

## Bushmeat and the Fate of Trees with Seeds Dispersed by Large Primates in a Lowland Rain Forest in Western Amazonia

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### ABSTRACT

In Neotropical forests, large fruit-eating primates play important ecological roles as dispersal agents of large seeds. Bushmeat hunting threatens to disrupt populations of primates and large-seeded trees. We test the hypothesis that otherwise intact Neotropical forests with depressed populations of large primates experience decline in recruitment of large-seeded trees. We quantify the proportion of small juveniles (> 0.5 m tall–1 cm diameter at breast height, DBH) of large primate-dispersed tree species found underneath heterospecific trees that are also dispersed by large primates at two protected sites in Manu National Park and one hunted site outside Manu N.P. in southeastern Peru. The forests are comparable in edaphic and climatic qualities, successional stage, and adult tree species composition. We found that hunting locally exterminates populations of large primates, and reduced primates of intermediate body size (hereafter “medium primates”) by 80 percent. Moreover, tree species richness was 55 percent lower and density of species dispersed by large and medium-bodied primates 60 percent lower in hunted than in protected sites. In addition, richness and density of abiotically dispersed species and plants dispersed by non-game animals are greater in hunted sites. Overhunting threatens to disrupt the ecological interactions between primates and the plants that rely on them for seed dispersal and recruitment. Sustainable wildlife management plans are urgently needed, because protected areas are at risk of becoming “island” parks if buffer zones become empty of animals and have impoverished flora.

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

*Key words:* bushmeat; conservation; hunting; Manu; Peru; primates; recruitment; regeneration; seed dispersal; tropical forest.

THE EXPLOITATION OF BUSHMEAT poses a major threat to populations of tropical forest vertebrates worldwide (Robinson & Bennett 2000, Fa *et al.* 2001, Peres 2007). The harvest of wildlife is reaching devastating levels in the tropics due to rising human population and migration, increasing access to forests, and the use of increasingly efficient hunting technology (Robinson *et al.* 1999). As a result, populations of vertebrates are severely depressed and in some cases locally extinct (Bodmer *et al.* 1997) even in the absence of other forms of habitat disturbance (Peres & Lake 2003). Animals preferred by hunters are involved in key processes that aid the maintenance of forest diversity, such as pollen and seed dispersal, and seed and seedling predation (Emmons 1989, Redford 1992). Consequently, effects of overhunting vertebrates are not limited to the loss of animals' biomass. Overhunting also profoundly alters tropical plant dynamics (Dirzo & Miranda 1996, Wright 2003) with severe implications for conservation.

Seed dispersal is an essential process for the successful recruitment of many tropical tree species, and for the maintenance of tropical plant diversity (Janzen 1970, Harms *et al.* 2000, Webb & Peart 2001, Wang & Smith 2002, Howe & Miriti 2004). Seeds dispersed away from parent trees have higher probabilities of survival and hence a higher likelihood of producing seedlings (Howe *et al.* 1985, Harms *et al.* 2000, Nathan Muller-Landau 2000). In tropical rain forests, vertebrates are the main seed dispersers of 70–90 percent of woody plants (Willson *et al.* 1989); thus, it is likely that the reduction or the loss of fruit-eating vertebrates could alter the population dynamics of trees dependent on animals for seed

dispersal (Wang *et al.* 2007), and decrease tree diversity. Moreover, among tree species, seed size varies up to six orders of magnitude (Westoby *et al.* 2002). Small-seeded tree species produce numerous seeds, whereas large-seeded species produce fewer seeds, although with a higher per-capita probability of seedling establishment than smaller seeds (Westoby *et al.* 2002). Small-seeded plant species are dispersed by a wide variety of small and large frugivores (Shanagan *et al.* 2006), while large-seeded species have a restricted assemblage of potential dispersal agents (Wheelwright 1985), many of which are large-bodied animals that are often depleted by overhunting (Peres & van Roosmalen 2002, Peres 2007). The loss of seed dispersal due to the hunting of large fruit-eating animals can change the spatial distribution and demographic prospects of recruiting seedlings, particularly those of large-seeded plants (Peres & van Roosmalen 2002, G. Nunez-Iturri, pers. obs.). To the degree that many tropical tree species depend on seed dispersal, one expects reduced plant species diversity in the initial stages of forest regeneration in areas that have lost most of their large vertebrate frugivores, even if these forests are otherwise intact.

In tropical forests, large primates are important seed dispersal agents for many large-seeded species (Peres & van Roosmalen 2002). It is reasonable to predict that the loss of large primate seed dispersal may depress or preclude recruitment of large-seeded tree species, and will change the spatial distribution of seedlings that do establish. In forests with a complete assemblage of frugivorous animals, one could expect that over a long time, much of the seed transport by large and medium primates is directed in such a way that fruiting tree species “synergize” each other's recruitment by attracting frugivorous primates. Previous work in the protected Manu National Park supported the hypothesis that small saplings

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(< 1 cm DBH) of 14 primate-dispersed tree species would be more likely to occur under the crowns of primate-dispersed heterospecifics than elsewhere in the forest. Numbers of small saplings underneath primate-dispersed trees were significantly higher (by 2.5-fold) than under the crowns of abiotically dispersed species or at random points in the forest floor (Terborgh & Nunez-Iturri 2006). Here we explore how the overexploitation of large Neotropical primates (>2 kg) alters vegetation structure in species-rich communities in the western Amazon. We ask how the recruitment patterns of small saplings of large and medium primate-dispersed species underneath large-seeded, primate-dispersed heterospecifics differ between defaunated forests and forests protected from hunting.

## METHODS

**STUDY SITES.**—Our study was conducted in one hunted and two protected sites in mature flood plain forests of the Manu River in the department of Madre de Dios in Southeastern Peru. The climate is characterized by one dry (May–September) and one wet (October–April) season with an average annual rainfall of 2400 mm, and an average annual temperature of 25°C (Dallmeier *et al.* 1996). These sites are at elevations of 300–350 m above sea level. The forests are located on silty entisol soils in the mature floodplain of the Manu River, are extremely diverse and present late successional tree species with diameters over 1 m (Dallmeier *et al.* 1996, Terborgh *et al.* 1996). The mature phase of the flood plain forests in the Manu River basin are unflooded forests (Dallmeier *et al.* 1996) with uniform species composition (Terborgh *et al.* 1996). The remarkably high number of tree species shared between the study sites (J. Terborgh, pers. comm.) reveals the oligarchic composition of similar species that characterizes forests in Western Amazonia (Pitman *et al.* 2001).

The protected forests are in the Manu National Park located around Cocha Cashu Biological Station (11°52' S, 71°24' W) and Pakitza Biological Station (11°57' S, 71°17' W) situated 20 km further downstream from Cocha Cashu on the opposite side of the river. The sites are effectively protected from poaching. Cocha Cashu has a permanent presence of researchers and/or staff, and Pakitza has a permanent park guard station. The two sites are relatively far from the community of Tayacome of Matsigenka indigenous people, situated 30 km upriver from Cocha Cashu. Inhabitants of Tayacome concentrate most of their hunting near their village, use traditional methods (bow and arrow) to hunt, and hunt mostly during the wet season when animals have enough fat, and during the dry season Matsigenka people obtain protein mostly from fish. They do not have motorized vehicles to move within the park. The area surrounding their village contains populations of large primates and other preferred game (G. Nunez-Iturri, pers. obs.). The heavily hunted studied forest is located at the northeast boundary of the Manu National Park (12°15' S, 70°55' W), near the villages of Boca Manu and Isla de los Valles, situated across an oxbow lake from Isla de los Valles (60 km downstream from Pakitza). Residents of Boca Manu are Spanish-speaking colonists, and those from Isla de los

Valles are a mixture of people from Yine (Piro) and Matsigenka indigenous tribes that have abandoned their traditional methods of hunting. Inhabitants of both communities use shotguns to hunt, and are engaged in commercial hunting, selling bushmeat to other families in the village, to restaurant owners, and to merchant boats that stop by the village (G. Nunez-Iturri, pers. obs.). The forest near the villages has been intensively hunted for more than 30 yr (J. Terborgh, pers. comm.). Logging does not occur inside Manu N.P. or at the hunted forest site; inhabitants from Isla de los Valles protect the hunted forest from commercial logging. At the villages, the majority of men are boat artisans who collect tree trunks (primarily redwood *Cedrela odorata*) that fall into the Manu River and wash down during the rainy season.

**ABUNDANCE OF FRUGIVOROUS PRIMATES.**—To estimate primate density at each site, we performed diurnal and nocturnal standardized line transect censuses (Peres 1999), during the dry season in 2003 and the wet season in 2004. Censuses were performed along a 4-km transect marked every 25 m. Trails were prepared with the minimal disturbance possible, and after being established, transects were left undisturbed for at least 4 d prior to censuses to allow the distribution of animals to normalize. Each transect was walked for 13–16 consecutive days; no census was performed during rainy days. Diurnal and nocturnal censuses began at 0600 and 1800 h, respectively. The observer walked at an average speed of 1 km/h, recorded the number of animals seen along the trail, and estimated the perpendicular distance from the transect line to the animal or the center of the group for gregarious species. Detection was through visual and/or acoustic cues. For social species, we recorded number of groups and number of individuals per group. Total distance walked at Boca Manu-Isla de los Valles was 208 km, at Cocha Cashu 220 km, and at Pakitza 234 km.

**RECRUITMENT OF SMALL SAPLINGS UNDER TREES WITH SEEDS DISPERSED BY LARGE AND MEDIUM PRIMATES.**—We selected five target tree species predominantly dispersed by large and medium primates (>2.5 kg). Underneath each individual tree, we assessed species richness and density of small saplings by dispersal mode. The target tree species were *Brosimum alicastrum* (Moraceae), *Manilkara inun-data* (Sapotaceae), *Matisia cordata* (Bombacaceae), *Spondias mombin* (Anacardiaceae) and *Ziziphus cinnamomum* (Rhamnaceae). These species produce fruits that are highly preferred by large and medium primates (Terborgh 1983, Zhang & Wang 1995, Stevenson *et al.* 2002, Wehncke 2003, Dew 2005). All the species have seeds  $\geq$  1.5 cm (J. Terborgh, pers. comm.). All the target trees were reproductive, as indicated by the presence of fruits. All trees were  $\geq$  80 cm DBH, with complete crowns and a minimum of 12 m radius. Between three and nine trees per species were selected at each site. Underneath each tree, we placed two plots of 12.5 m  $\times$  4 m, extending from the base of the trunk in random but not overlapping directions. In each plot, we identified and counted all individuals of small saplings (> 50 cm height–1 cm DBH). We classified saplings according to their dispersal mode into one of three categories: (1) Large and medium primate-dispersed species (fruits with seeds  $\geq$  1.5 cm long); (2) Plant species dispersed by nongame

animals (ants, bats, small primates, and birds); and (3) Wind or ballistic-dispersed species (hereafter, “abiotic”). Primate-dispersed species were divided between those usually dispersed by large and medium primates, and species usually dispersed by small primates (fruits with seeds < 1.5 cm long). Those species dispersed by large and medium primates with seeds  $\geq$  1.5 cm, and that were known also to be dispersed by bats (Geiselman *et al.* 2006), were excluded from the large and medium primate-dispersed species category (*e.g.*, *Iriarteia deltoidea*). The dispersal mode of each individual was assigned to one of these three categories based on its fruit and seed morphology (Janson 1983, FMNH 2006, Geiselman *et al.* 2006, MBG 2066, STRI 2006, J. Terborgh, pers. comm.), and data on primate diet from the Cocha Cashu Biological Station (Terborgh 1983, Symington 1987). Individuals not identified in the field were assigned to morphospecies, and botanical samples were collected for later identification and deposition at the Herbario Vargas (CUZ) at the Universidad Nacional San Antonio Abad del Cuzco.

**DATA ANALYSIS.**—We compared the abundance of groups of primates found per day between the sites with the Kruskal–Wallis nonparametric ANOVA. We classified primates according to their body size and time of activity. Thus, there were small, medium, and large diurnal primates, and the medium-bodied nocturnal primates (Table 1). To evaluate the difference in abundance between the

sites, we performed subsequent planned contrasts using the non-parametric Tukey multiple comparisons “Nemenyi” test (Zar 1996). To assess the community of small saplings, we analyzed the mean richness and the mean density of saplings underneath individual target trees by dispersal mode between the sites. Each individual tree constitutes a replicate within site in the sapling analyses; saplings conspecific with the focal trees were not included in the counts for the density analysis. We categorized the species of plants according to their primary seed dispersal agent: dispersed mainly by (1) large and medium primates; (2) nongame animals; or (3) abiotic mechanisms. We square-root transformed the data to meet the assumption of a normal distribution, and we assessed the homogeneity of variances among the samples using the Levene test (Sall *et al.* 2001). Depending on whether the groups had equal or unequal variances, we used a one-way ANOVA or a Welch ANOVA, respectively (Zar 1996). We used the Tukey–Kramer posthoc test to investigate significant differences between group means. Analyses were performed with JMP IN version 4.0.4 (SAS Institute Inc.).

## RESULTS

**EFFECT OF HUNTING ON THE ABUNDANCE OF FRUGIVOROUS PRIMATES.**—Large frugivorous primates had been extirpated at Boca

TABLE 1. Encounter rate and density of frugivorous primates at Boca Manu-Isla de los Valles hunted site (h), and at Cocha Cashu and Pakitza protected (p) forests in southeastern, Peru. Target species are monkeys, *Ateles chamek* (black spider), *Alouatta seniculus* (howler), *Lagothrix lagotricha* (common woolly), *Cebus apella* (brown capuchin), *Cebus albifrons* (white-fronted capuchin), *Callicebus moloch* (dusky titi), *Saimiri sciureus* (squirrel), *Aotus nigriceps* (night monkey), *Saguinus fuscicollis* and *S. imperator* (saddleback and emperor tamarins). Also are included the encounter rate and densities of other potential large seed disperser as *Dasyprocta variegata* (agouti), and other forest ground herbivores that feed on seeds, fruits, and trample seedlings as *Mazama americana* (red brocket deer), *Tayassu pecari* (white-lipped peccary) and *Pecari tajacu* (collared peccary).

Target species	Cocha Cashu (p) Mean groups/day ± SE (Individuals/km <sup>2</sup> )	Pakitza (p) Mean groups/day ± SE (Individuals /km <sup>2</sup> )	BMIV (h) Mean groups/day ± SE (Individuals /km <sup>2</sup> )
Seed dispersers, Diurnal			
Large primates > 5–10 kg (spider, howler, wooly monkeys)	11.6 ± 1.3 (67)	17.3 ± 1.9 (61)	0
Medium primates > 2–5 kg (capuchin monkeys)	13.0 ± 2.0 (99)	13.5 ± 1.9 (66)	2.3 ± 0.6 (8)
Small primates < 2 kg (titi, squirrel, and tamarin monkeys)	6.5 ± 2.3 (70)	18.0 ± 5.8 (129)	18.7 ± 10.7 (86)
Seed dispersers, Nocturnal			
Small primates < 2 kg (night monkeys), and kinkajou <sup>a</sup>	2.8 ± 0.5 (21)	2.1 ± 0.4 (27)	3.0 ± 0.6 (34)
Secondary seed disperser			
Agouti <sup>b</sup> (scatter hoarder, 3 kg)	1.1 ± 0.2 (17)	2.0 ± 0.3 (26)	1.1 ± 0.3 (10)
Ground herbivores			
Red brocket deer <sup>b</sup> (35 kg)	0.32 ± 0.13 (3.4)	0.43 ± 0.16 (3.6)	0
Collared peccaries (25 kg)	0.14 ± 0.07	0.37 ± 0.12	0.17 ± 0.08
White-lipped peccaries (35 kg)	0.5 ± 0.13	0.6 ± 0.15	0.04 ± 0.04

<sup>a</sup>The fruit-eating kinkajou (*Potos flavus*). Kinkajous were included in the nocturnal census because a study in central Panama showed that this species includes in its diet about 90 percent of the plant species that the Central American spider monkey (*Ateles geoffroyi*) consumes (Keys 1998).

<sup>b</sup>Encounter rates of agouti and deer are mean number of individuals per day.

Manu-Isla de los Valles hunted forest site (Kruskal–Wallis,  $\chi^2_2 = 52.78$ ,  $P < 0.0001$ ). Medium-bodied primates were 83 percent less common when compared to the protected sites (Kruskal–Wallis,  $\chi^2_2 = 24.82$ ,  $P < 0.0001$ ), whereas the abundance of small diurnal primates did not differ between the hunted and the protected sites (Kruskal–Wallis,  $\chi^2_2 = 1.74$ ,  $P = 0.42$ ). Abundance of medium-bodied nocturnal frugivores (night monkeys and kinkajous) did not differ significantly between the hunted and the protected sites (Kruskal–Wallis,  $\chi^2_2 = 1.47$ ,  $P = 0.48$ ) and (Kruskal–Wallis,  $\chi^2_2 = 1.4$ ,  $P = 0.5$ ), respectively (Table 1). Subsequent planned comparisons (nonparametric Tukey) showed significant differences in abundance of groups of medium and large primates between the hunted and both protected sites, but no differences between the two protected forests, and no significant differences in the abundance of groups of the small primates and the medium-bodied nocturnal frugivores between all sites.

**EFFECTS OF HUNTING ON SMALL SAPLING RECRUITMENT UNDER TREES DISPersed BY LARGE AND MEDIUM PRIMATES.**—The total area sampled in the hunted site at Boca Manu-Isla de los Valles was 3200 m<sup>2</sup> (32 target trees, 2882 saplings), whereas in the protected sites of Cocha Cashu and Pakitza, the sampled areas were 2400 m<sup>2</sup> (24 target trees, 1972 saplings) and 2300 m<sup>2</sup> (23 target trees, 1801 saplings), respectively. The saplings included 106 species (25 families) mainly dispersed by large and medium primates, 497 species (59 families) dispersed by nongame animals, and 85 species (16 families) dispersed abiotically. In Boca Manu, only 9 percent of target trees (3 individuals) had conspecific saplings growing underneath, range (1–4 saplings); in Cocha Cashu, 12 percent of target trees (3 individuals), range (1–3 saplings); and in Pakitza 9 percent of target trees (2 individuals), presented a single conspecific sapling growing underneath.

Species richness and density of small saplings by dispersal mode beneath the adult target trees differ greatly between the hunted and nonhunted sites (Fig. 1). At the hunted site, Boca Manu-Isla de los Valles, the richness of large primate-dispersed species was 55 percent lower ( $F_{2,42.29} = 47.94$ ,  $P < 0.0001$ ) and density was 60 percent lower ( $F_{2,40.95} = 37.21$ ,  $P < 0.0001$ ) than the protected sites. However, the richness of species dispersed by nongame animals was 35 percent higher at the hunted site ( $F_{2,75} = 12.34$ ,  $P < 0.0001$ ) and the density of these species was 49 percent higher ( $F_{2,75} = 14.9$ ,  $P < 0.0001$ ). Moreover, richness of abiotically dispersed species was 56 percent higher ( $F_{2,71} = 7.4$ ,  $P < 0.005$ ) and the density 81 percent higher ( $F_{2,71} = 6.63$ ,  $P < 0.005$ ) in the hunted than protected sites. Posthoc comparisons (Tukey–Kramer HSD) found significant differences in richness and density between the hunted and both protected sites but no differences between the two protected forests.

## DISCUSSION

This study strongly suggests that hunting disrupts the ecological interactions between large frugivorous primates and their dependent plants. The compared sites are located in continuous tracts of for-

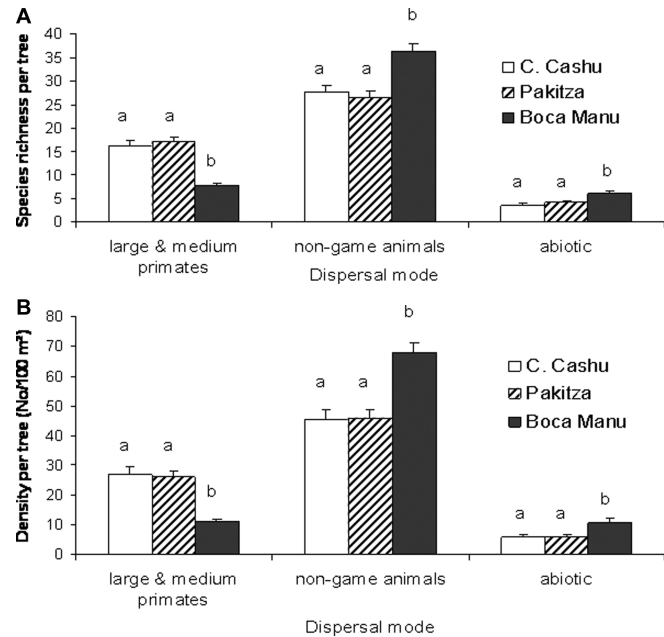


FIGURE 1. (A) Species richness of small saplings (> 0.5 m tall–1 cm DBH), by dispersal mode and by site, underneath individual trees that are dispersed by large and medium primates. (B) Density of small saplings (> 0.5 m tall–1 cm DBH), by dispersal mode and by site, underneath individual trees (heterospecific) dispersed by large and medium primates, nongame animal-dispersed and abiotically dispersed. The areas of study are unfragmented forests in southeastern Peru, Cocha Cashu and Pakitza in Manu National Park (protected), and Boca Manu-Isla de los Valles (hunted), outside the border of Manu N.P. Figure shows mean species richness and mean density per individual tree,  $\pm 1$  standard error.

est without anthropogenic habitat disturbance other than hunting. These mature flood plain forests of the Manu River are characterized by remarkable similarity in species composition (Terborgh *et al.* 1983, pers. comm.), a pattern evident throughout Madre de Dios and most of the western Amazon (Pitman *et al.* 2001). Overhunting depletes these forests of their large frugivorous vertebrates, despite the compositional similarity of tree species in southeastern Peru, hunting threatens to change the composition and spatial distribution of vertebrate dispersed trees. We found that hunting locally exterminated the large primates and severely reduced the abundance of medium primates (80% reduction), but did not have a significant effect on the density of small primates, nocturnal monkeys, and kinkajous. The decline in numbers of the larger seed dispersers was reflected in the community of the small saplings. Hunting appeared to have a significant negative effect on the number of species and density of small saplings of large-seeded primate-dispersed trees. In addition, we found a significantly higher abundance and species richness of plants dispersed by nongame animals or by abiotic means at the hunted forest compared to the protected areas. We conclude that loss of seed dispersal by large primates threatens to change the structure and forest composition in hunted areas, which could in turn feed back and further reduce the abundance of frugivore

primates with severe consequences for the conservation of tropical species-rich forests.

Commercial hunting can locally exterminate large frugivorous vertebrates. In tropical forests where hunting depleted most of the frugivorous primates, seed removal and dispersal of dependent trees is reduced (Beckman & Muller-Landau 2007, Wang *et al.* 2007). In intact flood plain forests of the western Amazon in Peru, fruit-eating primates represent up to 45 percent of the nonflying frugivore biomass (Janson & Emmons 1990). However, large primates are especially vulnerable because of their low reproductive rates (Bodmer *et al.* 1997), and are often depleted by overhunting in Neotropical forests (Peres 2007). In some forests, primates are the main dispersal agents of up to 40 percent of woody plants (Southeastern Peru: Janson 1983; Amazonas, Brazil, and Central Surinam: Peres & van Rossmalen 2002) and their depletion can have extensive negative consequences on the regeneration of the plant species that rely on them for dispersal. For instance, Chapman and Chapman (1995) estimated that 60 percent of primate-dispersed trees would be more prone to extinction if primate dispersers were absent from west Ugandan forests. Peres and van Rossmalen (2002) hypothesized that large-seeded plants would be more susceptible to recruitment failure if populations of large Neotropical primates are extirpated or severely reduced from hunted areas, and estimated a decline of 50 percent on the probability of effective dispersal of large seeds. Our independent results support these predictions, and show that forests where populations of large and medium primates are depressed exhibit a 55 percent reduction in species richness and a 60 percent reduction in abundance of small saplings ( $\geq 1$  m tall–1 cm DBH) of primate-dispersed plants with seeds  $\geq 1.5$  cm long. We foretell pervasive changes in the structure and composition of the advance regeneration of hunted forests. Commercial hunters that extirpate large frugivorous primates jeopardize forest structure and composition, and may decrease the probability of large primate population recovery by reducing the abundance of preferred fruit crop trees. Our analysis provides evidence that the loss of primate dispersal services leads to a decline in the population recruitment of dependent trees.

Our results confirm that in areas where hunters exterminate most of the medium and large frugivores the seedling recruitment of abiotically dispersed and nongame animal-dispersed plants is favored (Wright *et al.* 2007, G. Nunez-Iturri, pers. obs.), and provide evidence that hunting suppresses the recruitment of medium and large-seeded species dispersed by medium and large primates. In general, small primate species are not preferred targets of hunters in Amazonian forests, nor are small birds, bats, or other small members of the forest frugivore community (Peres 2007). However, in overexploited forests, hunting could indirectly increase the abundance of small primates (Peres & Dolman 2000). Large and medium primates eat a large proportion of the small fruits consumed by smaller monkeys (Terborgh 1983, Stevenson 2000). In severely hunted areas, therefore small frugivorous primates could show competitive release due to reduced exploitation competition from larger primates, and could potentially move the seeds formerly dispersed by the larger primates. However, small primates such as tamarins preferentially consume small seeds ( $< 1.5$  cm long; Peres

& van Rossmalen 2002, Knogge 2003) and prefer to forage in the lower strata (10–30 m; Terborgh 1983, Knogge 2003). It is thus unlikely that they will forage in large canopy trees where the large primates do. In this study, we found no evidence of density compensation of small primates or nocturnal arboreal frugivores in the hunted forest. Furthermore, we show that the hunted site has lower recruitment of large-seeded trees dispersed mostly by large and medium primates. Even if the small primates consumed fruits with large seeds in the hunted forest, there is no evidence that they compensated for the loss of dispersal services by larger primates. In this study, hunting appeared to increase indirectly the species richness and abundance of plants dispersed by nongame animals and abiotically. It is not known if compensatory increases among other nongame frugivorous animals exist in hunted forests that are depleted of large dispersers but are otherwise intact, and how this would affect the regeneration of nongame animal-dispersed plants. An experimental approach could distinguish whether the regeneration of abiotically dispersed and clonal plants is favored by reduced competition of nondispersed large seeds. In forests where most of the large frugivores are locally extinct, we urge more comprehensive studies of seed dispersal by remaining fauna to understand the regeneration dynamics in increasingly overhunted tropical forests.

Loss of seed dispersal by primates changes forest composition and alters the spatial distribution of large-seeded species dispersed by large and medium primates. The extermination of large primates can change seed deposition patterns (Wang *et al.* 2007), resulting in most seeds falling directly underneath parent trees. Disperser foraging movement and behavior after seed ingestion establishes the initial distribution of seeds (Bleher & Bohning-Gaese 2001, Wenny 2001), and sets the template for subsequent processes that ultimately lead to adult recruitment (Schupp & Fuentes 1995, Howe & Miriti 2004, Nathan & Muller-Landau 2000). In Neotropical forests, large and medium fruit-eating monkeys from the family Cebidae ingest big seeds (Stevenson 2002, Wehncke *et al.* 2003), carry large volumes of seeds in their guts, have relatively long (2–4 h) gut retention times (Milton 1981, Lambert 1998, Wehncke *et al.* 2003), have large home ranges ( $> 150$  ha), and travel long distances daily (Terborgh 1983, Wehncke *et al.* 2003). They drop seeds in a scattered pattern (Zhang & Wang 1995, Andresen 1999) with seeds of several species often dropped at the same time (Wehncke *et al.* 2003, Dew 2005). Consequently, large and medium primates provide long distance dispersal for several tree species (Chapman & Chapman 1995, Stevenson 2000, Wehncke *et al.* 2003), and they play an essential ecological role as dispersal agents of large and medium seeds (Peres & van Rossmalen 2002). Seed dispersers can aggregate seeds in a nonrandom fashion (Howe & Smallwood 1982, Wenny 2001, Schupp *et al.* 2002), for instance, under fruiting trees (Clark *et al.* 2004). In Cocha Cashu, Manu N.P., Terborgh and Nunez-Iturri (2006) found higher numbers of small saplings of trees dispersed by large primates, growing underneath heterospecific trees that were also dispersed by the same primates. We show that the loss of large and medium primates from hunted forests has the potential to disrupt the population dynamics and alter the dispersion of large- and medium-seeded trees.

Extirpation of large seed dispersal agents potentially could negatively affect the ecological and economical value of forested areas. Large and medium primates disperse the seeds of many “keystone” plant species that maintain other frugivores in times of scarcity (Terborgh 1983), and their disappearance may ignite an ecological disaster. In addition, large primates disperse several commercial timber species (*e.g.*, *Chrysophyllum* spp., *Duguetia* spp., *Manilkara* spp., *Otoba* spp., *Protium* spp., *Virola* spp., etc.) and other species that contribute nontimber forest products (fruits: *Anacardium*, *Anona*, *Genipa*, *Matisia*, *Theobroma*, several palm trees, etc.). Therefore, hunting could decrease the economic forest value of buffer zones contiguous to national parks, and thus threaten their long-term preservation if they become virtual “islands” parks surrounded by a fragmented and devalued landscape.

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