

Bushmeat Hunting Alters Recruitment of Large-Seeded Plant Species in Central Africa

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ABSTRACT

We investigated the effect of local hunting on plant recruitment at the community level in the Ngotto Forest, Central African Republic. It is the first study of this kind in the afrotropics. To compare our results with previous studies conducted in the neotropics, we used the protocol proposed by Nuñez-Iturri and Howe. We compared animal relative abundances and seed length, density and diversity of seedlings at two sites with contrasting anthropogenic pressures: one with low hunting pressure (LH) and one with high hunting pressure (HH). Furthermore, we investigated how density and diversity of recruitment vary with seed length in the two sites. Both sites exhibit similar soil, climate and tree species composition, and have never been logged. Large mammals (frugivores and herbivores) were extirpated from HH and relative abundance of medium-sized frugivores drastically decreased in HH compared with LH. In HH, diversity of seedlings was reduced compared with LH, especially for large-seeded plant species dispersed by large game mammals. The approach used in this study shows promising perspectives to investigate the effects of human disturbances on the regeneration of tropical forests. Furthermore, in the afrotropical context of a lack of data on plant–animal ecological relationships, seed length appears to be a good predictor of the strength of the deficit of plant recruitment due to large mammal extirpation because of hunting. Thus, more efforts are needed to study the ecological roles of large-seeded plants in order to better understand the effects of their disappearance on tropical forest resilience.

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

Key words: Central African Republic; forest regeneration; Ngotto Forest; seed dispersal; seed predation.

WILDLIFE HUNTING IS A MAJOR THREAT for forest vertebrates in the tropics (Robinson & Bennett 2000, Bennett *et al.* 2002, Peres 2007). Hunting preferentially targets species of large mammals that rapidly decline whereas smaller animals generally exhibit better resilience (Bennett & Robinson 1999). In tropical rainforests, the targeted large mammals are terrestrial (elephant, tapir, artiodactyls) and arboreal (primates) animals (Fa *et al.* 2002, Peres 2007). In extreme cases, preferred large game species may become locally extinct and smaller animals may be strongly depleted, leading to an 'empty forest' (Redford 1992). Although many authors have investigated the consequences of hunting on forest vertebrates, it is only recently that the effects of hunting on forest regeneration have been explored (Wright 2003, Wright *et al.* 2007b). Because plant regeneration is a key ecological process of forest resilience to disturbance (Elmqvist *et al.* 2001), the way hunting may affect it is of crucial importance.

Large terrestrial game mammals are mainly herbivores or herbivore/frugivore. Reduction in their abundance should lower seed-seedling predation in hunted sites (Wright 2003), leading to an overall increase of recruitment densities. But large vertebrates are also essential to disseminate the larger seeds of animal-dispersed plants (Stoner *et al.* 2007, Wright *et al.* 2007a). Thus, for those plants, dispersal of small seeds should be favored compared with large ones in a hunted zone. Following the Janzen–Connell hypothesis (Janzen 1970, Connell 1971), we expect more regeneration among insect-free and predator-free plant species dispersed away from their parent tree (Guariguata & Pinard 1998, Terborgh *et al.* 2008). Thus, animal-dispersed plants with large- to medium-

sized seeds that are preferentially dispersed by large game mammals should exhibit less recruitment than small-seeded species in a hunted forest. Following the same reasoning, regeneration of plants dispersed by other means (gravity, explosion, wind or water) should not be affected or less affected in hunted areas.

Most data on the effect of hunting on plant regeneration at the community level concerns the neotropics, but no such studies were done in the afrotropics (Stoner 2007, Stoner *et al.* 2007). In Panama, Wright *et al.* (2007a) showed that recruitment was lower in a hunted site than in a protected site for plants dispersed by game animals, but recruitment of large-seeded plants was favored in hunted site compared with protected site. They stated that, in their hunted sites, the reduction of large-seed predation caused by the depletion of large-seed predator outweigh the reduction of large-seeded plant dispersal. On the contrary, in Peru, Nuñez-Iturri and Howe (2007) and Terborgh *et al.* (2008) both found the same susceptibility of plants dispersed by game animals to hunting, but showed that recruitment was lower in a hunted site than in a protected site for plants with large seeds. Nuñez-Iturri and Howe (2007) presented an interesting protocol to address the question. Instead of quantifying regeneration in plots settled at random in the forest, they focused on heterospecific regeneration (postdispersal) found under mature trees known to attract large seed dispersers, where the effect of hunting on plant regeneration is likely to be the strongest. They studied regeneration by quantifying density and diversity of seedlings, as with Wright *et al.* (2007a). The common controversial point in all these studies is how plant species of recruitment are assigned to unique groups of dispersal modes differentially impacted by hunting. It is recognized that data are lacking on plant–animal relationships, especially in the paleotropics

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(Stoner *et al.* 2007, Wright *et al.* 2007a). A few observations of animals feeding on trees, or fruits in stomach contents are not sufficient to conclude that the particular species of plant and animal have an ecologically significant relationship (Wright *et al.* 2007a). Thus, authors often use fruits and seeds morphology to hypothesize main dispersers for each plant species.

This study aimed to assess the impact of hunting of large vertebrates on forest regeneration in Central Africa. It is the first study of this kind in the afrotropics. Given the paucity of data on plant–animal relationships in the paleotropics (Stoner *et al.* 2007; but see Forget *et al.* 2007, Corlett 2009), we tested whether seed size of dispersed seedlings beneath focal fruiting trees could be a reliable tool to assess the effect of hunting on plant recruitment in Africa. Therefore, we used the protocol proposed by Nuñez-Iturri and Howe (2007). Because most frugivores are likely to swallow large seeds lengthwise, seed diameter appears as the most accurate index of seed size. In this study, we considered only seed length; first because it is often the only metric available in published records, so using it allowed us to draw from a larger sample size; and second because it has been demonstrated that seed measurements increase isometrically between small- and large-seeded species in Central Africa (Forget *et al.* 2007). We compared seed length, density and diversity of established seedlings under trees known to attract large frugivores, in one site with low hunting pressure (LH) and one site with high hunting pressure (HH). Following Nuñez-Iturri and Howe (2007) and Terborgh *et al.* (2008), our hypotheses are (1) mean seed length is reduced at HH compared with LH for plants dispersed by animals and this reduction is due to the loss of the longest seeds; (2) density of seedlings is greater in HH than in LH, and this effect is stronger for small-seeded species that are more likely to be dispersed and to regenerate than large ones, following the expected decline in inter-specific competition; and (3) density and diversity are reduced for large-seeded plants dispersed by animals in HH compared with LH due to the expected lack of dispersal among this plant category.

METHODS

STUDY SITES.—We conducted this study in the southwestern forest block of the Central African Republic (CAR), in the Ngotto Forest (3°50' N, 17°10' E; 430–660 m asl; Defourny *et al.* 1997). This forest covers *ca* 1700 km², limited by the Republic of Congo to the south, and extending along the wooded savannahs of the Guinea–Sudanian transition zone to the north (Brugière *et al.* 2005). Climate in the area is tropical with one dry season (December–January) and one wet season (September–October). Average rainfall is 1500–1800 mm/yr and annual average temperature is *ca* 26°C (range: 19–31°C). The Ngotto Forest is semi-deciduous, belonging to the Congo–Guinean sector and consists of two main forest types: a non-flooded forest and a flooded *Raphia* spp. forest bordering the Mbaéré and Bodingué main permanent rivers (Boulvert 1986). In the Ngotto Forest, Meliaceae (*Entandrophragma* spp., *Guarea* spp. and *Trichilia* spp.) dominate, along with Sapotaceae (*Aurtranelia congolensis*, *Gambeya* spp. and *Manilkara* spp.), Cannabaceae (*Celtis* spp.) and the Lecythidaceae

Petersianthus macrocarpus. Fabaceae are poorly represented, with the exception of local patches of evergreen forest dominated by *Gilbertiodendron dewevrei*. Sterculiaceae and especially *Triplochiton scleroxylon* are absent (Lejoly 1995, Grosjean & Malaisse 1997).

All the Ngotto Forest has been traditionally hunted. We assumed that higher hunting pressure occurred as early as in the 1950s while shotguns and snares were more often used by local people, and that it was concentrated around major human settlement, while remote areas were experiencing very little pressure (Robinson & Bennett 2000). Nowadays, off-takes of the people in the Ngotto Forest are dominated by ungulates (80% of biomass; mostly duikers), followed by primates (11%; mostly *Cercopithecus* and *Cercocebus* species) and large rodents (6%). Large birds and fruit bats, which may play a significant role in seed dispersal of large seeds, are rarely taken. People hunt mostly around villages with snares and craft shotguns and 43 percent of the game biomass is sold to markets (Dethier & Ghiurghi 2000). In the area, consumption rates are estimated at 0.16 kg of bushmeat per person per year (Delvingt 1997) and in CAR's forests, it is estimated that 213–248 kg/km²/yr of bushmeat are extracted (Wilkie & Carpenter 1999, Fa *et al.* 2002). The Mbaéré-Bodingué National Park was created in one of the remote parts of the Ngotto Forest in 2007, although the area was already protected with the presence of the ECOFAC project, funded by the European Union, since 1993 (Vanthomme 2008). The entire Ngotto Forest but the park is now dedicated to planned selective logging.

The LH site was situated in the Mbaéré-Bodingué National Park, an area only rarely subjected to poaching due to the strong protection by the ECOFAC project, and the HH site was situated in the logging concession no. 169 of the IFB Company, in the hunting territory of the Bofi village of Banga. The distance between the two sites is 30 km. We chose these sites in the denser, old growth areas of the Ngotto Forest that exhibit almost the same profile of dominant trees and that were never logged before (Mille & Petrucci 1997).

WILDLIFE CENSUSES.—We performed diurnal censuses using pre-existing paths established by local hunters and scientists. A team of three persons composed of one local hunter, one field assistant and one of the authors, walked all paths in each site at 0600–1500 h between April and November 2008. However, because hunters' paths may be avoided by many mammals (Barnes *et al.* 1991, Benhaiem *et al.* 2008), the same team also performed REConnaisance (RECCE) transects (Barnes & Jensen 1987) between July and October 2008, by following an azimuth across the forest between paths without cutting new transect, to reduce the impacts of the study on hunting levels in the sites. The team walked quietly at an average speed of 2 km/h on the paths and 1 km/h on RECCE transects. All direct observations (*i.e.*, animals seen or heard) or indirect (*i.e.*, tracks, feces, resting sites, feeding sites) of groups of animals were recorded. All tracks or other indirect signs of the presence of groups of animals were removed after being registered. No census was performed on rainy days. Total distance walked at LH site was 305.7 km (225.3 km on hunting paths and 80.4 km on RECCE transects) and 281.9 km at HH site (201.5 km on hunting

paths 80.4 km on RECCE transects). During these censuses we also recorded all signs of hunting activities in the two sites (*i.e.*, traps, sockets and gun shots heard).

Game species recorded during the censuses were pooled in the following categories of plant-eating vertebrates: (1) frugivorous species including elephant (*Loxodonta africana cyclotis*), duikers (*Cephalophus silvicultor*, *Crocothemis nigrifrons*, *Cephalophus leucogaster*, *Cephalophus dorsalis*, *Cephalophus callipygus*, *Philantomba monticola*), apes (*Gorilla gorilla*, *Pan troglodytes*), large primates (*Cercocebus agilis*, *Lophocebus albigena*), medium-sized primates (*Cercopithecus nictitans*, *Cercopithecus cephus*, *Cercopithecus pogonias*), and birds (Musophagidae and Bucerotidae); (2) ground herbivorous species including tragelaphinae (*Tragelaphus euryceros*, *Tragelaphus spekei*); and (3) the ground omnivorous red river hog (*Potamochoerus porcus*). The three above-cited categories describe the major diet category of the censused vertebrates, most species playing a seed dispersal role to some extent (see "Discussion").

RECRUITMENT BENEATH TREES.—We studied regeneration of all plant species at LH and HH by randomly establishing 50 m² plots of 12.5 × 4 m by pairs (100 m²/pair). Each pair of plots was placed under the crown of an old reproductive tree known to attract large mammal frugivores (game and non-game species). We chose to place our plots under adult trees instead of random sampling to better standardize conditions between our sites and because regeneration in these zones was most likely to be affected by changes in vertebrate community due to hunting (Carrière *et al.* 2002b, Nuñez-Iturri & Howe 2007). All the target trees (Table 1) were reproductive, have large or medium seeds, were ≥ 70 cm diameter at breast height (dbh) and had a complete crown of ≥ 12 m radius. Each pair of plots was extending from the base of the trunk in random and non-overlapping directions. In each plot, we identified and counted all seedlings measuring 0.5–2 m in height. When a plant species could not be identified in the field, a botanical sample of the seedling was collected, dried and later identified with the help of botanists from the University of Bangui.

We determined the dispersal mode of each plant species based on life-history traits and morphology of seeds and fruits (Aubréville 1950, Pope 1961–2007, Satabié 1978, Aubréville *et al.* 1978–1999, Vivien & Faure 1985, Carrière *et al.* 2002a) and from records of the literature (Hladik 1973, Gautier-Hion *et al.*

1985a, b; Tutin & Fernandez 1985, Forget *et al.* 2007). From this review, we were able to distinguish plant species dispersed by abiotic means from plant species dispersed by animals, but it was not possible to connect each species of plant with its animal disperser species because this information was unknown for 43.2 percent of them (38 of 88 species). We therefore distinguished only two dispersal modes: (1) species dispersed by abiotic means (gravity, explosion, wind or water); and (2) species dispersed by animals.

DATA ANALYSIS.—We calculated a Kilometric Abundance Index (KAI) by dividing all direct and indirect observations of groups of animals by the distance walked during the censuses. We compared KAI of the categories of species per day per site using Wilcoxon–Mann–Whitney non-parametric (WMW) tests (Scherrer 2007). KAI were also similarly computed for hunting activities.

We compared the frequency distributions of seed lengths (*L*) between sites for plants dispersed by abiotic means, and for plants dispersed by animals, using the Kolmogorov–Smirnov test (Scherrer 2007). Then we compared density (*D*) and diversity (*H*) of plant seedlings at the community level under each focal tree at LH and HH, on one hand when plants species are grouped by dispersal modes, and, on the other hand, for animal-dispersed plants, when seed length is used as a predictor. For the density analysis, we only counted heterospecific seedlings below the focal tree, *i.e.*, the seeds that have been dispersed away from their parent plant. Data from each pair of plot were pooled and constitutes a replicate within site for this analysis. We tested for differences in density of seedlings across sites with species grouped by dispersal modes using WMW tests (Scherrer 2007). Simple linear regression was then used to determine the correlation between density of saplings and seed length. After testing residuals' normality (Shapiro–Wilk test), and their variance (*F*-test; Scherrer 2007), we log-transformed density. Differences in the slope of the two regression lines obtained with log-transformed data were tested with a Student *t*-test (Scherrer 2007). Finally, we estimated species diversity of plants under the trees at LH and HH with the Shannon–Wiener Index (Zar 1984), when plants were grouped by dispersal mode and by seed length classes. Standard deviation of this index was calculated according to the formula proposed in Jayaraman (1999). Plant species dispersed by animals were ascribed to three seed length classes: (1) small (*L* ≤ 10 mm); (2) medium (*L* = 10–18 mm) and (3) large (*L* ≥ 18

TABLE 1. Old reproductive animal-dispersed trees under which pairs of plots were installed to analyze regeneration in sites with low hunting (LH) and high hunting (HH) pressures in the Ngotto Forest.

Tree species	Commercial name(s)	Sango names	Family	Seed length (mm)	#/site	
					LH	HH
<i>Antrocaryon klaineianum</i>	Onzabili	Naniénié	Anacardiaceae	22.0	1	0
<i>Canarium schweinfurthii</i>	Aiele	Motoua	Burceraceae	30.6	1	1
<i>Manilkara maboikeensis</i>	Manilkara	Monguinza	Sapotaceae	12.0	2	1
<i>Ricinodendron heudelotii</i>	Essessang (Erimado)	Mbomboko	Euphorbiaceae	16.7	1	1
<i>Staudtia kamerunensis</i>	Niove	Molanga	Myristicaceae	21.4	2	1
Total					7	4

mm). Each class had an equal number of species. We tested for differences in diversity of recruitment in each seed length class across sites using an adaptation of the classic Student *t*-test for comparing Shannon–Wiener Indices (Jayaraman 1999). Statistical analyses were performed with the R 2.9.0 open source software (available at <http://www.r-project.org>).

RESULTS

KAI for hunting activities was significantly ($P < 0.001$) greater at HH (1.41 observations/km, SD 0.90) than at LH (0.30 observations/km, SD 0.26). For the animal analysis, the larger the game species, the lower its relative abundance at HH compared with LH (Table 2). The largest frugivores appear to be extirpated from HH.

Of the 88 plant species (3127 individual seedlings; Table S1) found under trees at the two sites, only two species (2.3% of species and 0.2% of seedlings) were of unknown seed length and were excluded from the analysis. Overall, mean seed length was significantly ($P < 0.001$) lower at HH ($L_{HH} = 10.1$ mm, SD 6.6) than at LH ($L_{LH} = 13.8$ mm, SD 8.3). The comparison of the frequency distributions shows that seed lengths are significantly ($P = 0.04$) greater at HH compared with LH for plants dispersed by abiotic means (Figs. 1A and B) and significantly ($P < 0.001$) lower at HH compared with LH for plants dispersed by animals (Figs. 1C and D).

Overall, there was no significant difference ($P = 0.07$) for density of seedlings across sites, although there was a trend for density to be greater at HH than at LH. The Shannon–Wiener Index was significantly ($P < 0.001$) lower at HH than at LH.

No significant differences in density ($P = 0.33$) or diversity ($P = 0.17$) of seedlings were found between the two sites for abiotic-dispersed species (Fig. 2A and B). Although non-significant ($P = 0.07$), density of seedlings dispersed by animals tended to be greater at HH compared with LH (Fig. 2A). Diversity of animal-dispersed plants was significantly ($P < 0.001$) lower in HH compared with LH (Fig. 2B).

No significant correlation was found between the log of density of seedlings and seed length in the two sites for plants dispersed by animals ($R^2_{LH} = 0.03$, $P = 0.16$ and $R^2_{HH} = 0.05$, $P = 0.11$). The slope of the regression line in HH ($b_{HH} = -0.04$) was not significantly ($P = 0.19$) different from that of LH ($b_{LH} = -0.02$), although there was a tendency for it to be smaller (Fig. 2C).

Diversity of plants with large- and medium-sized seeds was significantly lower (P both < 0.001) while diversity of plants with small-sized seeds increased significantly ($P < 0.001$) at HH compared with LH (Fig. 2D).

DISCUSSION

Overall, our three hypotheses were supported by our results. The main working hypothesis was that hunting would contribute to a disadvantage for large- to medium-seeded plants species that are dispersed by large mammals. As expected, once hunting extirpated large mammals and severely reduced relative abundance of medium-sized mammals as observed at the most impacted site (HH), plant species diversity was reduced. This effect was even greater among large-seeded, animal-dispersed species (Fig. 1). Given that seedling density tended to be greater in HH, we can hypothesize that a major effect of hunting in the Ngotto Forest is an overall reduction of seed–seedling predation associated with a reduction in seed shadow among animal-dispersed plants with large seeds, as observed elsewhere for *Balanites wilsoniana* (Chapman *et al.* 1992, Babweteera *et al.* 2007) and *Antrocaryon klaineianum* (Wang *et al.* 2007). The disappearance of ecological functions of the largest mammals seemed not to be compensated for by those of smaller non-game species like large birds and fruit bats. The reduction of predation of the larger seeds in the hunted site may explain why seed lengths appeared to be greater in the HH site for plants dispersed by abiotic means. This result, however, must be regarded with caution as the significance of the difference was only due to the presence of one small-seeded species in LH, which was absent in HH.

TABLE 2. Kilometric Abundance Index (KAI, observations/km) and SD of animal species in sites with low hunting (LH) and high hunting (HH) pressures in the Ngotto Forest. Wilcoxon–Mann–Whitney test: NS, non-significant; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

Categories of animal species (weight range)	On hunting paths (SD)			On RECCE transects (SD)		
	LH	HH	<i>P</i>	LH	HH	<i>P</i>
<i>Frugivores</i>						
Elephant (2100 kg)	0.11 (0.07)	0.00 (0.02)	***	0.07 (0.08)	0	**
Duikers (6–65 kg)	1.88 (0.18)	0.23 (0.10)	***	30.44 (1.17)	26.5 (0.95)	***
Apes (35–140 kg)	0.03 (0.03)	0	*	0.42 (0.09)	0	***
Large primates (5–10 kg)	0.12 (0.08)	0.08 (0.07)	NS	0.35 (0.17)	0.14 (0.07)	**
Medium-sized primates (2–5 kg)	0.35 (0.14)	0.28 (0.11)	NS	0.60 (0.28)	0.57 (0.24)	NS
Birds (0.5–1 kg)	0.08 (0.07)	0.09 (0.08)	NS	0.05 (0.03)	0.05 (0.02)	NS
<i>Ground herbivores</i>						
Tragelaphinae (80–250 kg)	0.01 (0.02)	0.00 (0.02)	NS	0.29 (0.18)	0	***
<i>Ground omnivore</i>						
Red river hog (80 kg)	0.22 (0.07)	0	***	1.48 (0.30)	0.31 (0.10)	***
<i>Total</i>	2.76 (0.31)	0.62 (0.15)	***	34.06 (1.28)	27.52 (0.94)	***

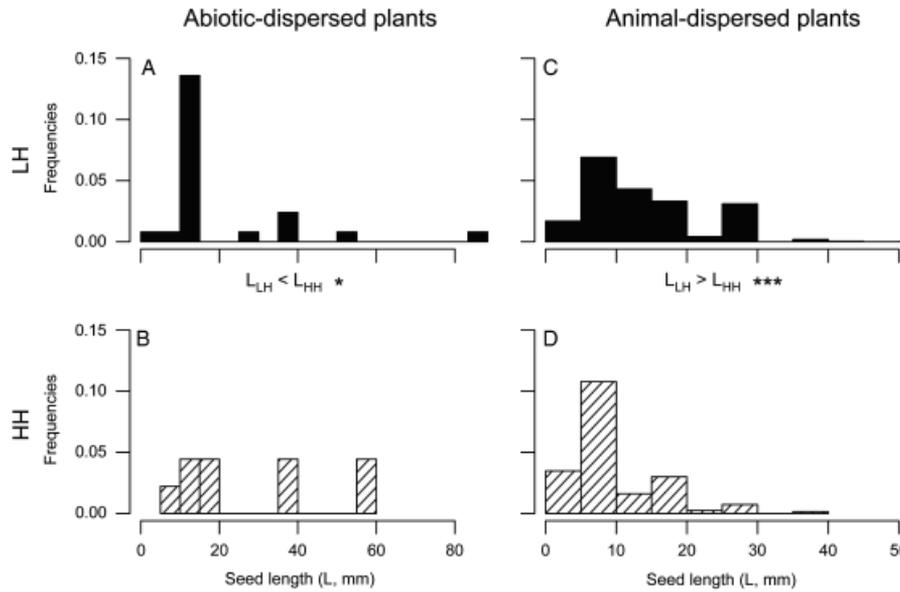


FIGURE 1. Frequency distributions of seed lengths for plants dispersed by abiotic means in sites with low hunting (LH, A) and high hunting (HH, B) pressures and for plants dispersed by animals in LH (C) and HH (D). Relationships between the distribution of seed length and results of the Kolmogorov–Smirnov tests are shown in the graphs. Asterisks denote significant differences ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

Although other studies in the neotropics (Guariguata & Pinard 1998, Nuñez-Iturri & Howe 2007, Stoner *et al.* 2007, Terborgh *et al.* 2008) and in tropical Asia (Corlett 2007) are in agreement with our results, Wright *et al.* (2007a) found the oppo-

site pattern in Panama concluding that ‘hunters favor large seeds by removing large vertebrate seed predators and increasing survival rates for large seeds.’ First, it should be noted that Wright *et al.* (2007a) included in their analysis species dispersed by all means,

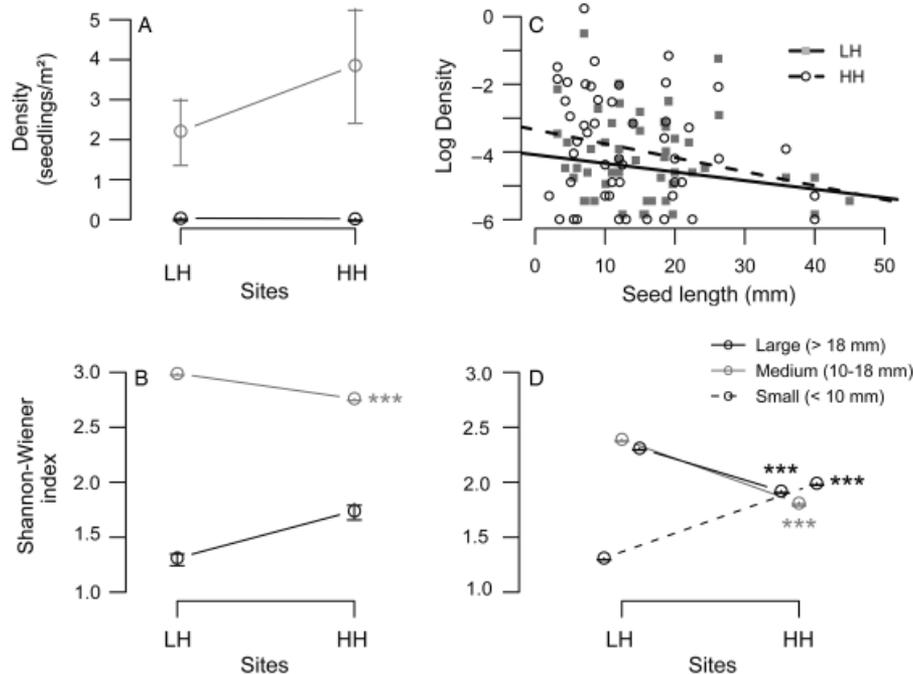


FIGURE 2. Density and Shannon–Wiener Index of plants in sites with low hunting (LH) and high hunting (HH) pressures when species were grouped by dispersal modes (A and B; black, abiotically dispersed, grey, animal dispersed) and when seed length is used as predictor (C and D). Wind-dispersed species are not shown in the seed length analysis. Error bars for densities and diversity represent 1 SD; $***P < 0.001$.

including those dispersed by wind, in contrast to our study. Wind-dispersed species can have very large seeds (Forget *et al.* 2007) and may affect the significance of the effect. Second, game species play several roles in forest regeneration. Even if a single animal species may have contradictory effects on forest regeneration (*e.g.*, small primates can be predispersal seed predators and primary seed dispersers in the same time; see Gautier-Hion *et al.* 1985b), main ecological roles have been defined for different taxa: they can be arboreal seed and foliage predators (such as primates); primary seed dispersers (*e.g.*, primates, African elephant); secondary seed dispersers (*e.g.*, rodents); or ground seed predators and herbivores (*e.g.*, rodents, artiodactyls) (Wright 2003). Whether or not each of these guilds affect predominantly plant recruitment is difficult to predict. Furthermore, extirpation of some species of granivorous, frugivorous and folivorous species by hunting may favor other non-game species through competitive interactions (Stoner *et al.* 2007). These non-game animals may in turn prey on plants in an unpredictable way. This complex set of interaction preclude any prediction to be done a priori for a given site (Guariguata & Pinard 1998, Stoner *et al.* 2007).

Because possible responses of tropical forests to human disturbances are driven by complex relationships, we cannot solely rely upon specific case studies (Forget *et al.* 2001, Wang *et al.* 2007) to predict the effects of human disturbances on forest regeneration, especially when the disturbance is not spectacular, and is silently developing as with hunting. We strongly advocate that the protocol used in Nuñez-Iturri and Howe (2007) and in this study should be the starting point for monitoring tropical forest regeneration in disturbed sites. In a cost-efficient, rapid and simple manner the protocol (1) enables assessment of the net effect of disturbance on plant recruitment, summing the effects of dispersal, predispersal and postdispersal predation, structure of animals communities and weather over decades; (2) emphasizes the more vulnerable plant species to disturbance, which enables managers to prioritize conservation actions and scientists to choose appropriate species to further test hypotheses; (3) produces data that could be used in ecological models to predict the future diversity of tropical rain forest plant species. The central caveat of such a protocol is that, due to field constraints and lack of replication of hunted and non-hunted treatment at the landscape level, this study at two sites is subject to pseudo-replication (Hurlbert 1984). Indeed, in the field, it is almost impossible to find replicates of sites with similar hunting pressure and habitat (*e.g.*, Rist *et al.* 2009). These results, however, contribute to building a hypothesis, which can then be tested, at smaller scales, in controlled field experiments (Hargrove & Pickering 1992). First, however, a tropical inter-continental (South and Central America, Africa and Asia) comparison of regeneration with a unified protocol is highly desirable to investigate the differences in tropical forests response to hunting and to better understand the ecological mechanisms involved.

More importantly, our study shows that seed length appears to be a reliable predictor of the effect of hunting on plant recruitment. As pointed out in the literature (Stoner *et al.* 2007, Wright *et al.* 2007a), data on dispersers in this study were available for only 43 percent of censused plants. Furthermore, as stated by Wright *et al.*

(2007a), ‘there is probably not a single plant species whose seeds are only dispersed by game species,’ thus opening a theoretically possible compensation of seed dispersal by other unknown, non-game animals. In this context of this lack of data on plant–animal ecological relationships, one can question the relevance of the group of plants ‘dispersed by game animals’ that can be found in some previous studies, and the significant statistical relations between this group and an altered recruitment. Because large seeds dispersed by mammals rely upon a reduced set of large dispersal agents compared with smaller seeds (Nuñez-Iturri & Howe 2007), and because these large dispersal agents are the main target species of hunters and the first to disappear (Fa *et al.* 2002, Peres 2007), mean seed length of recruitment of species dispersed by animals is expected to be reduced in hunted sites. This pattern was found in our study. Furthermore, the large-seeded group suffered reduced diversity while it was higher in the small-seeded group, along with density. These results are justified because we were able to determine seed length for 98 percent of censused plants, while we were only able to find dispersers for only 57 percent of plant species. The loss of large-seeded plant species in tropical forests where large seed dispersers are removed by hunting is probably a major trend throughout the tropics, and also possibly in temperate regions. The ecological consequences of this situation on forest resilience have need to be better understood, by conducting specific studies on the ecological roles of the most threatened large-seeded plant species, and the consequences of their disappearance.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Species of seedlings counted in the Ngotto Forest presented by dispersal modes, along with their families, seed lengths, plant types and densities in sites with low and high hunting pressures.*

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