Deforestation and hunting effects on wildlife across Amazonian indigenous lands

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ABSTRACT. Deforestation and hunting are main wildlife threats in Amazonia, affecting the ecosystem and dwellers that rely on game meat. Data from 9109 hunted animals from 35 villages of 8 Pano indigenous lands in Brazilian Amazonia were used to build 4 indicators of wildlife status based on ecological models and to analyze the effects of deforestation, hunting pressure, and socioeconomic aspects on wildlife variation. Although variation in wildlife status indicated depletion in certain locations, hunters from most villages continued to hunt their preferred game after decades of intensive hunting. Indigenous hunting resulted in local depletion of species because of the dispersal of animals away from the source of hunting. This local effect can be explained by the permanent hunting of wildlife in the region, the behavior of Pano hunters, and the design and scale of this study analysis. Regionally, however, deforestation and associated factors are the cause of reduced population density and hunting success, extirpating sensitive species. Roads exacerbated hunting effects through disturbance, encroachment, and provision of access to livestock meat at markets. To avoid local depletion, indigenous people must review their subsistence hunting practices, whereas to achieve regional wildlife conservation and to maintain indigenous societies in Amazonia, wildlife habitat loss should be limited.

Key Words: *Amazonia; game species; habitat loss; indigenous hunting; Katukina; Kaxinawá; road*

INTRODUCTION

The recent decline in populations of large-bodied wildlife species in tropical forests has led to a global bushmeat crisis, threatening forest ecosystems and the people that depend on wild meat (Milner-Gulland et al. 2003). Habitat loss at unprecedented rates and overhunting to supply rural and urban human populations are the main human-mediated disturbances threatening game species (Davidson et al. 2009). These disturbances affect large game communities by dispersing individuals and populations away from the source of disturbance, by reducing population abundance, and by extirpating species, resulting in depleted assemblages where sensitive species are consistently absent (Peres 2001, Laurance et al. 2011). Consequently, in areas with depleted wildlife, smaller prey is hunted farther away from settlements, with a lower meat return rate and from fewer species (Weinbaum et al. 2013, Iwamura et al. 2014).

Although the effects of deforestation and hunting may interact, it is essential to distinguish their individual effects to assess sustainable disturbance levels and impact on wildlife (Laurance and Useche 2009). Habitat loss is identified as one of the most important large-scale threats to large vertebrates, leading to several local extinctions (Kinnaird et al. 2003). Although development initiatives are the main drivers of deforestation in Amazonia, inside protected areas small-scale and subsistence agriculture plays a major role in habitat loss that leads to wildlife depletion. Hunting, in turn, can locally deplete Amazonian wildlife even when indigenous people hunt for subsistence (Souza-Mazurek et al. 2000, Peres and Nascimento 2006). For centuries, indigenous people have hunted wildlife, but it is controversial whether their impact alone depletes game species at regional scales (Robinson and Bodmer 1999, Milner-Gulland and Rowcliffe 2007, Levi et al. 2009). In such remote areas, these direct drivers of wildlife depletion can vary associated to socioeconomic variation in human communities (Sirén et al. 2006, Godoy et al. 2010, De la Montaña et al. 2015).

As in other Neotropical forests, Amazonian indigenous groups increasingly hunt in undisturbed and altered habitats (Smith 2005). Hence, game species in indigenous lands (ILs) are subject to multiple depletion drivers. The indigenous groups of the Pano linguistic family that live in the state of Acre hunt for subsistence in ILs dispersed throughout the state (Constantino 2015). Also, their lands are subject to small-scale and subsistence agriculture inside and in surrounding areas that changes forest cover. An investigation of hunting in their lands can provide insights about the drivers of variation in the hunted wildlife in Amazonian protected areas.

Pano hunting in indigenous lands

Kaxinawá and Katukina are ethnic groups of the Pano linguistic family with cultural similarities (Cunha and Almeida 2002) that, in Brazil, live in a 70,000 km² region that has been intensively hunted for decades (Peres and Palacios 2007). Their villages were created over the years since the 1970s, and have populations ranging from 50 to 140 people, with different linkage levels to the cities. The villages in Campinas and Igarapé do Caucho ILs have road access to cities, whereas the other villages have river access to markets (Fig. 1). Hunting is a prestigious male activity. Wildlife is the preferred meat source, which is fundamental to community structure through provision and sharing, and is significant for medicine and cosmology. The preferred preys are large species such as ungulates, large primates, reptiles, and understory birds and are chased whenever encountered. The second preference for prey is smaller species that are hunted incidentally when hunters do not succeed in hunting preferred animals (Kensinger 1995, Lima 2002). The most common hunting strategy is the single-man, one-day search for animals, although there is occasional overnight hunting in more remote areas or hunting with dogs or flashlights for specific prey (Constantino 2015). For several decades, shotguns have mostly replaced the bow and arrow. The ideal hunting territory of a remote Pano village is a 5-km circular area from the center of the village that is exclusively used by village

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members (Constantino 2015). Pano hunters evaluate wildlife abundance by estimating the straight distance, in minutes of walking, to the highest number of preferred animals (Kensinger 1995, Constantino et al. 2008).

Fig. 1. Kaxinawá and Katukina indigenous lands studied in Acre State, Brazilian Amazon. Indigenous lands' labels: (a) Kaxinawá do Igarapé do Cauho, (b) Katukina do Campinas, (c) Kaxinawá da Praia do Carapanã, (d) Kaxinawá do Baixo Rio Jordão, (e) Kaxinawá do Rio Jordão, (f) Kaxinawá/ Ashaninka do Rio Breu, (g) Kaxinawá do Humaitá, and (h) Alto Purus.
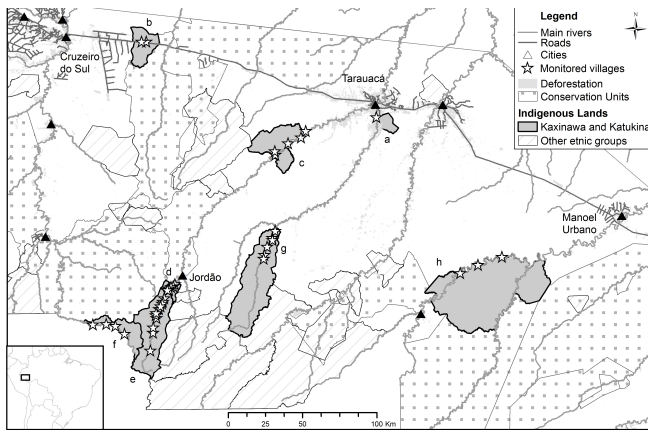
Assessing wildlife status using hunting data
Variations in game species conservation status and hunting sustainability have been extensively assessed using hunting data, which is easier to collect than animal counts, in tropical areas (Jerozolimski and Peres 2003, Fa et al. 2005, 2015, Ohl-Schacherer et al. 2007, Parry et al. 2009a, Espinosa et al. 2014, Ochoa-Quintero et al. 2015). Indexes based on hunting data, if carefully designed according to ecological models, can provide reliable information about wildlife species and communities (Milner-Gulland and Rowcliffe 2007, Weinbaum 2013).

The central place foraging model links local harvesting intensity to resource depletion. This model assumes that hunting pressure from a settlement within a limited territory first depletes wildlife close to the settlement, and then at increasing distances from the settlement (Sirén et al. 2004, Levy et al. 2011). If the model only includes data for species that are always pursued, the hunting distance from the settlement is an indicator of wildlife status that varies with central place hunting pressure (Alvard et al. 1997, Ohl-Schacherer et al. 2007, Levi et al. 2011).

In extreme cases of extirpation or drastic reduction in species density, the species is no longer hunted. In the Amazon, certain large primates, birds, and ungulates that are sensitive to habitat disturbance and hunting pressure are prone to extirpation (Robinson 1996, Peres and Palacios 2007). Therefore, their presence in wildlife assemblages is often used as a proxy for wildlife depletion near hunter settlements (Daily et al. 2003, Parry et al. 2009b).

Wildlife populations can also be assessed using indicators derived from the optimal foraging theory. This theory predicts that more animals of lower ranked species are hunted as the cost of hunting them declines compared with higher ranked species (Hames and Vickers 1982, Smith et al. 1983). The addition of new species and increasing frequency of less preferred species in a hunter's prey profile are a response to a decline in abundance of the preferred species (Rowcliffe et al. 2005, Parry et al. 2009a). The factors relating to reduced mean prey weight drive the reduced abundance of preferred species.

In addition to the mean prey weight, the capture per unit of effort (CPUE) for preferred species can be used to evaluate the variation in the abundance of these species. However, this indicator uses a different set of data, the biomass of preferred species and the time spent hunting. This indicator is supported by the behavior of hunters who have to increase their effort in areas with depleted populations of preferred large-bodied species to achieve the required meat return rates (Souza-Mazurek et al. 2000, Sirén et al. 2004, Parry et al. 2009a, b). Therefore, factors that relate to a decrease in CPUE of preferred species cause the reduced abundance of these species.

This research identified the drivers of game variation across villages at the regional level and at the village level using indicators of wildlife status. I developed indicators based on ecological models using hunting data from 35 Kaxinawá and Katukina villages from 8 ILs in Acre, Brazilian Amazonia, to assess different wildlife responses to anthropogenic disturbances. The potential drivers were land use change, hunting pressure, and socioeconomic features of indigenous communities.

METHODS

Data collection
The Pano monitors from 35 villages (33 Kaxinawá and 2 Katukina) in 8 ILs (7 Kaxinawá and 1 Katukina) collected data. Between 2004 and 2009, monitors recorded data for hunting effort (number of hunters and time spent hunting) and success (species, weight, and straight distance in minutes from the point of capture to the village). Socioeconomic data, e.g., population, number of hunters and employees, permanent goods, and livestock, were collected via household interviews in all villages in 2004 and 2005 and were updated in 2009 (Constantino et al. 2012a). Deforestation in each village was calculated for the hunting territory (5-km radius from the village center) using PRODES data for Brazil. Deforestation around villages was estimated to be zero at the Peruvian border near the four villages located in the Kaxinawá/Ashaninka do Rio Breu IL; this is one of the most remote and unchanged forests in Peru (Oliveira et al. 2007).

Indicators of wildlife status
According the aforementioned ecological models, I assessed wildlife status in response to anthropogenic disturbance across the 35 villages using 4 indicators. (1) The mode of straight hunting distance from the settlement was assessed using the central place forager model. I used the Gaussian kernel density estimator to estimate the distances (Gitzen et al. 2006). (2) The species richness of wildlife assemblages that are sensitive to habitat disturbance and hunting pressure was determined. I calculated the sensitive-

species richness by combining the number of sensitive hunted species always pursued by the Pano, thereby limiting the analysis to selectively hunted species (Weinbaum et al. 2013). (3) The mean prey weight of hunted animals was obtained from the optimum foraging theory. A fourth indicator was based on data of 21 villages: I used the CPUE (with biomass) for animals of preferred species, using the optimum foraging theory to indicate overall variation in species abundance.

I conducted pairwise Pearson's correlations between the four indicators of wildlife status to assess the differences in information. Data from all indicators were normally distributed. No indicators correlated with monitoring effort ($0.1 < r < 0.2$; $p > 0.05$), except for the sensitive-species richness. The sampling effort varied between the villages; therefore, I used Mao Tao analysis to correct the differences. The results for the multiple linear regressions using samples corrected for the number of sensitive species were similar to the results for the uncorrected species richness. Therefore, I assumed no effect of sampling on the observed variation and used the uncorrected sensitive-species richness.

Analysis of drivers of wildlife variation
For each of wildlife status indicators, I used multiple linear regression to detect the drivers of wildlife status across villages. The explanatory variables relating to hunting pressure, land-use change, and socioeconomic condition of Pano villages were transformed (log_{10} or square root) when required to achieve normal distribution. I conducted pairwise Pearson's correlations between the 12 continuous explanatory variables before running the regression models to avoid multicolinearity. Variables with fewer correlations and lesser uncertainty were selected. The continuous variables used to build full models were the density of indigenous people in a 5-km radius, village age, indigenous population in the village (hunting pressure), animal unit (socioeconomic condition), and log_{10} deforested area in a 5-km radius (land use). The nominal variable "road presence" was also used in the model.

I selected the minimal model for each wildlife indicator, excluding unrelated explanatory variables ($p > 0.1$) from the full model through backward stepwise elimination. An analysis was also performed of all possible subset models checking for the corrected version of the Akaike information criterion (considering a variation of 2.0 as significant), the consistency in variables' entrance in models, and the signals of estimates. I selected all the possible final models for each response variables.

To verify the spatial dependence of the wildlife status indicators across villages and the residuals of the minimal regression models, I used the Moran's I test for each kilometer between 7 and 15; smaller distances had fewer than 28 points and could not be tested for spatial dependence. Reduced sample size prevented testing the spatial dependence of CPUE.

RESULTS

Pano hunter's prey profile
The Kaxinawá and Katukina communities hunted 9109 animals comprising 54 wildlife species or higher taxa (e.g., Dasypodidae), among which at least 8 are highly sensitive to human disturbance and 2 are nationally threatened (Table 1). The preferred, large-bodied vertebrates were the most hunted (55.7%) and provided the largest amount of meat (83.95%). Of the hunted animals, 32% were sensitive species and contributed to almost half of the consumed meat (46.25%). Ungulates, were the most hunted in almost all villages, particularly the white-lipped peccary (*Tayassu pecari*), which provided up to 60% of wild meat in some villages. Species of secondary preference that were frequently hunted included paca (*Cuniculus paca*), agouti (*Dasiprocta fuliginosa*), armadillos (Dasypodidae), capuchin monkey (*Cebus* sp.) , squirrels (*Sciurus* sp.), and coati (*Nasua nasua*), but they only provided 14% of the total consumed meat. Although low-ranked species represent the higher number of hunted species, they were rarely hunted (9.6%) and provided only 2% of the total meat. Only 0.1% of all animals were threatened and provided only 0.2% total meat consumed.

Drivers of wildlife variation across Pano villages
The indicators of wildlife status, such as the mean prey weight, sensitive-species richness, and CPUE of preferred species, significantly correlated with each other. In turn, the mode distance of preferred animals from the village did not correlate with other indicators, suggesting that a different process caused its variation (Table 2).

The 51% variation in mean prey weight across villages in the single significant minimal model was because of deforestation and presence of roads (Tables 3 and 4). Clearing the first 10 hectares of forests near villages resulted in prey weighing 3 kg less. However, the rate of prey size reduction decreased as deforestation increased. Hunters in roadside villages harvested animals that averaged 6 kg more than those of riverside villages. The variation in CPUE of preferred species and sensitive-species richness in the minimal models was explained by deforestation, respectively accounting for 30% and 59% of the variation (Tables 3 and 4). Losing the first 10 hectares of forest in a 5-km radius around the villages resulted in the absence of more than 2 sensitive species in the prey profiles, but the rate of species absence decreased as deforestation increased. Only hunters from four villages in one IL hunted all sensitive species. In terms of hunting success, hunters caught less meat with the same effort in deforested areas. After the first 10 hectares of the forest were cleared near villages, hunting decreased to 0.65 kg/ha, which further decreased as deforestation increased. No explanatory variable proxy for hunting pressure was related to mean prey weight, CPUE, or sensitive-species richness. Conversely, the single significant minimal regression model explained that 30% of the variation in hunting distance of preferred animals hunted away from villages was due to hunting pressure, represented by the density of indigenous people and road presence (Tables 3 and 4). According to this model, an addition of 100 Pano people within 5 km, regardless of whether they belonged to the same village, or a combination of population growth between neighboring villages, would result in Pano people hunting most of their preferred prey approximately 230 m farther away. Hunters in roadside villages hunted animals approximately 1715 m farther away from the village center than hunters from riverside villages. Deforestation was not associated with hunting distance from the village. No indicator of wildlife variation was related with the socioeconomic factors analyzed.

Table 1. Wildlife species hunted by Pano communities in Acre, Brazilian Amazon, during this study. Preferred species (1), secondary species (2), and low-ranked species (3) are indicated according to Cunha and Almeida (2002) and Constantino et al. (2008). For some analysis in this study we grouped 2 and 3 representing species of secondary preference.

Scientific name	Common name	No. of animals	Weight of animals	Preference	Sensitive species
Tayassu pecari	White-lipped peccary	1335	24,455.6	1	X
Pecari tajacu	Collared peccary	1267	16,049.0	1	
Mazama americana	Red brocket deer	695	15,381.8	1	
Tapirus terrestris	Lowland tapir	68	6786.0	1	X
Alouatta seniculus	Howler monkey	539	3343.5	1	X
Chelonoides denticulate	Yellow-footed tortoise	536	3161.3	1	X
Ateles chamek	Spider monkey	258	1937.5	1	X
Caiman sp.	Caiman	177	1614.5	1	
Lagothrix lagotricha	Woolly monkey	72	536.2	1	X
Mitu tuberosum	Razor-billed currasow	96	457.1	1	X
Mazama gouazoubira	Brown brocket deer	10	136.0	1	
Pipile cujubi	Piping guan	18	37.5	1	X
Cuniculus paca	Paca	524	3933.1	2	
Dasypodidae[†]	Armadillo	427	2368.5	2	
Dasiprocta fuliginosa	Agouti	411	1812.2	2	
Nasua nasua	Coati	313	1450.8	2	
Cebus apela	Brown capuchin	266	1031.1	2	
Sciurus sp.[‡]	Squirrel	636	657.5	2	
Penelope jacquacu	Spix's guan	228	421.7	2	
Tinamus guttatus	Large tinamous	200	326.1	2	
Hydrochaeris hydrochaeris	Capybara	13	291.0	3	
Psophia leucoptera	Pale-winged trumpeter	132	251.3	2	
Dinomys branickii	Pacarana	31	236.0	3	
Pithecia sp.[§]	Saki monkey	68	203.0	3	
Myoprocta pratii	Acouchi	162	183.8	3	
Cebus albifrons	White-fronted capuchin	45	162.5	3	
Aotus nigriceps	Night monkey	88	119.8	3	
Priodontes maximus[#]	Giant armadillo	4	95.0	3	
Myrmecophaga tridactyla[#]	Giant anteater	4	87.0	3	
Ara sp.[¶]	Macaw	53	74.9	3	
Saimiri sciureus	Squirrel monkey	53	60.7	3	
Tinamus tao	Grey tinamous	24	55.8	2	
Callicebus moloch	Titi monkey	44	53.1	3	
Saguinus sp.[ǀ]	Tamarin	53	44.2	3	
Amazona sp.[¶]	Parrot	34	31.8	3	
Crypturellus cinereus	Small tinamous	30	21.6	3	
Ramphastos sp.[¶]	Toucan	26	20.5	3	
Ortalis guttata	Speckled chachalaca	23	16.8	3	
Crypturellus soui	Little tinamous	25	16.3	3	
Rallidae[¶]	Rail	23	15.0	3	
Coendou sp.	Quandu	3	15.0	3	
Tinamous major	Small tinamous	15	12.5	2	
Crypturellus sp.3	Small tinamous	15	11.9	3	
Crypturellus sp.2	Small tinamous	18	11.6	3	
Odontophorus sp.[¶]	Wood quail	11	6.9	3	
Jabiru mycteria	Jabiru	1	6.0	3	
Harpia harpyja	Harpy eagle	1	5.0	3	
Columbidae[¶]	Dove	14	4.3	3	
Anatidae[¶]	Duck	3	4.0	3	
Accipitridae[¶]	Kite	3	2.5	3	
Tupinambis teguixin	Common tegu	2	2.0	3	
Psarocolius sp.	Oropendola	5	1.9	3	
Psittacidae[¶]	Macaw	5	1.9	3	
Pteroglossus sp.	Aracari	2	0.9	3	
Total		9109	88,023.3		

[†]*Dasypus novemcinctus*, *Dasypus kapplery*, *Cabassous unicinctus*.
[‡]*S. ignitus* and *S. spadiceus*.
[§]*P. irrorata* or *P. monachus*.
[ǀ]*S. imperator*, *S. fusicolor*, *S. melanoleucus*, and possibly *S. mystax*.
[¶]taxa containing more than one species but with uncertain identification.
[#]Threatened species according to the International Union for Conservation of Nature (http://www.iucn.org/redlist).

Table 2. Pearson correlation matrix between simple indicator variables of wildlife depletion in Pano villages (upper) and excluding roadside villages (bottom) in Acre, Brazilian Amazon.

Indicators of wildlife status	Mean prey weight	CPUE preferred species	Number of sensitive species
Mean prey weight	1		
CPUE of preferred species	0.83**	1	
	0.82**		
Number of sensitive species	0.54*	0.62**	1
	0.73**	0.59**	
Mode distance of preferred	0.33	0.00	-0.04
species hunted from the village	0.19	0.14	0.25

CPUE indicates capture per unit of effort.
*p < 0.01;**p < 0.05.

Table 3. Backward stepwise regression models for all response variables at the village level.

Response variable	R^2_{adj}	DF	F ratio	p	n
Mean prey weight	0.51	2	18.62	< 0.001	35
CPUE preferred species	0.30	1	9.67	0.006	21
Sensitive species richness	0.59	1	49.78	< 0.001	35
Mode distance of preferred species hunted from the village	0.30	2	8.42	0.001	35

CPUE indicates capture per unit of effort; DF, degrees of freedom.

These results separated the effects of indigenous hunting and deforestation near villages in two different processes driving wildlife variation. Nevertheless, it was not possible to separate the effects of deforestation and indigenous hunting from the effects of nonindigenous hunting. No information was available on nonindigenous hunting pressures around or encroaching onto IL.

Human-sensitive species were consistently absent in hunters' prey profiles for several villages, particularly the piping guan (*Pipile cujubi*), razor-billed curassow (*Mitu tuberosum*), wooly monkey (*Lagothrix lagotricha*), spider monkey (*Ateles chamek*), and lowland tapir (*Tapirus terrestris*). Villages that hunted four or less sensitive species never hunted the piping guan, razor-billed curassow, and tapir, whereas only one hunted the spider monkey and four hunted the wooly monkey. Villages alongside roads did not hunt large monkeys or birds. However, the howler monkey (*Alouatta seniculus*), the yellow-footed tortoise (*Chelonoides denticulate*), and the white-lipped peccary were hunted in varying intensities in most villages. Other preferred large-bodied species resilient to anthropogenic disturbances, such as the collared peccary (*Pecari tajacu*) and the red brocket deer (*Mazama americana*), were hunted in all villages.

Spatial dependence of indicators across Pano villages
The mean prey weight and sensitive-species richness across villages were autocorrelated and increased with distances between 7 and 15 km (0.19 < r < 0.29; p < 0.05). The hunting distance from the village was not autocorrelated (-0.04 < r < 0.13, p > 0.1).

The residuals of the minimal regression models were not spatially dependent. The deforestation explanatory variable correlated with the Moran's I results for mean prey weight and sensitive-species richness analysis.

Table 4. Explanatory variables included in the final regression models after stepwise and supervised selection.

Response variable Parameters	Estimate	SE	t Ratio	Prob > t
Mean prey weight				
Intercept	18.90	1.66	11.38	< 0.001
Log deforested area	-3.36	0.61	-5.49	< 0.001
Road presence	3.02	0.64	4.72	< 0.001
CPUE of preferred species				
Intercept	2.84	0.46	6.13	< 0.001
Log deforested area	-0.65	0.21	-3.11	0.006
Sensitive species richness				
Intercept	10.51	0.86	12.24	< 0.001
Log deforested area	-2.68	0.38	-7.06	< 0.001
Mode distance of preferred species to village center				
Intercept	72.76	16.71	4.35	< 0.001
Road presence	31.50	10.71	2.94	< 0.01
Density of indigenous people	6.60	2.83	2.33	0.03

CPUE indicates capture per unit of effort; Prob, probability; SE, standard error.

DISCUSSION

Wildlife status across Pano villages
Even after several decades of wildlife harvesting and current intensive hunting pressure in a lightly deforested region, most Kaxinawá and Katukina communities still have preferred large-bodied species as their main meat source. The Pano hunt more ungulates, similar to Amazonian communities where game is not severely depleted (Alvard et al. 1995, Robinson and Bodmer 1999), including other Kaxinawá in Peru (Navarro 2004). This overall pattern suggests that wildlife is not depleted; even threatened species are rarely hunted because hunters prefer other species. Nonetheless, there was variation in wildlife status across villages.

Some villages substituted their main hunting for ungulates with hunting for smaller and less preferred but resilient species, which created a gradual shift in the mean prey weight, indicating depleted wildlife assemblages. In particular, villages located in the ILs of Kaxinawá da Praia do Carapanã and Baixo Rio Jordão have drastically changed their prey profile, including lots of animals of less preferred species. This pattern can be because of several factors, including persistent hunting (Iwamura et al. 2014), and is observed across multiple sites in a protected area in the same region (Ramos 2005) as well as at larger tropical spatial scales (Jerozolimski and Peres 2003, Fa and Brown 2009). Another indication of localized game depletion is the absence of razor-billed curassow, piping guan, spider monkey, wooly monkey, and tapir in prey profiles from several villages. Except for the four villages in the IL of Kaxinawá/Ashaninka do Rio Breu, at least

one species was absent in the prey profile of all the villages. In the Neotropics, these species are the most sensitive to anthropogenic disturbance and are likely to be the first locally extirpated animals, being consistently absent among hunted species at single depleted sites (Daily et al. 2003, Parry et al. 2009*b*) and across sites in the Amazon basin (Peres 2000). In addition, the variation of meat return rate across Pano villages indicates a decline in preferred game abundance, particularly ungulates. This was also observed in Peruvian communities where the decline in abundances of peccaries and tapir over 10 years resulted in a decline in the meat return rate (Bodmer et al. 1997). As a result, Pano living in depleted villages changed their social and cultural practices. They frequently consumed small livestock or fish and increased their purchase of meat from the markets, like the two villages in the Katukina do Campinas and the one in the Kaxinawá do Igarapé do Caucho ILs(Lima 2001, Constantino et al. 2012*b*).

Considering the optimal foraging theory, the CPUE for Pano hunters declined because of a change in assemblage structure, which was because of reduced abundances of preferred species and reduced species composition due to extirpation of some sensitive species. However, these indicators do not assume the underlying cause of wildlife variation a priori (Rist et al. 2009). Therefore, several factors could be driving wildlife depletion and status variation across the villages.

Conversely, the hunting distance from the village assumes that hunting pressure is the main driver of wildlife variation, which conforms to the premises of the central place forager model (Levi et al. 2009). Hence, the pattern observed across Pano villages could be related to indigenous hunting pressure. However, the effect of hunting on animal populations is not defined. If it affects population abundances, the increase in hunting distance from the village is related to reduced abundance of tropical game (Hill et al. 1997, Ohl-Schacherer et al. 2007) and lower meat return rate in other indigenous groups in the Amazon (Alvard et al. 1997, Sirén et al. 2004). These associations were not observed across Pano villages, where preferred animals were hunted farther away in villages with higher hunting pressures; however, wildlife assemblages were not considerably depleted.

Regional effects of deforestation on wildlife
The regression analysis results suggest that deforestation and indigenous hunting induced different responses in wildlife species, whereas the presence of roads exacerbated the effects of both drivers. Pano hunting and deforestation had different effects on game species because there were no associations between these explanatory variables, no correlation between the wildlife status indicator "hunting distance from the village" and the other three indicators, the models that explained the variation of wildlife status across villages differed, and there were different patterns of spatial dependence of indicators.

Across Pano villages, deforestation depleted wildlife by significantly inducing shifts in large game abundances and by declines in sensitive-species richness, leading to an increase in the effort needed to obtain meat from preferred species. This driver apparently affects wildlife at larger ecological spatial scales, given the autocorrelation of indicators and deforestation index across Pano villages. The rate of loss of two species related to deforestation across Pano villages is similar to the rate of species loss due to forest cover loss in a nearby region in Amazonia (Ochoa-Quintero et al. 2015).

Forest cover loss has an important influence in the depletion of tropical wildlife; it has been used to estimate future reductions in population range and size and species extinction (Kinnaird et al. 2003; Soares-Filho et al. 2006). Despite local hunting, regional deforestation has caused the loss of many game species across forest fragments in Mexico (Urquiza-Hass et al. 2009) and the Brazilian Amazonia (Michalski and Peres 2007). Nevertheless, in Amazonia, hunters catch more ungulates in primary forests in heterogeneous landscapes in the eastern region (Parry et al. 2009*b*), whereas ungulates hunted by local people declined in response to increasing deforestation density in another protected area in Acre (Ramos 2005).

Habitat loss and land-use practices inside Pano ILs corresponded to slash-and-burn agriculture and small-scale pastures bordered by forests prone to fire and fragmentation (Norris et al. 2008). In Amazonia, deforestation and associated processes such as fire (Barlow and Peres 2006) and fragmentation (Michalski and Peres 2007) have directly affected large game species by reducing their population and home range, and have indirectly affected resources, changing climate, and other ecological interactions (Laurance et al. 2011, Michalski and Peres 2007, Laurance and Useche 2009). Deforestation, fire, and fragmentation are related to the nonrandom extirpation of large frugivorous primates, birds, and the lowland tapir; whereas other game species may be resilient because of their generalism (Peres 2000). Therefore, these processes may be associated with deforestation that has directly depleted game species at the regional level in Pano ILs.

Local effects of indigenous hunting on wildlife
The Pano hunting pressure, in turn, was related to the variation in wildlife distribution near villages, but it did not cause game depletion at the regional level. Populations of preferred game species moved away from villages with more hunters and more wildlife consumption, which consequently changed the hunting distance from the village. This process affected wildlife responses across indigenous villages in Acre operating at the local level, closer than 7 km, and only within the indigenous hunting territory. The spread of animals away from the village center because of hunting pressure was reported for tropical areas where hunters go for one-day-walking, subsistence hunting trips (Stearman 1990). For example, local hunting was not responsible for regional wildlife depletion in several tropical forest regions, such as Mexico (Urquiza-Hass et al. 2009) and Africa (Fa et al. 2005). The hunting effect is local and does not extirpate primate populations at a regional level, particularly if the area is surrounded by underexploited forest (Levi et al. 2009).

The relatively small and localized effect of indigenous hunting on wildlife variation may be related to ecological factors as well as to the design of hunting research. Major declines in mammal densities due to hunting are more likely to occur in previously unhunted sites than in those already exploited because hunters in unaltered forests usually represent the only anthropogenic disturbance to game populations. A selective filter may operate after the initial hunting pressure, whereby tolerant species and population abundances remain stable until other processes begin adding to the negative effect of hunting (Cowlishaw et al. 2005, Fa and Brown 2009, Iwamura et al. 2014). The Pano people hunt in a region affected by centenary intense hunting, but major land conversion has only occurred recently. Some time ago, Pano hunting may have strongly affected current wildlife communities,

but now they are mainly affected by deforestation. In addition, when hunting pressure is concentrated in a few areas, game populations in larger forest areas may function as a source of individuals for other game populations in adjacent disturbed sink areas (Woodroffe and Ginsberg 1998). Therefore, undisturbed areas near Pano villages may be a source of animals (Constantino et al. 2008), whereas Pano villages surrounded by depleted areas may not have the wildlife population to be a source of animals for hunting territories (Hansen and DeFries 2007).

Severe impacts of hunting were discovered based on meta-analyses of studies with decades of differences, conducted at continental or intercontinental scales (Robinson and Bennett 2004; Fa and Peres 2001) using a small sampling effort but including hunters from different cultures (Peres 2001, Jerozolimski and Peres 2003, Fa et al. 2005). Because of the present study design, the data had little variation in temporal, spatial, and cultural aspects across villages, which could introduce uncertainties (Redford and Robinson 1987, Lupo and Schmitt 2005, Peres and Palacios 2007). The results from Pano ILs clearly differentiated the effects of indigenous hunting and deforestation on wildlife, which are difficult to distinguish (Fa and Brown 2009, Parry et al. 2009b). Because most tropical forest game species sensitive to hunting are also sensitive to habitat loss (Michalski and Peres 2007, Laurance et al. 2012) and fire effects (Barlow and Peres 2006), it is hard to clearly delimit hunting pressure (Rist et al. 2008).

Moreover, the spatial scale of research can alone explain much of the wildlife variation in response to habitat loss (Dumbrell et al. 2008) and human occupancy (Pautasso 2007). Pano hunting had only local effects on wildlife, which may have been suppressed by landscape differences in deforestation. Robinson and Bodmer (1999) claim that indigenous hunting has been sustainable at the landscape level, whereas many species must have been locally extirpated by hunting. Sirén et al. (2004) found that at the local scale a model of hunting sustainability indicated overharvested populations, whereas at regional scales, populations would be sustainably harvested. At a spatial scale similar to that of the present research, species richness is expected to have no relationship with human presence (Pautasso 2007), and the effects of deforestation exceed the effects from local hunting of game animals (Michalski and Peres 2007, Urquiza-Hass et al. 2009).

The effect of roads on indigenous hunting

In Amazonia, roads have affected hunter-prey systems by changing hunter behavior and prey ecology (Espinosa et al. 2014). Roads had a dual effect on Pano hunting systems. First, they exacerbated the negative effects of indigenous hunting on hunting distance from roadside villages, probably through their associated disturbances (Laurance et al. 2006, Fahrig and Rytwinski 2009) and by increasing poacher access to Pano ILs (Lima 2001). Second, roads are related to a shift in roadside village behavior toward a market-dependent diet. Because ammunition is expensive in the small cities in Acre, sometimes more expensive than livestock meat, the Pano prefer not to shoot small species that have low meat return rates. Hence, in Amazonia (Redford 1993, Jerozolimski and Peres 2003, Sirén and Wilkie 2014), Pano hunters substitute livestock meat for hunting small species and restrict their hunting to large mammals, even when wildlife is depleted. Therefore, CPUE and mean prey weight in these villages

reflect human processes more than prey abundances (Ling and Milner-Gulland 2006), and hence, these should not be used to infer wildlife status. Nonetheless, these results are important for understanding the effects of roads on indigenous community behavior and society.

Implications for conservation of game species and indigenous well-being

Discerning the effects of different drivers of change in game populations is crucial for determining correct conservation action and mitigating the main threats to wildlife. This research indicates a relatively higher importance of deforestation and associated factors than indigenous hunting for regional game depletion in Amazonia. These findings are alarming because of the negative consequences of deforestation to game species even in well-conserved tropical forest regions. Wildlife conservation, therefore, should target this threat instead of blaming subsistence hunting for the massive loss of diversity. Nonetheless, indigenous people should be aware that their hunting pressure leads to local wildlife depletion and consequently affects their communities. The effect of roads on indigenous societies and game populations must be taken into account when conservation is designed on a large scale. In this case, protecting the surroundings of these protected areas and opposing encroachment would help to guarantee the sustainability of wildlife for use by indigenous people and their integrity and autonomy as a society.

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