



# Correlation and persistence of hunting and logging impacts on tropical rainforest mammals

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**Abstract:** *Humans influence tropical rainforest animals directly via exploitation and indirectly via habitat disturbance. Bushmeat hunting and logging occur extensively in tropical forests and have large effects on particular species. But how they alter animal diversity across landscape scales and whether their impacts are correlated across species remain less known. We used spatially widespread measurements of mammal occurrence across Malaysian Borneo and recently developed multispecies hierarchical models to assess the species richness of medium- to large-bodied terrestrial mammals while accounting for imperfect detection of all species. Hunting was associated with 31% lower species richness. Moreover, hunting remained high even where richness was very low, highlighting that hunting pressure persisted even in chronically overhunted areas. Newly logged sites had 11% lower species richness than unlogged sites, but sites logged >10 years previously had richness levels similar to those in old-growth forest. Hunting was a more serious long-term threat than logging for 91% of primate and ungulate species. Hunting and logging impacts across species were not correlated across taxa. Negative impacts of hunting were the greatest for common mammalian species, but commonness versus rarity was not related to species-specific impacts of logging. Direct human impacts appeared highly persistent and lead to defaunation of certain areas. These impacts were particularly severe for species of ecological importance as seed dispersers and herbivores. Indirect impacts were also strong but appeared to attenuate more rapidly than previously thought. The lack of correlation between direct and indirect impacts across species highlights that multifaceted conservation strategies may be needed for mammal conservation in tropical rainforests, Earth's most biodiverse ecosystems.*

**Keywords:** biodiversity conservation, bushmeat hunting, habitat disturbance, Heart of Borneo, indirect effects, selective logging, species richness, tropical conservation, tropical deforestation

Correlación y Persistencia de los Impactos de la Caza y la Tala sobre los Mamíferos de los Bosques Tropicales

**Resumen:** *Los humanos influyen directamente sobre los animales de los bosques tropicales por medio de la explotación e indirectamente por medio de la perturbación de hábitat. La caza de animales silvestres y la tala ocurren de manera extensiva en los bosques tropicales y tienen grandes efectos sobre especies particulares, pero sigue sin saberse cómo alteran la diversidad animal en las diferentes escalas de terrenos y si sus impactos están correlacionados entre las especies. Usamos medidas espacialmente esparcidas de la presencia de mamíferos a lo largo del Borneo malayo y modelos jerárquicos de múltiples especies desarrollados recientemente para evaluar la riqueza de especies de mamíferos terrestres de tamaños medianos a grandes*

*mientras representamos la detección imperfecta de todas las especies. La caza se asoció con el 31% de la riqueza más baja de especies. Además, la caza siguió siendo alta incluso cuando la riqueza fue muy baja, resaltando cómo la presión de la caza persiste en áreas con exceso crónico de caza. Los sitios recién talados tuvieron un 11% de riqueza de especies más baja que los sitios sin tala, pero los sitios talados previamente durante más de 10 años tuvieron niveles de riqueza similares a aquellos en los bosques de crecimiento viejo. La caza fue una mayor amenaza a largo plazo que la tala para 91% de las especies de primates y ungulados. Los impactos de la caza y la tala en las especies no estuvieron correlacionados en los taxones. Los impactos negativos de la caza fueron mayores para las especies de mamíferos más comunes, pero la frecuencia contra la rareza no estuvo relacionada con los impactos específicos de especie de la tala. Los impactos humanos directos aparecieron persistentemente y resultaron en la pérdida de fauna de ciertas áreas. Estos impactos fueron particularmente severos para especies de importancia ecológica como los dispersores de semillas y los herbívoros. Los impactos indirectos también fueron severos pero parecieron atenuarse más rápido de lo que se pensaba anteriormente. La falta de correlación entre los impactos directos e indirectos en las especies resalta que las estrategias de conservación multifacéticas pueden ser necesarias para la conservación de mamíferos en los bosques tropicales, los ecosistemas más biodiversos del planeta.*

**Palabras Clave:** caza de animales silvestres, conservación de la biodiversidad, conservación tropical, Corazón de Borneo, deforestación tropical, efectos indirectos, perturbación de hábitat, riqueza de especies, tala selectiva

## Introduction

Earth's most species-rich ecosystems are tropical rainforests. Animals in these systems are subject to 2 main anthropogenic threats: logging and hunting (Corlett & Primack 2011). Logging and hunting both occur over vast expanses of tropical forest. Numerous studies have assessed their impacts on particular taxa or at specific sites, but assessing their individual and joint effects on species richness at landscape scales remains critical (Poulsen et al. 2011; Urquiza-Haas et al. 2011).

Logging continues at a rapid rate in many tropical forests and has mixed effects on forest animal diversity (Wilcove et al. 2013). Logging reduces habitat quality for many taxa (Fimbel et al. 2001; Parry et al. 2007). However, not all rainforest animals depend exclusively on closed-canopy forests (Gubista 1999), and logging can benefit certain species (Castro-Luna et al. 2007; Bicknell & Peres 2010) and even attract some new species to an area (Dahaban et al. 1996). The effects of logging also change over time. In many taxa, species composition in logged forests approaches that of unlogged forests just a few decades after logging has ceased (Dent & Wright 2009). In short, though the impacts of logging on mammal diversity remain critical to understand, they are far from fully understood in a general, predictive framework. This has fueled a debate about whether regenerating forests can sustain regional diversity of tropical wildlife (Wright & Muller-Landau 2006; Laurance 2007).

Hunting occurs over even larger areas in the tropics than logging, and often (Robinson et al. 1999), though not always (Poulsen et al. 2011), accompanies logging. Much research has focused on determining harvest rates and assessing whether levels of exploitation are sustainable (e.g., Robinson & Bennett 2000; Fa & Brown 2009; Kumpel et al. 2010). Recent strides have been

made in the understanding of how various socioeconomic drivers affect hunting rates (e.g., Coad et al. 2013; Vega et al. 2013). Hunters in many areas prefer ungulates, primates, or large rodents (Fa & Brown 2009). However, an extremely wide spectrum of smaller or rarer species may be taken opportunistically (Bennett et al. 2000; Fa & Brown 2009). Thus hunting, in addition to reducing the abundance of primary target species, can decrease overall mammal species richness in many areas (Robinson & Bennett 2000). Although knowledge of hunting impacts in particular areas is considerable, fewer studies have examined hunting at landscape scales, for example, concurrently assessing multiple spatially separated sites subject to different environmental conditions and human disturbances (Peres & Palacios 2007; Urquiza-Haas et al. 2011).

It is also important to determine whether impacts of logging and hunting are correlated across species. Certain taxa may be vulnerable to extirpation due to both logging and hunting (leading to a positive correlation between the impacts of logging and hunting) or susceptible to either hunting or logging but not the other (no correlation). Negative or no covariation between logging and hunting impacts across species could make conservation more difficult because separate strategies would be needed to address each threat.

Our objectives here are to quantify how exploitation (hunting) and logging individually and jointly affect mammal occurrence and species richness, assess how logging impacts on mammal alpha diversity changed over time, and determine if logging and exploitation strongly affected the same species or if species tended to be affected by either one factor or the other. We focused on terrestrial (nonvolant, ground occurring), medium- to large-bodied mammals amenable to detection with camera traps. We included some species that are mainly arboreal but also occur on the ground. Although mammals

represent a tiny fraction of rainforest diversity, their disproportionately high risk of extinction in Southeast Asia (Wilcove et al. 2013) and the important ecological roles of some species as herbivores and seed dispersers (Brodie et al. 2009) make them among the highest conservation priorities.

## Methods

### Study System

We sampled 7 study areas in the Malaysian states of Sabah and Sarawak on the island of Borneo (Fig. 1). Study areas were chosen to include unlogged sites, where we expected hunting to vary from little to none (e.g., Maliau Basin) to heavy (e.g., Mulu), and logged sites, where we expected hunting to vary from little (e.g., Hose Mountains) to heavy (e.g., Ulu Trusan). The study areas differed in type and degree of human influence and in natural environmental conditions such as elevational range. Therefore we sought to assess general patterns in hunting and logging impact while controlling for between-area differences.

Forests across our study region are classified as tropical moist forests and have >2000 mm of rainfall/year and extremely high tree species diversity. Forests in the lowlands tend to be tall (canopy approximately 30–50 m), have an uneven canopy, and are dominated by Dipterocarpaceae. As elevation increases the trees become shorter in stature, the canopy becomes more even, and in montane forests dominance shifts to Fagaceae, Lauraceae, and Myrtaceae (Corlett 2009). Most of Borneo is composed of sedimentary rocks; soils in most of our study areas formed from sandstones and claystones. Maliau Basin Conservation Area contains large tracts of sandy, acidic, kerangas soils, and Mulu National Park has limestone outcrops. Preliminary evidence suggests soil variation may have limited influence on terrestrial mammal diversity (Brodie & Giordano 2011).

Industrial logging is widespread across Borneo. Most logging is selective (as opposed to clearcut); that is large, commercially valuable trees are removed whereas smaller individuals are left. Data on extraction levels from logging operations are seldom publicly available in Malaysia, but removal rates are often on the order of 10–15 trees above 60 cm diameter per hectare (G. Reynolds, personal communication). Collateral mortality of non-target trees can be considerable (G. Reynolds, personal communication). Logged forests tend to have lower tree basal area and altered plant species composition (Johns 1996). Reduced-impact logging techniques were practiced in one of our study areas, Maliau Basin Conservation Area, and involved similar removal rates to conventional logging in flat areas, but there was greater effort to avoid damage to unharvested trees and to reduce removal rates on steep slopes.

Hunting is almost ubiquitous in forests of interior Borneo. Muslim populations in some, mainly coastal, areas may avoid killing certain native mammals such as bearded pigs (*Sus barbatus*), but our study areas in the interior of Borneo had mostly Christian people with no strong hunting taboos of which we were aware.

### Field Sampling

We deployed Reconyx RM45 and Bushnell TrophyCam camera traps at 153 locations spanning the 7 study areas from 2010 to 2012. These are digital, motion-triggered units active 24 h/d; an infrared flash operates at night. Some cameras malfunctioned or were stolen, resulting in usable data from 134 locations. Cameras were attached to the bases of trees, usually 30–70 cm above the ground. The camera traps take fairly wide-angle photographs, so cameras placed at this height recorded species ranging in size from rats to elephants. Some cameras were placed on potential movement routes for wildlife such as human or animal trails, abandoned logging roads, or stream courses, whereas others were placed off trail. This afforded the detection of species that either used or avoided trails.

Sampling locations within each of 7 study areas in Malaysian Borneo (Table 1) were selected to span gradients in elevation, logging pressure, and human accessibility, while maintaining approximate spacing between cameras of usually at least 1 km, and with no prior knowledge of wildlife abundance or richness at any sampling location. We sought to stratify sampling locations across logging histories as much as possible, but this was constrained by the fact that logging operations were not designed with replicable experiments in mind. Some unlogged forests were sampled in all study areas, but only 3 areas had old logged forest available for sampling.

### Logging Assessment

Assessment of habitat disturbance was restricted to selective logging, rather than clearcutting, because the former is a more spatially widespread disturbance in much of the tropics (Edwards & Laurance 2013). Cameras were not placed in unforested areas such as plantations or agriculture. As is nearly always the case in studies of animal responses to forest disturbance (Dent & Wright 2009), we assessed changes in logging impacts on mammal diversity over time with a space-for-time substitution. In other words, we measured mammal occurrence across sites that were unlogged or had been logged at different times in the past, but we did not conduct decadal-term monitoring at any given site.

Logged sites were divided into classes based on how long prior to the study logging occurred. This course-scale approach necessitates glossing over some of the nuances of how altered forest conditions from selective logging can potentially affect animal communities (Kitching et al. 2013; Woodcock et al. 2013). But the

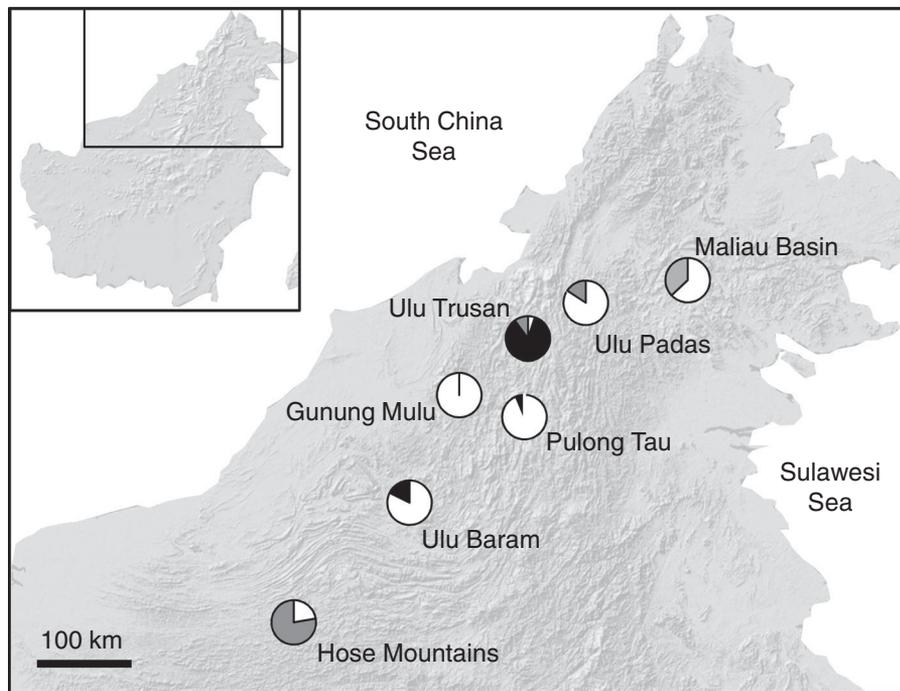


Figure 1. Map of the study region in northern Borneo (inset) showing for each study area the proportion of camera stations in unlogged (white), newly logged (<10 years ago) (gray), and older logged (black) forest.

Table 1. Details of sampling of mammals for each study area in Malaysia.

Study area (state)	Centroid latitude (°N)	Centroid longitude (°E)	IUCN protected area category <sup>a</sup>	Total number of sites, with number of logged sites in parentheses	Mean (SD) camera days/site <sup>b</sup>	Mean (SD) proportion of days with ≥1 hunter detected at each site			Elevation (m)		
						Min	Mean	Max	Min	Mean	Max
Hose Mountains National Park (Sarawak)	2.2310	113.6862	Proposed	18 (14)	84.2 (14.7)	0.004	0.013	524	1075	1436	
Maliau Basin Conservation Area (Sabah)	4.7264	116.9354	Ia	27 (10)	193.8 (93.6)	0.000	0.001	214	561	1115	
Gunung Mulu National Park (Sarawak)	4.0992	114.8809	II	17 (0)	137.1 (51.3)	0.083	0.166	64	319	1326	
Pulong Tau National Park (Sarawak)	3.8277	115.4944	Proposed	16 (1)	191.9 (44.8)	0.023	0.057	1106	1459	1792	
Ulu Baram (Sarawak)	3.2992	115.2228	Not protected	17 (3)	83.8 (29.1)	0.039	0.045	304	730	1429	
Ulu Padas (Sabah)	4.3611	115.7108	Not protected	19 (3)	96.9 (50.9)	0.035	0.045	1009	1256	1682	
Ulu Trusan (Sarawak)	4.3889	115.4717	Not protected	20 (19)	59.7 (35.9)	0.048	0.080	400	742	1012	

<sup>a</sup>IUCN, International Union for Conservation of Nature; Ia, strict nature reserve; II, national park.

<sup>b</sup>Number of days during which camera traps were operational at each camera location.

cycle of logging rotations is a critical factor that managers can control (Brukas et al. 2013); therefore, it is important to understand how animal diversity changes as a function of time since logging. Moreover, prior research suggests that for selectively logged forests (Adum et al. 2013) and regenerating secondary forests (Dent & Wright 2009), the

time since logging occurred is a very strong predictor of diversity in a number of animal taxa.

Information on when logging occurred in given areas is not publicly available, so in each study area we used informal interviews with local villagers or forestry department staff to determine when the area was logged.

We did not believe these estimates were accurate enough to use as a continuous time-since-logging metric, but we determined they were suitable for gross categorization of logging into  $\leq 10$ -year-old (new logging) and  $> 10$ -year-old (older logging) classes. Ten years is approximately the time required for re-establishment of a low tree canopy following logging (Johns 1996). All logged sites areas were contiguous with unlogged forest patches.

### Hunting Analysis

We analyzed our camera trap photographs to determine the proportion of days at each camera site where at least one hunter was detected (encounter rate). Assessing prey responses to predator distribution or relative abundance is common, though it only allows us to measure current predator (in this case, human) impacts and not legacies of potential historical impact. By default, we assumed humans in the forest were hunters. In most cases this was verifiable because they carried hunting implements (shotguns or blowpipes) or were accompanied by hunting dogs. We excluded humans who were obviously tourists (e.g., in several of the national parks in which we worked) or were unarmed park staff or guides accompanying tourists.

Hunter encounter rates could potentially not be a good metric of hunting intensity if they declined over time at given sites because hunters became aware of the cameras and avoided them. To test this, we ran general linear models of encounter rate versus time at each site and used Bonferroni-corrected alpha levels to account for family wise error rate.

We used Bayesian generalized linear models to examine whether hunter encounter rates were affected by accessibility, indexed as the distance to the nearest village, logging camp, navigable river, or drivable road (measured with GIS or in the field with handheld GPS; hereafter “distance”). We also tested the effects of road density (cumulative linear roads per square kilometer), human population density as indexed by nighttime light pollution captured by the VIIRS satellite program (NOAA 2012), logging, and a distance  $\times$  logging interaction term. Light emission serves as an approximate index, rather than an exact measure, of human populations because small rural communities may not use power at night. The interaction terms allowed an explicit test of whether logging exacerbated the impacts of hunting via timber roads increasing forest accessibility, as has been noted in other tropical areas (e.g., Robinson et al. 1999).

### Species Richness Analysis

Many, even most, animals in these ecosystems are naturally rare and cryptic. Historically, this has made it impossible to achieve sufficient sample sizes for quantitative population analysis of any but the most common

species (Robinson & Bennett 2000). As a result it has been problematic to untangle true human impacts from false absences stemming from limited detection ability. We used hierarchical Bayesian multispecies occupancy models (Royle & Dorazio 2008) to elucidate how anthropogenic stressors affect individual taxa and species richness while accounting for imperfect and low detectability in most species.

We assumed species occurrence,  $Z_{i,j}$ , at a given location was a Bernoulli process, where the probability that species  $i$  occurs at site  $j$ , denoted as  $\psi_{i,j}$ , can be modeled with a logit-link function and relevant covariates. We denote the occurrence of species  $i$  at location  $j$  as  $Z_{i,j}$  and model occurrence probability as:

$$\begin{aligned} \text{logit}(\psi_{i,j}) = & \beta 0_i + (\beta 1_i \times \text{elevation}_j) + (\beta 2_i \times \text{elevation}_j^2) \\ & + (\beta 3_i \times \text{hunting}_j) + (\beta 4_i \times \text{new logging}_j) \\ & + (\beta 5_i \times \text{old logging}_j) + (\beta 6_i, \text{study area}_{(j)}), \end{aligned} \quad (1)$$

where  $\beta 0_i$  is the average occurrence probability for species  $i$  (the intercept term) and  $\beta 1_i - \beta 5_i$  are the effects of each covariate, standardized to have a mean of zero and standard deviation of one. We used elevation as a proxy for environmental conditions because it is the strongest driver of natural variation in forest composition in our study region (Culmsee & Leuschner 2013) and correlates strongly with other abiotic conditions such as temperature. We included an elevation quadratic term to account for potential mid-elevation peaks in diversity. To address unmeasured differences in environmental conditions between study areas and potential autocorrelation from our clustered sampling design, we included a categorical (7 levels) random effect  $\beta 6_i$  based on the study area in which point  $j$  is located, where  $\beta 6_i, \text{study area}_{(j)} \sim \text{normal}(0, \sigma_i)$ .

True occurrence of species is detected imperfectly. We modeled the detection probability of each species ( $p_{i,j,k}$ ) as a Bernoulli process conditional on species presence. We used 2 covariates for estimating the detection probability of species at camera traps: number of camera hours per sampling period (i.e., how many hours cameras were operational at each site) and sampling period (to account for time-varying detection), both of which were standardized. We used 5-d increments as sampling periods.

To link each of these single-species models, we assumed that the species-specific parameters in both the occurrence and detection models were random effects derived from a normal distribution, such that there was a common mean and variance for the parameter estimates of each covariate across all species in the community (Royle & Dorazio 2008; Burton et al. 2012).

To assess correlations between the effects of hunting and logging, we included explicit correlation coefficients

when we specified the community-level parameters for these variables. We also added a large number of all-zero encounter histories to the data set to account for species that were not detected during sampling. Such data augmentation is a well-documented process for estimating species richness and is a more mechanistic approach than nonparametric estimators for estimating richness (Royle & Dorazio 2008). We ran 3 chains for 70,000 iterations after a burn-in of 30,000. We used the  $\hat{R}$  statistic and visual exploration of the MCMC chains to assess model convergence. We examined whether rarity was related to species responses to different human disturbances by examining correlations between species-specific estimates of mean occurrence and coefficients for logging and hunting.

We assumed independence of detections among sites, which could be violated if several sampling sites were within the home range of a single individual animal. We tested this and found no evidence of nonindependence in detections (Supporting Information).

## Results

### Hunting Analysis

We had 16,608 trap days. There was a significant change in hunter encounter rate over time at only one of the 134 camera stations. The effect at that station was slight (regression slope more than an order of magnitude lower than the intercept).

Of the factors potentially related to hunter encounter rates, Euclidean distance from each camera site to the nearest village, logging camp, drivable road, or navigable river was negatively related to encounter rate (Fig. 2).

Road density, human population density, logging, and the distance  $\times$  logging interaction had weak or negligible relationships with encounter rate.

### Species Richness Analysis

Our model estimated a mean total species richness of 30.91 (95% CI 30–34), nearly the same as the 30 species we observed in the study region (Table 2). The model fit the data well; the Bayesian posterior predictive check was 0.55 (a model fits the data well if the check is toward the middle of the 0–1 range). Mammal species richness peaked at approximately 1200 m (elevation: community-level  $\beta = 0.20$ , Bayesian 95% CI =  $-0.35$  to  $0.74$ ; elevation<sup>2</sup>:  $\beta = -0.33$ , CI  $-0.61$  to  $-0.09$ ) (Fig. 3). During preliminary analysis we also ran a model that included trail as an occurrence covariate because occurrence of human and nonhuman mammals could be affected by the presence of trails. This model had a worse posterior predictive check (0.23) than the model without the trail covariate; trail had a weak effect ( $\beta = -0.28$ , CI  $-0.65$ – $0.11$ ) and coefficients for the remaining covariates were similar to the model without trail.

Across our study region, recent logging was negatively associated with mammal species richness ( $\beta = -0.30$  & CI  $-1.84$  to  $-0.32$ ) (Fig. 3). With all other factors constant, mammal richness in newly logged forests was 11.3% lower than in unlogged forests. Older logging had ambiguous effects on mammal richness; beta coefficient credibility interval substantially overlapped zero ( $\beta = 0.14$ , CI  $-0.61$ – $0.96$ ). On average, occurrence was reduced in newly logged forests for all species and lower in forests that had been logged  $>10$  years ago for 63.3% of species (Fig. 4).

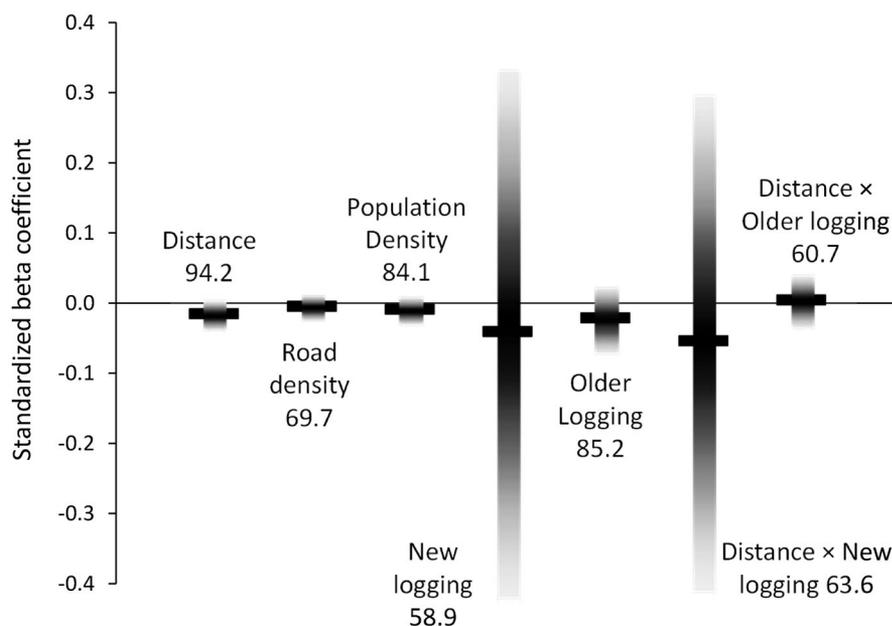


Figure 2. Beta coefficients for factors related to relative local abundance of hunters. Black bars show coefficient means; posterior distributions shown from high (dark) to low (light) probability. Numbers under each factor show the percent posterior distribution in the same direction (+ or -) as the mean. Distance is the distance from each camera to the nearest village, road, or navigable river.

Table 2. Mammal species detected via camera trapping in Malaysia.<sup>a</sup>

Species code	Species	Scientific name	Order	IUCN status	Number of trap days with $\geq 1$ detection <sup>b</sup>	Model intercepts (SE); (detection)
BACA	Bay cat	<i>Pardofelis badia</i>	Carnivora	Endangered	3	-1.16 (1.64); -5.36 (0.88)
BACI	Banded civet	<i>Hemigalus derbyanus</i>	Carnivora	Vulnerable	132	-0.79 (0.65); -1.75 (0.10)
BALI	Banded linsang	<i>Prionodon linsang</i>	Carnivora	Least concern	9	-1.62 (1.39); -4.26 (0.53)
BANT	Banteng	<i>Bos javanicus</i>	Cetartiodactyla	Endangered	11	-3.62 (1.41); -2.99 (0.57)
BEPI	Bearded pig	<i>Sus barbatus</i>	Cetartiodactyla	Vulnerable	555	1.37 (0.74); -1.22 (0.05)
BINT	Binturong	<i>Arctictis binturong</i>	Carnivora	Vulnerable	8	-1.30 (1.69); -4.72 (0.60)
CLLE	Sunda clouded leopard	<i>Neofelis diardi</i>	Carnivora	Vulnerable	92	-0.88 (0.87); -2.60 (0.15)
COPO	Malayan porcupine	<i>Hystrix brachyura</i>	Rodentia	Least concern	285	0.06 (0.58); -1.30 (0.07)
CPCI	Common palm civet	<i>Paradoxurus bermaphroditus</i>	Carnivora	Least concern	3	-1.50 (1.79); -5.55 (0.93)
FHCA	Flat-headed cat	<i>Prionailurus planiceps</i>	Carnivora	Endangered	2	-1.89 (1.69); -5.53 (1.32)
HOCI	Hose's civet	<i>Diplogale bosei</i>	Carnivora	Vulnerable	29	-2.16 (1.03); -2.33 (0.25)
HOLA	Hose's langur	<i>Presbytis bosei</i>	Primates	Vulnerable	4	-1.24 (1.52); -5.15 (0.82)
LECA	Leopard cat	<i>Prionailurus bengalensis</i>	Carnivora	Least concern	41	-1.01 (0.84); -2.68 (0.24)
LTMA	Long-tailed macaque	<i>Macaca fascicularis</i>	Primates	Least concern	29	-1.31 (0.78); -2.83 (0.27)
LTPO	Long-tailed porcupine	<i>Trichys fasciculata</i>	Rodentia	Least concern	88	-1.10 (0.86); -1.93 (0.14)
MACA	Marbled cat	<i>Pardofelis marmorata</i>	Carnivora	Vulnerable	20	-0.85 (0.72); -3.46 (0.39)
MACI	Malay civet	<i>Viverra zanzalunga</i>	Carnivora	Least concern	125	-0.56 (0.96); -1.95 (0.11)
MALA	Maroon langur	<i>Presbytis rubicunda</i>	Primates	Least concern	4	-2.50 (1.84); -4.41 (0.82)
MONG	Mongoose	<i>Herpestes brachyurus</i> and <i>Herpestes semitorquatus</i>	Carnivora	Least concern & data deficient, respectively	99	-0.51 (0.45); -2.14 (0.12)
MOON	Moonrat	<i>Echinosorex gymnura</i>	Insectivora	Least concern	3	-2.72 (1.42); -3.76 (1.08)
MOUS	Mousedeer	<i>Tragulus kanchil</i> and <i>Tragulus napu</i>	Cetartiodactyla	Least concern	301	-0.84 (0.93); -0.94 (0.07)
MPCI	Masked palm civet	<i>Paguma larvata</i>	Carnivora	Least concern	67	-1.77 (1.05); -2.20 (0.16)
MUNT	Muntjac	<i>Muntiacus muntjak</i> and <i>Muntiacus atberodes</i>	Cetartiodactyla	Least concern	838	2.01 (0.66); -0.58 (0.04)
PANG	Sunda pangolin	<i>Manis javanica</i>	Pholidota	Endangered	7	-0.94 (1.81); -4.96 (0.46)
PTMA	Pig-tailed macaque	<i>Macaca nemestrina</i>	Primates	Vulnerable	519	1.71 (0.50); -1.19 (0.05)

Continued

Table 2. Continued

Species code	Species	Scientific name	Order	IUCN status	Number of trap days with $\geq 1$ detection <sup>b</sup>	Model intercepts (SE); (detection)
SAMB	Sambar	<i>Rusa unicolor</i>	Cetartiodactyla	Vulnerable	300	-0.10 (0.43); -1.39 (0.07)
SUBE	Sun bear	<i>Helarctos malayanus</i>	Carnivora	Vulnerable	114	-0.11 (0.74); -2.71 (0.14)
TSPO	Thick-spined porcupine	<i>Hystrix crassispinis</i>	Rodentia	Least concern	164	-0.77 (0.74); -1.42 (0.10)
WFLA	White-fronted langur	<i>Presbytis frontata</i>	Primates	Vulnerable	3	-2.27 (1.86); -4.59 (1.61)
YTMA	Yellow-throated marten	<i>Martes flavigula</i>	Carnivora	Least concern	45	-1.69 (0.60); -2.25 (0.20)

<sup>a</sup>Taxonomy and status follow the International Union for the Conservation of Nature (2013).

<sup>b</sup>Number of trap days (i.e., number of days during which camera traps were operational at each camera location) is out of a possible total 16,608.

Hunting also had a strong negative relationship with mammal species richness ( $\beta = -0.30$ , CI  $-0.60$  to  $-0.04$  & Fig. 3). Hunting was associated with a 30.7% average decrease in mammal local species richness across its observed range of variation (when all other factors were held constant). Individually, the mean predicted effects of hunting were negative for 87% of species (Fig. 4).

We determined that hunting was a greater conservation threat than logging for a particular species if the hunting coefficient was both negative and lower than the logging coefficient. Recent logging had more serious negative impacts than hunting for all species. In older logged forests, however, hunting was a more serious conservation threat than logging for 10 of the 11 primate and ungulate species, including all of the IUCN at-risk taxa. For carnivores, 8 of the 14 species were more negatively affected by hunting than by older logging, including 5 of the 8 at-risk taxa. The effects of hunting on occurrence probabilities across species were not significantly correlated with either new logging ( $R = 0.02$ , 95% CI  $-0.94$ – $0.95$ ) or older logging ( $R = -0.39$ , 95% CI  $-0.97$ – $0.85$ ).

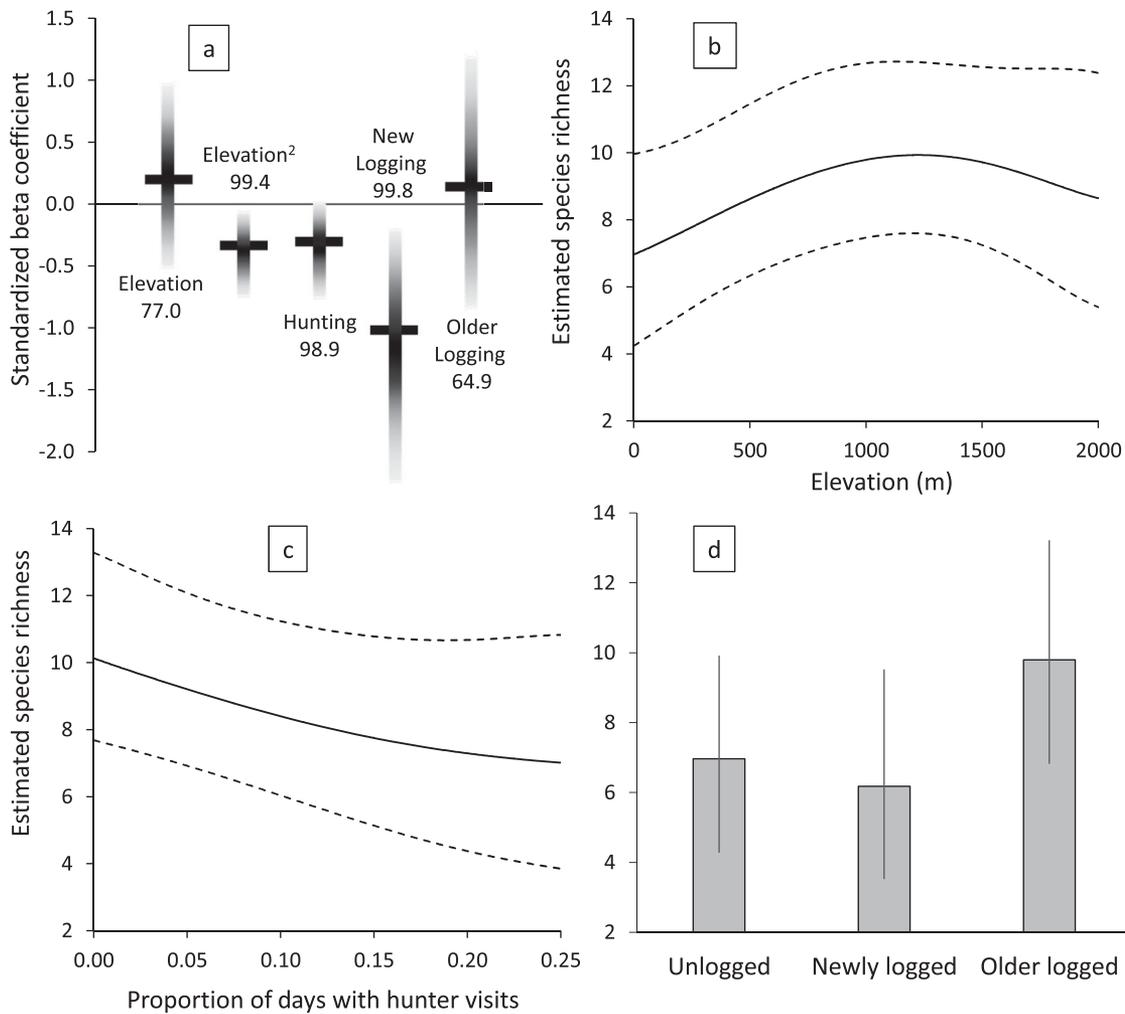
Mean occurrence was negatively correlated with species-specific hunting impacts ( $R = -0.48$ , CI  $-0.72$  to  $-0.14$ ). Mean occurrence was not correlated with species-specific impacts of recent logging ( $R = 0.03$ , CI  $-0.34$  to  $0.38$ ) or older logging ( $R = 0.12$ , CI  $-0.25$  to  $0.46$ ).

## Discussion

Our results show that both indirect human impacts from logging and direct impacts from hunting had large effects on the species richness of native medium- to large-bodied terrestrial mammals in Borneo rainforests. Despite our unbalanced sampling design, we detected general patterns in which logging initially had strong negative impacts

on mammal richness, but these negative effects were greatly attenuated in forests that had been logged over 10 years previously, indicating a fairly rapid recovery of local species richness. Other studies have demonstrated high variability in logging impacts among species; some species respond positively and others negatively (e.g., Castro-Luna et al. 2007; Bicknell & Peres 2010). Our results suggest that such patterns may emerge only after a certain level of forest regeneration has occurred. On average, every species in our study was negatively affected by recent logging. Only after a decade since logging did differences in the direction of response appear; older logged forests provided good habitat for large herbivores such as sambar (*Rusa unicolor*) and banteng (*Bos javanicus*) as well as omnivorous macaques (*Macaca* spp.) but suboptimal conditions for many carnivores. For many taxa, species composition in secondary forests comes to resemble that of unlogged forests after several decades (Dent & Wright 2009). We documented relatively fast (approximately 10 years) recovery of local species richness for medium- and large-bodied terrestrial mammals in selectively logged forests. Although patterns of occurrence and species richness were similar between older logged and unlogged forests, population density could take longer to recover; density of several large mammals in the Republic of Congo remain lower than in unlogged forests 2–3 decades after logging (Poulsen et al. 2011).

Hunting was a greater conservation threat than logging for primates and ungulates, many species of which are important as seed dispersers and herbivores in tropical forests (Brodie et al. 2009). Although hunters here prefer ungulates such as the bearded pig, they are also opportunistic in their prey selection and broad in their diet breadth (Bennett et al. 2000). Such generalist foraging by other predator species can increase species richness. For example, predation on herbivore species in proportion to their relative abundance can restrict competitive



**Figure 3.** (a) Beta coefficients for the analysis of mammal species richness (black horizontal bars, coefficient means; dark to light shading, posterior distributions from high to low probability, respectively; numbers under factors, percent posterior distribution in the same direction [+ or -] as the mean). Relationships between estimated species richness and 95% credibility intervals and (b) elevation, (c) hunting pressure, and (d) logging. Apparently higher richness in older logged forest (d) is not statistically significant (a).

exclusion by any herbivore (Paine 1966), a pattern known as predator-mediated coexistence. Across our sites, however, generalist hunting by humans reduced mammal richness. Although humans have been hunting in Southeast Asian forests for tens of millennia (Corlett 2007), their current strong influence on mammal richness likely stems from a growing human population, expansion of central-place foraging rather than nomadism, increased harvest efficiency afforded by firearms, demands of international markets (Lenzen et al. 2012), and, unlike with obligate predators, the fact that human populations are substantially subsidized by plant-based foods.

We did not find a correlation between logging and hunting impacts across species such that strong responses by a given mammal to one factor were not associated with strong responses to the other. This has practical applications, in that conservation strate-

gies addressing one threat cannot be expected to implicitly mitigate the other. With a few notable exceptions (e.g., Bennett 1996), current conservation strategies in Borneo tend to focus on avoiding deforestation rather than on limiting hunting (e.g., Phelps et al. 2010; Greenwood 2012). In terms of vertebrate conservation, logged forests regain conservation value relatively quickly and even provide optimal habitat for vulnerable and endangered ungulates, whereas hunting appears to persist as a long-term threat even when mammal populations are depleted (Tungittiaplakorn & Dearden 2002).

Though we used models to statistically partition the effects of hunting and logging, our sampling design cannot fully disentangle the 2 because in many areas they are tightly linked (Bennett & Gumal 2001). Thus the avoidance of newly logged forests by sambar, even though

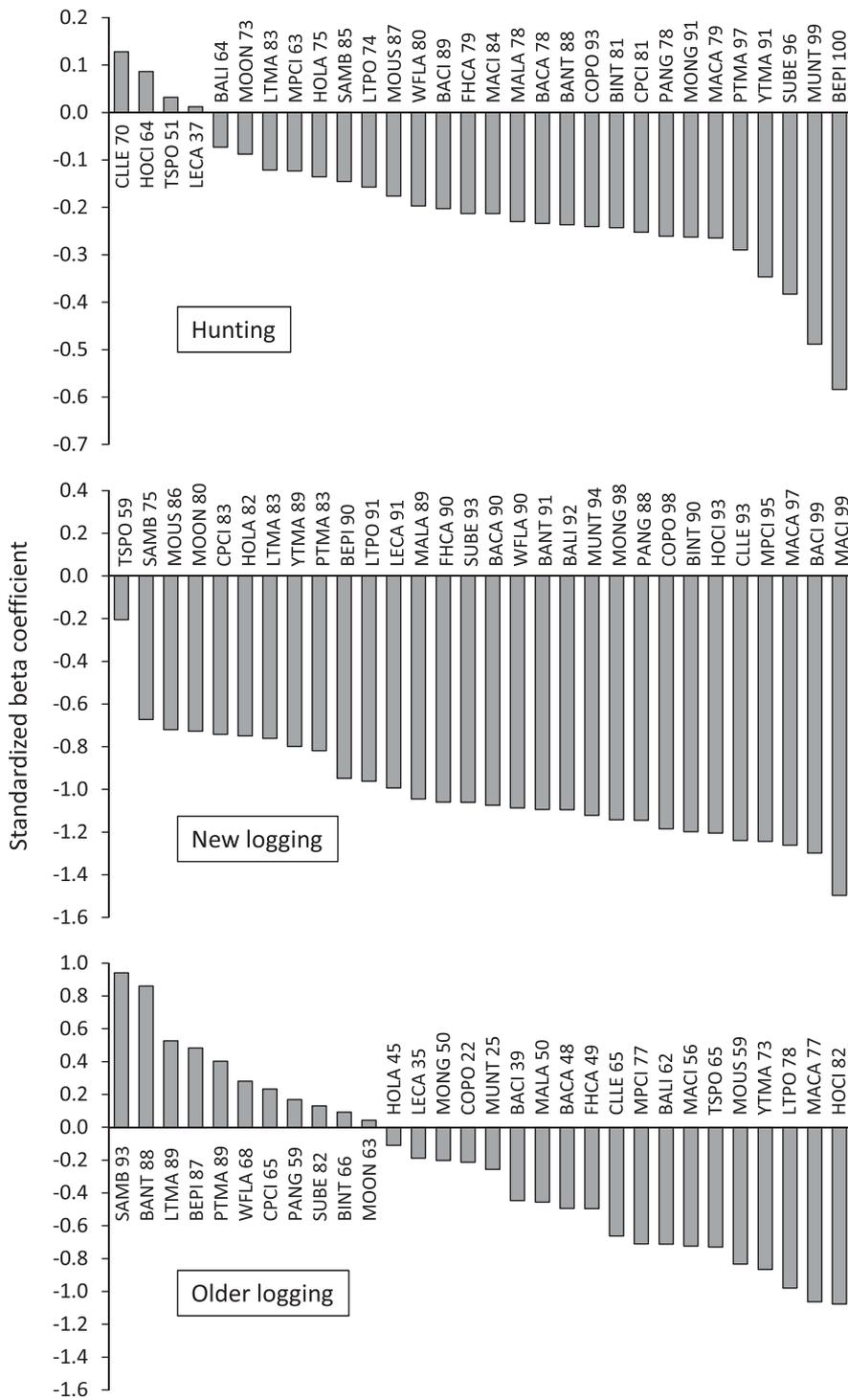


Figure 4. Species-specific beta coefficients of hunting and logging parameters. Species codes are in Table 2. Number after the species code is percentage of model runs with the same direction (+ or -) as the mean for each species.

such habitats may have abundant forage (Dahaban et al. 1996), could be due to higher hunting there. Though several of the larger ungulates are more abundant in older logged forests, Sunda clouded leopards appeared to avoid such areas. Little is known about clouded leopard diet, but perhaps they were more closely tracking the abundance of small prey such as mousedeer, muntjac, or porcupines that also avoided older logged habitat.

The negative effects of hunting were stronger for common species than rare ones. On the one hand, this is unsurprising because hunters would be expected to target readily available prey (Robinson & Bennett 2000; Urquiza-Haas et al. 2011). On the other hand, this pattern also ignores hidden historical legacies. The banteng was once a widespread ungulate in Bornean rainforests, but it has been extirpated via hunting from much of its former

range (Payne et al. 1985). The only study area where we detected banteng was Maliau Basin, currently a well-protected conservation area. The hunting coefficient for banteng in our analysis was therefore relatively weak, but this only reflected conditions at the time; past hunting had a dramatic effect on this species.

Although our analysis produced illuminating results, there are caveats that warrant exploration. Use of relative local abundance of hunters as a metric of hunting pressure would not be appropriate if the hunters had distributed themselves across the landscape in proportion to prey availability. For example, if human hunters exhibited an ideal free distribution (Fretwell & Lucas 1970), the relationship between hunter and wildlife abundance would be a linear positive correlation where per capita hunter impacts are effectively constant relative to wildlife abundance. In our system, however, there are several reasons why these conditions do not apply. First, nomadism, formerly common in certain cultures in Borneo, has become increasingly rare (Bennett et al. 2000). As far as we could tell, all the hunting we observed was by central-place foragers based in villages or logging camps. Indeed, accessibility of sampling locations (their distance to the nearest village, road, or river) was the major predictor of relative hunter local abundance. Second, although wild meat supplements the diets of many people in Borneo, it has never been the sole staple resource. Villages, logging camps, and nomadic peoples are likely spatially distributed based on cultural and agricultural considerations, timber availability, and wild food plants, respectively, rather than by wildlife availability. Third, hunting is performed for many cultural and recreational reasons beyond the simple provisioning of food (Bennett & Robinson 2000). Much of the hunting in our study areas was conducted by local villagers who were supported economically by other means and did not depend on wild meat for subsistence. Taken together, these factors suggest why hunting effort can still remain high even in areas that have been depleted of animals, as our results confirm. Thus local relative abundance of hunters can be a useful predictor (rather than response) variable in relation to wildlife occurrence. This contention is further supported by the fact that we observed a negative relationship between relative local hunter abundance and both mammal species richness and occurrence rates for most species, rather than positive relationships as would be expected if the hunters were efficiently tracking prey availability.

A second caveat to our analysis is that terrestrial-based camera trap sampling is likely suboptimal for assessing arboreal species. Our models account for this, in part, by parsing out estimated occurrence probabilities from detection rates, which may be low for species that spend a lot of time in trees. It is possible that arboreal species spend more time on the ground in logged than in unlogged forests. If this were true in the study area, our

estimates of logging impacts on arboreal species occurrence would be conservative because detection rates would have been enhanced in logged forests through behavioral mechanisms rather than true changes in occurrence probability.

Maintaining abundant vertebrate populations in logged and unlogged tropical forests should be in the best interests of both conservationists and local people living in these systems. Achieving sustainable exploitation levels is possible where the local hunting community deems it important (Robinson & Bennett 2000) and can ultimately benefit biological conservation and human livelihood.

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## Supporting Information

Additional information on testing the assumption of independent detections among sites (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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