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Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees

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ABSTRACT

The responses of plant–animal interactions to forest fragmentation can vary. We hypothesized that large-seeded plant species would be more susceptible to forest fragmentation than small-seeded species because large-seeded species rely on a few, extinction prone dispersers. We compared seed dispersal of the large-seeded, mammal dispersed *Duckeodendron cestroides* and the small-seeded, avian dispersed *Bocageopsis multiflora*. The number, percentage, distance, and distributions of dispersed seeds were all reduced in fragments for *Duckeodendron* but not for *Bocageopsis*. Other fragmentation research in tropical communities supports this hypothesis through three lines of evidence: (1) Large-seeded plant species are more prone to extinction, (2) Fragmentation restricts or alters the movement of large animal dispersers more than small dispersers, and (3) Large and small-seeded species seem to be differentially linked to primary and secondary forest habitats. Therefore, small-seeded plants may be more resilient to forest fragmentation while large-seeded species may be more susceptible and should be a priority for conservation.

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1. Introduction

Responses of mutualisms to forest fragmentation can be very diverse. Declines in animal or plant species can result in the loss of mutualistic functions, jeopardizing connected species (Andresen and Levey, 2004; Bruna et al., 2005). Alternatively, some mutualisms are more resilient to fragmentation because the behavior of animal mutualists is not altered, lost mutualists are replaced by other species (Dick, 2001), or lost mutualistic functions are replaced by the plant itself through self-fertilization (Powell and Powell, 1987). Given the diversity of individual responses to fragmentation, are there generalizations that allow us to predict the effects of forest fragmentation for some tropical rainforest trees?

It has been hypothesized that populations of large-seeded plants will be highly susceptible to fragmentation (Fortuna

and Bascompte, 2006; Jones and Crome, 1990; Kitamura et al., 2004; Melo et al., 2006; Silva and Tabarelli, 2000; Tabarelli and Peres, 2002). In contrast, small seeded plants may sustain viable populations in or across forest fragments (Silva and Tabarelli, 2000; Tabarelli and Peres, 2002). Seed dispersal of large and small-seeded tree species may be differentially affected by forest fragmentation because their dispersers have varying responses to fragmentation for several reasons. First, large-seeded species rely on fewer animal species for dispersal (Christian, 2001; Hamann and Curio, 1999). Second, dispersal agents of large-seeded species are often larger and therefore at greater risk of extirpation in fragments, given greater hunting pressures, their low reproductive rates, and small populations (Bodmer et al., 1997; Gilbert and Setz, 2001; Hamann and Curio, 1999; Willis, 1979). In addition, large-animals cannot subsist even in large fragments (100-ha) because their home

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ranges are too extensive (Chapman, 1989; Woodroffe and Ginsberg, 1998). After forest fragmentation, the loss of the few dispersal agents available for large-seeded plants can effectively eliminate all seed dispersal. On the other hand, small-seeded fruits can be dispersed by many species of frugivores and extinction of any single disperser might have little effect on a tree's net dispersal ability (Corlett, 1998). The added vegetative diversity provided by edge habitats and the matrix around fragment attracts small, omnivorous frugivores (Galetti et al., 2003; Pizo, 1997), potentially increasing the dispersal community for small-seeded species (Blake and Loiselle, 2001; Jules and Shahani, 2003).

Here, we offer a preliminary test of the hypothesis that forest fragmentation negatively impacts seed dispersal of a large-seeded tree species more than that of a small-seeded tree species. We examined the effects of forest fragmentation on the seed dispersal of two Amazonian tree species in a year of high fruit production. *Duckeodendron cestroides* Kuhl. (Solanaceae) is a Central Amazon endemic with large fruits (5.9 cm long). *Bocageopsis multiflora* Mart. (Annonaceae) is more widely distributed and has small fleshy berries (0.8 cm diameter).

This study is the first comparison of fragmentation effects on the seed dispersal of two coexisting tree species with different fruit sizes in the aseasonal tropics. As such, we confronted several challenges: individuals of most species are rare (Oliveira, 1997), tree species fruit supra-annually usually with different fruiting phenologies; furthermore, measuring dispersal of large and small-seeded species requires different sampling methods (Herrera et al., 1998). Our results are tempered accordingly.

2. Materials and methods

2.1. Study site

We sampled trees within the experimentally fragmented reserves of the Biological Dynamics of Forest Fragments Project (BDFFP), a collaboration between Brazil's Institute for Amazonian Research (INPA) and the Smithsonian Tropical Research Institute (STRI). The BDFFP reserves are located north of Manaus at 2°30' S and 60°00' W in the State of Amazonas Brazil. Vegetation is upland terra firme tropical moist forest with an elevation range of 50–100 m. Mean annual rainfall is 2651 mm with a mild dry season from June to October. The BDFFP has 11 isolated reserves distributed in 1-ha, 10-ha, 100-ha forest fragments and control plots in nearby continuous forest, established between 1980 and 1984. Each reserve includes at least one hectare where all trees ≥ 10 cm d.b.h. (diameter at breast height) are censused. This database of trees allowed us to identify and locate individuals of our target species from over 400 000 living, tagged trees across 66-ha of tropical forest.

2.2. Study species

We identified one large-seeded species and one small-seeded species, based on fruit crops that were large enough to sample. As the two species exhibited different fruiting phenologies, they were sampled during consecutive dry and rainy seasons.

D. cestroides (Solanaceae) is a large-seeded emergent tree endemic to the Central Amazon. It is one of the largest trees in the area with a maximal d.b.h. of 153.2 cm (Laurance et al., 2004). Adults are rare at the BDFFP with recorded densities of 1.3 ha^{-1} (Oliveira, 1997) and 0.5 ha^{-1} (BDFFP database). In the dry season trees produce narrowly ovate fruits that average 5.9 by 3.4 cm in size and 26.8 g fresh weight ($n = 50$). Pulp of *D. cestroides* is very thin, so fruit and seed sizes are about the same. When ripe, fruit pulp is orange-yellow with a strong, musty odor. *Duckeodendron* has been recorded in the diets of two primate species – red howler monkeys (*Alouatta seniculus*) (Neves and Rylands, 1991) and bearded sakis (*Chiropotes sagulatus*) (S. Boyle, pers. obs.). Once fruit has fallen terrestrial mammals may be important dispersers (Cramer et al., 2007; Yabe et al., 1998).

The small-seeded species, *B. multiflora* (Annonaceae) is a canopy tree that grows maximally to 33.1 cm d.b.h. (Laurance et al., 2004). This species is locally rare, BDFFP adult densities are 3.7 ha^{-1} (Oliveira, 1997) and 2.3 ha^{-1} (BDFFP database), although widely distributed throughout the Brazilian Amazon and Guianas (Webber and Gottsberger, 1995). In the wet season, between February and May (Oliveira, 1997), trees produce ripe fruits that are 0.8 cm in diameter, with a watery orange to purple pulp around 1–2 seeds. Seed size is 0.5 cm diameter when there is one seed per fruit, and about half this size when there are two seeds. Fruit size and color implicate frugivorous birds of all sizes as consumers of this species, and seeds have been found in bird feces (M. Gordo, pers. obs.).

Fruit and seed sizes of *D. cestroides* and *B. multiflora* are representative, respectively, of large- and small-seeded tropical species (Hammond and Brown, 1995). Pantropically, fruit size among the eight largest families that rely on animals for dispersal ranges from 0.5 to 15 cm long (Mack, 1993). In the Neotropics, the smallest seeds, less than 0.1 cm long or 0.001 g wet weight, come from figs (*Ficus* spp.) and the Melastomataceae. Generalized, frugivorous birds disperse small seeds (up to 1 cm long), like *B. multiflora* (Howe and Westley, 1986). In contrast, mammals disperse seeds greater than 5 cm long (Howe and Westley, 1986) with an average wet weight of 12.6 ± 2.5 g (Hammond and Brown, 1995). *Duckeodendron* seeds, 5.9 cm long and 26.8 g wet weight, are among the largest seeds and fruits in Neotropical forests.

2.3. Seed dispersal

Given their different seed sizes, we sampled dispersal differently for the two species, trying to employ parallel methodologies. The large *D. cestroides* produces a small number of large fruits whose seeds persist on the ground many months after dispersal, so we located them in the leaf litter. *B. multiflora* seeds are small and impossible to census in the leaf litter, so we sampled them using seed traps. For both species, the area censused or trapped increased with distance from the parent tree to compensate for decreased seed densities (Clark et al., 2005; Cramer et al., 2007).

Duckeodendron seed dispersal was censused during the dry season of 2002 (June–Oct.) using 11 fruiting adults; four in 10-ha fragments, two in 100-ha fragments, and five in continuous forest. We established two wedge-shaped transects originating at the center of each focal tree's canopy in 2002

(Cramer et al., 2007). Each transect had a 45° base angle and together the two transects represented 25% of the tree's potential dispersal area for censused distances. We counted all seeds within these transects and measured distances, to the nearest meter, from the edge of maternal tree crowns. Transects were terminated after three to four consecutive distance classes revealed no seeds. See Cramer et al. (2007) for a more detailed description of transect construction and placement.

In the following wet season (Feb.–April 2003), we identified eight fruiting adults of *B. multiflora* for study: one in a 1-ha fragment, one in a 10-ha fragment, two in 100-ha fragments, and two each in two continuous forest sites. We placed seed traps around *B. multiflora* individuals along a single line-transect originating from the center of the crown of each focal tree. As with *D. cestroides*, these transects were oriented to avoid dispersal overlap from other fruiting conspecifics, fragment edges, trails, or plot edges where tree composition was unknown. The tree in the 1-ha fragment was virtually in the center of its fragment where edge effects are less severe. Ten seed traps were mounted along each transect: one trap each mid-way between crown center and crown edge, at 5 m and 10 m from the crown edge, two traps each at 20 m and 35 m from the crown edge, and three traps at 50 m from the crown edge. We chose not to place traps where there would be unusually low volumes of seeds such as directly underneath palm fronds or other low branches that would deflect seeds, or in gaps where there were no available perches for bird dispersers.

Seed trap frames were constructed with 0.71 m long pieces of 1/2 in. PVC, creating a 0.5 m² trapping area. To reduce seed predation, traps were raised 0.5 m off the ground. Along three points of each side of the PVC frame we secured fiberglass mesh screen (18 × 16 squares per inch) with 0.11 in. diameter wire (Phifer Wire Productions, Tuscaloosa, USA). The screen was fastened so that it created a sagging net that would catch and cushion falling seeds. We removed and counted all intact and partial fruit, and seeds from each trap biweekly until fruiting and dispersal ended. Seeds that were clean with no remaining pulp were considered dispersed; All seeds found in traps beyond the crown were clean.

2.4. Statistical analyses

To test for an effect of fragment sizes on seed dispersal and the validity of lumping all fragment sizes together, we ran a generalized linear mixed model (PROC GLIMIX) (SAS Institute Inc., 2005) with a Poisson distribution on the percentage of seeds dispersed more than 1 m past the crown for each species. This analysis revealed no difference in dispersal between fragment sizes for *Duckeodendron* ($F_{1,4} = 0.68$, $P = 0.46$) and for *Bocageopsis* ($F_{2,1} = 2.7$, $P = 0.40$). Therefore, for each species we grouped trees from all fragment sizes as fragment trees ($n = 6$ for *Duckeodendron*, 4 for *Bocageopsis*) and compared them to continuous forest trees ($n = 5$ for *Duckeodendron*, 4 for *Bocageopsis*) in all analyses.

To test for effects of forest fragmentation on the seed dispersal of each species we performed three types of analyses. The first was a generalized linear mixed model (GLMM) with a binomial distribution and a logit transformation to examine the percentage of seeds that were dispersed more than 1 m

beyond the crown. The second was a set of GLMMs to test the effect of fragmentation on dispersal distances including (1) the mean distance of all dispersed seeds, (2) the mean distance of the five furthest dispersed seeds for each tree (Poisson distribution and log transformation), and (3) the number of seeds dispersed more than 10 m beyond parent crowns (Poisson distribution and log transformation). Each of these analyses included fixed effects of forest type (fragments and continuous forest) and random effects of individual trees. The third type of analysis was a two-sided Random Coefficient Regression Analysis (RCR) with random intercepts only, and assuming a Poisson response to compare distributions of dispersed seeds across distances censused. An RCR is a generalized linear mixed model that fits subject-specific models about population-averaged models, similar to an analysis of covariance except that it assumes random effects for the covariate (Littell et al., 1996; Moser, 2004). We natural-log transformed both seed number and dispersal distance variables for regressions used in the RCR analysis for *Bocageopsis* ($R^2 = 0.20$ – 0.82 , 4 of 8 values significant to $P = 0.05$), but regressions using untransformed values for seed number provided better fits for *Duckeodendron* ($R^2 = 0.40$ – 0.81 , 8 of 11 values significant to $P = 0.05$). Offsets of total number of fruits and sample area (natural log-transformed), were included for the percentage of dispersed seeds and the RCR analysis, respectively, to accommodate each tree's differentially sized fruit crops and sampling areas. Response variables were divided by the offset, transforming them into proportions. The fractional degrees of freedom seen throughout the paper are a result of a Kenward-Rogers adjustment to the degrees of freedom, which provides a conservative Type I error control for small sample sizes. All analyses were performed with the SAS System for Windows (Version 9.1).

3. Results

A total of 1805 *D. cestroides* seeds were counted in the dry season of 2002. A total of 1367 *B. multiflora* fruits were captured in seed traps, of which 396 were classified as dispersed seeds. Seed production in continuous forest was not different than in fragments for *D. cestroides* (continuous = 196, fragment = 84, $F_{1,9} = 4.07$, $P = 0.07$) or *B. multiflora* (continuous = 201, fragment = 67, $F_{1,6} = 3.5$, $P = 0.11$, dependent variable natural-log transformed for normality), although we still controlled for differential fruit production across individuals by including total fruit count as an offset variable in the analysis that included dispersed and undispersed seeds. Likewise, large trees might produce more fruit than small trees but the d.b.h. of our trees in continuous forest (*D. cestroides* = 97 cm ± 14.5, *B. multiflora* = 31 cm ± 1.8) was not different from the d.b.h. in forest fragments for either species (*D. cestroides* = 77 cm ± 13.2, *B. multiflora* = 33 ± 1.8) (*D. cestroides*, $F_{1,9} = 1.06$, $P = 0.33$; *B. multiflora*, $F_{1,6} = 0.52$, $P = 0.50$).

All analyses indicated a difference in dispersal between continuous forest and forest fragments for *D. cestroides*, but none indicated a difference for *B. multiflora*. In continuous forest 48% ± 6 of *D. cestroides* seeds were dispersed more than 1 m past parent crowns whereas in fragments only 16% ± 3 of seeds were dispersed that far ($F_{1,7} = 23.2$, $P = 0.002$; Fig. 1a). In addition, *D. cestroides* seeds were dispersed one and a half times fur-

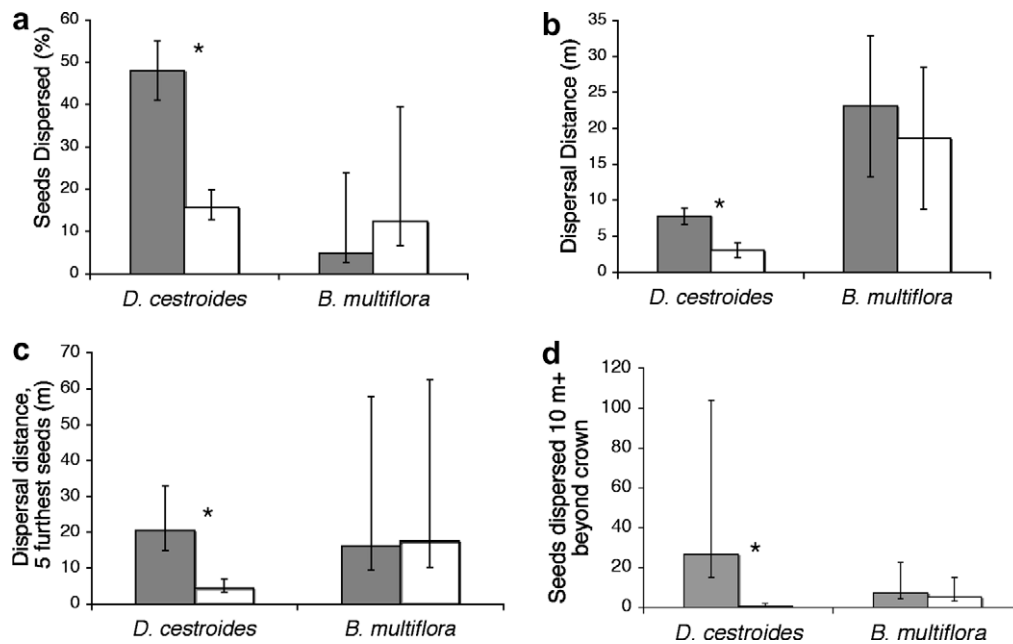


Fig. 1 – Seed dispersal for each species in continuous forest (shaded bars) and forest fragments (open bars). (a) Percentage of seeds dispersed more than 1 m past the crown. (b) Mean distance dispersed seeds were found from the crown of each tree. (c) Mean dispersal distance of the five furthest dispersed seeds for each tree. (d) Number of seeds dispersed more than 10 m beyond the crown of each tree. Graphed values represent LSMs with 95% CI from 1-way ANOVAs of each species. Significant differences between fragments and continuous forest are indicated (*).

ther in continuous forest (mean = 7.8 m \pm 1) than in forest fragments (mean = 3.0 m \pm 0.9) ($F_{1,9} = 12.22$, $P = 0.007$; Fig. 1b). The five furthest dispersed seeds of *D. cestroides* were dispersed five times further in continuous forest (mean = 20.5 \pm 6.7) than in forest fragments (mean = 4.4 \pm 1.5; Fig. 1c) and many more seeds per tree were dispersed 10 m beyond the crown in continuous forest (mean = 24.7 \pm 19) than in forest fragments (mean = 0.4 \pm 0.4; $F_{1,8.3} = 11.02$, $P = 0.01$; Fig. 1d).

In contrast, for *B. multiflora* there was no difference between continuous forest and fragments in either the percentage of dispersed seeds (continuous forest = 5% \pm 5, fragments = 12% \pm 10, $F_{1,5} = 0.47$, $P = 0.52$), mean distance of dispersed seeds (continuous forest = 23.1 m \pm 8.0, fragments = 18.6 m \pm 8.0, $F_{1,6} = 0.15$, $P = 0.71$), distance of the five furthest dispersed seeds (continuous forest = 16.2 \pm 10.7, fragments = 17.6 \pm 11.2, $F_{1,4} = 0.01$, $P = 0.93$), or number of seeds dispersed more than 10 m (continuous forest = 7.2 \pm 4.3, fragments = 5.0 \pm 3.0, $F_{1,4.1} = 0.2$, $P = 0.68$) (Fig. 1).

Although distributions of dispersed seeds in continuous forest and forest fragments were non-linear and highly variable among individuals of both species, Random Coefficient Regressions showed that the number of seeds dispersed per 10 m² declined as distance from the parent crown increased for both species (*D. cestroides* $F_{1,9.4} = 6$, $P < 0.0001$, *B. multiflora* $F_{1,26.8} = 4.57$, $P = 0.04$). The slopes of the regressions were not different in fragments versus continuous forest for either species (*D. cestroides* $F_{1,85} = 0.66$, $P = 0.41$, *B. multiflora* $F_{1,26.8} = 0.80$, $P = 0.38$). However, intercepts were significantly lower in forest fragments than in continuous forest for *D. cestroides* ($F_{1,9.4} = 6$, $P = 0.035$), indicating that more seeds were dispersed to all distances beyond the crown in continuous forest than in forest fragments (Fig. 2). In contrast, intercepts were not different be-

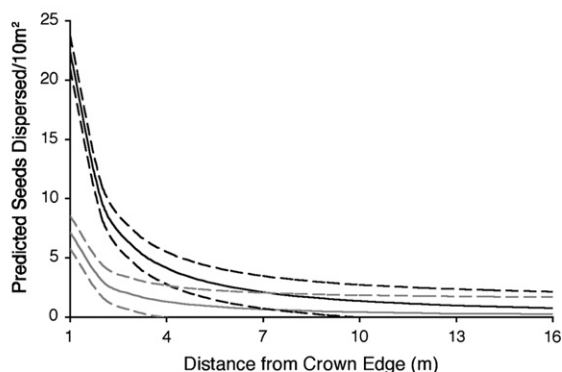
tween continuous forest and fragments for *B. multiflora* ($F_{1,33} = 0.58$, $P = 0.45$), indicating that seed dispersal was distributed similarly across distances for both continuous forest and forest fragments (Fig. 2).

4. Discussion

Our results demonstrate that forest fragmentation does not alter the seed dispersal of the small-seeded *B. multiflora*, but dramatically reduces the seed dispersal of the large-seeded *D. cestroides*. For *D. cestroides* there is a threefold reduction in the percent of seeds dispersed and the mean distance of dispersed seeds in forest fragments. More dramatic results were that each tree's five furthest dispersed seeds were five times farther from the crown in continuous forest and that fifty times more seeds were dispersed 10 m beyond the crown in continuous forest. Finally, distributions of dispersed seeds across distances from the parent tree also showed fewer seeds at all distances.

We attribute the differences in seed dispersal of *D. cestroides* and *B. multiflora* to the differential effects of forest fragmentation on the dispersal guilds of small and large-seeded species. Effective dispersers for large-seeded species like *D. cestroides* are limited to medium and large mammals because smaller animals are simply incapable of handling large fruits (Jordano and Schupp, 2000; Wheelwright, 1985) whereas disperser size is not as limiting for small fruits (Dowsett-Lemaire, 1988; Kitamura et al., 2004; Wheelwright, 1985). The average number of dispersers in a Philippine submontane rainforest was twice as great for species with fruits <20 mm (8.5 dispersers $N = 13$) as for species with fruits >20 mm (4.8 dispersers $N = 11$) (Hamann and Curio, 1999). In a survey of the Oriental Region, Corlett (1998) found that fruits with a

Duckeodendron cestroides



Bocageopsis multiflora

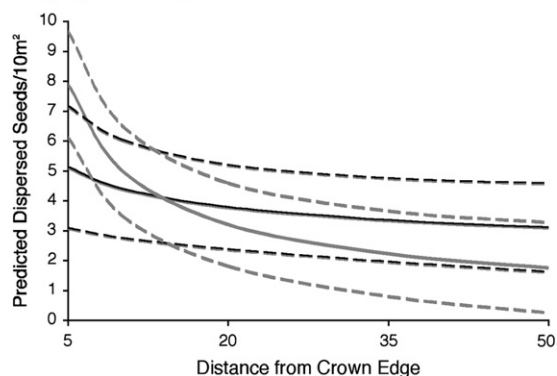


Fig. 2 – Predicted density of dispersed seeds per 10 m² (solid lines) and 95% confidence intervals (dotted lines) across distances from maternal trees in fragments (grey) and in continuous forest (black) for *D. cestroides* and *B. multiflora*. For visual clarity, the X-axis of *D. cestroides* graph is abbreviated.

diameter larger than 30 mm can only be consumed by the ecosystem's largest frugivores – hornbills, fruit pigeons, and fruit-eating mammals.

Large-seeded species also tend to be highly specialized with respect to their dispersers. In Peru, the large-seeded *Virola calophylla* (mean seed length = 17 mm) relies on spider monkeys (*Ateles paniscus* body length = 43–62 cm) to disperse 92% of its seeds (Russo, 2003). Similarly, in Thailand, virtually 100% of seed dispersal of the large-seeded *Aglaia spectabilis* (seed length = 3.0–4.6 cm) was accomplished by four species of hornbill, of which only one (*Buceros bicornis* body length = 120 cm), accounted for 65% of dispersal (Kitamura et al., 2004). Finally, in a Philippine rainforest three tree species depend solely on two species of hornbill (*Aceros waldeni* and *Penelopides panini*) for seed dispersal and two other species depend entirely on the visayan warty pig (*Sus cebifrons*) for seed dispersal (Hamann and Curio, 1999).

In addition to large-seeded trees being specialized to their dispersers, these dispersers are often specialized on their plant species. Specialist frugivores are usually large (>250 g), depend on fruit for a critical portion of their diet, and exist in small populations (Howe, 1993). Primates, large terrestrial mammals, and large birds are commonly considered specialist frugivores. In contrast, small-seeded trees are more reliant on generalist

dispersers, including passerines and frugivorous bats. Generalist frugivores are smaller (<50 g), supplement their diet with fruit, and exist in large populations (Howe, 1993). Specialized interactions in dispersal mutualisms are uncommon, making them more susceptible to fragmentation, whereas weak generalist interactions are abundant, making them more resilient to fragmentation effects (Bascompte et al., 2006).

At the BDFFP responses of primates and large mammals to fragmentation mirror the changes in seed dispersal of *D. cestroides*. More than six times the number of medium and large terrestrial mammals were recorded in fragments than in continuous forest, with especially large differences for brocket deer (*Mazama* spp.), white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Tayassu tajacu*), and agoutis (*Dasyprocta leporina*) (Timo, 2003). Half of the BDFFP's primate species have disappeared from fragments (Gilbert and Setz, 2001; Rylands and Keuroghlian, 1988). In contrast, many guilds of frugivorous birds did not suffer declines in density following forest fragmentation (Stouffer et al., 2006), suggesting that entire guilds or some species within each guild were resistant to fragmentation. Remaining species of frugivorous birds are the current dispersers of *B. multiflora* in fragments.

The scope, length, and methods of our study each limit our interpretations about seed dispersal. First, seed dispersal among individuals of the same species and within the same forest type were highly variable. One *D. cestroides* individual in continuous forest had a seed dispersal distribution more similar to fragment trees than other continuous forest trees. *B. multiflora* trees in both fragments and continuous forest had anywhere from 0% to 40% of their seeds dispersed. This variability may reflect the probabilistic character of seed dispersal, such that the effects of fragmentation appear in a non-deterministic fashion.

Second, our study was limited to one-year and cannot account for effects of supra-annual variation in fruit abundance, although we do know that fruit production was high in the year of our study. Fruit production can directly impact disperser visitation which may be important to overall seed dispersal. Multiple years of sampling might show that the lack of differences in dispersal between fragments and continuous forest for *B. multiflora* was a result of annual variation in disperser abundance or behavior, not fragmentation.

Finally, our sampling methods impose some limits on the interpretation of our results. Although the design of our study limits the certainty of each seed's parental origin, the isolation of each individual from fruiting conspecifics limits problems associated with parental origin (Cramer et al., 2007). Also, our study cannot account for long-distance seed dispersal, although we believe that our samples are representative of seed dispersal for each tree (Cramer et al., 2007). Furthermore, sampling one species with seed traps and the other by counting seeds on the forest floor opens the possibility of methods affecting the results. However, the nature of our study, comparing two species with contrasting seed sizes, precluded our using the exact same methodology and the exact same sampling months.

With these limitations we achieved a modest comparison of a single large and a single small-seeded species from over a thousand species in the BDFFP forests (Gascon and Bierregaard, 2001). Thus, we are unable to generalize our results to

differences between all large and small-seeded fruits. However, our data in conjunction with other research on fragmentation support the hypothesis tested.

Evidence from tropical fragmentation literature: Three lines of evidence from research on disperser responses to fragmentation support the hypothesis that in the tropics the dispersal of large-seeded tree species is more threatened by forest fragmentation than the dispersal of small-seeded tree species. First, large-seeded species are prone to extinction, especially in fragments, because they depend on large dispersers that require large home ranges and are susceptible to edge effects and hunting. The extinction of the four largest frugivorous pigeons in Tonga (Polynesia) left 18 large-seeded plant species with no dispersers (Meehan et al., 2002). In Madagascar the extinction of 16 large-bodied mammals left the collared brown lemur (*Eulemur fulvus collaris*) as the sole disperser for five large-seeded species (Bollen et al., 2004b). In the highly fragmented Atlantic forest of Northeastern Brazil, the largest frugivorous bird (*Mitu mitu*) is extinct, and large-bodied frugivores are the most vulnerable to extirpation as a result of fragmentation (Silva and Tabarelli, 2000; Tabarelli and Peres, 2002). In Ugandan forests, the loss of elephants has left *Balanites wilsoniana* regeneration concentrated under parent plants (Babweteera et al., 2007). At the BDFFP, primates are less common or often absent from fragments (Gilbert and Setz, 2001). Highly frugivorous primates, such as *Ateles*, are found only in large tracts of forest whereas more folivorous primates, such as *Alouatta*, still occur in forest fragments (Estrada and Coates-Estrada, 1996). In forest remnants in Singapore and Hong Kong, entire fruit crops remain underneath parent crowns of large-seeded trees, evidence that their dispersers are absent from these fragments (Corlett and Turner, 1997).

In contrast, dispersal of small seeds may remain unaltered by fragmentation because their dispersers are unaffected by fragmentation. In the Atlantic Forest of Brazil, fragmentation reduced the number of bird visitors and effective dispersers for the small-seeded *Cabralea canjerana* (mean size = 4 mm/diaspore) (Pizo, 1997). However, there was no indication that the residual guild of dispersers at the fragmented site did not continue to provide effective seed dispersal for *C. canjerana*. Bird assemblages visiting *Dendropanax arboreus* (fruit length = 4–7 mm) in Mexico were different between a 650-ha forest reserve and riparian remnants, but these differences did not translate into different fruit removal rates (Graham et al., 2002).

The second line of evidence is that forest fragmentation restricts or alters the movement of large dispersers more than small ones. Primates seldom move between fragments, especially when patches are devoid of preferred food sources (Bollen et al., 2004a; Estrada et al., 1994; Gascon et al., 2002; Gilbert and Setz, 2001; Ratiarison and Forget, 2005; Schwarzkopf and Rylands, 1989). Movement of frugivorous bats and small omnivorous birds is not as disrupted by forest fragmentation (Corlett, 1998). Bats are important dispersers in disrupted landscapes and often contribute the majority of dispersed seeds across fragments or in the regenerating matrix (Bollen et al., 2004a; Gorchov et al., 1993; Parrotta et al., 1997). Avian dispersers are very mobile and track fruit resources among rainforest patches (Price, 2004) even ventur-

ing into open habitats when perches are available (Shiels and Walker, 2003).

Finally, there is some evidence that large and small-seeded fruits, respectively aligned with specialist and generalist dispersers, are differentially linked with primary versus secondary forests in the tropics. Pioneer plant species have smaller seed masses than mature forest species (Foster and Janson, 1985; Richards, 1996) and large-seeded species are less represented in regenerating forest than in primary forest (Parrotta et al., 1997). Mammal dispersed trees (excluding bats) are more abundant in late-successional habitats than early-successional habitats (Hamann and Curio, 1999). On the other hand, recently cleared and early successional habitats that characterize edge communities and small fragments are composed of wind, generalist bird and bat dispersed seeds (Foster et al., 1986; Gorchov et al., 1993; Ingle, 2003; Medellín and Goina, 1999; Parrotta et al., 1997). In fact, 82% of seeds larger than 15 mm were only recorded in the interior of a 3500 ha fragment (Melo et al., 2006). In contrast, at forest edges, species with seeds smaller than 6 mm were more abundant in the seed rain (Melo et al., 2006) and small artificial fruits were visited by birds more frequently than in forest interiors (Galetti et al., 2003). In the fragmented Atlantic Forest, the percentage and number of small-seeded (<0.6 cm) species were reduced as the successional age of plots increased, while the percentage and number of medium-sized (0.6–1.5 cm) species increased with plot age (Tabarelli and Peres, 2002). At the BDFFP, genera that decline in fragments were characterized by many factors including large seeds and later successional status (Laurance et al., 2006a). In disturbed habitats, remaining populations of generalist disperser assemblages are likely to consist of species with partially omnivorous diets that do well in early to mid-successional habitats (Shiels and Walker, 2003) while large specialist dispersers are reluctant to cross open habitats. Therefore, although large-seeded species could succeed in early-successional habitats, their large size limits the likelihood of their arrival there (Foster et al., 1986; Wunderle, 1997). In a fragmented Kenyan forest, pioneer plant species were abundant in the seedling community but 75% of non-pioneer species showed reduced regeneration (Githiru et al., 2002a).

How do these different patterns of dispersal for early and late-successional species relate to forest fragmentation? At the BDFFP, there is clear evidence that forest fragments accumulate secondary forest trees in deference to primary forest species (Laurance et al., 2006b). We found *D. cestroides* only in continuous forest or the core of 10 and 100-ha forest fragments. On the other hand, *B. multiflora* can be found throughout the forest fragments and in secondary forests, indicating that its dispersers not only move between fragments, but also frequent the regenerating matrix around fragments.

Other studies on seed dispersal in forest fragments support the hypothesis that dispersal of small-seeded species is less affected by fragmentation than large-seeded species. Nine small-seeded tree species (<14 mm) in southeastern Kenya showed high fruit consumption in forest fragments, although there was low disperser mobility between fragments (Githiru et al., 2002b). Second, fewer dispersal agents and reduced seed dispersal were detected in fragments compared

with continuous forest for the endemic large-seeded *Leptonychia usambarensis* (seed size = 90–133 mm) in Tanzania (Cordeiro and Howe, 2003). Two other studies have examined frugivore assemblages in isolated habitats for differences based on guilds of dispersers. In the first, large and medium birds (except the fig-bird) with highly frugivorous diets declined in fragments, compared to continuous forest sites, whereas small-gaped birds with mixed diets increased in fragments (Moran et al., 2004). In the second, more primates were recorded visiting fruiting trees at mainland sites than at islands isolated for 10 years in French Guiana, but no differences in bird assemblages were detected between the two locations (Ratnarison and Forget, 2005).

Interestingly, many studies on the effects of fragmentation on the seed dispersal of a single-species focus on endemics (Cordeiro and Howe, 2003; Cramer et al., 2007; Galetti et al., 2006). For all of these studies, fragmentation (and sometimes hunting) reduces seed dispersal for both large (Cordeiro and Howe, 2003; Cramer et al., 2007) and small-seeded (Galetti et al., 2006) endemic species. Therefore, it is possible that endemic species have more specialized dispersers and are especially susceptible to fragmentation, regardless of their seed size.

Our study is significant because it compares forest fragmentation effects on seed dispersal for two coexisting species with contrasting dispersal agents, using direct counts of dispersed seeds to characterize seed dispersal in forest fragments and continuous forest. In forest fragments, small-seeded species like *B. multiflora* may continue to receive the adequate seed dispersal needed to persist as healthy populations of seedlings and adults. The fate of large-seeded species such as *D. cestroides* seems to be quite the opposite. In forest fragments large-seeded species have reduced seed dispersal making them more susceptible to extirpation. Small-seeded species are probably more resilient to fragmentation than large-seeded species because they have a greater number of generalist dispersers that are less prone to extinction and that utilize secondary forests in the surrounding matrix. In addition, endemic species may be more threatened by fragmentation regardless of seed size. Accordingly, conservation of large-seeded species and their dispersal agents will require reserves that are large enough to harbor reproductive populations of both mutualists.

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