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# Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru

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## ABSTRACT

Hunting with firearms decimates primates of large and medium body size (>2 kg) that disperse the seeds of large-seeded trees. In continuous, un-fragmented forests of southeastern Peru regularly hunted with firearms for 30–40 years, large primates are extirpated and medium-sized (medium) primates are reduced 61% compared with protected forests. At hunted sites seedlings and small juveniles (<1 m height) of trees dispersed by primates heavier than 2 kg are reduced 46%, a loss of one species m<sup>-2</sup>, and abiotically-dispersed plants are 284% more common, adding eight individuals m<sup>-2</sup>, compared with protected forests. Here we provide evidence consistent with the long-held prediction that commercial hunting changes plant communities. We show that the composition of seedling and small juvenile tree communities that ultimately regenerate future forests differs markedly in forests hunted with firearms compared with protected forests. This opens the possibility of shifts in tree species composition, even in hunted forests that are not logged or fragmented, towards forests dominated by trees dispersed by wind or non-game animals.

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## 1. Introduction

Extirpation of vertebrate populations threatens the ecological integrity of ecosystems worldwide through disruption of plant–animal interactions (Dirzo and Miranda, 1991; Myers and Knoll, 2001; Cordeiro and Howe, 2003; Cramer et al., 2007). As in Old World rainforests (e.g. Fa et al., 2005, 2006; Lee et al., 2005), bushmeat consumption in Neotropical forests has greatly increased in recent decades as roads increase access to forests and facilitate the removal of meat, and shotguns kill animals far more efficiently than bows and arrows or blowpipes (Robinson et al., 1999). In the Brazilian Amazon alone, hunters kill at least 16 million mammals each year (Peres, 2000). Commercial hunting for local and re-

gional markets follows histories of exploitation, some of it excessive, of subsistence hunting in expanding human populations (Marshall et al., 2006; Gavin, 2007). Overhunting is widely recognized as a threat to vertebrate populations, but more subtle and potentially more pervasive effects of hunting are disruption of plant and animal interactions that affect the seed dispersal, and seed and seedling predation that drive forest dynamics (Muller-Landau, 2007; Wright et al., 2007). Here we address effects of extirpation of primates that serve as key agents of seed dissemination for a large proportion of the flora in extensive, unbroken Peruvian lowland forests.

Large fruit-eating animals are thought to play important ecological roles in the maintenance of tropical forests (Em-

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mons, 1989; Redford, 1992; Peres and Palacios, 2007). Because plant recruitment often depends on seed deposition at suitable sites far from the parent plant, local extermination of key seed dispersers could affect tropical forest regeneration (Wright, 2003; Nunez-Iturri and Howe, 2007). The potential effects of disperser loss are especially important in Neotropical rainforests, where 80% of plant species rely on frugivorous animals for seed dispersal (Levey et al., 1994), with large-seeded trees particularly vulnerable to loss of fruit-eating animals that are both less common than smaller frugivores, and are often game animals (Nunez-Iturri and Howe, 2007; see Cramer et al., 2007). We hypothesize that large-seeded plants with a limited array of dispersal agents are most affected by hunting. In undisturbed forests of the western Amazon, medium- (>2–5 kg) and large-bodied (>5–10 kg) primates comprise up to 40% of the non-flying mammal biomass (Janson and Emmons, 1990), and disperse the seeds of nearly 40% of woody plant species (Janson, 1983). In contrast, small-bodied primates (<2 kg) ingest and disperse small seeds (<15 mm long) (Peres and van Roosmalen, 2002; Knogge and Heymann, 2003). Large primates are particularly effective dispersers of large ( $\geq 25$  mm long) seeds (Zhang and Wang, 1995; Stevenson, 2000) of tree species, which in this primate-driven forest (Janson, 1983; Terborgh, 1983; see Russo, 2003) are unlikely to be consistently dispersed without them.

Hunters with firearms change the fortunes of many wild animals. In Neotropical forests, primates >2 kg are preferred game, and are sensitive to hunting (Bodmer et al., 1997; Peres, 2000). We hypothesize that over-hunting large and medium fruit-eating primates deprives trees with larger seeds of dispersal agents, exposing seeds and seedlings accumulated under parent trees to higher density-dependent mortality from insects and pathogens than would occur among widely-scattered seeds (e.g. Janzen, 1970; see Harms et al., 2000; Hardesty et al., 2006). The occurrence of few juvenile trees under fruiting adults of the same species implies general dependence on seed dispersal throughout the Neotropics, from Central America to the Amazon (Terborgh and Nunez-Iturri, 2006). It is becoming clear that community-level effects of hunting do impact plant populations in many disturbed sites in the tropics (e.g. Stoner et al., 2007a, b; Dirzo et al., 2007; Wright et al., 2007), and that other disturbances, such as logging, forest fragmentation, interference from domestic animals, and other factors have multiple effects on tree recruitment that may be independent of hunting (Benitez-Malvido, 1998; Lurance, 2005; Fleury and Galetti, 2006; Lopes de Melo et al., 2006; Huerta, 2007; Whiteman et al., 2007). Not yet well understood is how hunting alters forest floor plant dynamics in continuous forests of thousands of square kilometers that are otherwise unaffected by logging, fire, or other physical disturbances.

Here we test the prediction that loss of dispersal agents changes community-wide recruitment of trees bearing seeds consistently dispersed by primates of medium or large body size. We ask whether forest floor communities of hunted and protected sites differ in representation of seedlings and small juveniles of mammal-dispersed trees. In a pilot study, Nunez-Iturri and Howe (2007) used three of these sites with an alternative design directed at seedlings under primate-dispersed trees; more seeds of tree species dispersed by large pri-

mates occurred under reproductive trees dispersed by large monkeys in two protected forests, as compared with one hunted forest. The present study uses the context of an expanded mammal census (Nunez-Iturri, 2007) and an entirely different method of sampling community-wide plant composition to test for differences of forest floor composition independent of proximity to primate-dispersed trees. The goal is to test for distinctively different species compositions and plant densities of forest floor communities where primates have been extensively hunted with firearms, as compared with where they have not, in vast un-fragmented forests in which plant interactions are not confounded by commercial logging, habitat fragmentation, fire, or other anthropogenic disturbances.

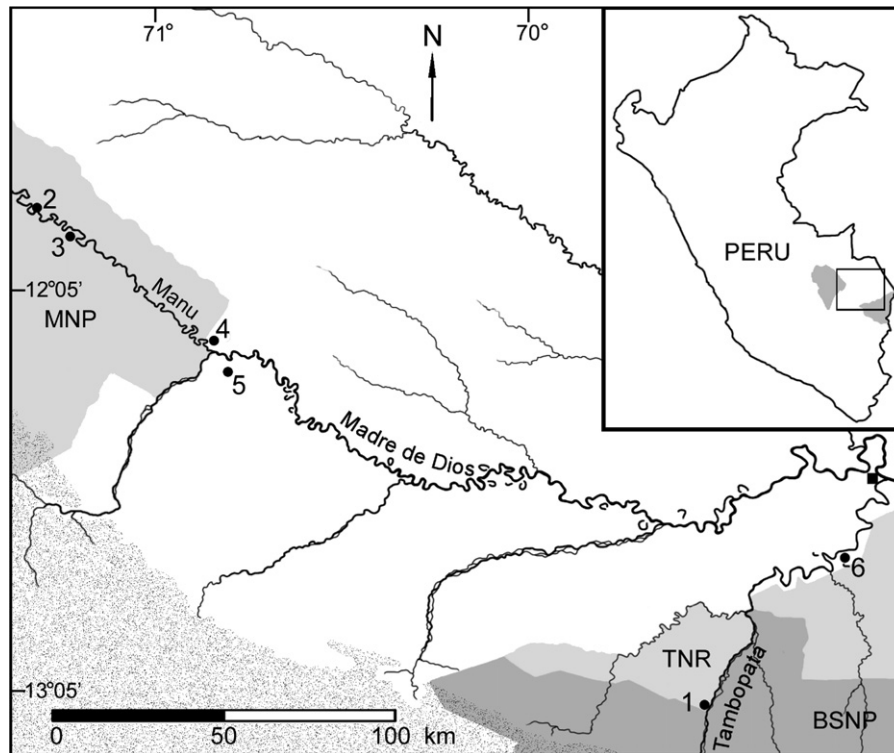
## 2. Materials and methods

### 2.1. Study sites

The study was carried out at six localities in the southwestern margin of the Amazon basin within the Manu and Tambopata regions of southeastern Peru (Fig. 1). All sites were in mature forests of the alluvial floodplain of the Madre de Dios and two tributaries, the Manu and Tambopata rivers. Three sites are inside National Protected Areas where hunting with firearms is not allowed; (1) near the Tambopata Research Center (13° 06' S, 69° 36' W) in the Tambopata National Reserve (TNR); (2) near Cocha Cashu (11° 52' S, 71° 24' W); and (3) Pakitza (11° 57' S, 71° 17' W) Biological Stations in Manu National Park (MNP), Peru. Members of the Machigenga people and uncontacted groups hunt with arrows and blowpipes in the Park, but firearms are strictly prohibited. Sites (2) and (3) were 20 km apart on opposite sides of ~160 m wide Manu River. Three sites hunted with firearms were contiguous with the National Protected Areas 3–8 km from three villages: (4) 3 km NNW from the village of Boca Manu (>250 inhabitants) (12° 14' S, 70° 55' W), across an oxbow from the Piro indigenous community of Isla de Los Valles, and 1 km from the Manu River; (5) 8 km ENE from the Piro indigenous community of Diamante (>400 inhabitants) (12° 18' S, 70° 53' W), 1.5 km from the Madre de Dios River; and (6) 8 km SSW from the center of the Esse'ja indigenous community of Infierno (>600 inhabitants) (12° 47' S, 69° 15' W), ~5 km NE from the Explorer's inn research station, 1 km from the Tambopata River. Infierno is 25 km from Puerto Maldonado (>40,000), the capital of the Department of Madre de Dios. Protected sites (4) and (5) were 10 km apart on opposite sides of the 380 m wide Alto Madre de Dios River. Distances between hunted and protected sites range from 50–160 km.

Villages along the rivers are inhabited by indigenous farmers and colonists engaged in slash-and-burn agriculture that participate in the regional market economy. All three sites have been intensively hunted with firearms for >30–40 years, and continue to be hunted for subsistence and commercial purposes (GNI personal observation), to the extent that preferred game are gone (below).

The lowland mature forests studied are comparable in geology, drainage, and climate. They share mean temperature of 25 °C, seasonal rainfall distribution, average annual rainfall



**Fig. 1** – Study sites in mature floodplain forests in the southwestern Amazon in Peru. Three sites are inside National Protected Areas where hunting is not allowed; (1) near the Tambopata Research Center in the Tambopata National Reserve (TNR); (2) near Cocha Cashu; and (3) Pakitza Biological Stations in Manu National Park (MNP), Peru. Three heavily-hunted sites were contiguous with the National Protected Areas 3–8 km from three villages: (4) near the villages of Isla de Los Valles and Boca Manu; (5) near the village of Diamante; and (6) near the village of Infierno. Puerto Maldonado (■) is the capital of the Department of Madre de Dios. See text for details.

of 2800 mm (Kalliola et al., 1993; Malhi et al., 2004; Phillips et al., 2004), and elevation of 200–350 m. Despite a flora of over 1400 woody plant species, these lowland mature floodplain forests have similar floristic composition in familial composition of adult trees established before firearms were commonly used in the region (Table 1 and Appendix A; see Foster, 1990; Gentry and Terborgh, 1990; Dallmeier et al., 1996; Pitman et al., 2001). Pre-existing tree inventories at four

of our sites show virtually complete overlap in the top 10 families, representing 55–65% of species present.

Detailed analyses of the most abundant *adult* trees at two protected and two hunted sites show comparable abundance of large-seeded tree species dispersed by primates of medium and large size, amounting to at least 17% of individual trees present (Nunez-Iturri, 2007). We have no reason to believe that differences in game mammal abundances in intensively

**Table 1** – Structural forest characteristics of two hunted (H) and two protected (P) of the six mature floodplain forests studied in southeastern Peru

Site	Stems (ha <sup>-1</sup> )	Families (ha <sup>-1</sup> )	Genera (ha <sup>-1</sup> )	Species (ha <sup>-1</sup> )	Species/100 stems	Stems/species	Basal area (m <sup>2</sup> )
Cocha Cashu <sup>a</sup> (P)	650	47	~120	201	31	3.23	35.1
Pakitza <sup>b</sup> (P)	610	45	108	157	26	3.89	37.2
Boca Manu <sup>c</sup> (H)	592	43	96	150	25	3.95	29.7
Infierno <sup>d,e</sup> (H)	526	41	–	155	29	3.39	36.1

Data shown are from previously established plots of one hectare each, including all stems  $\geq 10$  cm dbh.

a Site 2: Gentry and Terborgh (1990).

b Site 3: Dallmeier et al. (1996).

c Site 4: Terborgh J, unpublished data.

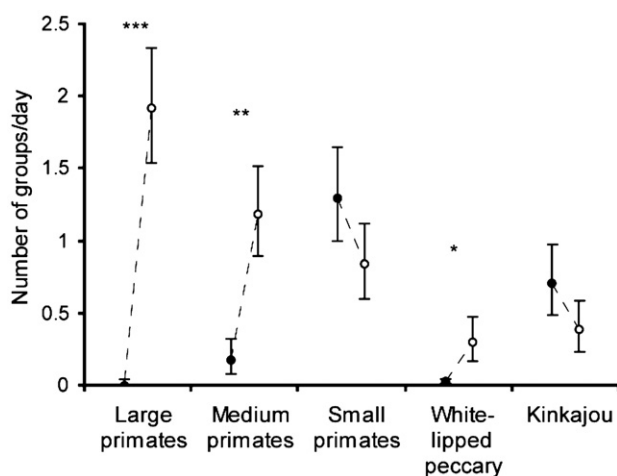
d Gentry (1988).

e Site 6: Phillips et al. (1994).

hunted and protected sites are due to differences in tree community composition.

We used transect counts to quantify evident differences in mammal abundance between hunted and protected sites. Censuses of mammals used a standardized line-transect method (Bodmer et al., 1997; Peres, 1999; Haugaasen and Peres, 2005) have documented dramatic differences in large mammal presence in protected forests as compared with those hunted >30 years with firearms (Fig. 2; see Nunez-Iturri, 2007). These censuses in the June–September dry season of 2003 and the February–May wet season of 2004 involved daytime census at protected sites of 375 km, and nighttime censuses of 325 km. Total census effort at hunted sites in the day was 330 km, at night 300 km (Nunez-Iturri, 2007). Of the 700 km of censuses for protected sites and 630 km reported for hunted sites, data for 454 and 208 km are summarized in Nunez-Iturri and Howe (2007). Data reported here add observations from three additional sites, doubling the total from the pilot study. Hunters in villages near the sites hunted with firearms confirmed that large primates and peccaries had been shot out years before.

Censused species were assigned to six animal categories 1. Large-bodied primates (*Ateles belzebuth*, *Lagothrix lagothricha*), 2. Medium primates (*Cebus albifrons*, *C. paella*), 3. Small primates (*Aotus nigriceps*, *Callicebus moloch*, *Saimiri sciureus*), 4. Kinkajous (*Potos flavus*), a solitary, non-game arboreal frugivore, 5. Agoutis (*Dasyprocta variegata*), a solitary scatter-hoarding rodent, and 6. White-lipped peccaries (*Tayassu pecari*). Small primates, agoutis and kinkajous are too small to be preferred game in these areas (“not worth a bullet” to hunters). An interesting result is that agoutis did not decline with hunting, we expect because they are an order of magnitude less com-



**Fig. 2 – Number of groups observed per day by frugivore category, including large primates (>5–10 kg), medium-sized primates (>2–5 kg), small primates (<2 kg), white-lipped peccaries (~40 kg), and kinkajous (~2 kg). Independent groups of mammals were sighted within three protected (○) and three hunted (●) sites during wet and dry census-seasons per site in mature floodplain forests in southeastern Peru. Means ± 1 standard error are shown. \*  $P \leq 0.025$ , \*\*  $P < 0.005$ , \*\*\*  $P < 0.0001$ . Adapted from Nunez-Iturri (2007).**

mon in forests of the western Amazon than in places, such as Panama, where tree composition is skewed towards rodent-dispersed trees (see Janson, 1983; Terborgh and Wright, 1994; Forget et al., 2002; but see Bodmer 1995). Details for these and other species will be given in a future publication.

## 2.2. Plant censuses

Censuses of seedling and juvenile plants were conducted to provide a community-wide sample of recruitment in the six sites. Censuses of small juvenile plants at each site used 30 randomly-located 1-m<sup>2</sup> plots in a 120-m-wide strip along the 4 km animal-census transect, resulting in 180 samples across the six sites. Distinguishing features of this design are that the 30 1-m<sup>2</sup> plots at each site sampled 480,000 m<sup>2</sup>, and no sites with the same treatment were <10 km apart, a substantially greater dispersion within and between sites than attempted elsewhere. Exceptions to randomization were occasional canopy gaps and occasional seedling carpets beneath parent trees. Small juveniles beneath parent trees were analyzed with a different method at three sites in a pilot study (Nunez-Iturri and Howe, 2007). Herbaceous and woody stemmed plants <1-m tall and seedlings with at least two true leaves were identified and counted. Censuses were conducted in the dry season (May–September). Plants were identified in the field or assigned to morphospecies, with vouchers later identified to species by botanist Percy Nuñez at the Herbario Vargas (CUZ) at the Universidad Nacional San Antonio Abad del Cuzco, Peru.

Plant species were classified by dispersal mode: 1. Dispersed by primates weighing more than 2 kg in mass (fruits with seeds >15 mm long), 2. Dispersed by non-game animals (fruits with seeds <15 mm long dispersed by ants, bats, small primates and birds), and 3. Dispersed by wind or ballistic ejection (hereafter “abiotic”). Species with seeds  $\geq 15$  mm long dispersed by primates known to be mainly dispersed by bats (Geiselman et al., 2006) were excluded from the large and medium primate-dispersed category (e.g. *Iriartea deltoidea*, *Socratea exorrhiza*, *Simphonia globulifera*, *Dipteryx micrantha*, *Otoba parvifolia*) to avoid confounding results. Dispersal mode was assigned to one of the three categories based on fruit and seed morphology (Janson, 1983), augmented by published data on plants consumed by primates (Terborgh, 1983; van Roosmalen, 1985; Symington, 1987) and online databases (Geiselman et al., 2006; Field Museum, 2006; Smithsonian Institution, 2006; Solomon, 2006).

## 2.3. Analysis

We used mixed linear modelling (the Mixed Procedure) in SAS 9.1 (SAS Institute, Cary, NC) to assess the effects of hunting on mammal abundance and the species richness and density of seedlings and small juveniles in relation to their dispersal mode. This is a maximum likelihood based generalization of standard linear models used in general linear models (GLM). Generalization lies in the fact that data are permitted to have correlation and non-constant variability, and therefore it is possible to model variances and covariances more flexibly than in GLM (e.g., homogenous variance is not necessary). Analyses used here are analogous to nested ANOVAs.

Analysis of seedling species richness and density by dispersal mode identifies the effect of hunting on plants with seeds dispersed by large and medium primates (seeds >15 mm long), as well as the effect of hunting on species with seeds dispersed by other animals that are not hunted, and species dispersed by abiotic means. We use site, plot by site, and dispersal mode by site in a variance components covariance structure to model the nested design. Negative covariances within plots reflect competition within plots. In the fully factorial version of the model, one analysis of total species richness of seedlings compared hunted and protected sites. Significance tests of fixed factors use Satterthwaite's method, allowing non-integer degrees of freedom (Satterthwaite, 1946). Dependent variables are square-root transformed as necessary to meet normality assumptions. Residuals from all analyses were inspected and found to be normally distributed.

### 3. Results

#### 3.1. Plant censuses

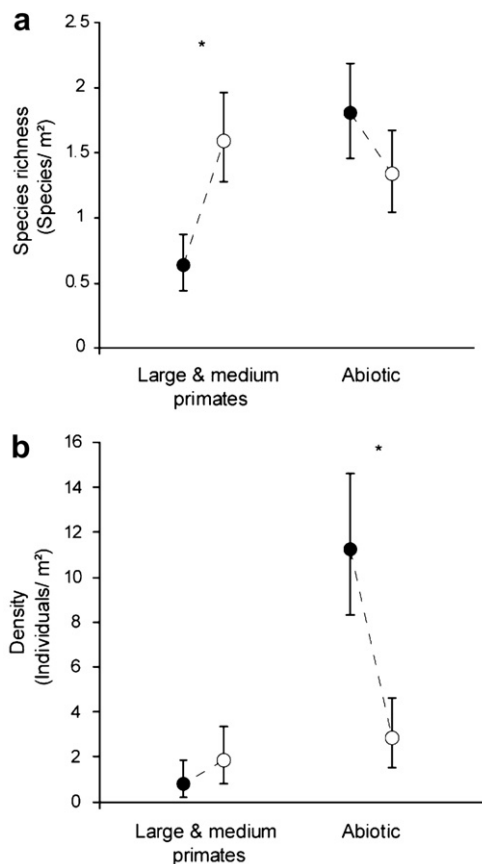
Seedling communities differed in hunted and protected sites. Overall, hunted sites had significantly lower plant species richness than sites without hunting ( $F_{1,4} = 18.1$ ,  $P = 0.013$ ), amounting to a loss of 26%, or two species per  $m^2$  on the forest floor. To separate the effect of hunting on species with different dispersal modes, we made a fully factorial mixed model with hunting and dispersal mode as factors (hunting:  $F_{1,4} = 4.56$ ,  $P = 0.099$ ; dispersal mode  $F_{2,8} = 26.6$ ,  $P < 0.001$ ; interaction term:  $F_{2,8} = 3.04$ ,  $P = 0.104$ ). The richness of seedlings dispersed by large and medium-bodied primates was significantly lower in hunted sites than in sites that were not hunted as was shown by a planned contrast from this model (planned contrast:  $t_{11,8} = 2.43$ ,  $P = 0.032$ ), amounting to a loss of 46%, or a loss of one species per  $m^2$  (Fig. 3a). In contrast, species richness did not differ between hunted and protected sites for wind-dispersed species and for species dispersed by non-game animals.

Plant density was affected by hunting and dispersal mode (Fig. 3b, hunting:  $F_{1,4} = 0.80$ ,  $P = 0.4$ ; dispersal mode:  $F_{2,8} = 4.60$ ,  $P = 0.047$ ; interaction:  $F_{2,8} = 2.94$ ,  $P = 0.11$ ). The density of individuals of species with abiotic dispersal was much higher in hunted areas (planned contrast:  $t_{11,8} = 2.53$ ,  $P = 0.027$ ), amounting to an increase of 284%, or eight individuals per  $m^2$ . The density of species dispersed by animals was not different between hunted and protected sites.

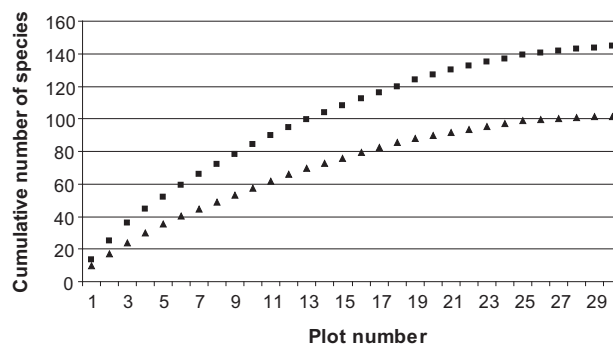
Species-area curves for plant samples show that hunted sites accumulate species to lower asymptotes than protected sites (Fig. 4). The approach to asymptote in both categories indicates adequate sampling effort for the communities evaluated; curves for each site separately show asymptotes of all three hunted sites well below all three protected sites.

### 4. Discussion

Vertebrates have long been assumed to affect plant communities through ecological interactions (Howe, 1977, 1984; Emmons, 1989; Redford, 1992), but tests of the assumption that



**Fig. 3 – Plant species richness and densities of seedlings and small juveniles (<1 m tall) by seed dispersal mode in three protected (○) and three hunted (●) areas in 180  $m^2$  plots in mature floodplain forests in southeastern Peru. Means  $\pm$  1 standard error are shown. Dispersal modes include plants disseminated by large and medium primates (seeds >15 mm long) or dispersed by abiotic means. \*  $P < 0.05$ .**



**Fig. 4 – Species-area curves for three hunted (▲) and three protected (■) sites in mature floodplain forests in southwestern Amazonia, Peru. Shown are the mean cumulative numbers of species per sampled site, with 30 plots of 1  $m^2$  per site. Curves for separate sites show no overlap between protected and hunted areas.**

hunting disrupts these interactions in forests where logging and fragmentation are partially controlled are limited (Forget

and Jansen, 2007; Wright et al., 2007). Early indications suggest important disruptions of dispersal mutualisms in physically disturbed or fragmented forests, especially in regions where roads permit access to logging or subsistence agriculture. Our data indicate major potential effects of hunting by itself on forest structure in extensive unbroken tropical forests not yet accessible by road.

Examples of tests in degraded land, forest fragments, and smaller areas of continuous forest indicate that the assumption is plausible. A classic comparison of the Los Tuxtlas understory with that of the Lacandon forest in Mexico suggests that terrestrial mammals maintain tree diversity through suppression of aggressive species, which become dominant if hunting eliminates the mammals (Dirzo and Miranda, 1991; Dirzo et al., 2007). In Madagascar, loss of the largest lemur species from forest fragments in dry deciduous forests is associated with reduced regeneration of trees that depend on it for seed dispersal (Ganzhorn et al., 1999). Similarly, combined effects of forest fragmentation and hunting in the Atlantic forest of Brazil depress seedling densities of the large-seeded endemic palm (*Astrocaryum aculeatissimum*) due to reduced densities of its main seed disperser (*Dasyprocta*) (Galetti et al., 2006). In Panama, a heavily-hunted mainland site has greater seed fall from wind-dispersed species, many of them vines, as compared with Barro Colorado Island and three nearby peninsulas, where hunting has been closely restricted for >25 years (Wright et al., 2007). There is ample basis for predicting that hunting, by itself, will eventually change forest structure by affecting the differential survival and recruitment of tree seeds and seedlings, and thereby ultimately alter forest composition.

Tests to date have been inconclusive because a variety of anthropogenic effects confound interpretation. Logging and forest fragmentation both accelerate and obscure effects of hunting for tree communities because it is often difficult or impossible to separate the effects of hunting from fragment size, isolation, and edge effects (Benitez-Malvido, 1998; Laurance, 2005; dos Santos et al., 2007). Domestic animals and fire near human settlements similarly obscure direct and indirect impacts of hunting (see Liddle et al., 2006; Whiteman et al., 2007). In other cases, reports of bushmeat hunting are not designed to test wider effects on the plant community, fail to compare hunted and protected sites, or lack sufficient replication for rigorous statistical analysis. What is missing from the literature are reports of clear effects of hunting on forest composition and structure, not confounded by logging, fire, habitat fragmentation, or other anthropogenic disturbances.

Our results are consistent with the prediction that hunting has significant indirect effects on seedling and small juvenile plant communities in unbroken forests of the western Amazon. Differences in the composition of communities of tree seedlings and small juveniles in hunted and similar protected forests are fully consistent with the hypothesis that loss of key primate dispersal agents changes regeneration dynamics of hyper-diverse tropical lowland forests. This inference is especially compelling because primate-dispersed *adult* trees that started growing before firearms were widely used in the western Amazon are still

common in the canopies of hunted sites, but their seedlings and juveniles are poorly represented in the understory. Local suppression to extermination of large fruit-eating primates appears to reduce the species richness of seedlings and small juveniles of trees dispersed by primates by half, and increases the density of abiotically-dispersed plants by nearly 3-fold. Our results suggest that hunting large fruit-eating monkeys reduces recruitment of large-seeded monkey-dispersed trees (Emmons, 1989; Peres and van Roosmalen, 2002), indirectly increases recruitment of abiotically-dispersed species, and alters understory composition in tropical forests (Phillips, 1997). Elimination of large seed-dispersal agents by hunting appears to drastically change understory communities that ultimately will regenerate forest canopies.

Forest floor plant communities are imperfect templates of canopies because processes of differential growth and mortality of seedlings, juveniles, saplings, and young adults intervene between seedling establishment and full reproductive maturity. One thorough study of these processes shows that fewer than half of the small tree or large tree categories sampled of 80 Panamanian tree species show detectable habitat associations (Comita et al., 2007). The site on the plateau of Barro Colorado Island has more topographic relief than mature lowland floodplain forests sampled in our study, so we expect less sorting by edaphic features, even in our much more species-rich assemblage. Species much diminished in numbers in heavily-hunted sites are likely to disappear, and species much more common in hunted than protected sites are more likely to persist to reach the canopy.

Extinction of fruit-eating vertebrates threatens important ecosystem processes that maintain long-term forest integrity (Roldan and Simonetti, 2001; Silman et al., 2003; Stoner et al., 2007b). Hunting suppression of key frugivorous primates and the tree species that they disperse suggest a troubled future for remaining tropical forests, even if they are protected from deforestation, intensive selective logging, fire, or fragmentation. New roads make vast expanses of continuous forest that were previously inaccessible increasingly threatened by poachers (Peres and Zimmerman, 2001; Peres and Palacios, 2007). We concur with Wright and colleagues (2000, 2007) that persistent hunting in Neotropical forests will ultimately change forest composition (also Nunez-Iturri and Howe, 2007). Notably, we found much lower numbers of seedlings and juveniles of large-seeded primate-dispersed species in our hunted sites, despite abundance of adult trees of such species in the same forests. This is not consistent with the finding of some authors that large-seeded species in Panama are favored by hunting (Wright et al., 2007; taxa not indicated). In our region in Peru, large rodents (e.g. *Dasyprocta*) that prey upon large-seeded species are an order of magnitude less common than in Panama (Terborgh and Wright, 1994), are not preferred commercial game, and indeed are about as common in pristine, protected sites in Peru as in heavily-hunted sites in Panama. Agoutis may remain sources of mortality for large seeds not dispersed by primates in hunted areas of the western Amazon, but they are probably one source among many.

An intriguing possibility is that some trees regularly fail to recruit genetic offspring close to parents, even if unrelated

conspecifics do recruit near fruiting trees (Hardesty et al., 2006). Under severe dispersal limitation, offspring recruitment near parents of such species would be negligible, as we discovered earlier (Nunez-Iturri and Howe, 2007). In both central Panama and forests of the southwestern Amazon Basin, hunting alters dynamics of seedling regeneration by accentuating seed-recruitment limitation among large-seeded primate-dispersed trees.

Further predictions are plausible in light of what we now know now (Stoner et al., 2007b). We predict that forests in which the numbers of trees dispersed by large monkeys decline will eventually contain few food resources suitable for those primates. Changes in canopy composition take decades, but once they occur, recovery of primate and tree interactions may be irreversible if tree species unsuitable for large primates claim the canopy. Even if hunting is later controlled, and large vertebrates are re-introduced or attempt to re-colonize on their own, we predict that altered forests will lack sufficient resources to maintain large fruit-eating vertebrates. Forests will remain, but we predict in alternative states that simply do not include or support large primates or the trees that depend on them (see Beisner et al., 2003). The particular effects will depend on many contingencies, reflecting the attributes of floras and faunas in forests that differ in complexity and character. However,

we believe that hunting large mammals is already altering plant species composition on the forest floor in mature lowland tropical forests in Peru. We predict that these effects will echo for centuries as altered understories reach the canopy.

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## Appendix A

### Ten best-represented tree families in hunted and protected sites in mature floodplain forests of southeastern Peru

Family	Protected		Hunted	
	Cosha Cashu <sup>a</sup>	Pakitza <sup>b</sup>	Boca Manu <sup>c</sup>	Infierno <sup>d,e</sup>
Annonaceae	9	7	8	9
Arecaceae	–	–	–	4
Bombacaceae	3	3	3	–
Clusiaceae	–	–	3	–
Euphorbiaceae	3	6	–	4
Lauraceae	8	6	8	8
Leguminosae	13	12	11	13
Meliaceae	6	3	5	4
Moraceae	10	9	8	10
Myristicaceae	3	3	4	4
Nyctaginaceae	–	–	–	4
Sapindaceae	3	–	–	–
Sapotaceae	6	5	6	6
Sterculiaceae	–	3	3	–
Total % of species	64	57	62	66

Percentage of tree species in a family is shown for each site. Data are from established plots of 1 ha, including stems >10 cm dbh.

a Site 2: Gentry and Terborgh (1990).

b Site 3: Dallmeier et al. (1996).

c Site 4: Terborgh J, unpublished data.

d Gentry (1988).

e Site 6: Phillips et al. (1994).

**Appendix B**

**Tree abundance per species in protected and hunted sites in mature floodplain forests in southeastern Peru**

Family	Species	Protected		Hunted	
		CC <sup>a</sup>	Pza <sup>b</sup>	BM <sup>c</sup>	Inf <sup>d,e</sup>
Annonaceae	<i>Annona hypoglauca</i>	6			3
Annonaceae	<i>Crematosperma leiophyllum</i>	8			
Annonaceae	<i>Duguetia quitarensis</i>	12	13		
Annonaceae	<i>Duguetia spixiana</i>				2
Annonaceae	<i>Malmea declina</i>			7	
Annonaceae	<i>Oxandra espintana</i>	8			
Annonaceae	<i>Ruizodendron ovale</i>	5			
Apocynaceae	<i>Aspidosperma megaphyllum</i>	4			
Arecaceae	<i>Astrocaryum murumuru</i>	36	60	29	16
Arecaceae	<i>Attalea butyraceae</i>	22	9	27	7
Arecaceae	<i>Iriarteia deltoidea</i>	38	50	40	86
Arecaceae	<i>Socratea exorhiza</i>				38
Bombacaceae	<i>Matisia cordata</i>	8	7	17	
Bombacaceae	<i>Quararibea wittii</i>	27	43	19	6
Burceraceae	<i>Protium</i> sp.				2
Chrysobalanaceae	<i>Hirtella excelsa</i>				2
Chrysobalanaceae	<i>Hirtella triandra</i>		8		
Clusiaceae	<i>Caraipa densifolia</i>			7	
Clusiaceae	<i>Caraipa myrcioides</i>	8			
Euphorbiaceae	<i>Croton tessmannii</i>	5			
Euphorbiaceae	<i>Drypetes amazonica</i>		10	10	3
Euphorbiaceae	<i>Mabea nitida</i>				12
Euphorbiaceae	<i>Pausandra trianae</i>		8		
Euphorbiaceae	<i>Sapium marmieri</i>	6			2
Fabaceae	<i>Inga bourgonii</i>				2
Fabaceae	<i>Inga capitata</i>		10		
Fabaceae	<i>Inga chartacea</i>				2
Fabaceae	<i>Inga edulis</i>				6
Fabaceae	<i>Inga oerstediana</i>				3
Fabaceae	<i>Myroxylon balsamum</i>				6
Fabaceae	<i>Swartzia arborescens</i>				4
Lauraceae	<i>Caryodaphnopsis fosteri</i>	4			
Lauraceae	<i>Endlichera formosa</i>				4
Lauraceae	<i>Nectandra pulverulenta</i>				3
Lauraceae	<i>Pleurothyrium</i> sp.			9	
Meliaceae	<i>Guarea guidonia</i>	5			
Meliaceae	<i>Guarea macrophylla</i>	14	21	20	2
Meliaceae	<i>Trichilia pleeana</i>	4	8		
Meliaceae	<i>Trichilia poeppigii</i>	11			
Moraceae	<i>Batocarpus costaricensis</i>	4			2
Moraceae	<i>Brosimum alicastrum</i>			7	2
Moraceae	<i>Brosimum utile</i>				2
Moraceae	<i>Castillan ulei</i>				4
Moraceae	<i>Clarisia racemosa</i>	4			2
Moraceae	<i>Poulsenia armata</i>	4			
Moraceae	<i>Pseudolmedia laevis</i>	8	13	14	8
Myristicaceae	<i>Iryanthera olacoides</i>	4		21	
Myristicaceae	<i>Iryanthera juruensis</i>		9		5
Myristicaceae	<i>Otoba parvifolia</i>	42	44	82	5
Myristicaceae	<i>Virola duckei</i>		7		
Myristicaceae	<i>Virola elongata</i>				8
Myristicaceae	<i>Virola flexuosa</i>				2
Nyctaginaceae	<i>Neea floribunda</i>				4
Sapotaceae	<i>Manilkara inundata</i>		9		
Sapotaceae	<i>Manilkara surinamensis</i>				2
Sapotaceae	<i>Pouteria caimito</i>			8	
Sapotaceae	<i>Pouteria ephedrantha</i>	11			
Sapotaceae	<i>Pouteria</i> sp.				7

(continued on next page)

## Appendix B – continued

Family	Species	Protected		Hunted	
		CC <sup>a</sup>	Pza <sup>b</sup>	BM <sup>c</sup>	Inf <sup>d,e</sup>
Sapotaceae	<i>Pouteria torta</i>				2
Staphylacaceae	<i>Turpinia occidentalis</i>		9		
Sterculiaceae	<i>Theobroma cacao</i>	8	7	25	5
Ulmaceae	<i>Ampelocera</i> sp.	7			
Ulmaceae	<i>Celtis schippii</i>		11	11	17
Violaceae	<i>Leonia glycyarpa</i>			9	23
Violaceae	<i>Rinorea viridifolia</i>		8		
Total		323	364	362	311
Total stems/ha		650	610	592	530
Total trees with seeds dispersed by primates >2 kg		82	113	106	90
Percent represented by trees dispersed by primates >2 kg		13	19	18	17

Including species with two or more individuals. Data are from established plots of 1 ha, including stems >10 cm dbh. Cocha Cashu (CC), Pakitza (Pza), Boca Manu (BM), and Infierno (Inf).  
a Site 2: Gentry and Terborgh (1990).  
b Site 3: Dallmeier et al. (1996).  
c Site 4: Terborgh J, unpublished data.  
d Gentry (1988).  
e Site 6: Philips et al. (1994).

## REFERENCES

- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 7, 376–382.
- Benitez-Malvido, J., 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12, 380–389.
- Bodmer, R.E., 1995. Managing Amazonian wildlife: Biological correlates of game choice by detribalized hunters. *Ecological Applications* 5, 872–877.
- Bodmer, R.E., Eisenberg, J.F., Redford, K.H., 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* 11, 460–466.
- Comita, L., Condit, R., Hubbell, S.P., 2007. Developmental changes in habitat associations of tropical trees. *Journal of Ecology* 95, 482–492.
- Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed disperser and an endemic African tree. *Proceedings of the National Academy of Sciences, USA* 100, 14052–14056. doi:10.1073/pnas.2331023100.
- Cramer, J., Mesquita, R., Williamson, G.B., 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation* 137, 415–423.
- Dallmeier, F., Kabel, M., Foster, R.B., 1996. Floristic composition, diversity, mortality and recruitment on different substrates: lowland tropical forest, Pakitza, Rio Manu, Peru. In: Wilson, D.E., Sandoval, A. (Eds.), *Manu: The Biodiversity of Southeastern Peru*. Horizonte, Peru, pp. 61–88.
- Dirzo, R., Mendoza, E., Ortiz, P., 2007. Size-related differential seed predation in a heavily-defaunated neotropical rain forest. *Biotropica* 39, 355–362.
- Dirzo, R., Miranda, A., 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. In: Price, P., Lewington, T., Fernandes, G., Benson, W. (Eds.), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. Wiley, New York, pp. 273–287.
- Dos Santos, K., Kinoshita, L.S., dos Santos, F.A.M., 2007. Tree species composition and similarity in semideciduous forest fragments of southeastern Brazil. *Biological Conservation* 135, 268–277.
- Emmons, L.H., 1989. Tropical rain forests: why they have so many species and how we may lose this biodiversity without cutting a single tree. *Orion* 8, 8–14.
- Fa, J.E., Ryan, S.F., Bell, D.J., 2005. Hunting variability, ecological characteristics and harvest rates of bushmeat species in afro-tropical forests. *Biological Conservation* 121, 167–176.
- Fa, J.E., Seymour, S., Dupain, J., Amin, R., Albrechtsen, L., Macdonald, D., 2006. Getting to grips with the magnitude of exploitation: Bushmeat in the Cross-Sanaga rivers region, Nigeria and Cameroon. *Biological Conservation* 129, 497–510.
- Field Museum, 2006. Environmental Conservation Program 1999 Neotropical Herbarium Specimens. <<http://fm1.fieldmuseum.org/vrrc/>>, Neotropical Live Plant Photos. <[http://fm2.fieldmuseum.org/plantguides/color\\_images.asp](http://fm2.fieldmuseum.org/plantguides/color_images.asp)>.
- Fleury, M., Galetti, M., 2006. Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation* 131, 1–13.
- Forget, P.M., Hammond, D.S., Mileron, T., Thomas, R., 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: Consequences for seed dispersal and seedling recruitment. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology Evolution and Conservation*. CAB International, Wallingford, pp. 241–256.
- Forget, P.M., Jansen, P., 2007. Hunting increases dispersal limitation in the tree *Carapa procera*, a non-timber forest product. *Conservation Biology* 21, 106–113.
- Foster, R.B., 1990. Long-term change in the successional forest community of the Rio Manu floodplain. In: Gentry, A.H. (Ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven, pp. 565–572.
- Galetti, M., Donatti, C.I., Pires, A.S., Guimaraes, P.R., Jordano, P., 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest

- fragmentation. *Botanical Journal of the Linnean Society* 151, 141–149.
- Ganzhorn, J.U., Fietz, J., Rakotovo, E., Schwab, D., Zinner, D., 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology* 13, 794–804.
- Gavin, M.C., 2007. Foraging in the fallows: Hunting patterns across a successional continuum in the Peruvian Amazon. *Biological Conservation* 134, 64–72.
- Geiselman, C.K., Mori, S.A., Blanchard, F., 2006. Database of Neotropical bat/plant interactions. <[http://www.nybg.org/botany/tlobova/mori/batsplants/database/dbase\\_frameset.htm](http://www.nybg.org/botany/tlobova/mori/batsplants/database/dbase_frameset.htm)>.
- Gentry, A.H., 1988. Changes in Plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75, 1–75.
- Gentry, A.H., Terborgh, J., 1990. Composition and dynamics of the Cocha Cashu “mature” floodplain forest. In: Gentry, A.H. (Ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven, pp. 542–564.
- Hardesty, B.D., Hubbell, S.P., Bermingham, E., 2006. Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters* 9, 516–525.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495.
- Haugaasen, T., Peres, C.A., 2005. Mammal assemblage structure in Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 21, 133–145.
- Howe, H.F., 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58, 539–550.
- Howe, H.F., 1984. Implications of seed dispersal by animals for management of tropical reserves. *Biological Conservation* 30, 261–281.
- Huerta, M.A.O., 2007. Fragmentation patterns and implications for biodiversity conservation in three biosphere reserves and surrounding regional environments, northeastern Mexico. *Biological Conservation* 134, 83–95.
- Janson, C.H., 1983. Adaptation of fruit morphology to dispersal in a Neotropical forest. *Science* 219, 187–189.
- Janson, C.H., Emmons, L.H., 1990. Ecological Structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. In: Gentry, A.H. (Ed.), *Four Neotropical Forests*. Yale University Press, New Haven, pp. 314–338.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104, 501–528.
- Kalliola, R., Puhakka, M., Danjoy, W., 1993. Amazonia Peruana: Vegetación Humeda Tropical en el Llano Subandino. Gummerus Printing, Jyväskylä, Finland.
- Knogge, C., Heymann, E.W., 2003. Seed dispersal by sympatric tamarins *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74, 33–47.
- Laurance, W.F., 2005. The alteration of biotic interactions in fragmented tropical forests. In: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*. Cambridge University Press, Cambridge, pp. 441–458.
- Lee, R.J., Gorog, A.J., Dwyahreni, A., Siwu, S., Riley, J., Alexander, H., Paoli, G.D., Ramono, W., 2005. Wildlife trade and its implications for law enforcement in Indonesia: a case study from North Sulawesi. *Biological Conservation* 123, 477–488.
- Levey, D.J., Moermond, T.C., Denslow, J.S., 1994. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, pp. 282–294.
- Liddle, D.T., Brook, B.W., Mathews, J., Taylor, S.M., Caley, P., 2006. Threat and response: A decade of decline in a regionally threatened rainforest palm affected by fire and introduced animals. *Biological Conservation* 132, 362–375.
- Lopes de Melo, F.P., Dirzo, R., Tabarelli, M., 2006. Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. *Biological Conservation* 132, 50–60.
- Malhi, Y. et al., 2004. Wood productivity and net primary productivity in 100 Neotropical forests. *Global Change Biology* 10, 563–591.
- Marshall, A.J., Nardiyono, Engstrom, L.M., Parmungkas, B., Palapa, J., Meijaard, E., Stanley, S.A., 2006. The blowgun is mightier than the chainsaw in determining density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biological Conservation* 129, 566–578.
- Muller-Landau, H.C., 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39, 372–384.
- Myers, N., Knoll, A., 2001. The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences of the United States of America* 98, 5389–5392.
- Nunez-Iturri, G., 2007. The effects of hunting on the regeneration of trees in mature floodplain forests in southeastern Peru. Ph. D. Dissertation. University of Illinois, Chicago.
- Nunez-Iturri, G., Howe, H.F., 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in Western Amazonia. *Biotropica* 39, 348–354.
- Peres, C.A., 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. *Neotropical Primates* 7, 11–16.
- Peres, C.A., 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14, 240–253.
- Peres, C.A., Palacios, E., 2007. Basin-wide effects of vertebrate game harvest in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica* 39, 304–315.
- Peres, C.A., van Roosmalen, M., 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted tropical forests. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, pp. 407–421.
- Peres, C.A., Zimmerman, B., 2001. Perils in parks or parks in peril? Reconciling conservation in Amazonian reserves with and without use. *Conservation Biology* 15, 793–797.
- Phillips, O.L., 1997. The changing ecology of tropical forests. *Biodiversity Conservation* 6, 291–311.
- Phillips, O., Gentry, A.H., Reynel, C., Wilkin, P., Galvez-Durand, C., 1994. Quantitative ethnobotany and Amazonian conservation. *Conservation Biology* 8, 225–248.
- Phillips, O.L. et al., 2004. Pattern and processes in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society, B* 359, 381–407 (doi:10.1098/rstb.2003.1438).
- Pitman, N.C.A., Terborgh, J., Silman, M.R., Nuñez, P., Nelly, D.A., Ceron, C.E., Palacios, W.A., Aulestia, M., 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82, 2101–2117.
- Redford, K.H., 1992. The empty forest. *Bioscience* 42, 412–422.
- Robinson, J.G., Redford, K.H., Bennett, E.L., 1999. Wildlife harvest in logged tropical forests. *Science* 284, 595–596.
- Roldan, A.I., Simonetti, J.A., 2001. Plant–mammal interactions in tropical Bolivian forests with different hunting pressures. *Conservation Biology* 15, 617–623.
- van Roosmalen, M., 1985. *Fruits of the Guianan Flora*. Institute of Systematic Botany, Utrecht University, Netherlands.
- Russo, S., 2003. Response of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136, 80–87.

- Satterthwaite, F.E., 1946. An approximate distribution of estimates of variance components. *Biometrics Bulletin* 2, 110–114.
- Silman, M.R., Terborgh, J., Kiltie, R.A., 2003. Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* 84, 431–438.
- Smithsonian Tropical Research Institute, 2006. Plant Image Database. <[http://striweb.si.edu/esp/tesp/plant\\_images\\_info.htm](http://striweb.si.edu/esp/tesp/plant_images_info.htm)>.
- Solomon, J., 2006. Missouri Botanical Garden 2006 Neotropical Plant Data Base. <<http://mobot.mobot.org/W3T/Search/vast.html>>.
- Stevenson, P.R., 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothericha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* 50, 275–289.
- Stoner, K.E., Riba-Hernandez, P., Vilunec, K., Lambert, J.E., 2007a. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica* 39, 316–327.
- Stoner, K.E., Vilunec, K., Wright, S.J., Peres, C.A., 2007b. Hunting and plant community dynamics in tropical forests: A synthesis and future directions. *Biotropica* 39, 385–392.
- Symington, M.M., 1987. Ecological and social correlates of party size in the black spider monkey, *Ateles paniscus chamek*. Ph. D. thesis. Princeton University, Princeton.
- Terborgh, J., 1983. *Five New World Primates*. Princeton University Press, Princeton.
- Terborgh, J., Nunez-Iturri, G., 2006. Disperser-free tropical forests await an unhappy fate. In: Peres, C.A., Lawrance, W.F. (Eds.), *Emerging Threats to Tropical Forests*. University of Chicago Press, Chicago, pp. 241–252.
- Terborgh, J., Wright, S.J., 1994. Effects of mammalian herbivores on plant recruitment in two Neotropical forests. *Ecology* 75, 1829–1833.
- Whiteman, C.W., Matushima, E.R., Confalonieri, U.E.C., Palha, M.D.C., da Silva, A.S.L., Monteiro, V.C., 2007. Human and domestic animal populations as a potential treat to wild carnivore conservation in a fragmented landscape from the Eastern Brazilian Amazon. *Biological Conservation* 138, 290–296.
- Wright, S.J., 2003. The myriad effects of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology, Evolution and Systematics* 6, 73–86.
- Wright, S.J., Hernandez, A., Condit, R., 2007. The bushmeat harvest alters seed banks by favoring large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* 39, 363–371.
- Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C., Ibanez, R., 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14, 227–239.
- Zhang, S.Y., Wang, L.X., 1995. Fruit consumption and seed dispersal of *Ziziphus cinamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27, 397–401.