous forest as in fragments. The distances of each tree's five furthest dispersed seeds were three times greater in continuous forest than fragments. Over the 3-yr study, 20 times more seeds were dispersed more than 10 m from parent crowns in continuous forest than fragments. A regression analysis showed more dispersed seeds at all distances in continuous forest than fragments. Dispersal differences were strong in 2002 and 2004, years of large fruit crops, but weak or absent in 2003, when fruit production was low. As distance from parent crowns increased, the number of seedlings declined more rapidly in fragments than continuous forest. Distance-dependent mortality between the seed and seedling stages appeared to be more important in continuous forest than fragments. This research provides ample, indirect evidence demonstrating that forest fragmentation can result in the breakdown of a seed dispersal mutualism, potentially jeopardizing the reproduction of a rare, tropical tree.

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

Key words: Brazil; mutualism; random coefficient regression; seedling germination; tropical wet forest.

FRAGMENTATION OF ONCE CONTINUOUS FOREST CAN HAVE DRAMATIC EFFECTS. Animal and plant populations often decline and become less resilient to disturbance, with many species becoming extirpated from fragments (Silva & Tabarelli 2000, Laurance *et al.* 2002, Ferraz *et al.* 2003). Additionally, some tree species in fragments exhibit increased mortality (Laurance *et al.* 2000) and decreased recruitment (Benitez-Malvido 1998).

The effects of fragmentation may be exacerbated in tropical forests where biotic interactions prevail, interconnecting many species, especially through mutualisms (Gilbert 1980). Reduced plant regeneration in tropical fragments may be related to declines in animal species that are vectors for pollination and seed dispersal (Howe 1977, Howe 1984, Benitez-Malvido 1998, Tabarelli *et al.* 2004). Fragmentation can also cause changes in frugivore behavior, resulting in reduced seed dispersal (McConkey & Drake 2006). How forest fragmentation alters mutualistic processes, such as seed dispersal, is a priority for research (Laurance *et al.* 2002), given the paucity of studies (Wright & Duber 2001, Cordeiro & Howe 2003, Dick *et al.* 2003, Bruna *et al.* 2005, Galetti *et al.* 2006).

Here, we present evidence for changes in the seed dispersal of the rare tropical tree *Duckeodendron cestroides* Kuhlm. (Solanaceae), which are caused by forest fragmentation. *Duckeodendron cestroides* fruit is consumed by primates and terrestrial mammals such as peccaries, agoutis, and pacas. However, many of these medium-to-large vertebrates are rare in or absent from forest fragments in the Amazon Basin (Gilbert & Setz 2001). For *Duckeodendron*, we hypothesized that the decline in seed dispersers would result in reduced seed dispersal and seedling recruitment. Specifically, we ask the following: (1) Does forest fragmentation result in the reduced quantity (number of seeds) and/or quality (seed distance), *sensu* Schupp (1993), of seeds dispersed away from parent *D. cestroides*? (2) Are fragmentation effects on seed dispersal constant from year to year? (3) Are first-year seedling distributions a reflection of seed dispersal distributions or are they affected by distance-dependent mortality, *sensu* the Janzen-Connell hypothesis?

METHODS

STUDY SITE.—This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), a collaborative research program between Brazil's National Institute for Amazonian Research (INPA) and the Smithsonian Tropical Research Institute (STRI). The BDFFP reserves are located on nonflooded upland (terra firme) tropical moist forest, *ca* 80 km north of Manaus in the state of Amazonas, Brazil (2°30′ S, 60° W) (Lovejoy & Bierregaard 1990). Mean annual rainfall is 2651 mm, with a distinct, but mild, dry season (Laurance 2001). Mean annual temperature is 26°C (Bruna 2002). Density of trees $>$ 10 cm dbh averages 613 stems/ha and trees $>$ 60 cm dbh are uncommon with only 11 stems/ha (Laurance

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2001). Alpha diversity is high, with over 1000 species of trees in 61 families and 288 genera (Gascon & Bierregaard 2001).

Between 1980 and 1984, 11 fragments (five 1-ha, four 10-ha, and two 100-ha) were isolated from continuous rain forest by clear-cutting, often followed by burning around each fragment (Gascon & Bierregaard 2001). The BDFFP monitors tree species in these reserves every 6–13 yr.

STUDY SPECIES.—*Duckeodendron cestroides* is an emergent tree, endemic to the Central Amazon. With adult densities of 0.5/ha (BDFFP data base) to 1.3/ha (Oliveira 1997), *Duckeodendron* exhibits a rarity representative of nearly 80 percent (404/513) of the tree species in the Central Amazon (Oliveira 1997). Since its description in 1925, the genus *Duckeodendron* has been placed into various families, including its own, the Duckeodendraceae (Kuhlmann 1947). More recently, molecular data have assigned this species to a monospecific genus in the Solanaceae (Fay *et al.* 1998). To date, there have been no published studies on the ecology of *D. cestroides*.

Fruiting of *D. cestroides* peaks in the dry season (Oliveira 1997), although ripe fruits can be found on the forest floor throughout the year and old fruits without pulp can persist on the ground for months. Fruits are pyriform drupes *ca* 59 mm long by 34 mm wide (J. M. Cramer, pers. obs.). When ripe, the fruit possesses a thin, orange exocarp (the pulp) that covers a thick, fibrous mesocarp of hair resembling the husk of a coconut in texture (Santiago-Valentin & Olmstead 2003). The pulp has a strong, stinky odor. Fruits with pulp are twice as heavy as those without pulp (37.5 g and 18.6 g, respectively; J. M. Cramer, pers. obs.). Beneath the mesocarp's fibrous hair, the seed is further protected by a very hard, bony endocarp. Most fruits contain one seed (Kuhlmann 1947), although 2.3 percent of sampled fruits ($N = 478$) produced two stems, indicating either two seeds per fruit or two sprouts from a single seed (J. M. Cramer, pers. obs.).

Although *D. cestroides* fruit is anecdotally considered poisonous (C. F. da Silva, pers. comm.) or dispersed by extinct megafauna (Ribeiro *et al.* 1999), fruits are regularly removed from the forest floor (J. M. Cramer, pers. obs.). The fruits' size, odor, bright color, and the well-protected seed suggest that medium-to-large mammals are the primary seed dispersers (Van der Pijl 1982, Roosmalen 1985). *Duckeodendron* fruits at BDFFP have been recorded in the diets of two primate species—red howler monkeys (*Alouatta seniculus*) (Neves & Rylands 1991, P. Stouffer pers. comm.) and bearded sakis (*Chiropotes sagulatus)* (S. Boyle, pers. comm.). Arboreal mammals may strip the pulp from the fruit while in the canopy and then drop the fruits to the ground where they may be further handled and dispersed by terrestrial mammals. It has been suggested that acouchies (*Myoprocta* spp.) are probable dispersers (Ribeiro *et al.* 1999). As 73 percent of experimentally placed seeds were removed within 7 weeks (J. M. Cramer, pers. obs.), we believe terrestrial mammals contribute to secondary dispersal or to seed predation. Numerous seeds at our study site have tooth marks on the seed endocarp and lack seed kernels.

FIELD DATA COLLECTION.—In the 2002, dry season (July–October), we located 11 *D. cestroides* with at least 30 fruits on the forest floor: four trees in 10-ha fragments, two in 100-ha fragments, and five in continuous forest (tracts > 1,000,000 ha). Trees were selected based on the size of their 2002 fruit crop and location relative to other fruiting conspecifics. In 2003, another continuous forest tree was added to the census and, in 2004, a nearby treefall forced us to exclude a previously sampled *Duckeodendron* from a 100-ha fragment. The BDFFP's phytodemographic data base allowed us to accurately determine the location of fruiting as well as nonfruiting conspecifics within the census plots.

Two transects established around each individual in July and August 2002 were used to estimate seed dispersal for each tree (Fig. 1). We used wedge-shaped transects to accommodate increased dispersal area and decreased seed density as distance from the parent tree increased, similar to seed trapping methods used by Clark *et al.* (2005). Wedge-shaped transects eliminate census bias based on distance-dependent seed density. We chose this method because past seed dispersal studies have shown conventional seed trap methods failed to catch a single seed from as many as 88 percent of species over a 10-yr period (Hubbell *et al.* 1999) and that in a given year, only 7 percent of species have seeds that reach at least 10 percent of randomly placed seed traps (Muller-Landau 2001).

Transect placement accommodated irregular fruiting patterns throughout the crown, avoided overlap with other fruiting *D. cestroides*, and conformed to four criteria, in the following order of priority: (1) avoid transects of other focal trees; (2) capture the highest concentration of fruit on the ground under each tree;

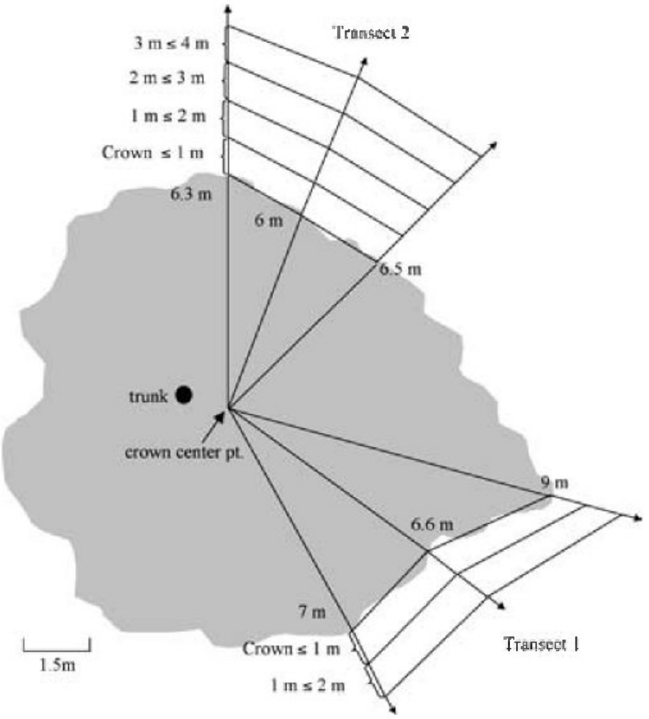

FIGURE 1. Transect layout for seed dispersal census, illustrated for Tree #5 from continuous forest, to scale except transect length that is abbreviated to conserve space.

(3) avoid fragment edges and trails; and (4) maximize the distance between transects of a given focal tree without violating the first three criteria. These criteria were established to maximize the quantity of fruit censused without transect overlap or other anomalies that would cause changes in disperser behavior (forest edges) or the likelihood of seed disturbance (researcher trails). When two fruiting individuals were within 50–100 m of each other, both were used only if sampling transects could be placed in directions radiating away from each other to minimize transect overlap.

Each census year, transects originating at the crown center, regardless of trunk location, were extended until no seeds were found in three to four consecutive distance classes. Therefore, the length of each transect was independent of the lengths of all other transects for the same or other focal trees and for different years. Terminating transects according to seed availability allows censusing for dispersed seeds without bias toward seed density. Transects of equal lengths may be biased because greater effort is given to searching for rarer occurrences of seeds around trees where seed dispersal is reduced. The crown edge was delineated at three points on each transect, at both edges, and the transect median. Because tree crowns are naturally variable in shape, it was not unusual for each of these three points to be at a different distance away from the transect origin (Fig. 1). Distance from the crown was marked independently along both transect edges and the transect median in the following intervals: 1-m intervals from the crown edge to 10 m from the crown, 2-m intervals from 10 to 40 m from the crown, and 3-m intervals beyond 40 m from the crown. Each wedge-shaped transect has a 45° base angle, so together the two transects constitute 25 percent of the tree's potential dispersal area for distances censused. Both transects were pooled for each tree for all analyses.

During the dry seasons of 2002, 2003, and 2004, we searched the leaf litter within transects to locate and record the positions of seeds relative to the parent's crown. Seed locations were individually marked with a small, wooden stake and subsequently checked 1–2 mo later (2002 and 2003, only). Disappearance of seeds after the initial census could represent either secondary dispersal or seed predation. All first-year seedlings, determined by the color and quality of the seed's mesocarp, were marked and counted concurrently with each year's census. These seedlings provide a snapshot of seed germination rates as virtually all *Duckeodendron* seeds that do not suffer from predation germinate (J. M. Cramer, pers. obs.).

Given the low density of *Duckeodendron* at the BDFFP, the 10- and 100-ha fragments were tested for differences in the percent of seeds dispersed and found to be similar, so they were combined into a single class, 'fragments,' for comparison to trees in unfragmented, continuous forest.

DATA ANALYSES.—We used several analyses to test for differences in seed dispersal between forest fragments and continuous forest. Primarily, we asked what proportion of seeds (dispersal quantity) were dispersed at least 1 m beyond the crown, what was the mean distance (dispersal quality) of those dispersed seeds, and what was the shape of the dispersal curve, always looking for a variation by forest type (fragments vs. continuous forest) and by year. We also focused on the most successful dispersal each year by repeating the mean distance analyses for the five furthest dispersed seeds. Finally, we examined the cumulative effect of fragmentation on dispersal quality by asking how many seeds were dispersed 10 m beyond the crown over all years. Because the same individual trees were repeatedly measured every year, the variable 'tree nested in forest type' was included as a random effect in our model. In SAS (PROC MIXED and GLIMMIX), random effects define repeated measures with constant variance and covariance. Details of the statistical treatments follow.

Generalized Linear Mixed Model (GLMM, SAS, PROC GLIMMIX) analysis (SAS Institute Inc. 2005) with a negative binomial distribution and natural log transformation was used to test for differences in the number of seeds dispersed more than 1 m past the crown of parent trees for fragmentation and year effects. Negative binomials are appropriate for natural count data because populations are often associated with overdispersion as a result of correlated errors in time and space. A negative binomial distribution accounts for overdispersion by allowing for larger variances relative to the mean, whereas Poisson distributions assume variances and means are equal. The total number of seeds found (fruit crop) was included in this analysis as an offset variable to adjust for different fruit crop sizes per tree. An offset variable is the same as a covariate with a fixed coefficient of one.

Two-factor ANOVAs (SAS, PROC MIXED) were used to test for differences in the total number of seeds found in the combined transects of each tree and the mean distance from the crown of dispersed seeds by forest type and year. The dependent variables, total number of seeds (+1) and mean distance from the crown of dispersed seeds, were natural log transformed to achieve normality and equal variances.

GLMM analysis with a Poisson distribution and natural log transformation was used to examine the effects of fragmentation and year on the mean dispersal distance of each tree's five furthest dispersed seeds in each year. We also examined the cumulative effect of fragmentation on dispersal distances for each tree over all 3 yr on (1) the number of seeds dispersed beyond 10 m from the parent crown (χ^2 analysis) and (2) the mean distance of the five furthest dispersed seeds for all 3 yr combined (SAS, PROC GLIMMIX).

A Random Coefficient Regression (RCR) was used to describe the number of seeds found as a function of distance from the crown, assuming a Poisson response (SAS, PROC GLIMMIX). A RCR is a GLMM that fits subject-specific models (individual trees) about a population-averaged model (fragments or continuous forest) (Moser 2004). RCR models are similar to analysis of covariance (ANCOVA), but the latter assumes fixed effects for the covariate, whereas an RCR assumes that the regression coefficient for one or more covariates is a random sample from some population of possible coefficients (Littell *et al.* 1996). We compared the regressions with intercepts that were allowed to vary randomly among trees and years. A one-tailed test determined if forest fragments had reduced dispersal relative to continuous forest. Variable-sized sampling areas, resulting from the irregular crowns, were included in the analysis as an offset variable. The equation of a triangle was used to extrapolate the sample areas of the crown and each distance interval (sum of two triangles). We removed the number of seeds found under the crown of each tree and the zeros at all distances after the last seed was found in each transect to limit the regressions to dispersed seeds only. Removing crown data eliminated large drops in seed numbers between the crown edge and first distance class after the crown (0–1 m). Removing excess zeros at the end of the dispersal curves eliminated variable sized tails and standardized the data for all regressions.

Finally, two-factor ANOVAs (SAS, PROC GLIMMIX) were employed to compare the total number of seedlings and percent of germinated seeds in fragments versus continuous forest for three different distance classes: under the parent crown, crown edge out to 10 m, and beyond 10 m from the crown to transect end. To achieve the best fit for normality and equal variances, the total number of seedlings was fit with a Poisson distribution and a natural log transformation, whereas the proportion of germinated seeds was fit with a binomial distribution and a logit transformation. The total number of seedlings and the percent of germinated seeds were used as response variables to determine if dispersal distance had an effect on first-year seedlings. When there was a significant interaction between the independent variables, separate effects of each variable were tested.

When appropriate, a Kenward–Rogers adjustment to the degrees of freedom was added to analyses to provide a conservative Type I error control for small sample sizes. The Kenward-Rogers adjustment results in fractional degrees of freedom seen throughout the results. Except for the Chi-squared test, the analyses for this paper were generated using SAS software, (SAS Institute Inc. 2002).

RESULTS

SEED DISPERSAL.—Over 3 yr, we marked and counted a total of 3767 *D. cestroides* seeds in the dispersal transects. Seed totals varied among years—1805, 734, and 1226, respectively, in 2002, 2003, and 2004. There were 2752 seeds in continuous forest and 1013 in fragments, with 17 tree censuses over all 3 yr for each forest type.

We tested for two potentially confounding factors, distances transects were sampled and fruit crop sizes, that might influence our interpretation of dispersal differences between continuous forest and fragments. The distance at which transects were searched was not significantly different between forest fragments (mean = 8.0 m ± 1.1) and continuous forest (mean = 7.8 m ± 1.1; $F_{1,33} = 0.03$, $P = 0.86$). However, for all 3 yr, total number of seeds per tree (fruit fall) was greater in continuous forest (ln(seeds) = 4.7 ± 0.33) than in forest fragments (ln(seeds) = 3.6 ± 0.33; $F_{1,10} = 5.8$, $P = 0.04$). Seed totals also fluctuated over the 3 yr ($F_{2,18} = 14.2$, $P = 0.0002$) with the fewest seeds in 2003. However, there was no significant interaction between these two variables, forest type and year ($F_{2,18} = 1.1$, $P = 0.36$). Given the absolute difference in fruit fall between fragments and continuous forest, subsequent tests that included both dispersed and undispersed seeds were adjusted for fruit crop sizes.

Only 16 percent of seeds were dispersed further than 1 m past the crown edge in forest fragments, compared to 31 percent in continuous forest (Table 1). Year was also significant with a smaller percent being dispersed in 2003 (13%) than in 2002 (26%) or 2004 (32%) (Table 1; Fig. 2A), and there was no significant interaction between year and forest type.

TABLE 1. *ANOVA (MIXED or GLIMMIX) results used to characterize dispersal of* Duckeodendron cestroides *in fragments and continuous forest and over the 3 yr (2002–2004). Each analysis may have been modeled with a different distribution (negative binomial, Poisson, normal) to get the best fit.*

Dispersal Source	df	*F*	*P*	Source	df	*F*	*P*
Percent dispersed				*Distance of five furthest dispersed seeds/yr*			
forest type	1.9	5.2	**0.05**	forest type	1.10	5.9	**0.04**
year	2.18	5.1	**0.02**	year	2.26	18.5	**< 0.01**
type × year	2.18	1.5	0.26	type × year	2.26	4.1	**0.03**
Dispersal distance				*Distance of five furthest dispersed seeds over 3 yr*			
forest type	1.10	7.3	**0.02**	forest type	1.10	9.4	**0.01**
year	2.15	6.7	**< 0.01**				
type × year	2.15	4.6	**0.03**				
Germination							
Number of seedlings				*Percent germination*			
forest type	1.94	1.1	0.29	forest type	1.93	0.1	0.72
distance	2.49	3.7	**0.03**	distance	2.93	0.5	0.61
type × distance	2.49	3.4	**0.04**	type × distance	2.93	3.0	**0.05**

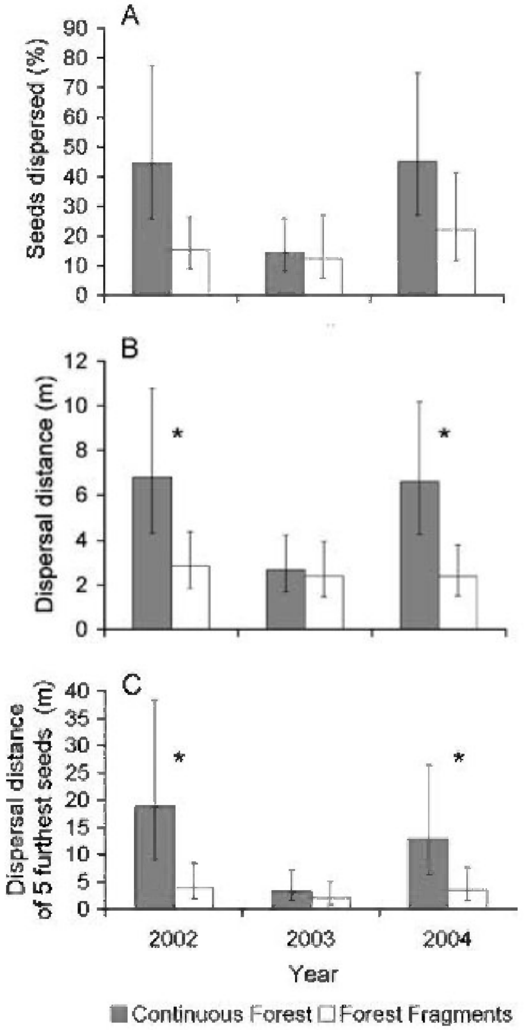

FIGURE 2. Continuous forest trees had a significantly greater (A) percent of seeds dispersed more than 1 m past the crown ($N = 34$ trees over 3 yr), (B) dispersal distances of seeds from the parent crown ($N = 31$ trees over 3 yr), and (C) dispersal distances of the five furthest seeds/tree/yr ($N = 32$ trees over 3 yr) than forest fragments. Asterisks above paired bars indicate significant differences between continuous forests and forest fragments for that year. Back-transformed LS Means (with 95% CI) are presented here, but significance tests were based on transformed means.

Seeds were dispersed for shorter distances beyond the edge of the crown in fragments (2.5 m) than in continuous forest (4.9 m) and shorter distances in 2003 (2.5 m) than in 2002 or 2004 (4.4 m and 4.0 m, respectively; Table 1). A significant interaction between forest type and year (Table 1) showed that continuous forest trees had greater mean dispersal distances than forest fragment trees in 2002 and 2004 ($F_{1,15} = 8.7$, $P = 0.01$ and $F_{1,15} = 11.7$, $P = 0.004$, respectively) but not in 2003 ($F_{1,15} = 0.11$, $P = 0.74$) (Fig. 2B).

For the five furthest dispersed seeds of each tree in each year, differences between fragments (3.0 m) and continuous forest (9.3 m) were even more exaggerated (Table 1). Year was again significant with greater dispersal distances in 2002 (8.7 m), and 2004 (6.7 m) than in 2003 (2.7 m; Table 1). Again, a significant interaction between forest type and year (Table 1) showed that the means were different between continuous forest and fragments in 2002 ($F_{1,11.4} = 10.6$, $P = 0.007$) and in 2004 ($F_{1,13.6} = 7.0$, $P = 0.02$), but not in 2003 ($F_{1,20.4} = 0.67$, $P = 0.42$) (Fig. 2C).

Over the cumulative 3 yr, the five furthest dispersed seeds averaged 18.7 m beyond the parent crown in continuous forest versus 5.0 m in forest fragments (GLMM $F_{1,10} = 9.4$, $P = 0.01$). In addition, 20 times more seeds were dispersed > 10 m from the parent crown in continuous forest (344 seeds) than in forest fragments (17 seeds)—a difference much greater than expected from the number of seeds recorded (2752 and 1013, respectively) in each forest type ($\chi^2 = 200$, $P < 0.0001$).

The number of seeds at each distance interval followed a negative trend with distance that was nonlinear and highly variable among trees and years (Fig. 3). For trees, seed number decreased with distance from the crown, but not monotonically as it was common to find many seeds in one distance interval, no or few seeds in the next distance interval, and then another increase in the seed number. Despite this variation, the regressions provided significant linear fits for most trees in most years when seed numbers were high, although not when seed production was low, as in 2003 (data not shown).

The RCR analysis showed that the number of seeds dispersed over all years for both continuous forest and forest fragments decreased with increasing distance from the edge of the tree crown ($F_{1154} = 424$, $P < 0.0001$). A comparison of fragments versus continuous forest revealed that the seed distributions of continuous forest and fragments differed in their intercepts ($F_{1,10.2} = 4.4$, $P = 0.03$) but not in their slopes ($F_{1149} = 0.01$, $P = 0.46$). As the dispersal regression for continuous forest was above the regression for fragments, the number of dispersed seeds was greater at all distances (Fig. 3D). Because the regressions were performed on log-transformed distances, the same slopes signify that the decline in seed number with the log of distance in fragments was similar to the decline in continuous forest, even though the fragments started with much fewer seeds at the intercept (crown edge). Finally, the furthest dispersed seeds were much further from the crown in continuous forest than in fragments (Fig. 3D). This last result is not an artifact of variable transect lengths, because we performed the RCR regressions on transect lengths uniformly truncated to 6 m from crown edge, the maximum distance with seeds for every tree, and obtained the same results.

Seed removal (secondary dispersal or seed predation) between censuses in 2002 and 2003 was a small percent of the total (mean = 4.7% ± 2.36). The mean percent of seeds removed between censuses in 2003 (7.1% ± 4.5) was more than triple that in 2002 (2.1% ± 0.77). However, the total number of seeds removed in 2003 ($N = 66$) was only double that removed in 2002 ($N = 32$).

SEEDLING ESTABLISHMENT.—Although there was no difference in the number of seedlings per tree found in continuous forest versus forest fragments (Table 1), seedling numbers were dependent on

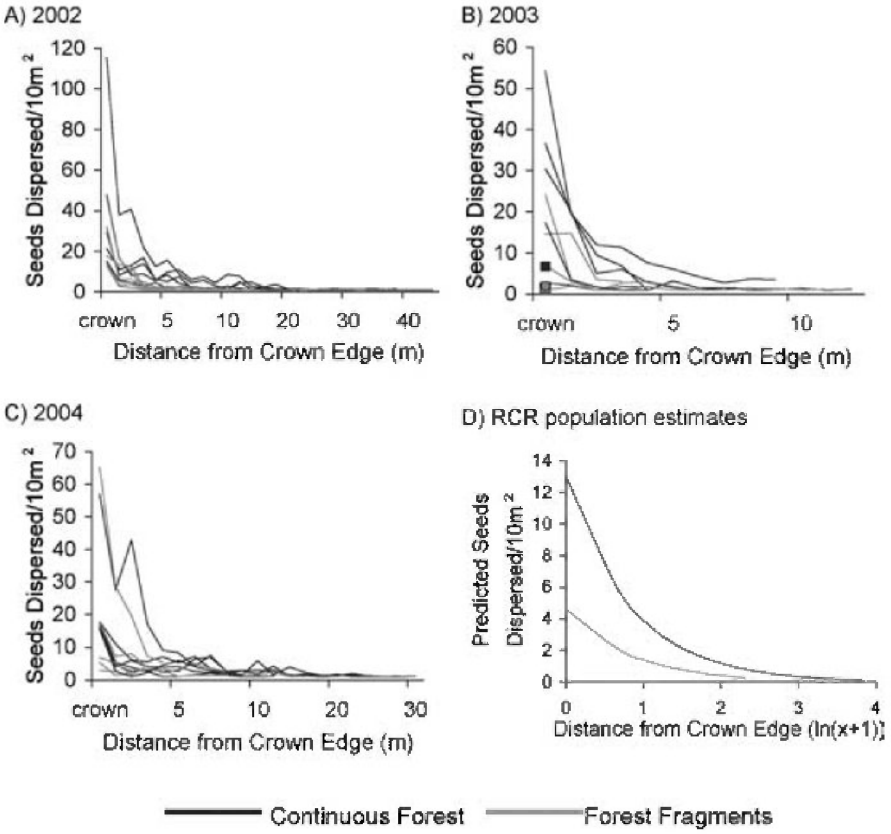

FIGURE 3. The density of dispersed seeds per 10 m^2 across distances from the maternal tree in fragments and in continuous forest for years 2002–2004, (A–C), and the RCR population estimates for all years combined (D). Trees in fragments typically have a lower density of seeds across all distances than trees in continuous forest. Each line represents an individual tree, solid shapes represent trees where seeds were only found under the crown (A–C). Note that the x-axis distance is greatly reduced in 2003 (B). The y-axis for the RCR estimate (D) is reduced because it only accounts for seeds dispersed beyond the crown.

distance from parent trees (Table 1; Fig. 4A) with significantly fewer seedlings 0–10 m from the crown than under the crown (Bonferroni pairwise comparisons $P = 0.05$). A significant interaction between distance and forest type indicated that seedling numbers declined at different rates for each forest type (Table 1). Separate tests by forest type showed significantly more seedlings under the crown and 0–10 m from the edge of the crown than beyond 10 m in continuous forest ($F_{2,18.7} = 6.7$, $P = 0.006$). In forest fragments, there were significantly fewer seedlings 0–10 m from the crown than under the crown ($F_{2,65} = 5.8$, $P = 0.005$). Continuous forest and forest fragments differed in the number of seedlings only for the 0–10 m distance class ($F_{1,37.7} = 7.9$, $P = 0.008$). Therefore, the number of seedlings declined immediately after the crown in forest fragments but only beyond 10 m from the crown in continuous forest. The net effect of this differential decline in seedlings with distance was no seedlings beyond 10 m from the crown over 3 yr for fragment trees in contrast to the 22 seedlings from nine different trees in continuous forest.

The proportion of seeds that became seedlings showed a significant interaction between forest type and distance class from a parent tree (Table 1). Separate tests by forest type showed no distance effect in forest fragments ($F_{2,93} = 0.60$, $P = 0.55$) but significant differences across distance classes in continuous forest ($F_{2,93} = 4.1$, $P = 0.02$) with a higher percent of seedlings germinating beyond the crown than under the crown (Fig. 4B). Separate tests by distance classes showed that the percent of germinated seeds was not significantly different between forest types for 0–10 m from the crown ($F_{1,39.4} = 0.03$, $P = 0.87$) but was nearly so under the crown ($F_{1,28} = 3.7$, $P = 0.07$) (Fig. 4B), and obviously different at 10+ m from the crown, as there were no seedlings this far in fragments.

DISCUSSION

SEED DISPERSAL.—Over all 3 yr, both the quantity (proportion) and quality (distance) of dispersed seeds in continuous forest were double those in fragments. In addition, the distance of the furthest dispersed seeds in continuous forest was triple that in fragments. Finally, predicted dispersal curves for each forest type show more seeds dispersed to all distances from parent crowns in continuous forest than in forest fragments.

The reduced seed dispersal of *D. cestroides* in forest fragments may be attributed to the declines of terrestrial and arboreal mammalian dispersers for this species. The responses of primates and

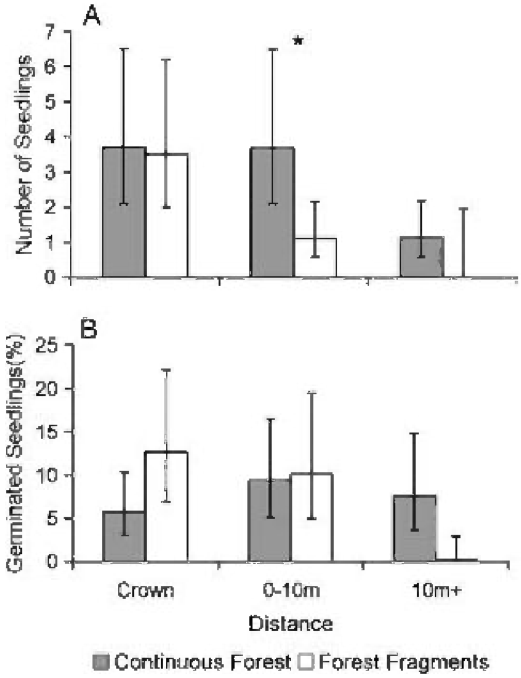

FIGURE 4. (A) Number of seedlings and (B) percent of germinated seeds in continuous forest and forest fragments at three distance classes from parent trees. Data show LS Mean ± 95% CI. Asterisks above paired bars indicate significant differences between continuous forest and forest fragments for that distance class.

large mammals to fragmentation at the BDFFP coincide with the changes in dispersal we observed in *Duckeodendron*. Of the six primate species at the BDFFP, black spider monkeys (*Ateles paniscus*) and bearded sakis disappeared from the forest fragments immediately after isolation and remained absent for at least 10 yr after isolation (Gilbert & Setz 2001). Bearded sakis are a known consumer of *D. cestroides* fruit. The other confirmed consumer of *Duckeodendron*, red howler monkeys, are less sensitive to fragmentation, occasionally occupying 10-ha fragments (Gilbert & Setz 2001). In a recent study, sand traps (ten 0.25 m^2 for a week) in fragments and continuous forest at the BDFFP recorded many fewer medium and large terrestrial mammals in fragments (9 records) than in nearby continuous forest (60 records) (Timo 2003). Thus, it appears that reduced seed dispersal in forest fragments resulted from overall mammal reductions, not the disappearance of a single species—an anticipated result given the asymmetry of most dispersal mutualisms (Bascompte *et al.* 2006) and the switching of dispersers among preferred fruit species (Herrera 1998, Levey & Benkman 1999).

Rates of *Duckeodendron* fruit removal 1–2 mo after initial censuses indicated that terrestrial animals were important secondary dispersers or seed predators. Over 6 weeks, a camera trap aimed at ten experimentally placed seeds under the canopy of a *D. cestroides* in a nearby continuous forest site recorded the Guianan squirrel (*Sciurus aestuans*, six visits), the brown four-eyed opossum (*Metachirus nudicaudatus*, five visits), and a *Marmosa* or *Marmosops* sp. (one visit) (Yabe *et al.* 1998). Over a 2-week period, our camera traps at two continuous forest sites photographed a Margay (*Leopardis wiedii*) and three gray-winged trumpeters (*Psophia crepitans*) at *Duckeodendron* fruits, and two agoutis (*Dasyoprocta* sp.), a capybara (*Hydrochaeris hydrochaeris*), and one Guianan squirrel (*S. aestuans*) in the bait vicinity. Other potentially important terrestrial mammals, such as acouchies, agouties, pacas, and rats (*Proechimys* spp. and *Oryxomys* spp.), are all present in fragments at the BDFFP. These species tend to hoard seeds, so they could be important secondary dispersers, although we did not track secondary dispersal. Scatterhoarding has been shown to increase seed survival and escape from seed predation by rats (Asquith & Mejia-Chang 2005). Undetected scatterhoarded seeds in fragments could counter our results by increasing the number of dispersed seeds in fragments and reducing the difference we saw in dispersal between fragments and continuous forest. If so, more scatterhoarded seeds in fragments should have resulted in more seedlings in fragments, but our results showed more seedlings in continuous forest. Also, fragmentation may reduce populations of scatterhoarders, resulting in a lower probability of scatterhoarded seeds in fragments (Galetti *et al.* 2003). Therefore, it is unlikely that undetected scatterhoarded seeds in fragments would change our interpretation of fragmentation effects on seed dispersal.

Fruiting of tropical trees is often highly variable with years of high fruit production interspersed with years of low or no fruit production (Herrera *et al.* 1998). Here, for *D. cestroides,* fruit crop fluctuated over the 3 yr of our study; total fruit production in 2003 was about half of 2002 and 2004 (40% and 60%, respectively). When fruit production was high, differences between fragments and continuous forest in the proportion of seeds dispersed and dispersal distances were significantly different or nearly so. In these years, seeds in continuous forest were found up to 46 m (2002) and 30 m (2004) from the parent tree, triple and double, respectively, the maximum dispersal distance (14 m) in any fragment. In contrast, in 2003 when fruit production was low, there were no detectable differences between continuous forest and forest fragments in the percent of seed dispersed or distance of dispersed seeds. Therefore, differences in dispersal between fragments and continuous forest were sharp during years of high fruit production, exactly when dispersal was important.

Reduced dispersal differences in 2003 may be a consequence of reduced *D. cestroides* fruit production. In 2003, a crash in fruit production in neighboring French Guiana resulted in frugivorous animals leaving the area (P. M. Forget, pers. comm.). Although reduced fruit crop sizes often do not affect the distance that seeds are dispersed (Laska & Stiles 1994, Bleher & Böhning-Gaese 2000), they appear to determine the attractiveness of a fruiting tree and, consequently, the likelihood of disperser visitation (Jansen *et al.* 2004). The lack of dispersal differences between forest types in 2003, when fruit production was low, may reflect poor visitation leading to poor dispersal.

Just as low disperser visitation could explain the lack of dispersal for all trees in 2003, it could be argued that smaller fruit crops of trees in forest fragments could result in poor disperser visitation (Jordano 1995, Saracco *et al.* 2005) and explain the reduced seed dispersal we recorded here. Forest fragmentation could reduce fruit crop sizes, perhaps as a result of poor pollinator visitation and resulting low fertilization. We found that trees in continuous forest did produce more fruits than trees in forest fragments over the course of 3 yr. To be conservative in the analyses, we incorporated the total number of seeds counted as an offset variable (SAS Institute Inc. 2005) in the analysis, comparing the proportion of seeds dispersed in continuous forest to forest fragments while adjusting for fruiting effort of each tree in each year. A greater proportion of seeds were dispersed in continuous forest than in forest fragments for all 3 yr, indicating that the differences in seed dispersal found here are strong despite modest differences in fruit production. Therefore, if poor disperser visitation is responsible for low dispersal in fragments relative to continuous forest, it is likely a result of changes in the disperser community, not simply differences in fruit crops.

Although we grouped 10- and 100-ha fragments as a result of limited sample sizes, both percent dispersal and the distance where the last seed was found had responses in 100-ha fragments that were intermediate to those in 10-ha fragments and continuous forest in years of high fruit production (2002 and 2004) but not in years of low fruit production (2003) (analyses not shown). These trends suggest that shifts in seed dispersal depended on fragment size, and that fragment area should be considered in dispersal studies wherever possible.

A critical assumption in our study is that the seeds found in the dispersal transects were assigned to the appropriate parent tree. A recent seed dispersal study on *Simarouba amara* in Panama found that the nearest adult was not always the maternal parent to a seedling (Hardesty *et al.* 2006). Without molecular markers, we cannot be definite of seed parentage and therefore of dispersal rates and distances for *Duckeodendron.* However, all of our parent trees were isolated from other fruiting conspecifics or were placed with their transects radiating away from fruiting conspecifics. The latter case occurred only once in our study, a pair of trees in continuous forest where any errors in assigning parentage would have underestimated dispersal distances. The net effect of underestimated dispersal distances would have yielded a greater actual difference in dispersal between continuous forest and fragments than we observed.

A limitation of sampling for dispersed seeds on the ground is that rare instances of long-distance dispersal are missed. In addition, as we did not monitor fruit removal from tree crowns, we could not account for seeds removed directly from trees and dispersed beyond our transects. Such differences could be problematic if dispersers in fragments behave differently from those in continuous forest (McConkey & Drake 2006). Seeds dispersed far beyond parent crowns and our transects may represent individuals of the highest dispersal quality, if they have the greatest likelihood of survival to adulthood because they escape distance-dependent mortality. We did analyze the tail of our distributions by looking at the five furthest dispersed seeds, and they exhibited more exaggerated differences between fragments and continuous forest than did all seeds.

Reduced seed dispersal resulting from forest fragmentation has been reported in three other studies, all in the tropics. Cordeiro and Howe (2003) found fragmentation reduced dispersal agents and seed removal of the endemic tree *Leptonychia usambarensis* in the East Usambara Mountains of Tanzania, although they did not report direct counts of dispersed seeds. Wright and Duber (2001) used direct counts of seeds to show that dispersal of *Attalea butyraceae* in Panama was less in areas where mammal populations were reduced by both hunting and fragmentation. Similarly, Galetti *et al.* (2006) found that in Brazil's fragmented Atlantic forest the probability of seed removal of the large-seeded endemic palm, *Astrocaryum aculeatissimum*, decreased as mammal dispersers were eliminated by hunting and fragmentation. These studies all linked reductions in dispersal in hunted fragments to reductions in seedlings numbers or densities. Results from our study further support these findings that forest fragmentation does reduce seed dispersal, here based on direct counts and on the distances seeds were dispersed in areas experimentally fragmented, where hunting was not a factor.

SEEDLING ESTABLISHMENT.—We estimated the effect of distance-dependent mortality on seeds and seedlings by looking for newly germinated seedlings shortly after fruitfall and comparing the percent of germinated seeds across distance classes. The Janzen–Connell hypothesis states that predators should operate more intensely at distances closer to the parent tree. In forest fragments, the pattern of seedling germination contrasted with the Janzen–Connell hypothesis as the percent of germinated seeds under the crown was not different from the percent at 0–10 m beyond the crown, and there were no seeds in the 10+ m class (Fig. 4B). While the percent did not change, there were more absolute numbers of seedlings under the crown because there were more seeds there (Fig. 4A). In continuous forest, distance-dependent mortality may be more important for *Duckeodendron* as the percent of germinated seeds 0–10 m beyond the crown was greater than under the crown.

Differences in the influence of distance from the parent tree on germination in continuous forest and forest fragments resulted in differences in the absolute numbers of seedlings. Although both forest types showed that the number of seedlings declined with distance, this decline occurred much closer to parent trees in fragments than in continuous forest (Fig. 4A). The accelerated decline in seedling numbers with distance from parent crowns in fragments resulted in significantly fewer seedlings 0–10 m from the parent crown. This difference in seedling numbers with distance can be attributed to the number of seeds dispersed over all distances: increased seed dispersal in continuous forest resulted in greater numbers of seedlings at distances beyond the crown. In fragments, the low number of dispersed seeds coupled with their decline in number as distance increased, resulted in few seedlings 0–10 m from parent crowns and a complete absence of seedlings more than 10 m beyond parent crowns. Although we did not detect a change in the percent of seeds that germinated in fragments 1–2 mo after fruitfall, seedlings close to parent trees might still show increased susceptibility to distance-responsive herbivores or pathogens over longer periods. In fragments, where all seedlings are concentrated around parent plants, distance-dependent seedling mortality could have an extreme effect, eliminating nearly all seedlings in fragments.

Fragmentation effects of disrupted mutualisms on trees may be difficult to detect because the results take longer to surface in long-lived species. In addition to reduced seed dispersal and fewer seedlings in fragments shown here, fragment trees may also be affected by decreased probability of fertilization (Cascante *et al.* 2002), increased seed abortion (Chacoff *et al.* 2004), increased seed predation by vertebrates (Francisco *et al.* 2002), and decreased seed predation by insects (Janzen 1978, Cascante *et al.* 2002). By studying the mutualistic processes involved in plant regeneration, such as seed dispersal and first-year seedling establishment, we can detect changes that forecast the next generation before they appear in the adult community.

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