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VARIABLE DENSITY RESPONSES OF PRIMATE COMMUNITIES TO HUNTING PRESSURE IN A WESTERN AMAZONIAN RIVER BASIN

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Abstract

Large-bodied game species are in decline in tropical forests worldwide due to unsustainable extraction levels by hunters, which can result in cascading effects on vertebrate community structure. In this study, we examine the density responses of primate populations to different levels of hunting pressure in the Madre de Dios river basin, Peru. Across three surveyed sites, both small- and mid-sized primates exhibited population-level density compensation in response to the extirpation of sympatric large primates. Small primate density at one heavily hunted site was 5x that of a comparable nonhunted site, while the highest density of mid-sized primates was recorded at mid-level hunting pressure. Primate response to hunting pressure appears to be influenced by reproductive rate, with strong interspecific variability. High reproductive rate, infrequent extraction, and the relaxation of competitive interactions with extirpated large primates appear to facilitate increasing density of the smallest-bodied species. Evidence from elsewhere in the Madre de Dios basin suggests that large primates are particularly slow to recover from past hunting pressure, with continuing recovery even in sites that have not been hunted for several decades. These variable density responses to hunting pressure alter inter-specific and community dynamics, with potentially expansive short- and long-term ecosystem-level effects.

Key Words: Competitive release; conservation; density compensation; distance sampling; game vertebrates; hunting; tropical forest.

Resumen

Los vertebrados de tamaño grande están en declive en los bosques tropicales a nivel mundial debido a niveles insostenibles de extracción por cazadores, lo cual puede resultar en efectos de cascada sobre la estructura de la comunidad de vertebrados. En este estudio, examinamos el efecto de diferentes niveles de presión de caza sobre primates en cuanto a la estructura de la comunidad y densidades de sus poblaciones en la cuenca del Río Madre de Dios, Perú. En los tres sitios estudiados, los primates de tamaños pequeño y mediano mostraron compensación de densidad al nivel de la población como respuesta a la extirpación de los primates grandes simpátricos. La densidad de primates pequeños en un sitio con alta cacería fue cinco veces más que en un sitio comparable sin cacería, mientras que la densidad más alta de primates de tamaño mediano fue registrada en el sitio con una presión mediana de caza. La respuesta de los primates a la presión de caza parece estar influida por la tasa de reproducción, con una fuerte variabilidad inespecífica. Altas tasas de reproducción, extracción infrecuente, y la disminución de interacciones competitivas con especies de primates grandes extirpados parecen facilitar una densidad creciente de primates de tamaño pequeño. Evidencia de otras partes de la cuenca del Río Madre de Dios sugiere que los primates grandes se recuperan lentamente de la presión de caza, presentándose recuperación continua aún en sitios en los cuales no se ha cazado por varias décadas. Estas respuestas de densidad variables a la presión de caza cambian las dinámicas interespecíficas y de la comunidad entera, con efectos potencialmente amplios al nivel del ecosistema a corto y largo plazo.

Palabras Clave: Liberación de competencia; conservación; compensación de densidad; muestreo de distancias; vertebrados de caza; cacería; bosque tropical.

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Introduction

Subsistence and commercial demand drives hunting pressure on primates and other game vertebrates, resulting in increasingly "empty" forests worldwide (Redford, 1992; Wilkie *et al*., 2011). In recent decades, expanding road networks have allowed unprecedented access to Neotropical forests for extractive purposes, with the extent of accessibility approaching 100% in the Brazilian Amazon (Peres and Lake, 2003). Our current understanding of tropical forest primate communities and associated ecological dynamics should therefore be reexamined in the context of human disturbance, particularly with regard to directly extractive activities such as hunting. Hunters in Neotropical forests can be highly selective, targeting large-bodied vertebrates (Redford and Robinson, 1987); in primate communities specifically, large Ateline monkeys (*Ateles* spp., *Lagothrix* spp.) are subject to intense hunting pressure while small and medium-sized primates are often ignored (Peres, 1990). In the absence of anthropogenic disturbance, the largest primate species are dominant, conspicuous, and highly abundant, particularly in sites that support high densities of fleshy-fruited tree species (Terborgh, 1983). When subject to hunting pressure, these ecological mainstays are increasingly replaced by their smaller counterparts (Peres and Dolman, 2000). Targeted hunting of the largest species can thus be a transformative force on the faunal assemblage.

If inter-specific competition for resources plays an important role in vertebrate population regulation, smaller vertebrates may exhibit a compensatory response from competitive release in the absence of large vertebrates, a phenomenon known as density compensation (MacArthur et al., 1972). Although density compensation has been studied most extensively in island and fragmented avifaunas (Diamond, 1970; Wright, 1980; Feeley and Terborgh, 2008) and its underpinnings have been debated (Faeth, 1984), some evidence of such responses exists for Amazonian primate communities, with increased abundance of small and mid-sized primates in response to the hunting-induced decline of large-bodied species (Peres and Dolman, 2000). However, more evidence of density compensation from additional sites – particularly for the smallest-bodied species – is necessary in order to better understand the long-term impacts of hunting on the vertebrate community of tropical forests. This study examines the density responses of primate populations to different levels of hunting pressure in the Madre de Dios river basin, Peru. We hypothesize that response to hunting pressure is influenced by reproductive rate, with strong interspecific variability. Infrequent extraction, higher reproductive rate, and the relaxation of competitive interactions with extirpated large primates may thus facilitate increasing density of the smallest-bodied species with hunting.

Methods

Field sites

The Madre de Dios river basin in southeastern Peru comprises ca. 80,000 km2 of lowland tropical forest, including several large protected areas. Human use of the area ranges from small-scale swidden agriculture to more intensive logging, mining, and hunting, as well as expanding development around urban centers such as Puerto Maldonado. Three sites under varying degrees of protection from hunting pressure were selected for faunal surveys (Fig. 1), based on documented and anecdotal historical information on human pressures, and an initial assessment of surrounding landuse via satellite imagery. We used the size of the focal protected area and straight-line distance to the nearest human settlement as proxies for ranking the degree of hunting pressure. The sites were selected to minimize potentially confounding natural variation and allow for the isolation of specific effects of hunting pressure from other forms of anthropogenic disturbance such as logging and agriculture.

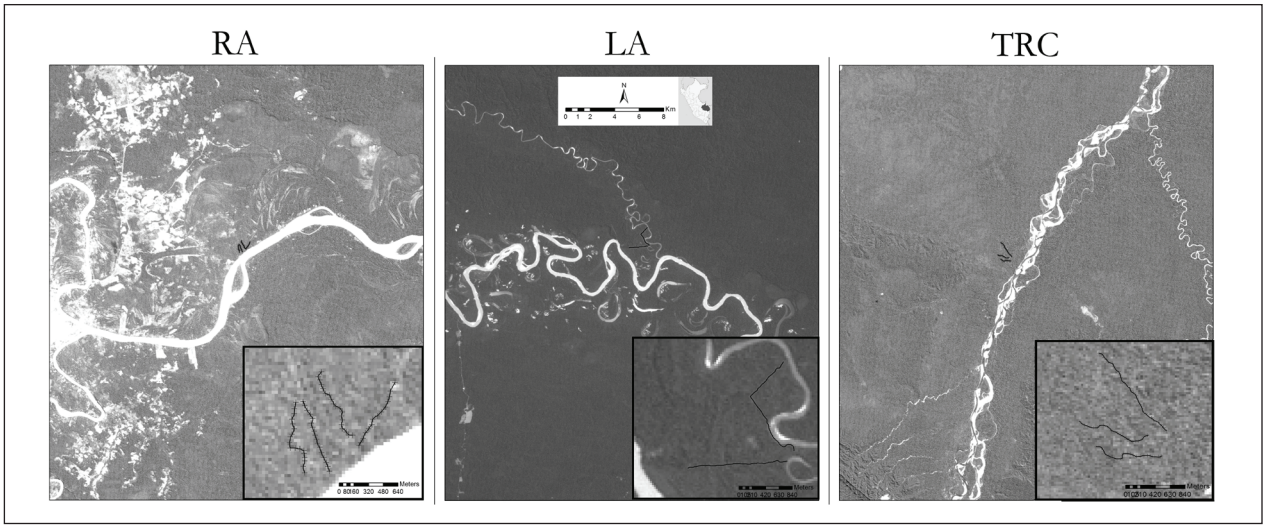


Figure 1. Field sites and transects in the Madre de Dios river basin, Peru; Reserva Amazónica (RA), Los Amigos (LA), and Tambopata Research Center (TRC). Human use surrounding field sites is evident in extensive landuse change (RA) and remnant mining pools (LA).

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Reserva Amazónica (RA) [12°32'4"S, 69°3'13"W] is a 17,000 hectare private ecological reserve, owned and managed by the Asociación Inkaterra, a Peruvian ecotourism company. Given its relatively small size and proximity to Puerto Maldonado (1km from nearest human settlement, 16 km from Puerto Maldonado population center), the forest within the RA site has faced substantial human pressure in recent years. The lands surrounding the reserve are dominated by human use, with forests converted for farming, mining, and urban expansion. The RA region is characterized as a site under low protection from hunting pressure. The Los Amigos Biological Station / Centro de Investigación y Capacitación Rio Los Amigos (LA) [12°34'10"S, 70°4'52"W] is a 453 hectare research center adjacent to the 146,000 hectare Los Amigos Conservation Concession (2km from the nearest human settlement, Boca Amigos). The Concession was established in 2001 by two non-governmental organizations: the Peruvian Asociación para la Conservación de la Cuenca Amazónica (ACCA) and the US-based Amazon Conservation Association. The immediate grounds and many of the station facilities themselves were formerly the headquarters of a large gold mining enterprise. During the peak period of mining activity on the station grounds, from the late 1980s to early 1990s, the high density of miners – up to 120 at one point (Pitman, 2010) – fueled active hunting in the immediate area. Although the permanent mining settlement was abandoned and later repurposed with the designation of the land as a conservation concession, artisanal mining persists, scattered along the river. Overall, LA is characterized as a site under medium protection from hunting pressure. The Tambopata Research Center (TRC) [13°7'9"S, 69°36'59"W] is an eco-lodge and research facility located within the 275,000 hectare Tambopata National Reserve, and adjacent to the million-hectare Bahuaja-Sonene National Park (>50km from the nearest human settlement). The facilities are managed by the eco-tourism company Rainforest Expeditions, while the majority of the land is managed for strict conservation by the Peruvian government. Prior to the 1990 establishment of the reserve zone, gold mining operations existed in the region, with activity tapering off after designation of the reserve and as a likely result of resource overexploitation in the region. The intensity of human disturbance is minimal and the site is well-protected from hunting. TRC is characterized as a site under high protection from hunting pressure.

Documenting vertebrate abundance

Our research team followed line transect protocol as described in the literature specific to tropical forest surveys of primates (Peres, 1999a; Marshall et al., 2008; Buckland et al., 2010), with minor modifications to account for site-specific circumstances. We implemented line transects of 1m width and varying length (from 750m to 1,500m, according to terrain conditions and station layout) at each site. Given the small size of each focal area, transects were placed in parallel or "zig-zag" orientations to ensure systematic and efficient sampling (Peres, 1999a; Buckland, 2001), with four transects at RA and three each at LA and TRC, spaced no fewer than 200m apart. Trail heads were located at a distance greater than 500m from the station base, and all transects were contained within mature floodplain forest. We flagged and georeferenced each transect at 50m intervals, and left all transects to rest for at least 1 day prior to sampling. Transects were surveyed in sequence during two daily periods corresponding to peak activity of study subjects: in the morning (0630-1100 h) and afternoon (1300-1730 h). We did not sample transects under rainy conditions. To survey each transect, a team of two (CR plus a trained field technician familiar with local fauna) walked quietly at a mean pace of ~1.5km/hour, listening for detection cues and scanning the transect line and surrounding forest. We stopped briefly approximately every 100m to listen for any additional cues. Focal species included diurnal primates present across the three study sites (Table 1). For each primate sighting, several data were recorded: time of day, species, number of individuals, perpendicular distance from transect ("PD", in meters), detection mode (visual or acoustic), and group diameter when applicable. For group encounters, PD was measured to the center of the group (Marshall et al., 2008). Large dispersed groups were sub-grouped to the greatest extent possible to maximize the likelihood that all individuals were counted and that PD measurements were accurate. PDs were measured via pacing, with regular re-calibration to ensure accuracy and consistency.

Analyzing transect data

For each species surveyed, we calculated an individual encounter rate per every 10km of sampled transect. Vertebrate transect data was modeled by functional group using the program Distance v. 6.0, a Windows-based computational package, to generate site-specific population density estimates for each focal species (Buckland, 2001). Distance allows for selection among several models; here, the Hazard-rate model with a Cosine adjustment offered the best density estimator for forest primates, as determined by the minimum Akaike information criterion (Peres, 1997; Buckland, 2001). All data were truncated to exclude the largest 5% of perpendicular distance values, which further benefitted model fit. Although sightings can be infrequent for some species – particularly when hunting reduces encounters of fauna already occurring at naturally low densities – small sample sizes can provide robust density estimates given a favorable distribution of data (Peres, 1999a). Given these constraints, we pooled detection data across sites to increase robustness of analysis. Analysis of Variance (ANOVA) comparing PD values across sites provided statistical support for data pooling. Data from the Monk Saki (Pithecia monachus) was not included in final density estimates, as the species did not occur at all three sites.

Results

We collected data over a total of 304.95km of transect survey effort, with 100.15km at RA, 102.3km at LA, and

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102.5km at TRC. The total number of encounters was 29 for large primates (Ateles chamek [23] and Alouatta seniculus [6]), 44 for mid-sized primates (Cebus apella and Cebus albifrons), and 43 for small primates (Saimiri boliviensis, Saguinas fuscicollis, and Saguinas imperator). The majority of detections (74%) resulted from an initial auditory cue, primarily from vocalizations or locomotion. Values of the coefficient of variation (CV) for some density estimates are expectedly high given constraints on detection frequency (see Figure 2 description). Data pooling benefitted statistical robustness of model outputs; ANOVA results were non-significant (p>.05), with the exception of Saimiri boliviensis, for which further ANOVA of a subset of the data indicated that pooling was appropriate across two – rather than all three – sites.

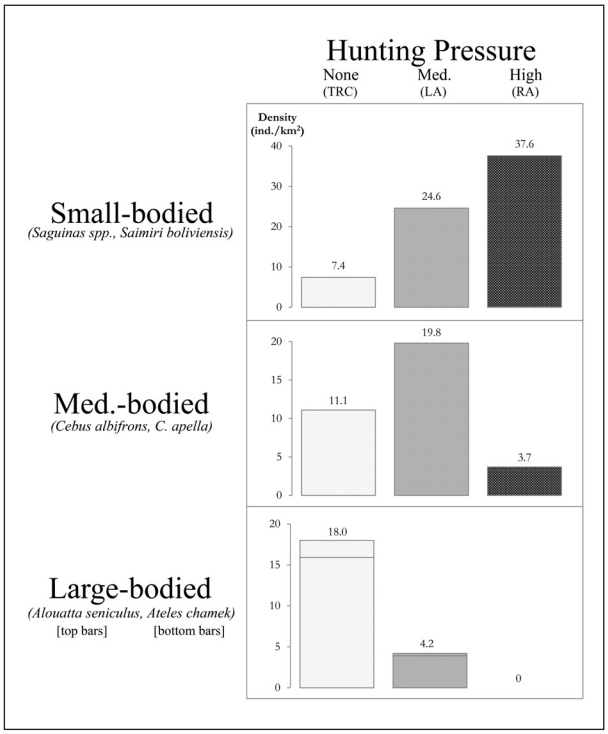


Figure 2. Densities of focal species by body size and hunting pressure at three sites: TRC site (no hunting), LA site (medium hunting pressure), and RA site (high hunting pressure). Large-bodied primates are further separated as folivorous (*Alouatta seniculus*: top bars) and frugivorous (*Ateles chamek*: bottom bars). CV values are as follows: small primates 26.8 (TRC), 31.5 (LA), 50.5 (RA); mid-sized primates 38.6 (TRC), 42.4 (LA), 85.7 (RA); large primates 58.8 (TRC), 89.7 (LA).

Observed encounter rates (Table 1) and *Distance*-derived density estimates (Fig. 2) reflect the impact of protection from hunting on relative densities of primate species at each site. At the RA site, large primates are completely absent, with low densities of mid-sized primates, and high densities of small primates. Conversely, at the large and well-protected TRC site, large primates are abundant, while mid-sized and small primates occur at lower densities. The LA site, representing a forest under moderate protection, exhibits mid-level densities for most species, with a notable abundance of mid-sized primates.

Discussion

Density responses to hunting

Hunting most dramatically affects large-bodied vertebrates – those greater than 5kg – which comprise the largest component (65-78%) of animal biomass at nonhunted sites (Peres, 1990; 2000). In primate communities, population declines of the Atelid monkeys (*Ateles chamek* and *Alouatta seniculus* in this study region) represent the main effect of hunting (Peres, 1990; 1999b). Such declines are the result of both hunter preference and low fecundity (see below). Large frugivorous primates are often abundant and highly conspicuous at nonhunted sites. Given their large body mass and gregarious social structure, large primates are prized prey species for human hunters, providing easy detectability and a large meat payoff. Hunter preference can vary based on several of these factors, as well as cultural taboos (da Silva *et al.,* 2005), but the strongest determinant of preference is large body size (see Table 1). Given this size selectivity, large game vertebrates may be drastically reduced at hunted sites while smaller non-target species escape hunting pressure. Our results support this assertion, with a complete absence of large primates at our least protected site.

Table 1. Body mass, hunter preference (Peres and Lake 2003), and encounter rate of focal species across three study sites.

Common Name	Latin Name	Body Mass (kg)	Hunter Preference*	Encounter Rate (ind./ 10km)		
				RA	*LA*	*TRC*
Spider monkey	*Ateles chamek*	9.0	4	–	1.4	6.8
Red howler monkey	*Alouatta seniculus*	6.5	3	–	0.3	2.2
Brown capuchin	*Cebus apella*	2.9	3	1.0	7.9	6.2
White-fronted capuchin	*Cebus albifrons*	2.7	2	0.4	2.8	–
Monk saki	*Pithecia monachus*	2.2	2	–	0.7	–
Squirrel monkey	*Saimiri boliviensis*	0.9	0	2.3	6.1	2.7
Saddleback tamarin	*Saguinus fuscicollis*	0.4	0	9.5	5.4	2.8
Emperor tamarin	*Saguinus imperator*	0.4	0	–	0.3	–

** Degree of hunter preference on a scale of 0 (always ignored) to 4 (never ignored)*

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Drastic reductions of dominant species such as the spider monkey (*Ateles chamek*) and the howler monkey (*Alouatta seniculus*) also impact the broader faunal assemblage. Results from this study suggest a compensatory response of smaller-bodied primates at hunted sites (Fig. 2). The density of small primates was lowest at the nonhunted site (TRC) and highest at the most heavily hunted site (RA). At the RA site, the predominant small primate was the saddleback tamarin (*Saguinas fuscicollis*). *S. fuscicollis* is normally subordinate to larger primates and subject to frequent agonistic displacement at fruiting trees (Terborgh and Stern, 1987). The absence of large primates frees up space, time, and resources previously unavailable due to inter-specific competition. *S. fuscicollis* could be considered hyperabundant at RA, given densities five times larger than our comparable non-hunted site and cohesive "supergroups" as large as 17 individuals – well above estimates of typical mean group size (5 individuals per group; Terborgh, 1983) and range (2-12 individuals per group; Emmons and Feer, 1997). The response of mid-sized primates (*Cebus spp.*) to hunting appears dependent on the degree of pressure. *Cebus spp*. occurred at very low density under intense hunting pressure, but increased to its greatest density in moderately hunted – rather than nonhunted – forest. This is likely due to two factors. First, under mid-level hunting pressure mid-sized primates are less targeted, while intense hunting pressure results in their being taken as well (Peres, 1990). Second, like *S. fuscicollis, Cebus spp.* may respond negatively to the presence of sympatric primates – particularly *Ateles chamek* – and benefit from relaxed competition for shared resources when these large primates are no longer abundant (Fig. 2). Both small- and mid-sized primates in this study appear to exhibit population-level density compensation responses to the extirpation of sympatric large primates. Though our scope of inference is limited to three sites within a small geographic range, these results are potentially indicative of similar changes to primate community structure in other hunted forests.

Observed composition and density of primate populations in forests subject to hunting are likely influenced by species-specific reproductive rates and strategies. In general, smaller relative body size is a strong predictor of higher intrinsic rates of population increase in mammals (Fenchel, 1974). For Neotropical primates specifically, shorter interbirth interval may be a function of smaller relative brain weight (Fedigan and Rose, 1995). Both factors offer smaller primates greater resilience and faster recovery when subject to hunting pressure. Evidence from elsewhere in the Madre de Dios basin suggests that even in forests that have not experienced any hunting pressure for decades, primate populations may still be undergoing recovery from past disturbances. Symington (1988), in a complete census of the local spider monkey (*Ateles chamek*) population in the vicinity of Cocha Cashu Biological Station in Manu National Park, documented the total presence of 77 individuals. In a follow-up census 19 years later, Gibson (2008) found that the same population had grown to 119 individuals. While this notable increase may be due to several factors, it is likely that these populations were still recovering from local hunting pressure during the rubber boom at the turn of the 20th century, more than 75 years prior to Symington's survey (Terborgh, pers. comm.). This may explain differences seen in population densities between other sites in the basin as well (e.g. Endo *et al.,* 2010). *Ateles chamek* population densities in TRC – less isolated and more recently protected than Manu – are considerably lower than those documented at Cocha Cashu (Gibson, 2008). This suggests that the TRC populations may also be in a state of recovery and increasing abundance. The fact that populations of game vertebrates such as Ateline primates can be so slow to recover from disturbance does not bode well for their long-term viability in unprotected forests.

Conservation implications

Hunting is not an ephemeral or geographically limited activity. Wild game can be a major food resource for subsistence hunters across the Neotropics (Redford, 1992). In tropical forest localities, the estimated carrying capacity for humans dependent exclusively on wildlife for protein may be as low as 1 person/km^2 (Robinson and Bennett, 2000), though population densities exceed this nearly everywhere across the tropics. Many large game vertebrates are inherently vulnerable to major population declines, given their low reproductive capacity. Atelid monkeys in particular take several years to reach reproductive age, and then have long interbirth intervals with extended nursing periods (Milton, 1981; Symington, 1987). Hunting of large primates is therefore likely to be unsustainable in many areas, except perhaps when adjacent to large, strictly protected source reserves (da Silva *et al.,* 2005; Ohl-Schacherer *et al*., 2007). Even moderate hunting pressure may be problematic, as large vertebrate dispersers need not be completely eliminated for hunting to have secondary impacts. Species in "half-empty forests" (Redford and Feinsinger, 2001) may be sufficiently reduced that they cease to provide ecological services such as seed dispersal before they become locally extinct (McConkey and Drake, 2006).

In addition to altering vertebrate population structure, hunting can have broad effects on the forest community as a whole. In general, frugivorous vertebrates suffer more severe declines at hunted sites than either granivorous or folivorous species, regardless of body size (Peres and Palacios, 2007). By mediating the dispersal of a majority of large-seeded fleshy-fruited canopy tree species, large vertebrate frugivores are crucial in maintaining biodiversity and regeneration dynamics in tropical forests (Janzen, 1970; Connell, 1971). Smaller non-targeted species, even with increased abundance, cannot adequately replace the dispersal function of larger ones due to inherent anatomical and physiological limitations (Peres and Van Roosmalen, 2002; Poulsen *et al*., 2002; Knogge and Heymann, 2003; Stoner *et al*., 2007). Under high hunting pressure, tree species most reliant on large frugivores may experience substantially reduced recruitment, which can dramatically

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alter forest regeneration processes at the community level (Wright *et al*., 2007; Nuñez-Iturri *et al*. 2008; Terborgh *et al.,* 2008). Increased population densities of smaller-bodied species may, however, favor the smaller-seeded plants which they consume, given limited dispersal distances of larger-seeded counterparts whose dispersers are hunted (Wright *et al*., 2007). Changes to plant recruitment success based on traits such as seed size and type of fruit may thus accompany shifts in faunal communities, to the detriment of species dependent on hunted wildlife and the benefit of those which are not. In the long term, the hunting-induced disruption of game- and non-game vertebrate population dynamics is thus likely to effect change beyond faunal density responses, with expansive transformations to tropical forest community composition and biodiversity.

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