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Differential Effects of Hunting on Pre-Dispersal Seed Predation and Primary and Secondary Seed Removal of Two Neotropical Tree Species

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ABSTRACT

Many of the mammals undergoing drastic declines in tropical forests worldwide are important seed dispersers and seed predators, and thus changes in mammal communities due to hunting will affect plant recruitment. It has been hypothesized that larger-seeded species will suffer greater reductions in seed removal and thus greater increases in predispersal seed predation than smaller-seeded species. We compared primary and secondary seed removal and predispersal seed predation of two tree species between hunted and nonhunted sites in Central Panama. Seeds of *Oenocarpus mapora* (Arecaceae) are 16-times greater in size than those of *Cordia bicolor* (Boraginaceae). We quantified primary seed removal and predispersal seed predation using seed traps, and we assessed secondary seed removal using seed removal plots. Primary removal of *C. bicolor* was 43 percent lower in the hunted sites, while primary removal of *O. mapora* was not significantly different. Secondary removal of unprotected *O. mapora* seeds on the ground was 59 percent lower in hunted sites, while secondary removal of *C. bicolor* was not significantly different. Predispersal seed predation of *O. mapora* by mammals was significantly lower in hunted sites, while predispersal seed predation by insects was not significantly different in either species. In combination with other studies, our results suggest that seed size is not a reliable predictor of the impacts of hunting. Mammal defaunation differentially affects stages and modes of seed dispersal and seed predation of different plant species, suggesting that these influences are complex and related to multiple plant traits.

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

Key words: conservation; *Cordia bicolor;* defaunation; life history traits; *Oenocarpus mapora;* Panama; seed dispersal; seed size.

ANTHROPOGENIC HUNTING AND FRAGMENTATION of tropical forests have caused global declines in animal abundances with unknown consequences for the plant communities with which these animals interact (Dirzo 2001, Wright 2003). Hunting directly causes mortality of large diurnal mammals, thereby decreasing abundances of preferred game species (Redford 1992). Habitat loss due to forest fragmentation decreases abundances of important mammal and bird seed dispersers (Laurance & Bierregaard 1997, Cordeiro & Howe 2001), and acts synergistically with hunting (Peres 2001). Because most mammals preferred by hunters are seed dispersers, seed predators, or herbivores, hunting alters plant community dynamics, including seed dispersal, seed predation, and seedling browsing (Dirzo 2001). Declines in mammal abundances are expected to significantly alter plant community dynamics, especially in the tropics where *ca* 80 percent of woody plants rely on vertebrates for seed dispersal (Willson *et al.* 1989, Jordano 1992) and where many plant species experience high rates of seed or seedling mortality due to consumption by mammals (Hammond & Brown 1998).

Over the last 15 yr, a number of studies have explored how depauperate, human-modified mammal communities affect early plant recruitment. These studies have shown that defaunation has significant impacts on seed dispersal, seed predation, seedling survival, and other recruitment processes in various plant species, as well as on community-level seedling abundance and diversity (Table 1). No common pattern has emerged, however, challenging our ability to predict the overall effects of mammal defaunation on plant communities. The variation in results among these studies can be attributed to two main causes. First, whereas all studies compare sites with relatively intact and altered vertebrate communities, the altered communities encompass diverse anthropogenic disturbances, many of which have effects beyond changes in the vertebrate community alone (Wright 2003). Second, plant species differ in their response to defaunation due to inherent variation in their interactions with affected seed dispersers and seed predators.

Wide variation in responses to defaunation among plant species does not necessarily indicate that there are no general patterns in these responses. Plant life history traits explain considerable interspecific variation in associations with affected animal species (*e.g.*, Gautier-Hion *et al.* 1985), and thus should explain considerable variation in the direction and magnitude of impacts of defaunation on plant demography (Leishman *et al.* 2000). For example, seed size, which ranges widely among plant species, is correlated with the mode of seed removal, seed survival probability, and susceptibility to pathogen attack (Leishman *et al.* 2000, Demattia *et al.* 2004). Therefore, direct effects of defaunation, specifically declines in vertebrate seed dispersal and seed predation, as well as indirect effects, such as increased pathogen-induced mortality among seeds remaining under parents, may be predictable from plant life history traits. Unfortunately, attempts to find general patterns are limited by the restricted number and diversity of plant species that have been studied so far. In particular, most studies have concentrated on plant species for which effects of hunting are expected to be particularly pronounced, especially large-seeded plant species (Fig. 1, Table 1).

Our objective in this study was to compare the impacts of hunting between tree species of two seed sizes, specifically examining seed removal and predispersal seed predation. We predicted that

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TABLE 1. *Results of studies that have looked at the effects of mammal defaunation on plant recruitment in tropical forests: + indicates an increase, − indicates a decrease, and 0 indicates no significant effect.*

					Effect of mammal defaunation								
Reference	Natural (high) vs. defaunated (low) mammal abundances	Study site	Species	Diaspore mass (mg)[a]	Seed removal	Seed dispersal[b]	Seed predation	Seed survival	Seedling damage	Seedling survival	Spatial genetic structure	Seedling density	Seedling diversity
Asquith *et al.* (1997)	Mainland vs. Small islands having no mammals, except spiny rats	Barro Colorado Nature Monument (BCNM), Panama	*Virola nobilis*	2,259	0	−	+			0			
			Gustavia superba	5,378	0	−	+			−			
			Dipteryx panamensis	11,218	0					−			
Asquith and Mejia-Chang (2005)	Mainland vs. Small islands having no mammals	BCNM, Panama	*Protium panamense*	511				+					
			Swartzia simplex	965				+	0	0			
			Oenocarpus mapora	1,661				+	0	0			
			Virola nobilis	2,259				+					
			Calophyllum longifolium	3,697				+					
			Gustavia superba	5,378				+	0	0			
			Astrocaryum standleyanum	7,565				+					
			Dipteryx panamensis	11,218				+	0				
			Prioria copaifera	25,548				+		0			
Guariguata *et al.* (2000)	Protected vs. Hunted; Continuous vs. Fragmented forests	La Selva Biological Station, Tirimbina Rain Forest Center; Costa Rica	*Virola koschnyi*	2,000	+	0							
			Otoba novogranatensis	3,000	0	−							
			Welfia regia	3,000	0	0							
			Minquartia guianensis	4,000	+	−							
			Lecythis ampla	6,000	−	−							
			Pentaclethra macroloba	6,000	−	0				+			
			Carapa nicaraguensis	20,000	−	−							
Guariguata *et al.* (2002)	Continuous vs. Fragmented forests	La Selva, Starke, Rojomaca, Paniagua; Costa Rica	*Dipteryx panamensis*	11,218	+	−							
			Carapa guianensis	14,328	0	-+							

TABLE 1.

Reference	Natural (high) vs. defaunated (low) mammal abundances	Study site	Species	Diaspore mass (mg)[a]	Effect of mammal defaunation: Seed removal	Seed dispersal[b]	Seed predation	Seed survival	Seedling damage	Seedling survival	Spatial genetic structure	Seedling density	Seedling diversity
Pacheco and Simonetti (2000)	Protected vs. Hunted	Beni Biosphere Reserve (EBB), Bolivia	*Inga ingoides*	NA							–		
Roldan and Simonetti (2001)	Protected vs. Hunted	EBB, Bolivia	*Astrocaryum murumuru*	7,400			–		–	+			
Stevenson *et al.* (2005)	Trees accessible to primates vs. isolated trees	Tinigua National Park, Columbia	*Bursera inversa*			–							
Wright *et al.* (2000)	Protected vs. Hunted	BCNM, Parques Nacionales Soberania (PNS), and Camino de Cruces (CC); Panama	*Astrocaryum standleyanum*	7,565		–	–/+[c]					+	
			Attalea butyraceae	11,101		–	–/+[c]					+	
Wright and Duber (2001)	Protected vs. Hunted	BCNM, PNS, and CC; Panama	*Attalea butyraceae*	11,101		–	–					+[d]	
Community level studies													
Chapman and Onderdonk (1998)	Continuous vs. Fragmented forests	Kibale National Park, Uganda	*Seedling community*									–	–[e]
Dirzo and Miranda (1991)	Protected vs. Hunted; Continuous vs. Fragmented forests	Tuxtla, Azules, Mexico	*Seedling community*						–			+	–
Roldan and Simonetti (2001)	Protected vs. Hunted	EBB, Bolivia	*Seedling community*									–	+

[a] Diaspore masses from S.J. Wright (pers. comm.) except for *A. murmuru* taken from Cintra and Horna (1997), *B. inversa* taken from Stevenson *et al.* (2005) and all seed sizes in Guariguata *et al.* (2000).

[b] Studies include primary removal (Stevenson *et al.* 2005), secondary dispersal (Asquith *et al.* 1997, Guariguata *et al.* 2002) and ecologically effective dispersal (Wright *et al.* 2000, Wright & Duber 2001).

[c] Predation by rodents and bruchid beetles respectively.

[d] Seedling recruitment under tree.

[e] Seedling species richness.

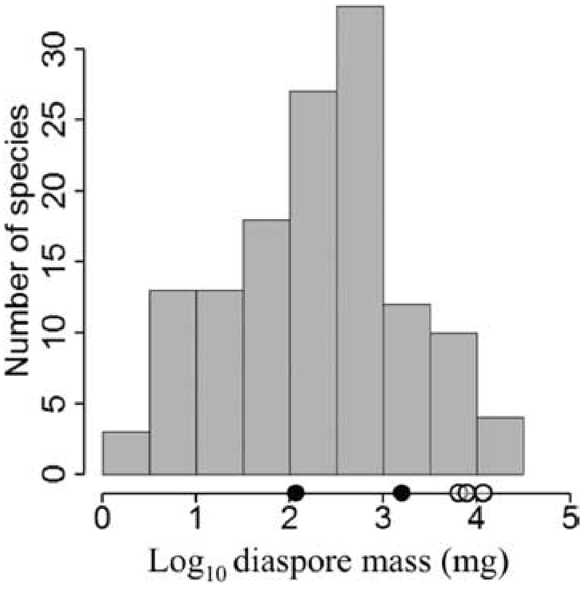

FIGURE 1. Size-distribution for known weights of diaspores of mammal-dispersed woody species on Barro Colorado Island, Panama ($N = 133$; S.J. Wright, pers. comm.). Closed circles indicate species included in this study; open circles indicate species included in other studies (Table 1; Wright *et al.* 2000, Roldan & Simonetti 2001, Wright & Duber 2001).

hunting would lead to a larger decline in seed removal rates for the larger-seeded species due to the interaction of seed size with dispersal mode as large and medium mammals tend to remove large seeds (Demattia *et al.* 2004). In contrast, we predicted that hunting would lead to no change or increased seed removal rates for the smaller-seeded species due to competitive release of nonpreferred game species (*i.e.*, small mammals and birds; Wright 2003). We also predicted hunting would increase predispersal seed predation due to longer exposure on the parent tree and competitive release of small mammalian seed predators. We further expected that this effect would be stronger in species experiencing greater reductions in seed dispersal (Thompson & Willson 1978). Our study is novel in the ecological literature on mammal defaunation in its investigation of primary seed removal and predispersal seed predation, and its inclusion of a small-seeded canopy tree, and thus sheds new light on the cascading effects of hunting on plant communities.

METHODS

STUDY SITE.—The study was conducted in protected and hunted forests of Central Panama. The protected and hunted areas are in close proximity to each other and are both in lowland rain forests with similar species composition (Wright & Duber 2001). The protected forests are on Barro Colorado Island (henceforth BCI); the hunted sites are in the Parque Nacional Soberania (henceforth Soberania; Wright *et al.* 2000). Annual rainfall averages 2188 mm near Parque Nacional Soberania and 2612 mm at BCI (Windsor 1990). BCI and Soberania were connected until 1914, after which the completion of the Panama Canal isolated BCI from the surrounding mainland. BCI has been protected and the hunted sites have had a strong human presence since the 1920s. We selected two sites each in both protected and hunted forests (Fig. 2). Sites within each hunting level were located at least 500 m apart; few mammals in this community have larger home ranges and thus seed dispersal and seed predation events at different sites should be independent (Janzen 1983, Kays & Gittleman 1995, Endries & Adler 2005). We selected three fruiting trees of *Oenocarpus mapora* and *Cordia bicolor* per site per hunting level (hunted vs. protected; 12 trees per species total).

STUDY SPECIES.—*Oenocarpus mapora* (Arecaceae) and *C. bicolor* (Boraginaceae) are both shade tolerant trees whose seeds are dispersed by mammals and birds (Croat 1978). *Oenocarpus mapora* is a clonal mid-story palm whereas *C. bicolor* is a canopy tree. Their seed masses average 1711 and 108.8 mg, respectively (diaspore dry weights; S. J. Wright, pers. comm.). *Oenocarpus mapora* fruits all year with peak fruiting in June through August, while *C. bicolor* fruits from April to August with peak fruiting in May and June (S. J. Wright, pers. comm.). The calyx of *O. mapora* and the exocarp of *C. bicolor* are nondispersed fruit parts of both species (S. J. Wright, pers. comm.), making it possible to estimate fruit production from the densities of fruits and these nondispersed parts under the crowns (Howe & Vande Kerckhove 1981). In the protected secondary forest of BCI, the average densities of *O. mapora* and *C. bicolor* are 48 trees/ha and 2 trees/ha, respectively (P. A. Jansen and S. J. Wright, pers. comm.), and in the hunted secondary forest of Soberania average densities are 38 and 5 trees/ha, respectively (R. Condit, pers. comm.).

Both species of tree are eaten and dispersed by a multitude of vertebrates. Likely primary seed dispersers of both species are

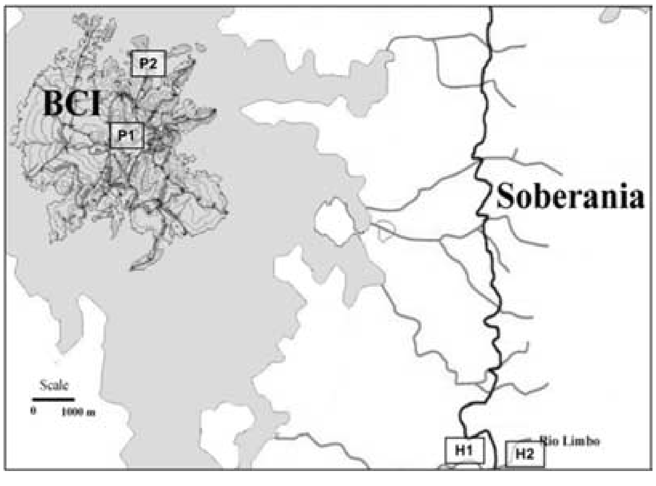

FIGURE 2. Map of Barro Colorado Island and Parque Nacional Soberania (Smithsonian Tropical Research Institute, Panama). Numbered rectangles represent locations of sites in protected (P1, P2) and hunted (H1, H2) forests.

TABLE 2. *Estimated fruit production and percent of removal for* Cordia bicolor *and* Oenocarpus mapora.

Species	Hunting	N	Estimated fruit production (Mean + SE)	Primary removal (Mean + SE)	Secondary removal[a] (Mean + SE)	Total removal (Mean+SE)
O. mapora	N	5	683.4 ± 208.6	21.6 ± 6.4	80.0 ± 7.5	84.3 ± 6.1
O. mapora	Y	6	454.2 ± 127.5	14.6 ± 5.1	10.8 ± 4.4	23.9 ± 5.9
C. bicolor	N	6	21,552.3 ± 14,021.0	42.0 ± 6.1	0 ± 0	42.0 ± 6.1
C. bicolor	Y	6	12,991.3 ± 8296.0	24.1 ± 5.4	10.6 ± 4.4	31.8 ± 6.4

[a] Secondary removal by day six.

howler monkeys (*Aloutta palliata*; Milton 1980), white-faced monkeys (*Cebus capucinus*; Wehncke *et al.* 2003), spider monkeys (*Ateles geoffroyi*; Milton 1993), Geoffroy's tamarins (*Sanguinus geoffroyi)*, common opossums (*Didelphis marsupialis)*, coatis (*Nasua narica*; N. Beckman, pers. obs.), red-tailed squirrels (*Sciurus granatensis*; Glanz *et al.* 1996), kinkajous (*Potos flavus*; Kays 1999), and various birds, especially the crested guan (*Penelope purpurascens*). Likely secondary dispersers and seed predators of both species include paca (*Agouti paca*), agoutis (*Dasyprocta punctata*; Smythe *et al.* 1996), collared peccaries (*Tayassu tajacu*), and spiny rats (*Proechimys semispinosus*; Adler 1995). All mammals present on BCI are present in Soberania, except for spider monkeys, which have been extirpated from that area (Wright *et al.* 2000, Ibanez *et al.* 2002). Abundances of howler and white-faced monkeys, agoutis, and spiny rats are lower in Soberania than in BCI, while guans are completely absent in Soberania; coatis, red-tailed squirrels, and collared peccaries also show decreased abundances in more intensely hunted areas in general (Wright *et al.* 2000).

PRIMARY SEED REMOVAL.—We assessed seed production and primary seed removal using seed traps. Under each infructescence of an *O. mapora* tree, we placed one 2 × 2 m seed trap made of 60 percent shade cloth 1–1.5 m above the ground, tied with twine to surrounding vegetation. Under each *C. bicolor* tree, we randomly placed at least three 1 × 1 m seed traps made out of 60 percent shade cloth. Seed traps accounted for 5–13 percent of crown area of this species. We calculated crown area by measuring distance from the trunk to the edge of the crown in the four cardinal directions and adding the calculated areas ($0.25\pi r^2$; Howe & Vande Kerckhove 1981). We counted all seeds, calyxes of *O. mapora* and exocarps of *C. bicolor* that fell into the seed traps weekly from May 2005 through December 2005. For each *C. bicolor* tree we calculated total fruits collected (by traps) by summing over all exocarps that fell into seed traps, and total fruit production by dividing total fruits collected by the proportion of crown area covered by seed traps. For each *O. mapora* tree*,* total fruits collected and total fruit production during the census were both calculated as total number of calyxes. For both species, primary seed removal for each tree was calculated as 1 − (total seeds collected / total fruits collected), where total seeds collected equals the total number of seeds caught in seed traps for that tree.

SECONDARY AND TOTAL SEED REMOVAL.—To quantify secondary seed removal, we compared seed removal from two 1-m-diameter circular plots next to each tree, one open to mammals and one from which mammals were excluded. Mammals were excluded using exclosures made out of 17-mm galvanized wire mesh, 0.9 m tall, buried 5 cm under the ground and were held fast to the ground with three 1-m iron rods. Plots were placed directly outside each crown, with the open access plots 2 m from the mammal exclusion plots. In each *O. mapora* plot, we set out 20 seeds in August 2005. We censused seeds the 1st, 3rd, and 6th day after seeds were set out and weekly thereafter from August through October. In each *C. bicolor* plot, we set out 20 seeds in June 2006. *Cordia bicolor* seeds were placed into 24.6 cm × 7.16 cm × 5.47 cm perforated plastic containers that were buried flush with the soil to limit the number of seeds washed away by rain. We censused seeds after 5 d. We treated the mammal exclusion plots as controls that accounted for seed burial by heavy rains (a frequent event in the small-seeded *C. bicolor*), and thus calculated secondary seed removal as 1 − (proportion seeds remaining in open access plots)/(proportion seeds remaining in mammal exclusion plots). We estimated total seed removal for each species as primary removal + (1 − primary removal) × (secondary removal). To compare estimated total seed removal between the two species, we used secondary removal by day six.

PREDISPERSAL SEED PREDATION.—For both *O. mapora* and *C. bicolor*, we counted the number of seeds with emergence holes and used the proportion of seeds with emergence holes as an indicator of insect seed predation. Specifically, we calculated the proportion of seeds predated by insects as the number of seeds with emergence holes divided by total seed fall. Our methods may underestimate total insect predation in two ways: (1) seeds infested with insects may be removed by frugivores and (2) seeds without visible emergence holes may contain insects (S. Riddle-Ford, pers. comm.). However, trials using similar methods showed that the proportion of seeds with insect emergence holes in *C. bicolor* was strongly correlated with the total proportion of undispersed seeds destroyed by insects, accounting for 68 and 98 percent of the variability in total insect predation at two sites in Panama (S. Riddle-Ford, pers. comm.).

For *O. mapora,* we also counted the number of seed fragments with tooth marks suggestive of mammalian seed predators (distinguished from insect predation; Demattia *et al.* 2004). We counted seed parts larger than three-quarters of a whole seed as whole seeds, between one-quarter and three-quarters as seed fragments and did not count seed parts less than one-quarter of a seed in size. We divided the counts of seed fragments by two to obtain an estimate

TABLE 3. *ANOVA table for proportion of seeds removed pooled over the season.*

a. Primary removal of *O. mapora* ($R^2 = 0.521$, $N = 11$)

	SS	df	MS	*F*	*P*
Hunting level	0.006	1	0.006	0.443	0.530
Ln (Fruit production)	0.023	1	0.023	1.700	0.240
Site (Hunting level)	0.076	2	0.038	2.746	0.142
Error	0.083	6	0.014		

b. Primary removal of *C. bicolor* ($R^2 = 0.752$, $N = 12$)

	SS	df	MS	*F*	*P*
Hunting level	0.145	1	0.145	6.326	0.040
Ln (Fruit production)	0.268	1	0.268	11.690	0.011
Site (Hunting level)	0.123	2	0.061	2.682	0.137
Error	0.160	7	0.023		

c. Secondary removal of *O. mapora* after 6 d ($R^2= 0.969$, $N = 12$)

	SS	df	MS	*F*	P^a
Hunting level	2.367	1	2.367	184.490	0.000
Ln (Fruit production)	0.173	1	0.173	13.511	0.016
Site (Hunting level)	0.061	2	0.031	2.391	0.324
Error	0.090	7	0.013		

d. Secondary removal of *C. bicolor* after 5 d ($R^2 = 0.371$, $N = 12$)

	SS	df	MS	*F*	*P*
Hunting level	0.034	1	0.034	4.689	0.062
Site (Hunting level)	0.000	2	0.000	0.015	0.985
Error	0.057	8	0.007		

e. Estimated total removal of *O. mapora* ($R^2 = 0.889$, $N =12$)

	SS	df	MS	*F*	*P*
Hunting level	0.669	1	0.669	54.326	0.000
Ln (Fruit production)	0.010	1	0.010	0.810	0.398
Site (Hunting level)	0.003	2	0.002	0.129	0.881
Error	0.090	7	0.013		

f. Estimated total removal of *C. bicolor* ($R^2 = 0.224$, $N = 12$)

	SS	df	MS	*F*	*P*
Hunting level	0.007	1	0.007	0.248	0.634
Ln (Fruit production)	0.024	1	0.024	0.811	0.398
Site (Hunting level)	0.009	2	0.005	0.153	0.861
Error	0.208	7	0.030		

[a] Bonferroni corrected *P*-values ($k = 2$).

of total seeds consumed by mammals and calculated the proportion of seeds consumed by mammals by dividing the total number of seeds consumed by mammals by total fruits collected for each *O. mapora* tree.

DATA ANALYSIS.—We used Analysis of Covariance (ANCOVA) to analyze variation in primary, secondary, and total seed removal and predispersal seed predation between hunted and protected areas, with sites nested within hunting level, and estimated total fruit production as a covariate. We used Analysis of Variance (ANOVA) to analyze variation in estimated total fruit production between hunted and protected areas, with sites nested within hunting level. In all cases, except where mentioned, we also performed repeated measures analyses on weekly data to see if the patterns were consistent across the fruiting season. Total estimated fruit production was log transformed and the proportion of seeds experiencing secondary removal was arcsine square-root transformed for these analyses. Analyses were done using SYSTAT (Version 11, Systat Software Inc., Richmond, California 2004).

RESULTS

PRIMARY SEED REMOVAL.—Hunting reduced total primary removal by approximately 18 percent for *C. bicolor* but did not affect total primary removal of *O. mapora* (Tables 2 and 3 (panels a and b); Fig. 3A). The repeated measures analysis showed similar results with no effect of time for either *O. mapora* (hunting: $F_{1,6} = 3.356$, $P = 0.117$; time: $F_{12,72} = 0.946$, $P = 0.508$) or *C. bicolor* (hunting: $F_{1,7} = 6.570$, $P = 0.037$; time: $F_{8,56} = 0.403$, $P = 0.914$). *Cordia bicolor* trees with higher fruit production had increased primary removal in the pooled analysis (Tables 2 and 3 (panel b); Fig. 4B) but not in the repeated measures analysis ($F_{1,7} = 2.619$, $P = 0.150$), whereas fruit production had no effect on *O. mapora* primary removal in either analysis (Tables 2 and 3 (panel a); Fig. 4A; repeated measures $F_{1,6} = 3.052$, $P = 0.137$). Fruit production did not differ between hunted and protected forests for *C. bicolor* ($F_{1,8} = 0.202$, $P = 0.665$) or *O. mapora* ($F_{1,8} = 0.047$, $P > 0.60$; Fig. 4) and declined over time for both species (*C. bicolor*: $F_{8,64} = 22.477$, $P < 0.001$; *O. mapora*: $F_{13,104} = 3.868$, $P < 0.001$). Interactions between factors were not significant for these and all subsequent analyses ($P > 0.05$).

SECONDARY AND TOTAL SEED REMOVAL.—Secondary removal of *O. mapora* was reduced in defaunated areas compared to intact mammal communities (Tables 2 and 3 (panel c); Fig. 3B). Six days after we set out seeds, 80 percent of seeds on average were removed from mammal access plots in the protected forest compared to 11 percent in the hunted forest (Tables 2 and 3 (panel c); Fig. 3B). After 59 d, 90 percent of seeds on average were removed from mammal access plots in the protected forest versus 31 percent in the hunted forest (N=12, $F_{1,7}$=28.841, P=0.001, R^2=0.821). Secondary removal of *C. bicolor* did not differ significantly between protected and hunted forests (Tables 2 and 3 (panel d); Fig. 3B). Estimated total seed

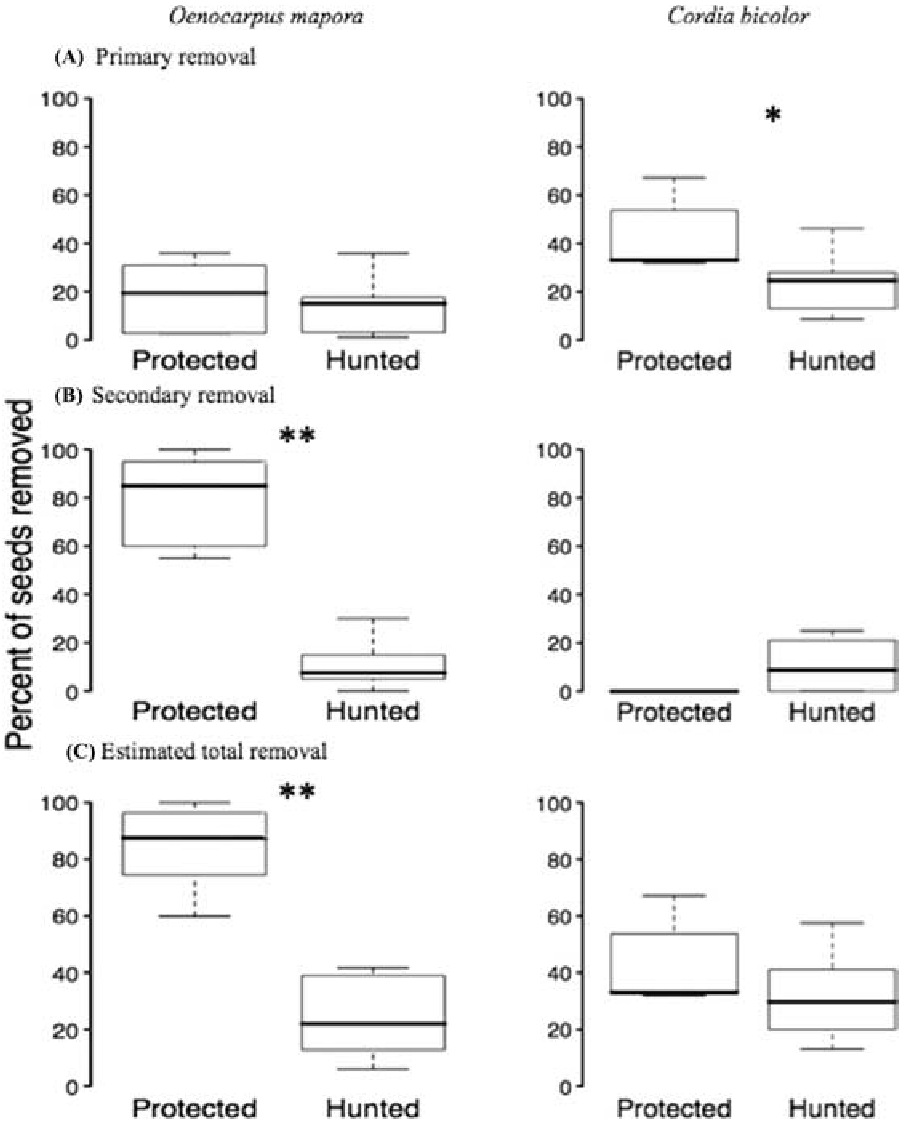

FIGURE 3. Primary removal (A), secondary removal (B), and total removal (C) of *O. mapora* and *C. bicolor* in protected and hunted forests. Asterisks depict the significance of a difference between protected and hunted forests (*, $P < 0.05$; **, $P < 0.01$.).

removal was reduced by 50 percent for *O. mapora* and did not differ significantly between protected and hunted forests for *C. bicolor* (Tables 2 and 3 (panels e and f); Fig. 3C).

PREDISPERSAL SEED PREDATION.—Predispersal seed predation by insects was not significantly different between hunted and protected forests for either *O. mapora* ($N = 12$, $F_{1,6} = 0.591$, $P = 0.471$, $R^2 = 0.495$) or *C. bicolor* (Table 4 (panel a); Fig. 5A). The repeated measures analysis for *C. bicolor* showed a similar result with no effect of time (hunting: $F_{1,7} = 3.248$, $P = 0.114$; time: $F_{8,56} = 1.007$, $P = 0.441$). Weekly predispersal insect predation was consistently too low in *O. mapora* to use repeated measures analysis. Overall, our measure of insect seed predation was much higher in *C. bicolor* than in *O. mapora*. Predispersal seed predation of *O. mapora* by mammals was approximately 150 times higher in protected areas than in hunted areas (Table 4 (panel b); Fig. 5B), whereas no predispersal predation by mammals was observed for *C. bicolor*. The repeated measures analysis for *O. mapora* showed a similar result including a significant effect of fruit production and a marginally significant effect of time (hunting: $F_{1,6} = 11.666$, $P = 0.014$; fruit production: $F_{1,6} = 12.412$, $P = 0.012$; time: $F_{10,60} = 2.018$, $P = 0.047$).

DISCUSSION

EFFECTS OF HUNTING ON SEED REMOVAL.—This study provides some support for our hypothesis that diaspore size predicts the

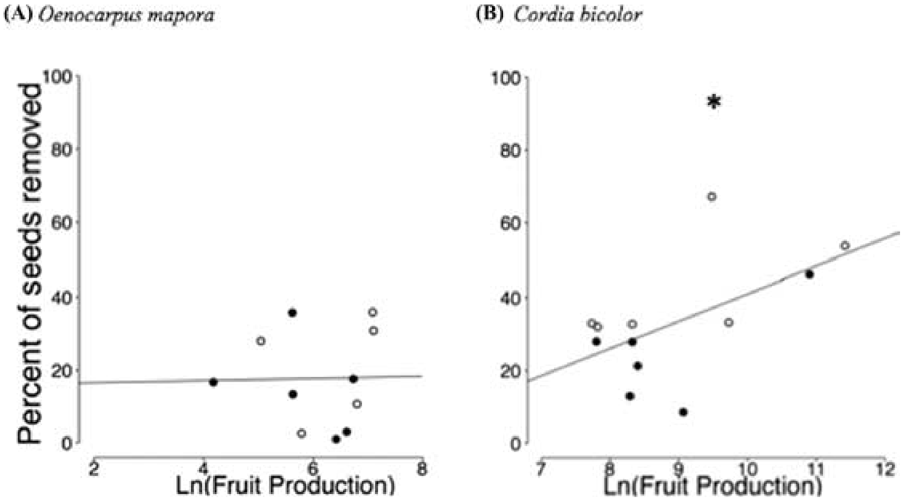

FIGURE 4. Relationship of fruit production to primary seed removal for *O. mapora* (A) and *C. bicolor* (B). Closed circles and open circles correspond to hunted and protected forests respectively; the line shows the linear regression fit (*, $P < 0.05$).

effects of hunting on total seed removal, with stronger reductions in the large-seeded species (Fig. 3C). In our study, hunting of large- and medium-sized mammals decreased total seed removal of *O. mapora* but not *C. bicolor,* whose seed mass is approximately one sixteenth as large as *O. mapora* (Fig. 3C). Partitioning the effects of hunting among the dispersal stages in these two species illuminates the complexity of this overall pattern: hunting led to significant reductions in primary removal in *C. bicolor* and in secondary removal in *O. mapora*.

Hunting did not significantly affect primary removal of *O. mapora,* but did reduce primary removal of *C. bicolor* (Fig. 3A). We interpret the stronger effects on the smaller-seeded species as due to the influences of attributes other than seed size on frugivore behavior and, thus, seed removal. These include fruit morphology, individual tree fruit production, and reproductive adult densities (Howe & Smallwood 1982). Several lines of evidence suggest that *C. bicolor* may be more attractive to primary dispersers than *O. mapora*. First, the fleshy pulp of *C. bicolor* makes up a much higher percentage of the diaspore than that of *O. mapora* (N. Beckman, pers. obs.). Second, the lower fruit production per tree and higher tree densities of *O. mapora* compared to *C. bicolor* may decrease the overall visits to individual *O. mapora* trees (Table 2; see Methods: STUDY SPECIES). Finally, previous studies suggest that white-faced monkeys prefer *C. bicolor* to *O. mapora* (Wehncke *et al.* 2003). In general, the difference in attractiveness to frugivores may reflect different dispersal strategies: *C. bicolor* potentially relies more heavily on primary dispersal than *O. mapora* and, consequently, has a greater response to hunting in the initial dispersal stage.

TABLE 4. *ANOVA table for predispersal seed predation.*

a. *Cordia bicolor* predispersal seed predation by insects ($R^2 = 0.495$, $N = 12$)

	SS	df	MS	F	P
Hunting level	0.305	1	0.305	3.807	0.099
Seed removed	0.065	1	0.065	0.816	0.401
Ln (Fruit production)	0.000	1	0.000	0.001	0.982
Site (Hunting level)	0.040	2	0.020	0.252	0.785
Error	0.481	6	0.080		

b. *Oenocarpus mapora* seed predation by mammals ($R^2 = 0.628$, $N = 11$)

	SS	df	MS	F	P
Hunting level	0.746	1	0.746	6.820	0.040
Ln (Fruit production)	0.163	1	0.163	1.490	0.268
Site (Hunting level)	0.323	2	0.161	1.475	0.301
Error	0.656	6	0.109		

Within species, vertebrate-dispersed trees with higher fruit production tend to attract more frugivore species, have higher frugivore visitation rates, and experience greater seed removal (Murray 1987, Stevenson *et al.* 2005). Consistent with these other studies, *C. bicolor* trees with higher fruit production did have higher proportions of seeds dispersed (Fig. 4B). In contrast, fruit production did not affect primary dispersal of *O. mapora* (Fig. 4A). Additionally, among the 12 *O. mapora* trees we studied, only four had removal rates greater than zero. Because of the small sizes of these palms, a larger sample size of trees may be needed to adequately compare primary dispersal between hunted and protected forests.

Hunting significantly decreased secondary removal of *O. mapora* but had no significant effect on the low rates of secondary removal of *C. bicolor* (Fig. 3B). *Oenocarpus mapora* may rely heavily on terrestrial mammals preferred by hunters for secondary dispersal of its seeds. In hunted forests, reduced secondary removal may

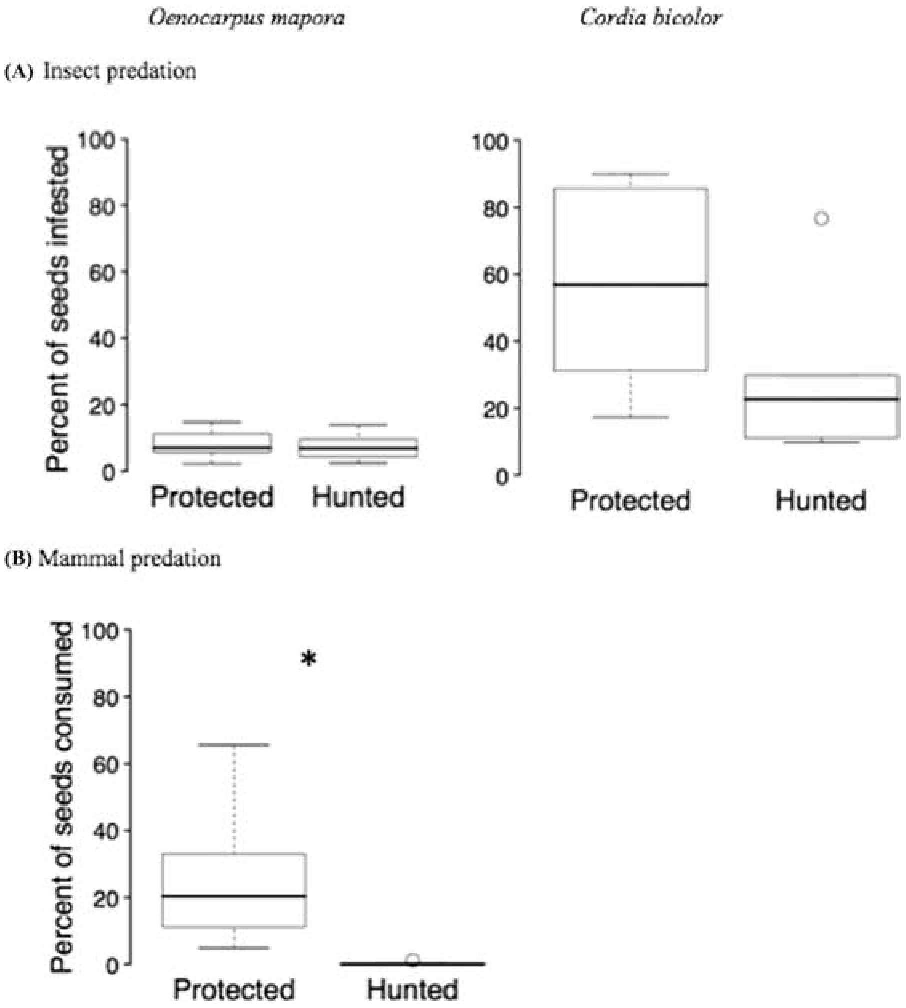

FIGURE 5. Predispersal seed predation of *O. mapora* and *C. bicolor* by insects (A) and predispersal seed predation of *O. mapora* by mammals (B) in protected and hunted forests. (*, $P < 0.05$).

explain the high densities of *O. mapora* seeds observed under parent crowns (N. Beckman, pers. obs.). The low rate of secondary removal of *C. bicolor* seeds in both hunted and protected forests suggests that terrestrial seed predators are not attracted to these seeds. However, the trend of higher removal rates in hunted forests implies that small rodents may be responsible for secondary removal of *C. bicolor*. A recent study including a larger number of species ranging in seed size supports the general prediction that hunting decreases seed predation for large-seeded species and increases seed predation for small-seeded species (Dirzo *et al.* 2007).

For both tree species, we observed seed removal rates without determining seed fate. Seeds removed by terrestrial mammals may be dispersed away from the parent tree or they may be consumed. Asquith *et al.* (1997) found that although removal rates for two large-seeded species did not differ among forests having different mammal communities, seed fates differed greatly. In our study, removal rates did differ between hunted and protected forests. Of the seeds removed, seed fates—dispersal versus predation—may differ due to hunting intensity, which will have different implications for plant communities.

EFFECTS OF HUNTING ON SEED PREDATION.—*Oenocarpus mapora* palms had lower predispersal seed predation by mammals in hunted forests than in protected forests. There was no association of predispersal mortality due to pathogens or insects with hunting, fruit production, or seed removal in either *O. mapora* or *C. bicolor*. We had expected hunting to increase predispersal seed mortality of mammal-dispersed canopy tree species indirectly because canopy trees not visited by mammal dispersers would retain higher densities of fruits for longer periods of time, and we expected such higher densities to be disproportionately more vulnerable to seed predation. Insect, avian, and mammal seed predators may be attracted to the high densities, have more time to find fruit in parent crowns (Thompson & Willson 1978), and would have less competition in the absence of seed dispersers, while pathogens may increase in a positive density dependent manner (Wright 2003). However, our results did not support these predictions for predispersal insect or pathogen damage.

Methodological limitations may have partly confounded our results. Our measure of the proportion of seeds predated by insects was based on the proportion of all seeds falling into our seed traps that showed visible signs of insect or pathogen damage. Thus, our estimates miss damage that leaves no obvious visible signature, and could be biased if frugivores prefer healthy and/or damaged fruits. Specifically, if frugivores avoid insect-infested seeds, our methods would overestimate seed predation in general, and lead to more severe overestimation in protected forests where primary removal rates are higher.

Hunting decreases the abundances of several mammalian seed predators (Wright 2003). This decrease is expected to have greater effects on predation of large-seeded species, which are typically preferred by larger mammals (Dirzo *et al.* 2007). The decrease in predispersal seed predation of *O. mapora* in the hunted sites parallels, and may be explained by, a decrease in arboreal mammal abundances (Wright *et al.* 2000).

INTEGRATING EFFECTS OF HUNTING ACROSS THE TREE COMMUNITY.—To understand the overall effects of hunting on plant communities, we must understand the variation in effects among plant species. The total effect on any one plant species requires integration over effects on multiple processes and life stages—primary and secondary dispersal, predispersal and postdispersal seed predation, seedling survival, etc (Nathan & Muller-Landau 2000). Each of these effects varies across plant species, and different plant traits may explain variation in different effects. In order to predict the consequences of hunting on plant communities, we can potentially use these plant traits to generalize effects across species. One of the few generalizations to have emerged so far is that total effects are predicted to be greatest for large-seeded trees, with these species disproportionately suffering decreased seed dispersal but also disproportionately benefiting from decreased seed predation, with the net result that they have higher recruitment in hunted forests (Dirzo *et al.* 2007, Wright *et al.* 2007).

A review of previous studies illustrates the difficulty of drawing general conclusions regarding the effects of hunting on early recruitment across plant species differing in seed size (Table 1). A major barrier to testing general hypotheses is the dearth of data on how hunting affects small-seeded species. Seed dispersal of large-seeded species generally decreases in defaunated forests (Asquith *et al.* 1997, Guariguata *et al.* 2000, Wright *et al.* 2000, Wright & Duber 2001, Guariguata *et al.* 2002, Stevenson *et al.* 2005); however, there are several exceptions (Guariguata *et al.* 2000, Guariguata *et al.* 2002). These studies suggest that plant responses to hunting are species specific and depend on the impact of hunting on the mammal community. Seed and seedling survival vary among sites in part due to differences in the intensity of mammal defaunation (Asquith *et al.* 1997, Roldan & Simonetti 2001, Wright 2003, Asquith & Mejia-Chang 2005). Studies of seedling densities and diversity have also found variable results of hunting in different communities (Dirzo & Miranda 1991, Roldan & Simonetti 2001, Wright *et al.* 2007). Integrating the effects on plant communities will require knowing the intensity of hunting as well as which mammals and fruiting species make up the community.

By favoring the regeneration of large-seeded species, hunting may eventually cause changes to the understory environment that further advantage these species. *Oenocarpus mapora* canopies decrease light availability and increase leaf litter depth under their crowns, resulting in lower overall seedling densities and seedling communities dominated by large-seeded, shade tolerant species (Farris-Lopez *et al.* 2004). In hunted areas, where mammalian predation on *O. mapora* is substantially decreased, this species may increase in density, subsequently reducing community diversity by increasing the mortality of small-seeded, light-demanding species. On small islands in the Panama Canal that have lacked mammals other than small rodents for 90 yr, *O. mapora* has become one of the dominant trees (Leigh *et al.* 1993).

The implications of hunting for plant communities are not straightforward. Different species in different sites are affected in different ways (Table 1; Dirzo & Miranda 1991, Asquith *et al.* 1997, Roldan & Simonetti 2001, Wright & Duber 2001). This variation is explained only partly by seed size and dispersal mode; many other plant traits are likely to be involved in determining the differential effects of hunting on different species. These responses may vary across the stages of plant recruitment and differ for each species, as shown here. Overall, because shade tolerance is correlated with seed size, the systematic differences in effects with seed size suggest that there will be changes in the proportion of shade tolerant species among recruiting seedlings, with implications for forest dynamics. A better understanding of the mechanisms structuring plant communities will help us predict how plant species respond when their interacting partners are extirpated and how plant communities will ultimately be affected (Muller-Landau 2007).

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