



Research Article

Manioc Losses by Terrestrial Vertebrates in Western Brazilian Amazonia

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ABSTRACT Tropical biodiversity benefits humanity. However, the costs of conserving topical biodiversity are largely borne by local communities. The damage caused by wild animals to human-cultivated plants (crop-raiding) in tropical ecosystems directly affects the livelihoods of local agriculturalists, which erodes their support for conserving biodiversity. We used data collected between 2013 and 2015 from 132 camera-trap stations and responses from 157 interviewees representing 47 semi-subsistence communities to quantify and contextualize terrestrial vertebrate crop-raiding damage to manioc (*Manihot esculenta*) agricultural fields (i.e., roçados) in the Médio-Juruá region of western Brazilian Amazonia. The 5 vertebrate species identified by respondents as the most damaging crop raiders were agoutis (*Dasyprocta fuliginosa*), collared peccaries (*Pecari tajacu*), pacas (*Cuniculus paca*), red brocket deer (*Mazama americana*), and spiny rats (family Echimyidae). These species were frequently detected by camera traps in early-successional forests. Respondents reported mean manioc stem losses to crop raiders of 7.3%/roçado. Proportional losses of more palatable manioc varieties were approximately 3 times higher than more phytochemically defended varieties, further constraining crop choice. Respondents estimated that in the absence of active crop-raider suppression, overall losses would have been 73.9%/respondent/annum, and therefore invested substantial effort in crop protection. Small communities, already economically disadvantaged by isolation from the material, service, and information monopoly of urban centers, were most affected by crop raiding. Although, the most damaging crop raiders are ideal candidates for sustainable subsistence hunting, we found only weak evidence of positive opportunities for agriculturalists to hunt crop raiders to compensate for crop losses. Our study indicated that crop raiding may continue to exacerbate the challenges inherent in tropical agriculture and represents a significant forest ecosystem disservice. © 2018 The Wildlife Society.

KEY WORDS Amazonia, camera trapping, conservation, crop raiding, human-wildlife interactions, hunting, local perception, subsistence agriculture, wildlife damage management.

In the context of increasing anthropogenic pressures on the global biota, reconciling the needs of rural development with biodiversity conservation has never been more pressing. Semi-subsistence rural dwellers in tropical forests live in the most biodiverse places worldwide (Gaston 2000) but are some of the world's monetarily poorest people (Sachs et al. 2001). Rural tropical communities are frequently called on by the international conservation community to protect their megadiverse surroundings (Mittermeier et al. 1998). Thus, the local agriculturalist communities often incur the costs of conserving biodiversity, whereas the benefits accrue internationally (Balmford and Whitten 2003). These socioeconomic costs and ecosystem disservices must therefore be recognized

when extolling tropical forest dwellers to coexist with and preserve biodiversity (Zhang et al. 2007).

The damage caused by vertebrate species of conservation concern including chimpanzee (*Pan troglodytes*) and Asian elephant (*Elephas maximus*) in the African and Asian tropics (Sukumar 1990, Naughton-Treves 1998) to human-cultivated plants (i.e., crop raiding) directly affects the livelihoods of local agriculturalists, which erodes their support for conserving biodiversity (Hill 2000, 2017). Crop raiding affects already precarious livelihoods through decreased yields and increased labor to protect crops (Gillingham and Lee 2003).

Globally important staple food crops depredated by wildlife include manioc (*Manihot esculenta*), maize (*Zea mays*), and Asian rice (*Oryza sativa*). Hill (2000) and Naughton-Treves (1998) estimated manioc crop losses in Uganda of 9.0% and 6.8%, respectively. Nchanji (2002) estimated manioc losses of 2.4–15.1% in Cameroon.

Manioc is the staple source of carbohydrates in Brazilian Amazonia and much of the humid tropics, where agriculturalists confront high rainfall, competition from vigorous weeds,

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high pest burdens and nutrient-poor soils with high levels of aluminium toxicity (Fraser 2010). Manioc plants produce multiple starchy tubers, tolerate nutrient-poor tropical soils, and are pest-resistant. Manioc farming often represents the only source of carbohydrates and income for semi-subsistence communities in the lowland Amazon (Newton et al. 2012). The main varieties of manioc are high-cyanide bitter manioc, and low-cyanide sweet manioc (Peroni et al. 2007). Sweet manioc requires far less intensive processing to render it palatable and the proportion of sweet manioc grown for local consumption is higher than that of bitter manioc.

Crop protection measures deployed by agriculturalists are time and labor intensive and include leaving some land fallow, building fences, guarding and patrolling fields, overnight vigils, and deploying snares, traps, poison bait, guard dogs, guard huts, fireworks, noisemakers, and bells to chase or otherwise repel undesirable animals (Naughton-Treves 1998, Hill 2000, Gillingham and Lee 2003, Linkie et al. 2007). In extreme cases, high crop-raiding rates result in farm abandonment (Sitati et al. 2005).

These livelihood effects may induce tropical agriculturalists to engage in pre-emptive hunting suppression and retaliatory killing of crop-raiding species (Kendall 2011, Hockings and McLennan 2016). These species, especially if they are slow-reproducing, may be vulnerable to overharvesting, and such culling may result in local extinctions (Redford 1992, Peres 2000). Hunting pressure, which influences the density of large tropical forest mammals, is highest in areas close to human settlements (Sirén et al. 2004). Overharvesting may be exacerbated in regions where wild food resources have been reduced through anthropogenic habitat disturbance or where forest vertebrates are attracted to palatable and high-calorie human crops (Yamada and Muroyama 2010). This potentially could create an ecological trap, whereby forest vertebrates succumb to high mortality by preferentially using anthropogenic areas (Battin 2004). The extirpation of these species may in turn cause widespread detrimental ecological effects, disrupting plant dispersal and recruitment dynamics (Wright 2003, Peres et al. 2016). The aforementioned effects on human livelihoods and populations of forest vertebrates underlie the need to balance rural development and biodiversity conservation (Agrawal and Redford 2006). This results in polarized support for fortress conservation on one hand (Hutton et al. 2005) and degazettement of protected areas on the other (Mascia and Pailler 2011).

Description and quantification of crop raiding in the neotropics is lacking (Estrada 2006). Naughton-Treves et al. (2003) reported that although crop losses were higher in remote areas of Tambopata, southern Peru, they were compensated by higher game meat harvest. Agriculturalists therefore experienced net livelihood benefits from coexisting with intact faunal assemblages in such locations. Pérez and Pacheco (2006) reported approximately 16% losses to crop raiders across 3 crop types in Bolivia.

Interview and camera trap techniques have been used separately to study the social and ecological dimensions of crop raiding (Hill 2000, Krief et al. 2014) but are rarely combined. Camera traps are increasingly used in biodiversity

surveys (Rowcliffe and Carbone 2008) because they have proved reliable compared to other survey methods (Benchimol and Peres 2015). Camera traps provide only a spatio-temporal snapshot, are expensive, are prone to failure and theft in the tropics, and when used to produce relative abundance estimates, may be unreliable when there are significant habitat-induced detectability biases (Sollmann et al. 2013). Interviews can distill decades of local knowledge and are relatively inexpensive to conduct. Interview reliability can, however, be questioned, given the sensitive nature of the topic (Gavin et al. 2010) and the propensity of respondents to over or underestimate crop damage by the species (Naughton-Treves 1998).

To provide better information regarding the effects of crop raiding on local communities and wildlife populations in the neotropics, we studied the livelihood effects of crop raiding for semi-subsistence agriculturalists in the Juruá region of western Brazilian Amazonia. We used data collected from local interviews with agriculturalists to 1) identify the species that use manioc fields (roçados) and those known to raid crops; 2) quantify perceived rates of crop-raiding damage to roçados; 3) determine if crop raiding impinges upon choice of manioc cultivar; 4) contextualize the relative importance of this damage in terms of livelihoods and local response strategies; 5) assess the degree to which the livelihood effects of crop raiding are offset by opportunities to hunt crop raiders; and 6) determine the anthropogenic and ecological correlates of losses to crop raiders. We used camera-trap data to determine the species composition in successional forests adjacent to roçados, and the anthropogenic and ecological factors associated with crop raider and non-raider metabolic biomass.

STUDY AREA

We conducted our study between April and August 2013–2015, within and around the Uacari Sustainable Development Reserve (623,929 ha) and the Médio Juruá Extractive Reserve (250,192 ha) in the Médio Juruá region of western Brazilian Amazonia. This region is bisected by the Juruá River, the second-largest white-water tributary of the Amazon (Fig. 1).

The region had a wet tropical climate and experienced a mean annual temperature of 27.1°C and an average annual rainfall of 3,679 mm. The rainiest period was between December and May, presaging an annual 12-m flood pulse (Hawes and Peres 2016). The region lay between 65 m and 170 m above sea level, with a 15–20-km wide floodplain encompassing each side of the Juruá River. The floodplain covered 20% of the region and was characterized by sediment-enriched, less floristically diverse white-water floodplain forest (locally várzea). Terrain became higher and more undulating farther from the river, and was characterized by unflooded forest (locally terra firme). Vertebrate community structure differed markedly between várzea and terra firme forest types (Emmons 1984).

The terrestrial ecosystem was dominated by highly diverse lowland moist deciduous forest, >98% of which was undisturbed contiguous primary forest with no apparent

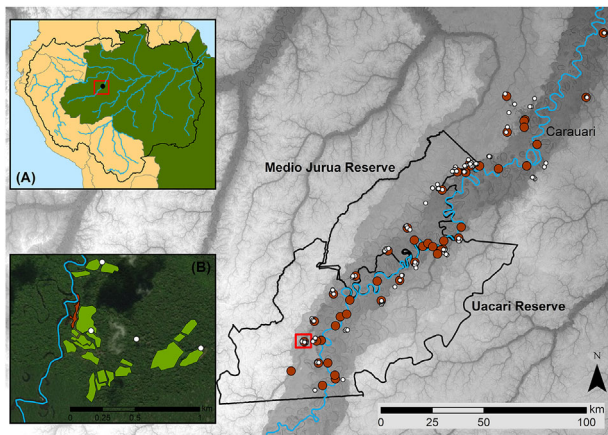


Figure 1. The Médio-Juruá study region, Brazilian Amazonia (2013–2015). Inset A shows the continental scale location of the study area, with major rivers (blue lines) and the main urban center of Carauari (black dot). The main panel (red square in A) shows the Médio-Juruá study region, where the background represents elevation above sea level. Low elevation areas (dark gray) adjacent to the river represent seasonally flooded (várzea) forests. Sustainable-use forest reserves are outlined in black and the Juruá River is indicated by a blue line. Brown circles indicate the 47 surveyed communities or urban neighborhoods, and white dots indicate the 132 camera-trap deployment sites. Inset B (red square in main panel) is an example of a surveyed local community, where the household cluster area is delimited by a brown polygon; a tributary of the Juruá (Anaxiqui River) is indicated by a blue line; and the background is a basemap consisting largely of primary forest. Second-growth areas (capoeiras) of mostly upland (terra firme) forests are indicated by green polygons and camera-trap deployment sites are indicated by white dots.

history of clearance. Terrestrial mammals considered to be manioc crop raiders inhabiting the area included pacas (*Cuniculus paca*), agoutis (*Dasyprocta fuliginosa*), acouchis (*Myoprocta pratti*), spiny rats (family Echimyidae), red and gray brocket deer (*Mazama americana* and *M. nemorivaga*), and collared and white-lipped peccaries (*Pecari tajacu* and *Tayassu pecari*).

The region is inhabited by Portuguese-speaking former rubber-tapper semi-subsistence communities of mixed-descent (i.e., ribeirinhos). The nearest towns were Carauari and Itamarati, which were located 88 and 120 fluvial km from the reserve boundaries, respectively. In the absence of regular and comprehensive demographic censuses, the number of permanent private households (Brazilian Institute of Geography and Statistics (IBGE) 2007–2009) was the *de facto* regional population metric, with a mean household size of between 5 and 6 individuals. There were an estimated 5,397 households distributed across 65 local communities and 19 urban neighborhoods throughout the study region, over 83% of which resided in the city of Carauari (IBGE 2007–2009).

Communities grew manioc in swidden agricultural fields called roçados. Manioc was grown clonally from single-stem cuttings. During a cultivation cycle, manioc may be grown year-round, and was typically harvested between 6 and 24 months after being planted. We follow local convention in using the number of manioc stems as the unit of agricultural production, rather than the number of tubers or the weight of processed manioc flour (i.e., farinha).

Roçados were generally active for 3 cultivation cycles or 4 years, until weed encroachment and declining soil fertility force their abandonment (Unruh 1988). These secondary forests (i.e., capoeiras) were left to undergo successional regrowth until standing biomass and soil nutrient loads were sufficient to permit re-clearing. This process created a mosaic of stands under different successional stages around village settlements, with shorter-rotation roçados generally closer to the community (Coomes et al. 2000).

METHODS

Camera Trapping

We used Bushnell Trophy-Cam, and Reconyx HC500 Hyperfire camera-trap models (Bushnell, KS, USA; Reconyx, WI, USA). We collected camera-trap data between April and August 2013–2015, avoiding the period of heaviest rainfall during which camera traps are often damaged. We deployed 132 camera-trap stations according to a standardized protocol adapted from the Tropical Ecology Assessment and Monitoring (TEAM) network (TEAM 2008). We did not repeat deployments in the same locations and we pooled data from all 3 years of deployments.

Mean functioning camera-trap nights per deployment was 31.9 ± 0.5 ($\bar{x} \pm SE$). Mean nearest neighbor distance between deployments was 974.4 ± 173.9 m, although we deployed camera traps along a 514-km nonlinear distance along the Juruá River. We stratified deployments between undisturbed contiguous primary forest and 4 land cover types within anthropogenic successional mosaics in the vicinities of local communities. The 4 anthropogenic land cover types were 1) disturbed forest including small primary forest fragments, natural rubber tapping areas, and degraded primary forest; 2) secondary forest older than 25 years; 3) secondary forest younger than 25 years; and 4) homestead areas close to community households. As per agriculturists' requests, we excluded deployments from active roçados to minimize disturbing agricultural activity, although all landscape elements within successional mosaics were typically adjacent to roçados.

We excluded camera-trap data from deployments farther than 1.8 km from community agricultural areas. We did not deploy camera traps in seasonally flooded (várzea) forests. Outside of contiguous primary forest, we placed camera traps 25 m from the stand edge to control for edge effects. We did not use bait. We did not choose camera-trap deployment locations to deliberately maximize detection, but we avoided conspicuous obstacles to detection. We chose locations with relatively flat ground and without large obscuring trees or other obstacles. We cleared thin vegetation in a cone of 7 paces long by 7 paces wide in front of camera traps.

We edited images to improve contrast and aid species identification. In the case of ambiguous images for which a subject could only be identified to a broader morphospecies, we calculated a deployment-specific detection ratio for each morphospecies sub-category. We used this ratio to apportion detections between sub-categories. For example, if we detected 2 red brocket deer, 1 gray brocket deer, and 1

ambiguous brocket deer at a camera trap, then the detection ratio of red to gray brocket deer for that camera-trap deployment would be 2:1. If that deployment included no photographs that could be identified with certainty to either sub-category, then we used the overall detection ratio for all deployments.

For each deployment we recorded 1) name and coordinates of the nearest local community; 2) coordinates of the camera-trap station; 3) date and time of deployment and removal; 4) date and time of last photograph if camera malfunctioned; 5) land cover type; and 6) if deployed in secondary forest, age since abandonment as determined by the roçado owner. We separated images per deployment by species. We excluded images of domestic animals, humans, vultures (family Cathartidae), bats (order Chiroptera), arthropods, small lizards, and non-human primates from further analyses. We defined independent detections of conspecifics as images at any given deployment recorded >30 minutes apart.

Local Interviews

We conducted 50 semi-structured livelihood interviews and 107 structured agricultural interviews at 47 local communities and city neighborhoods (i.e., communities), between April and August 2013–2015. To ensure that our sample was representative of the 84 communities in the region, we chose communities representing a range of population sizes (2–112 households), forest types (várzea and terra firme), and distances from an urban center (0–271 km). We conducted up to 3 livelihood and 6 agricultural interviews per community. Having sought permission from the community leader, we requested to interview adults who coordinated family agricultural production from independent extended households. Though we did not stratify households by socioeconomic status, surveying multiple independent households per community enabled us to capture variation within communities.

We conducted interviews in Portuguese. We recorded interviews using questionnaires adapted from the successfully implemented Projeto Médio Juruá (PMJ) livelihood survey (PMJ 2015). We reassured respondents that data would be kept anonymous and confidential. We did not pay respondents, but we employed 47 respondents as wage laborers to assist with camera trapping at the time of interviews.

During livelihood interviews, we asked 50 respondents to rank their most important livelihood activities, important sources of dietary protein, and the animals that they most frequently hunted. Subsistence hunting is legal within Brazilian extractive and sustainable development reserves and our respondents were not incriminating themselves. During agricultural interviews, we asked 107 respondents about up to 4 roçado patches they were currently cultivating ($n = 238$). We asked, per roçado, during that cultivation cycle 1) how many months ago the roçado had been planted; 2) the transport time to the roçado from the community and the mode of transport used (which allowed us to estimate transport distance); 3) which land cover types bordered the roçado (terra firme, várzea, secondary forest >10 years old, roçados abandoned 5–10 years ago, roçados abandoned <5

years ago, açai palm [*Euterpe precatoria*] or peach-palm [*Bactris gasipaes*] plantation, active roçados, pasture and fields, or the community household cluster); how many stems of sweet and bitter manioc 4) had been planted, 5) had been lost to flooding, and 6) had been lost to crop raiders; and 7) how many stems would they estimate would have been lost if they had not protected their roçados. In addition, we asked respondents to rank the species that most frequently entered their roçados and raided crops, how they respond to crop raiders, and if they had killed animals in their roçados, which species did they kill. We gave respondents opportunities to ask questions and expand upon responses with their opinions and experiences. In interviews relating to 49 roçados, respondents did not differentiate manioc type. We therefore excluded these data from analyses of crop choice.

When summarizing interview data, where single numeric responses were given, we calculated means. Where multiple unranked categorical responses were given, we summed the number of responses per category. Where multiple, ranked categorical responses were given, we calculated a summed, rank-weighted score per category. To convert agricultural data reported per roçado into data per agriculturalist per year, we summed data for all the roçados planted by a given respondent in a given year and calculated the mean of all years.

We received approval to work with human and animal subjects using interviews and camera traps from the University of East Anglia Research Ethics Committee. Our study forms part of the PMJ. The PMJ was authorized and licensed by the Protected Areas Center of Amazonas and the Chico Mendes Institute for Biodiversity Conservation to conduct ecological and socio-economic surveys (authorization 38357-1).

Species Traits

For species that were the subject of interviews or reliably detected by camera traps, we compiled a series of species traits (Table 1). We used interview data to create rank-weighted scores of species propensity to enter roçados, propensity to raid crops, frequency of being killed by hunters, and frequency of being killed in roçados. We designated the 5 species most commonly identified in interviews as crop raiders (accounting for >99% of summed weighted scores) and summed the metabolic biomass of crop raider and non-raider species per camera-trap deployment. Following Kleiber's rule (Kleiber 1932) for any given species i , we defined the group metabolic biomass as mean adult body mass _{i} ^{3/4} × mean group size _{i} .

We obtained values for adult body mass per species from Carboneras (1992), Dunning (1992), Baptista et al. (1997), Emmons and Feer (1997), Nowak (1999), and unpublished data (C. A. Peres, Projeto Médio Juruá, unpublished data). We used the mean male and female adult body mass for dimorphic species. Where only a range of adult body mass was known for a given species, we used the median of the upper and lower limits. Because camera traps may fail to detect some group members, we did not use camera-trap images to assess group size. We instead applied a mean group

Table 1. Trait database of vertebrate species reported during interviews or detected by camera traps in the Médio-Juruá region of Brazilian Amazonia, 2013–2015. NA = indicates species not reliably detected by camera traps or mean group size not known. Camera-trap rate = Detections per 100 camera-trap nights (all land cover types). Hunted = reported frequency of being killed by hunters. Crop raider = reported propensity to enter agricultural fields (roçados) and raid crops. Non raider = reported propensity to enter roçados but not raid crops. Interview data (hunted, killed in roçados, crop raider, non-raider) are percentages of summed weighted scores. Mass = mean adult body-mass (g). Camera-trap data could not always distinguish between small armadillo species.

Class or order	Species	Camera-trap rate	Habitat selectivity index	Hunted	Killed in roçados	Crop raider	Non-raider	Group size	Mass
Aves									
Anseriformes	Muscovy duck	NA	NA	0.37	1.00	0.10	0.00	NA	2,550
Anseriformes	Orinoco goose	NA	NA	0.13	0.00	0.00	0.00	NA	1,396
Columbiformes	White-tipped dove	0.64	-1.42	0.00	0.00	0.07	1.67	1.3	149
Galliformes	Razor-billed curassow	2.23	-0.10	8.21	0.00	0.07	2.22	1.6	3,000
Galliformes	Speckled chachalaca	0.12	0.52	0.00	0.00	0.00	0.45	5.0	1,200
Galliformes	Spix's guan	0.19	-0.86	0.32	0.00	0.00	0.08	4.9	1,280
Galliformes	Wood quail	0.07	-1.54	0.00	0.00	0.00	0.00	5.4	310
Gruiformes	Pale-winged trumpeter	1.88	-1.31	0.00	0.00	0.00	0.00	5.8	1,200
Tinamiformes	Tinamou large	0.57	-1.07	4.75	1.00	0.07	1.10	1.3	1,200
Tinamiformes	Tinamou small	0.83	-0.64	2.35	1.00	0.07	1.10	1.4	420
Mammalia									
Artiodactyla	Collared peccary	1.07	0.09	17.0	25.00	15.89	0.00	4.9	25,000
Artiodactyla	Gray brocket deer	0.89	-0.96	1.25	0.00	0.00	0.00	1.2	18,000
Artiodactyla	Red brocket deer	6.57	0.34	8.22	6.00	3.77	15.63	1.1	30,000
Artiodactyla	White-lipped peccary	0.05	-0.05	20.74	0.00	0.00	0.19	68.3	32,000
Carnivora	Margay	0.10	-1.43	0.00	0.00	0.00	0.52	1.0	6,000
Carnivora	Ocelot	1.21	0.04	0.00	0.00	0.00	0.09	1.3	15,000
Carnivora	Short-eared dog	0.24	-2.05	0.00	0.00	0.00	0.00	1.2	7,750
Carnivora	Tayra	0.86	-0.83	0.00	0.00	0.00	1.35	1.3	4,850
Carnivora	Coati	0.14	-1.83	0.00	0.00	0.00	0.00	11.9	5,100
Carnivora	Jaguar	0.17	-0.79	0.15	0.00	0.00	1.70	1.4	80,000
Carnivora	Jaguarundi	0.10	-1.43	0.00	0.00	0.00	0.00	1.0	8,000
Carnivora	Puma	0.48	0.04	0.15	0.00	0.00	1.17	1.1	45,000
Cingulata	Giant armadillo	0.14	-0.34	0.00	0.00	0.00	1.59	1.2	30,000
Cingulata	Greater long-nosed armadillo	NA	NA	0.00	0.00	0.04	1.96	NA	10,150
Cingulata	Nine-banded armadillo	NA	NA	0.00	0.00	0.04	5.02	1.1	4,500
Cingulata	Small armadillos	1.40	-0.44	2.73	0.00	0.14	9.17	1.0	4,800
Cingulata	Southern naked-tailed armadillo	NA	NA	0.00	0.00	0.04	0.23	NA	3,200
Didelphimorphia	Brown four-eyed opossum	0.52	-0.57	0.00	0.00	0.00	0.00	1.0	390
Didelphimorphia	Common opossum	1.19	0.09	0.00	0.00	0.00	0.00	1.0	1,088
Perissodactyla	Lowland tapir	0.02	-1.09	5.50	0.00	0.00	3.09	1.2	160,000
Pilosa	Giant anteater	0.76	-0.27	0.00	0.00	0.00	0.48	1.2	30,500
Pilosa	Southern tamandua	0.17	-1.90	0.00	0.00	0.00	0.00	1.1	4,500
Primates	Howler monkey	NA	NA	4.03	0.00	0.00	0.00	6.2	6,500
Primates	Squirrel monkey	NA	NA	0.00	0.00	0.00	0.10	23.9	940
Primates	Titi monkey	NA	NA	0.00	0.00	0.00	0.07	3.9	1,125
Primates	White-fronted capuchin monkey	NA	NA	0.00	0.00	0.00	0.14	15.1	2,700
Primates	Woolly monkey	NA	NA	1.31	0.00	0.00	0.00	19.6	8,710
Rodentia	Agouti	6.99	-0.07	8.01	53.00	23.02	0.29	1.2	4,500
Rodentia	Bolivian squirrel	0.12	1.68	0.00	0.00	0.00	0.00	1.2	700
Rodentia	Capybara	NA	NA	0.41	0.00	0.00	0.29	8.8	50,000
Rodentia	Green acouchi	0.78	-0.90	0.00	1.00	0.00	0.14	1.0	750
Rodentia	Paca	4.92	-0.04	14.36	12.00	12.74	0.58	1.0	9,500
Rodentia	Southern Amazon red squirrel	0.54	-0.74	0.00	0.00	0.00	0.00	1.4	1,200
Rodentia	Spiny rats	1.02	-0.75	0.00	0.00	0.84	0.00	1.0	560

size per species, using line-transect census data from our faunal monitoring program (PMJ 2015).

We estimated a primary forest habitat selectivity index (HSI) for each vertebrate species by summing the total number of detections per species and associated camera-trap nights (CTNs) for all deployments either within or outside undisturbed contiguous primary forest (see study area and methods). We estimated camera-trap rates per land cover type (contiguous primary forest and all other anthropogenic land cover types combined) as the number of independent detections per species divided by the total sampling effort (as measured by CTNs). The HSI for any given species i was a

log-abundance ratio that handles zero detections according to the formula below, with negative values representing greater primary forest habitat specificity.

$$\log_{10} \left[\frac{\left(\frac{\text{detections}_{\text{non-primary forest } (i)} + 0.1}{\text{functioning CTNs}_{\text{non-primary forest } (i)}} \right)}{\left(\frac{\text{detections}_{\text{primary forest } (i)} + 0.1}{\text{functioning CTNs}_{\text{primary forest } (i)}} \right)} \right]$$

Anthropogenic and Ecological Spatial Data

We extracted comparable anthropogenic and ecological spatial data for camera-trap deployments and roçados using Program ARCGIS Version 10.3 (Environmental Systems

Research Institute, Redlands, CA, USA). These data included metrics of land cover type, disturbance, urban proximity, proximity to community, and community size.

For each camera-trap deployment, we calculated the area of deforestation and várzea forest within a 500-m buffer using data from the Instituto Nacional de Pesquisas Espaciais Monitoramento da Floresta Amazônica Brasileira por Satélite (2009), Global Forest Change (Hansen et al. 2013), and the Brazilian Amazonian Radar Project vegetation polygons (Veloso and Góes-Filho 1982; see Spatial Data, available online in Supporting Information). We determined the degree of forest disturbance and extent of várzea forest adjacent to each roçado through interview scores (Table S1, available online in Supporting Information). We summed scores per roçado and divided by the number of responses, to derive the mean intactness and várzea of the land cover surrounding each roçado.

To measure transport distances in our study region and thereby calculate human proximity and population density metrics, we used ARCGIS Network Analyst to combine a map of households, with a region-wide transport network. We used spatially explicit household data from the IBGE (2007–2009) population census of rural households, validated against IBGE (2007–2009) municipal census data. We constructed a transport network from global positioning system (GPS) track logs taken over successive fieldwork years. Our network accounted for all main rivers, tributaries, known navigable perennial streams, paved and unpaved roads in the vicinity of all interviewed communities and camera-trap deployments.

To measure human population density in proximity to camera traps, we summed the number of households within a 4-km transport distance of each camera-trap deployment. We recorded the number of households in the nearest community from each roçado. We calculated the number of households per community from 3 data sources: 1) interviews conducted during this study; 2) Projeto Médio-Juruá interviews; and 3) The Sustainable Amazon Foundation (FAS) community census (FAS 2015). As no single dataset was complete, we used the mean of the available data per community.

To measure the transport distance from communities to roçados, we multiplied transport times reported in interviews, by average transport velocities per reported transport type (Parry and Peres 2015). For 3 out of 238 roçados, no mode of transport was reported by the respondent. We therefore applied the mean transport speed for the entire community. We calculated the population of and distance to the nearest urban center per camera-trap deployment and interviewed community, using the aforementioned transport network and the IBGE (2007–2009) census data. We then created a metric of urban proximity by dividing the total urban population by the square-root of the transport distance.

Data Analysis

We created generalized linear mixed effects models (GLMMs) using Program R (R version 2.15.1, www.r-project.org,

accessed 1 Jan 2016) to describe the determinants of reported losses to crop raiders, proportion of manioc plantation allocated to bitter manioc, and camera-trap-detected crop raider and non-raider metabolic biomass. We treated these dependent variables as counts with associated log-transformed offset variables, which were number of manioc stems planted that had not been lost to flooding, the number of months since the roçado was brought into cultivation, and CTNs (as appropriate). For both camera-trap and interview data, we designated the local community as a random effect.

We created comparable explanatory variables for models using either interview or camera-trap data. These included disturbance (interview-derived intactness score or deforestation within 500 m of a camera-trap deployment), várzea (interview-derived várzea score or várzea within 500 m of a camera-trap deployment), local human population density (number of households per interviewed community or number of mapped households within a 4-km travel buffer, centered around each camera-trap station), distance to a roçado from community (crop models only), urban proximity score, and land cover type in which camera traps were deployed (biomass models only).

We used a Poisson error structure to check for overdispersion. Because we detected overdispersion, we substituted a negative binomial error structure, which can be used to calculate Akaike's Information Criterion (AIC), used in information-theoretic model selection (Ver Hoef and Boveng, 2007).

Semi-subsistence agriculturalists were acutely aware of agricultural losses because such losses compromised an important livelihood activity (PMJ 2015). Therefore, we did not consider crop loss data to be zero-inflated. To model losses to crop raiders, we therefore additionally created generalized linear mixed effect Hurdle models (GLMMHs) that separately explored whether a roçado was raided and how many stems were lost. We used a binomial error structure in GLMMH zero models. In GLMMH count models, truncated negative binomial structure failed to converge and we therefore used a truncated quasi-Poisson structure.

We rescaled the continuous explanatory variables to aid model convergence and comparisons of effect size. We examined collinearity between independent variables using Spearman's rank and Kruskal-Wallis rank sum tests. Where explanatory variables had bivariate $Rho > 0.70$ or $P < 0.05$, we modeled them separately. We selected the best models based on their Akaike weights (w_i) and the change in AIC corrected for small sample sizes (ΔAIC_c). We considered models with $\Delta AIC_c < 2.0$ and $w_i > 0.1$ as equally plausible to explain observed patterns (Burnham and Anderson 2003). Where multiple plausible models were retained, we weighted and averaged them using the `model.avg` function in the R package MuMIn.

We performed Spearman's rank correlation tests to ascertain the degree to which species reported to enter roçados were detected by camera traps outside contiguous primary forest, and the species reported to raid crops were reportedly hunted. When comparing camera-trap and

interview data, we excluded primates because these arboreal species were not reliably detected by camera traps and we summed the interview scores for all small-bodied armadillos (order Cingulata) because these were not differentiated in camera-trap data. We created a univariate GLMM to test if the number of manioc stems raided per roçado differed by type of manioc. We performed a Wilcoxon signed rank test to determine if the number of manioc stems planted per roçado differed significantly by type of manioc. We additionally analyzed vertebrate species composition using nonmetric multidimensional scaling and permutation analysis of variance (Anderson 2001). These analyses supported our main study by investigating whether disturbed habitats were associated with depauperate species compositions and whether crop raiding and non-raiding species were affected differently by anthropogenic disturbance (see Vertebrate Species Composition, available online in Supporting Information).

RESULTS

Detected Species and Associated Land Cover Type

Respondents reported that the 5 most damaging crop raiders were (in descending order of frequency) agouti, collared peccary, paca, red brocket deer, and spiny rats (Fig. 2A). These rodents and ungulates represented >99% of all weighted crop-raiding scores. Agoutis, pacas, and collared peccaries reportedly fed on, or otherwise damaged manioc tubers, whereas cervids were reported to feed on young manioc foliage. The impact of agouti crop raiding was reportedly disproportionate to the amount of manioc consumed because, unlike pacas, agoutis damaged multiple stems, thereby inflicting higher crop mortality. The other taxa reported to cause negligible damage crops were small armadillos (including greater long-nosed armadillo [*Dasyopus kappleri*], nine-banded armadillo [*Dasyopus novemcinctus*] and

southern naked-tailed armadillo [*Cabassous unicinctus*]), Muscovy duck (*Cairina moschata*), razor-billed curassow (*Mitu tuberosum*), large and small tinamous (*Tinamus* spp. and *Crypturellus* spp.) and white-tipped dove (*Leptotila* spp.). The taxa reported to enter roçados, but not raid or damage crops, were (in descending order of frequency) lowland tapir (*Tapirus terrestris*), jaguar (*Panthera onca*), giant armadillo (*Priodontes maximus*), tayra (*Eira barbara*), puma (*Puma concolor*), margay (*Leopardus wiedii*), giant anteater (*Myrmecophaga tridactyla*), speckled chachalaca (*Ortalis guttata*), capybara (*Hydrochoerus hydrochaeris*), white-lipped peccary, green acouchi, white-fronted capuchin monkey (*Cebus albifrons*), squirrel monkey (*Saimiri sciureus*), ocelot (*Leopardus pardalis*), Spix's guan (*Penelope jacquacu*), and titi monkey (*Callicebus* spp.).

The 20 taxa reportedly hunted or killed in roçados (in descending order of frequency) were white-lipped peccary, collared peccary, paca, red brocket deer, razor-billed curassow, agouti, tapir, large tinamou, howler monkey (*Alouatta* spp.), small armadillos, small tinamou, woolly monkey (*Lagothrix* sp.), gray brocket deer, capybara, Muscovy duck, Spix's guan, jaguar, puma, Orinoco goose (*Neochen jubata*), and green acouchi (Fig. 2B). Hunted species were often reported crop raiders (Rho = 0.41). The 4 top-ranking species reportedly killed in roçados were also the top-ranked crop raiders. The first and seventh most commonly reported hunted species, white-lipped peccary and tapir respectively, were large-bodied ungulates that were infrequently detected by cameras and were not reported as crop raiders.

We detected 33 vertebrate taxa using camera traps, which yielded a steeper rank-abundance curve than did interview data (Fig. S2, available online in Supporting Information). Most detected species had proportionally higher detection rates inside primary forests than in all anthropogenic land covers combined. The 3 most frequently detected species

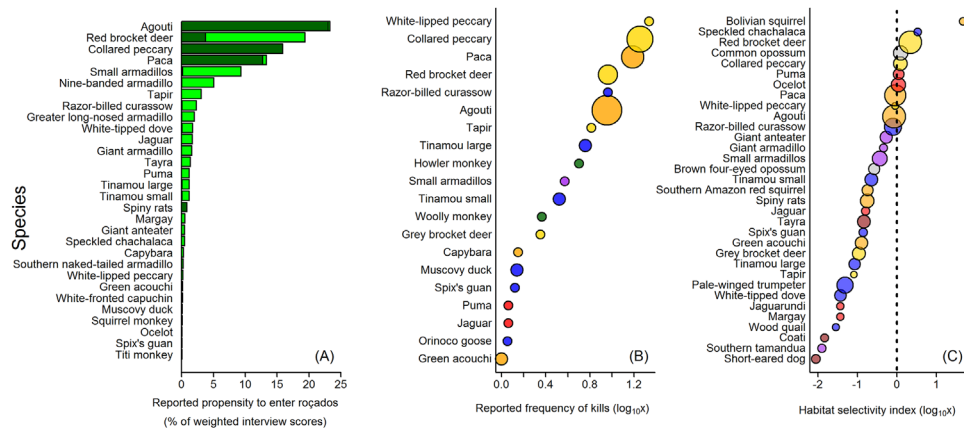


Figure 2. Prevalence of vertebrate species detected in the Médio-Juruá region of Brazilian Amazonia (2013–2015). Species were detected by camera traps and reported during interviews. Horizontal stacked bars (A) represent known species propensity to enter agricultural fields (roçados) as reported in interviews and local species perceptions as operating as either crop raiders (dark green) or non-raiders (light green). We also present frequency of kills as reported by respondents (B); circle sizes are proportional to the frequency killed in roçados. For each species, we present the habitat selectivity index (HSI) derived from camera-trap images (C; HSI scores < 0 indicate species that had a higher detection rate in primary forest); circle sizes are proportional to camera-trap rates. Symbol colors (B and C) represent taxonomic grouping: blue = birds, brown = carnivores, gray = marsupials, orange = rodents, purple = xenarthra, red = felids, and yellow = ungulates.

(agouti, red brocket deer, and paca) were also frequently reported crop raiders and proportionally equally detected in either primary forest or successional mosaics as measured by HSI (Fig. 2C). Species frequently reported to enter roçados were also frequently detected by camera traps outside primary forest ($Rho = 0.47$, $n = 36$). The 10 species detected by camera traps but not reported in interviews were Bolivian squirrel (*Sciurus ignitus*), brown four-eyed opossum (*Metachirus spp.*), coati (*Nasua nasua*), common opossum (*Didelphis marsupialis*), jaguarondi (*Puma yagouaroundi*), pale-winged trumpeter (*Psophia leucoptera*), short-eared dog (*Atelocynus microtis*), southern Amazon red squirrel (*Sciurus spadiceus*), southern tamandua (*Tamandua tetradactyla*), and wood quail (*Odontophorus spp.*).

Crop-Raiding Damage and Crop Choice

On aggregate, respondents reported planting 1,961,575 manioc stems ($11,009.4 \pm 894.9$ stems per respondent per annum [PRPA]). Assuming the mean stem density (1.1 stems/ m^2), which was largely constant across communities, a mean yield of 6.5 (50 kg) sacks of farinha/1,000 stems, and an average transaction price as reported by respondents of \$12.41 (U.S.)/sack of farinha (inflation-uncorrected 2015 prices), this corresponds to an aggregate roçado area of 178.3 ha, potentially yielding 12,750.2 sacks of farinha, which would have been worth \$158,230.

Unpredictable early flood pulses damaged or destroyed 2.2% of the overall manioc crop ($2.1 \pm 1.0\%$ PRPA; Fig. 3). An additional 5.5% of the overall manioc crop was lost to all vertebrate crop raiders combined ($8.0 \pm 1.2\%$ PRPA). At the 189 roçados for which we had data per manioc type, the number of manioc stems planted differed between bitter and sweet manioc ($P < 0.001$). Of all manioc stems planted 64.1% and 35.9% were bitter and sweet manioc, respectively ($58.0 \pm 3.5\%$ of bitter manioc and $42.0 \pm 3.5\%$ of sweet manioc PRPA). Overall losses to crop raiders differed between bitter and sweet manioc ($P < 0.001$). Overall losses to crop raiders were 3.7% for bitter manioc and 9.3% for sweet manioc ($4.7 \pm 1.2\%$ and $15.8 \pm 2.9\%$ of bitter and sweet manioc PRPA). In 40% of roçados that were the subject of interviews, no manioc stems were reportedly lost to raiders. Respondents estimated that the proportion of manioc stems PRPA that would have been raided if crop raiders were neither discouraged nor depleted by hunters, would have increased to $73.9 \pm 3.0\%$ ($37.1 \pm 8.4\%$ for bitter manioc and $85.7 \pm 9.2\%$ for sweet manioc).

Respondents explicitly stated that they planted less sweet manioc than bitter manioc because of the higher crop-raiding rates associated with the former. Some stated that they diluted planting of sweet manioc hidden amongst bitter manioc to reduce the chance of it being raided. Nonetheless, our GLMMs did not conclusively identify factors that influenced the proportion of sweet manioc planted (Fig. 4D).

The Livelihood Context of Crop Damage

Livelihood and agricultural interview respondents had resided in their communities for 21.8 ± 3.2 and 20.1 ± 1.3 years, respectively. Livelihood interview respondents ($n = 50$) considered agriculture, representing 43% of the

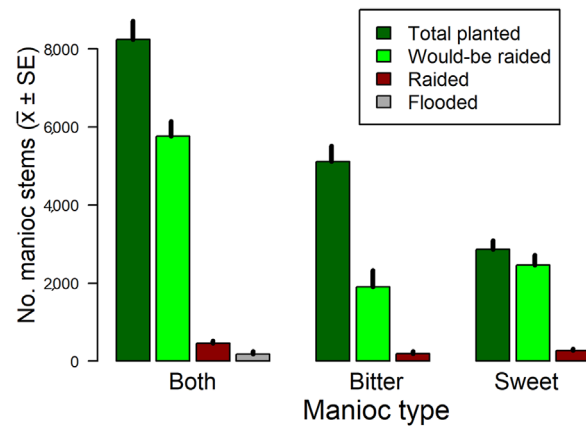


Figure 3. Quantification of manioc crop cultivation and losses in the Médio-Juruá region of Brazilian Amazonia (2013–2015). Agricultural interview data summarize manioc planted and lost to crop raiders and floods in agricultural fields (roçados), separated by type of manioc. Bar height represents the mean value for all roçados of all respondents, which were under cultivation at the time of interview. Vertical black lines represent standard errors. Dark green bars indicate the mean total number of individual manioc stems planted per roçado light green bars indicate those that respondents estimated would have been lost if crop raiders had not been suppressed by hunting. Dark red bars indicate the number of manioc stems reportedly lost to crop raiders, and gray bar indicates those lost to seasonal floods.

summed weighted interview scores, to be the most important livelihood activity. This was followed by fishing (19.9%), social welfare programs (14.1%), non-timber forest product extraction (14.0%), subsistence hunting (3.9%), wage labor (3.8%), timber (1.2%), and livestock (0.2%). Over 89.8% of respondents considered wild fish a more important source of food than hunted meat, whereas 6.1% considered terrestrial game more important, and 4.1% considered them equally important.

Agricultural interview respondents ($n = 107$) reported mean 1-way journey time to roçados from the community of 30.6 ± 2.8 minutes, and most respondents (57%) reported killing crop raiders in their roçados. Lethal methods to suppress crop raiders included hunting (38.6% of responses), dogs (17.1%), and traps (3.2%). Nonlethal methods included tending the roçado and maintaining vigilance (12.0%), using scarecrows (7.6%), creating firebreaks (7.0%), scaring animals away (4.4%), setting up net enclosures (3.2%), maintaining the roçado weed-free (3.2%), and praying for divine intervention (0.6%). Only 2.5% reported doing nothing to combat raiders, often because their roçado plot was too far away, and only 0.6% reported that their roçados did not succumb to crop raiders, thereby requiring no response.

Determinants of Crop-Raiding Rates and Vertebrate Metabolic Biomass

Anthropogenic factors at the landscape and local scales mediated crop-raider metabolic biomass (Fig. 4E) and crop losses to forest vertebrates (Fig. 4A–C). Crop-raider metabolic biomass detected by camera traps increased with distance to the nearest town (Fig. 4E). Larger communities were likewise associated with lower reported losses to crop

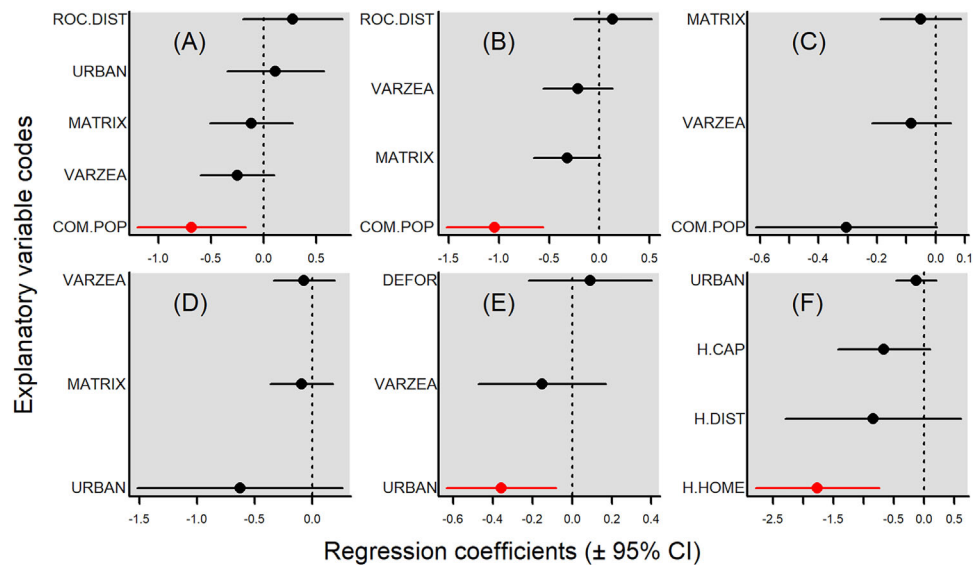


Figure 4. Key predictors of manioc crop raiding in the Médio-Juruá region of Brazilian Amazonia (2013–2015). We present coefficients and 95% confidence intervals of the explanatory variables retained in the averaged best performing models. Variables whose confidence intervals do not overlap zero are in red. Models include generalized linear mixed effects model (GLMM) of losses to crop raiders (A), Hurdle binomial model of losses to crop raiders (B), Hurdle truncated count model of losses to crop raiders (C), GLMM of the proportion of sweet manioc planted (D), GLMM of crop-raider metabolic biomass (E), and GLMM of non-raider metabolic biomass (F). COM.POP = community size (number of households); H.HOME = homestead; H.DIST = disturbed forest; H.CAP = secondary-growth (reference land cover is primary forest); MATRIX = degree to which land cover matrix adjacent to the agricultural field (roçado) can be defined as undisturbed; ROC.DIST = distance between the roçado and the nearest community; VARZEA = amount of floodplain forest (várzea) adjacent to roçado or camera trap; URBAN = urban proximity index.

raiders (Fig. 4A and B). Hurdle models indicate that respondents from more populous communities experienced a lower chance of their roçados being raided, and smaller crop losses in raided roçados (standardized coefficients of community size in the zero and count GLMMHs were -1.04 ± 0.24 and -0.31 ± 0.16 , respectively). Our models suggest that roçados surrounded by more intact habitat were somewhat less likely to be raided and that agriculturalists planted a somewhat lower proportion of more vulnerable sweet manioc in roçados close to primary forest, but large confidence intervals imply that these relationships were weak (Fig. 4B and D).

Our GLMMs of non-raider metabolic biomass suggested that overall forest vertebrate species composition detected by camera traps was predicated upon local land cover type (Fig. 4F). More disturbed land cover types exhibited lower non-raider metabolic biomass (non-raider biomass in homesteads had a standardized coefficient of -1.62 ± 0.38 compared to contiguous primary forest) and a non-random nested subset of primary forest species.

DISCUSSION

Crop-Raiding Species and the Human Landscape

Respondents overwhelmingly implicated agouti, collared peccary, paca, red brocket deer, and spiny rats as the most burdensome manioc crop raiders. These species were also identified in other neotropical crop-raiding studies (Naughton-Treves et al. 2003, Pérez and Pacheco 2006). Vertebrate species that were either reported to enter roçados or camera-trapped in their vicinities were a small proportion of the entire assemblage

detected by camera traps, and crop raiders were a smaller proportion. The high camera-trap rates and low primary forest habitat specificity of these few species, suggest that neotropical manioc crop raiders comprised a select group of locally abundant, disturbance-tolerant habitat generalists.

Tropical forest vertebrate community structure becomes impoverished in areas of high structural forest disturbance and deforestation (Gibson et al. 2011). Most Amazonian forest vertebrates persist at low densities and are intolerant of highly disturbed habitats. Among the most habitat-generalist, disturbance-tolerant species, only a small proportion were capable of digging and ingesting manioc tubers or grazing their leaves, both of which were highly toxic to generalist herbivores (Gleadow and Woodrow 2002). Marked differences in toxicity between manioc varieties may explain the much higher crop-raiding rates observed for the more palatable sweet manioc.

Our crop loss models implied that roçados surrounded by more intact habitat were less likely to be raided. However we anticipated the opposite effect, as neighboring undisturbed habitat acts as a reservoir for crop raiders (Hartter et al. 2010). Other studies have shown that crop raiding was strongly associated with areas near forest (Linkie et al. 2007). This was an unexpected result that we view with caution. Large confidence intervals suggest that the relationship was weak.

Roçados planted near primary forest may have been less attractive to crop raiders because agriculturalists planted a lower proportion of more vulnerable sweet manioc in them. Neotropical crop raiders may persist in highly heterogeneous successional mosaics to a greater degree than anticipated.

This was not the case for non-raiders, whose biomass was markedly lower in more disturbed habitats. Unlike other crop-raiding study areas throughout the tropics, the Médio Juruá region largely consists of vast tracts of contiguous primary forest with deforestation and regrowth representing only ~1.8% of the landscape. Primary forest was therefore not a limited habitat at the landscape scale and habitat-generalist raiders were likely attracted to anthropogenic resources.

Crop Losses to Terrestrial Vertebrates

The aggregate reported losses to crop raiders was considered to be substantial, and masked high variability in the extent to which crops were ruined every year. Losses to crop raiders compounded the hardship faced by semi-subsistence agriculturalists, whose livelihoods were also affected by unpredictable flood pulses and restricted access to markets.

Though sweet manioc was more palatable and required less laborious processing (Fraser 2010), the nearly triple raiding rates associated with it, seemingly relegated it to a secondary horticultural alternative within roçados. Viable crop choices for Amazonian agriculturalists, already severely curtailed by high rainfall and thin, infertile soils, were further restricted to phytochemically defended crop varieties by the constant threat posed by crop raiders. Perhaps most importantly, agriculturalists invested substantial amounts of time and effort in protecting their fields, incurring attendant opportunity costs (Barua et al. 2013). We estimated that they would suffer nearly 10 times higher crop losses in the absence of crop-raiding suppression. These high estimated counterfactual losses were consistent with findings in experimental plots in Bolivia that were unguarded for >1 week, which experienced near total crop losses to crop raiders (Pérez and Pacheco 2006).

Crop-raider abatement strategies along the Juruá included setting nets and traps and deploying hunting dogs, scarecrows, and firebreaks. These were labor-intensive and time-consuming, which is consistent with other studies. For example, Ugandan agriculturalists seasonally spent over 20% of their time guarding against crop raiders (Hill 2000), and Tanzanian agriculturalists guarded their fields on a full-time basis during high-risk months (Gillingham and Lee 2003). Terrestrial crop raiding on food crops cultivated by semi-subsistence forest dwellers in Amazonia thus imposed the burdens of direct crop loss, restricted crop choice, and increased efforts invested in crop protection.

As reported elsewhere, more isolated agriculturalists living in small communities far from towns, contended with higher crop-raider biomass and experienced the highest losses to crop raiders (Naughton-Treves et al. 2003). Human population density is a key determinant of tropical forest vertebrate population density (Peres 2000). Smaller communities and those far from urban areas exert lower hunting pressure (Alvard et al. 1997) and were less able to repel or deplete populations of crop raiders. These communities had the highest barriers to markets and lowest incomes (Parry et al. 2010), thereby suggesting a triple disadvantage in terms of their socioeconomic welfare. Several urban respondents reported that losses to crop raiders were formerly higher. A

respondent from a Carauari suburb reported seeing agoutis eating manioc 5 times in 1 day. This may reflect expanding urban populations with attendant-elevated hunting pressure and anthropogenic disturbance.

Hunting Crop Raiders

Hunting crop raiders around roçados could constitute a positive strategy that reduces raiding rates while providing meat for local communities (Smith 2005). We found that the most prolific crop-raiding species were also the most commonly hunted and the 19 species reportedly hunted in our study were in accord with game offtake profiles reported in other Neotropical studies (Jerozolinski and Peres 2003).

The species responsible for most of the widespread crop damage in our study region often had high reproductive rates, were disturbance tolerant and ubiquitous and were not of high conservation concern (Robinson and Redford 1991). They were therefore good candidates for sustainable subsistence hunting. Agouti, paca, and collared peccary are classified as of least concern by the International Union for the Conservation of Nature (IUCN), and the red brocket deer is classified as data deficient (IUCN 2015). Subsistence hunting in this region has a limited depletive effect on these harvest-tolerant species in proximity to local communities (Abrahams et al. 2017). This contrasts with the Afrotropics and Asian tropics, where habitual crop raiders, such as chimpanzee and Asian elephant, are classified as endangered. This suggests that in our study region, the existing practice of lethally controlling crop raiders may be less problematic for biodiversity conservation and that crop raiding need not constitute an intractable human-wildlife interaction. We caution however that the limited crop-raiding effects of large-bodied or large-group-living species such as tapir and white-lipped peccary may be due in part to depletion and repulsion caused by hunting.

However, hunting crop raiders provided limited benefits to semi-subsistence agriculturalists in our study area. Nonlethal methods to suppress crop raiders were as frequently reported as lethal methods. Terrestrial game hunting in the Médio Juruá was secondary to fish as a source of animal protein (Endo et al. 2016), and a modest livelihood component (Newton et al. 2012), which was consistent with other studies of ribeirinho communities in lowland Amazonia (Murrieta et al. 1999). Lastly, the most hunted species, white-lipped peccary, was not considered a significant crop raider; its large herds rarely entered roçado areas. This scenario was consistent with a study in the Peruvian Amazon where, on average, crop losses to raiders were more valuable than hunting gains in terms of meat acquisition (Naughton-Treves et al. 2003). Nevertheless, Naughton-Treves et al. (2003) also reported that in remote areas where hunting pressure had not reduced large-game abundance, hunting gains compensated crop losses. This supported the notion that community location represented a decisive livelihood trade-off between access to natural resources and access to critical goods and services (Parry et al. 2010).

White-lipped peccaries are anomalous. Foraging in large herds and ranging over vast areas, this species was a stochastic

windfall for hunters and impossible to overlook even by those otherwise disinclined to hunt. Although not regarded as an important crop raider because of its infrequent occurrence, several respondents commented that in the unfortunate event that a white-lipped peccary herd entered their roçado, the entire crop would be ruined. Additionally, the nutritional benefit of wild meat may be disproportionate to the quantity consumed. Indigenous Amazonians and ribeirinho groups placed extremely high nutritional and cultural value on game meat (Neel et al. 1964, Redford and Robinson 1987).

Lastly, the key terms hunting and livelihood were understood differently by respondents. Some respondents did not equate carrying a gun to their roçado and opportunistic kills as hunting, which was only defined as such when specifically setting out with the primary objective of killing game. Similarly, some respondents did not consider strictly subsistence activities such as hunting, even if those were frequently engaged in, to be a primary livelihood component. Thus our interviews may have underestimated the incidence and importance of opportunistic and subsistence hunting.

Forest Ecosystem Disservice

Crop raiding can be considered a forest ecosystem disservice (Zhang et al. 2007). Anthropogenic pressures negatively influenced rates of crop raiding, so that Amazonian communities sometimes pay a heavy price for living at low densities in a high species-richness, intact environment (Barua et al. 2013). A biodiverse ecosystem in itself may not be at fault. Crop-raiding species tolerated human disturbance, and could persist in simplified ecosystems. Indeed, biotic disturbance and simplification may exacerbate levels of crop raiding because of the relative shortage of primary forest resources available to vertebrate herbivores (Yamada and Muroyama 2010).

Furthermore, camera-trap and interview data suggested that crop raiders were closely attended by their natural predators in faunally intact vertebrate assemblages such as those along the Juruá, presumably buffering raiding rates. However, this was insufficient consolation to local villagers who often incur significant losses to forest carnivores. Predators of dasyproctid and echimyid forest rodents, such as ocelots and tayras, were frequently implicated in livestock depredation. Likewise, apex predators, such as large felids (jaguar, puma), may exercise top-down control over ungulate raiders, such as red brocket deer and collared peccaries, but were feared as killers of livestock and people, as occasionally reported by the communities of the Médio-Juruá region, where we have worked continuously since 2007 (PMJ 2015).

Promising Mixed Methods

A coherent picture emerged because of the complementarity between our interview data, comparable studies (Naughton-Treves 1998, Nchanji 2002), and our camera-trap data. Species frequently detected by camera traps, especially in anthropogenic land cover types, were those reported to frequent roçados. Likewise, nearby human population density (as quantified by community size or proximity to urban centers) was associated with lower reported crop losses

and lower crop-raider metabolic biomass. By contrast, disturbance (measured by land cover type or amount of nearby deforestation) was associated with lower non-raider biomass and a more depauperate species composition. Given the complementary strengths and weaknesses of these data collection methods, we suggest that combining different sampling techniques hold promise for understanding complex socio-ecological problems.

MANAGEMENT IMPLICATIONS

Our study indicated that the trapping and hunting of crop raiders within roçados, including hunting using domestic dogs, are important methods employed to reduce rates of otherwise devastating crop loss. Strategies to conserve the biological diversity and ecological interactions of neotropical forests include prohibitions and limitations on the hunting of forest vertebrates. Such strategies should prioritize the protection of slow-reproducing, large-bodied, and large-group-living species, which are extremely vulnerable to overhunting. The species we identified as the most damaging crop raiders are harvest-tolerant and common. Their lethal control within agricultural mosaics, insofar as these are within a landscape also including strictly protected areas, may therefore be compatible with the conservation of neotropical biodiversity.

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