# Irreplaceable socioeconomic value of wild meat extraction to local food security in rural Amazonia

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**Abstract**. Wild vertebrates play a decisive role in the subsistence economy of human populations worldwide. The food security value of wild-meat extracted from natural ecosystems remains poorly quantified. Here, we provide an economic valuation of the nutritional and monetary benefits of year-round wild-meat hunting across a large trinational region of southwestern Amazonia using data from indigenous and non-indigenous settlements from 30 sites. We then build scenarios to explore whether three ubiquitous sources of regional-scale household income (i.e. wage labour, horticultural revenues from manioc flour production and the harvest of Brazil-nuts) could match the purchase costs of alternative meat demand to meet domestic consumption of animal protein should game stocks collapse for any reason. We also considered a fourth valuation scenario in terms of game meat substitution with bovine beef. We conservatively estimate a total annual consumption of ~1431.8 tons of undressed animal carcasses, equivalent to a mean per-capita meat consumption of 54.75 kg person$^{-1}$ yr$^{-1}$, or ~10.9 kg of animal protein person$^{-1}$ yr$^{-1}$. This overall consumption of terrestrial wildlife meat provides US$7.875 million $yr^{-1}$ across the study region. However, household income levels were too low to enable transitions into domestic livestock consumption indicating low adaptation capacity to alternative animal protein; replacement purchases of domestic meat would amount to 90% of aggregate annual wages, 194% of overall income from manioc flour, and 67% of all Brazil-nuts collected. Complete beef replacement by the population in this 16,541-$km^2$ region would require further inputs of US$2.658 million $yr^{-1}$ and the conversion of 4,310 ha of Amazonian forests into pasture. Our results emphasize the extraordinarily valuable and irreplaceable role of wild meat in the food security of tropical forest dwellers. Proposing consumption of alternative sources of animal protein for monetarily deprived forest dwellers is clearly an unrealistic, if not environmentally-damaging, strategy. Conservation scientists, wildlife biologists and policy makers should therefore prioritize adding value to standing forests by managing sustainable wild-meat offtake from natural ecosystems.

**Keywords:** bushmeat harvest, ecosystem services, household income, protein consumption, rainforest, wildlife conservation

## 1. Introduction

Despite advances towards reducing world hunger over the past two decades, about 11% of the world's population (~805 million people) still live in a chronic state of malnutrition (FAO, 2014). A large part of this population inhabits economically marginal tropical regions and depends on daily offtake of terrestrial vertebrates or local fisheries to supplement their diets as they cannot afford to purchase alternative protein, including meat, eggs and dairy (Milner-Gulland et al., 2003; Robinson and Bennett, 2002). Consumption of wild vertebrate protein is mandatory for rural, forest-dependent families with annual incomes lower than US$1,041 (Wilkie and Godoy, 2001). About two thirds of their indirect income comes from subsistence harvest of forest products, agricultural crops, and bushmeat (Angelsen et al., 2014; Crookes et al., 2007; Nielsen et al., 2018). While subsistence overhunting by tropical forest dwellers is one of the drivers of wildlife population declines (Peres, 2001; Peres and Lake, 2003; Ripple et al., 2016), both the socioeconomic benefits of wild meat and the environmental costs of enabling transitions from wild to domestic meat consumption have rarely been estimated.

With the world population projected to reach ~9.7 billion people by 2050, the production of animal protein will have to increase by more than 200 million tons per year to meet burgeoning consumption demand (FAO, 2009). Such increased production will drive the conversion of additional natural habitats, accelerate land-use change, threaten native biodiversity, reduce the provision of several ecosystem services and increase poverty or social vulnerability (Alves and van Vliet, 2018; Barlow et al., 2018; Chaves et al., 2017; Costanza et al., 2017; Green et al., 2005; Laurance et al., 2012; Peres et al., 2010). For residents of (semi)natural ecosystems, whether traditional or otherwise, this may generate food insecurity by impairing subsistence hunting and favouring severe nutritional deficiencies of iron, zinc, vitamins A and $B_{12}$, and many fatty acids (Golden et al., 2011; Sarti et al., 2015).

Although the effects of unsustainable hunting have been historically more damaging in the Asian and African tropics compared to the Amazon (Fa and Peres, 2001), it is unclear to what degree the domestic economy of Amazonian populations can realistically afford the acquisition of alternative sources of animal protein. To address this gap in the literature, we assessed the prey harvest profile and the annual consumption of wildlife meat and animal protein by indigenous and non-indigenous populations in the southwest Amazon. We specifically assessed the economic benefits of wild-caught meat consumption and examined whether local household incomes can finance realistic substitution values of domestic meat consumption under scenarios of either chronic game depletion or banned subsistence hunting.

We examined the purchasing power of households in buying domestic meat based on three sources of income: (a) annualized expected household-scale wages, (b) revenues from manioc flour production, and (c) monetary yields from Brazil-nut harvesting, the dominant extractive trade across the study region. In addition, we estimate how much forest area would need to be converted and how many head of cattle would be required to replace consumption of wild-meat with bovine beef. If household economies are sufficient to ensure such replacement, and little additional forest conversion is required, management actions could be more restrictive and limit subsistence hunting. However, if household economies cannot meet baseline costs of beef acquisition, rendering the full transition into a market economy unaffordable, managing game hunting by rural Amazonians should be more flexible, and take into account the demography of game species and their subsistence value to humans.

## 2. Methods

*2.1 Study region and data compilation*

We used data on game vertebrate extraction in a 16,541-km$^2$ study region of Southwest Amazonia, including parts of Brazil, Peru and Bolivia, based on a review of hunting studies ranging from 14 days to seven years of sampling at 30 sites (mean ± SD = 379 ± 545 days). We conducted a comprehensive literature search using secondary data from peer-reviewed papers, technical reports and theses available on the World Wide Web. These documents were compiled from an initial survey using the Google and Google Scholar search platforms with the terms 'hunting', 'forest', and 'Amazon' (in Portuguese, Spanish and English). Bibliographic references of these articles also led to others with secondary hunting data in the study region. Most of this information was, however, extracted from non-indexed journals. One of us (AVN) also carried out a supplementary study yielding primary game harvest data over a 12-month period from 15 riverine communities within the 340,000-ha Riozinho da Liberdade Extractive Reserve in the Brazilian state of Acre (for further details, see Nunes et al., 2019).

The species-specific number of animals killed at each site was obtained from 30 studies conducted between 1966 and 2016 in the state of Acre, Brazil, the Peruvian departments of Ucayali, Huánuco, Pasco and Madre de Dios, and the Bolivian Amazon department of Pando (Fig. 1). Forests across the study region are defined as open ombrophilous forest, alluvial ombrophilous dense forest, and lowland ombrophilous dense forest sustained by soils with variable nutrient loads, which may affect large-scale forest productivity (Moulatlet et al., 2017). Sampling sites are located along four main watersheds: Juruá and Purus in Brazil, and the Ucayali, Purus and Madre de Dios in Peru and Bolivia (see Table 1 for a brief description of study sites).

We searched for studies whose results included a list of hunted species with their respective numerical offtakes. We excluded papers that estimated hunting of only a single species or a specific taxonomic group (e.g. hunting of either mammals or birds) because they fail to represent the total game meat consumption at each site. Households identified in these studies encompass indigenous, riverine and neocolonist settlements. Although we believe that wild meat trade occurs across all sites, at least as small fractions of the total offtake, these data were not available. Hunting studies recorded all species comprising the most important game vertebrates, including cracids, primates, ungulates, caviomorph rodents, reptiles and species contributing with smaller offtakes, such as carnivores. Hence, these samples can be considered representative of the overall game biomass consumed by rural populations in the southwest Amazon.

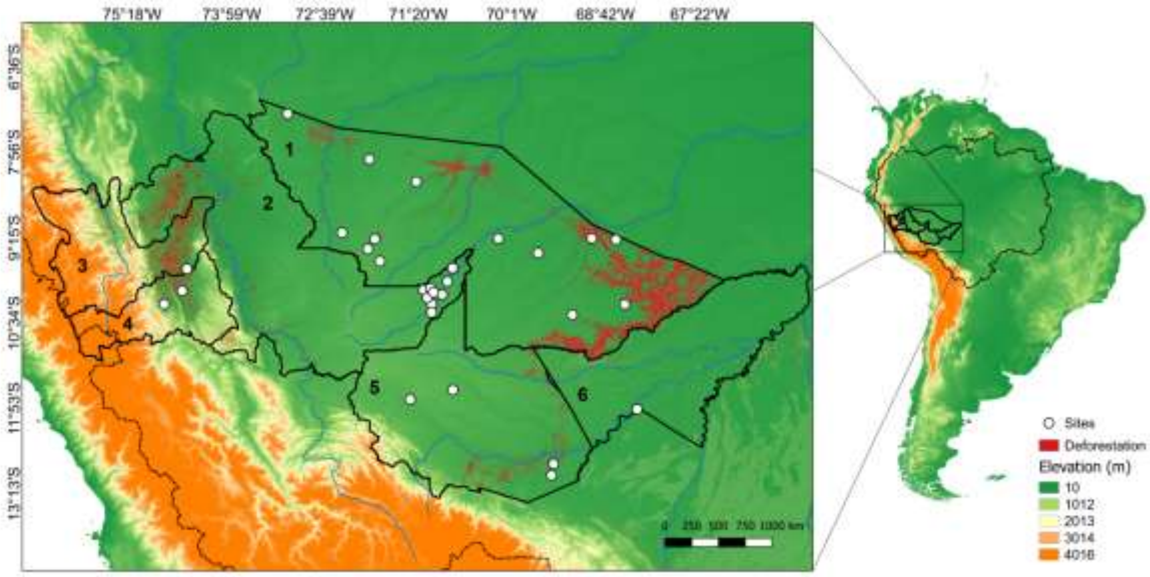



**Fig. 1**. Location of sites sampled across a ~16,541-km$^2$ trinational region of southwestern Amazonia, including administrative provinces or states in Brazil [(1) Acre]; Peru [(2) Ucayali; (3) Huánuco; (4) Pasco; (5) Madre de Dios], and Bolivia [(6) Pando]. Background colour-coding represents deforestation and elevation (asl).

**Table 1.** Region and human population (number of residents) of the 30 study sites in the southwestern Amazon where game offtake data were obtained to estimate wild-meat consumption and the cost of bovine beef substitution.

| Country (State) | Site | Population | Source |
|---|---|---|---|
| Brazil (Acre) | Alto Juruá Extractive Reserve | 850 | Ramos, 2005 |
| | Alto Tarauacá e Extractive Reserve | 250 | Moura, 2013 |
| | Cazumbá-Iracema Extractive Reserve | 280 | Oliveira, 2012 |
| | Chico Mendes Extractive Reserve | 1794 | Medeiros and Garcia, 2016 |
| | Riozinho da Liberdade Extractive Reserve | 1200 | A.V. Nunes (unpubl. data) |
| | Chico Mendes settlement | 390 | Rosas and Drumond, 2007 |
| | São Salvador settlement | 800 | Fragoso et al. 2000 |
| | Settlement along the Iaco river | 405 | Martins, 1993 |
| | Antimary State Forest | 383 | Calouro, 1995 |
| | Kaxinawá do Baixo Jordão Indigenous Land | 172 | Constantino, 2008 |
| | Kaxinawá do Rio Jordão Indigenous Land | 1470 | Constantino, 2008 |
| | Kaxinawá Praia do Carapanã Indigenous Land | 571 | Constantino, 2012 |
| Peru (Huánuco) | Indigenous Campa of the Pichis river | 6600 | Guedes, 1981 |
| Peru (Ucayali) | Native Community Amahuaca de Laureano | 32 | Arco, 2013 |
| | Native Community Gasta Bala | 178 | Sheppard, 2007 |
| | Native Community Santa Rey | 72 | Navarro, 2004; ProPurús, 2011 |
| | Native Community Balta | 541 | Navarro, 2004; ProPurús, 2011 |
| | Native Community Triunfo | 20 | Navarro, 2004 |
| | Native Community Columbia | 34 | Navarro, 2004 |
| | Native Community Nueva Esperanza | 49 | Navarro, 2004 |
| | Alto Purús Reserved Zone | 3150 | Amanzo, 2002 |
| | Native Community Monterey | 32 | ProPurús, 2011 |
| | Native Community Bufeo, Pikiniki and Nuevo Belén | 622 | Pacheco and Amanzo, 2000; Sherpad, 2007 |
| Peru (Madre de Dios) | Tambopata-Candamo Reserve | 3200 | Ascorra, 1999 |
| | Native Community Yomibato y Tayacome | 322 | Ohl-Schacherer et al. 2007 |
| | Communities in the Madre de Dios river | 100 | Loja-Alemán and Ascorra, 2004 |
| | Native Community Infierno | 480 | Loja-Alemán and Ascorra, 2004 |
| Peru (Pasco) | Communal Reserve Yanesha | 34 | Gonzales, 2003 |
| | Pachieta River | 950 | Pierret and Dourojeanni, 1966 |
| Bolívia (Pando) | Provincia Iturralde | 884 | Rumiz and Maglianesi, 2012 |

*2.2 People and socioeconomic profiles*

Our study region has been occupied by indigenous populations, mostly belonging to the Pano and Arawak linguistic families, since at least the first European expeditions into South America. Twelve out of 30 settlements were, however, occupied by non-indigenous former rubber-tappers and *colono* populations. Immigration into southwest Amazonia began in the late 19$^{th}$ century as new settlers established natural rubber estates to extract rubber tree latex (*Hevea brasiliensis* L.), culminating with the arrival of 55,000 northeastern Brazilians into the state of Acre alone (Wilkinson, 2013). Following the collapse of the rubber boom (1942-1945), there was significant rural exodus into large cities, and those who remained in native rubber stands continued to practice a subsistence economy in which hunting, wild animal skin trade and manioc cultivation (*Manioc esculenta* Crantz) became the most traditional livelihood modes (Dean, 1987; Nunes et al., 2019).

The Peruvian Amazon region examined here is inhabited by some 60 indigenous groups, including 15 that remain in voluntary isolation (INDEPA, 2009). Occupation of this region occurred 300 A.D, especially along the Ucayali River and its tributaries (Myers, 1974). Between 1880 and 1920 there was a natural rubber extractive industry boom, which was later replaced by timber, gold, animal skins, and currently palm oil extraction (Aparicio and Bodmer, 2009). During the rubber boom, many indigenous communities in the Madre de Dios region were enslaved; and more accessible areas along major waterways were only recolonized in the last 35 years (Vallve, 2010).

Rubber was also the main colonization driver of northern Bolivia (Heath, 2012), including extractive labour demand for both indigenous peoples and war prisoners, especially in remote areas (Vallori, 2012). Following the collapse of the rubber boom, several ethnic groups either disappeared or became severely depleted (Vallve, 2010). In sum, human populations of the southwest Amazon can be characterized by extreme rural poverty. In Brazil, household income is usually below US\$7.88 day$^{-1}$ (IBGE 2010). In southwest Peru, the rural subsistence economy is based on manioc, horticulture, hunting and fishing. However, per capita income is approximately US\$4.5 day$^{-1}$ (INEI-ENAHO 2014) and lower than that in neighbouring Brazil. Similarly, average income in northern Bolivia's Department of Pando, where populations rely heavily on the seasonal harvest of Brazil-nuts (*Bertholletia excelsa*) (Stoian, 2000), is about US\$4.3 day$^{-1}$ (INE 2016).

*2.3 Protein calculations and bushmeat consumption*

We calculated the undressed carcass yield for all species hunted by multiplying the adult body mass of each species by a factor of 0.6 (Rushton et al., 2005). This represents the total weight of fresh edible meat excluding skeletal parts, viscera and skin. We assumed that the amount of protein in wild-meat equates to 20% of overall undressed carcasses (Ojasti, 1996). To estimate body mass values of slaughtered game species, we used data for the same species from studies elsewhere in the Amazon (Parry et al., 2009; Peres, 2001; Terborgh et al., 1990). We estimated per-capita mean meat consumption as follows (Eq. 1; Redford and Robinson, 1987):

$$Mean\ per\ capita\ consumption = \frac{total\ undressed\ carcasses}{no.consumers \times study\ duration} \quad (1)$$

When the number of consumers was unavailable in the study, we consulted databases from the Brazilian Institute of Geography and Statistics (IBGE), Instituto Socioambiental (ISA) (https://terrasindigenas.org.br/pt-br/brasil; https://uc.socioambiental.org/uc/pesquisa), and Instituto del Bien Común (IBC) (http://www.ibcperu.org/mapas/sicna/). In Brazilian rural villages, for instance, we assumed an average of six persons per household following IBGE census data. To estimate wild-meat consumption at each site, we multiplied the per capita consumption by the total population at that site.

*2.4 Replacement cost of wild-meat consumption*

We quantified annual household economic benefit from wild meat (AHE) consumption as follows (Eq. 2):

$$AHE = (household\ consumption \times price\ of\ bovine\ meat\ kg) - income^{a,b,c} \quad (2)$$

We considered three income scenarios: (a) average annual net household wages of US$2,001 (IBGE 2010, INEI-ENAHO 2014, INE 2016); (b) revenues from sales of manioc flour production of US$931.26 per yr, equivalent to 60-80 sacks of 50 kg produced per hectare; (c) and monetary yields from seasonal Brazil-nut harvesting of US$2,660, based on the average price of US$0.43 per kg and an annual production of 6,187 kg per household (Duchelle et al. 2011). We aggregated the replacement value of wild meat with bovine beef because this is the main source of domesticated red meat consumed by Amazonian communities (Nardoto et al., 2011). This is also the main agricultural activity contributing to historical deforestation rates in the Amazon (Simon and Garagorry, 2005). We therefore assumed a mean value of US$5.50 per kg of bovine beef. This represents the average price (US$/kg) of bovine meat purchased at the nearest towns from the study communities. In addition, we estimated the total protein content from bovine beef biomass required to substitute animal protein from wild game meat from all available sources. We considered a mean body mass of 418 kg per head of cattle (~251 kg per undressed carcass), and 25% of protein per 100 g of beef (Wilson et al., 1979). In this context, we quantified how many head of cattle would be required to replace game meat, and the monetary cost of this replacement. We also included the basic costs of livestock husbandry, which involves the process of pasture creation (6 kg of *Brachiaria humidicola* per hectare; Embrapa, 1980; ~US$270.50), essential veterinary care (e.g. brucellosis vaccination; ~US$13.53), and the market value of each calf (~US$332.59). Moreover, we assumed a mean stocking density of one animal unit per hectare, which is an approximate estimate for SW Amazonia (Barbosa et al., 2015).

All values were recorded in Brazilian, Peruvian and Bolivian currencies [reais (R$), nuevo sol (PEN) and boliviano (Bs)] and subsequently converted into US dollars (US$). As a conversion rate, we used the US$ value at the time of the last study in our database. Monetary quotes were based on the year 2016 (1 US$ = R$ 3.25; PEN 3.35 and Bs 6.93). We aimed to be deliberately conservative in our estimates in this study, as we did not include costs of livestock transportation between rural villages and urban centres and other livestock rearing costs, including labour inputs.

## 3. Results

### *3.1 Wild meat and protein consumption*

We recorded 28,349 terrestrial vertebrates representing 58 species harvested at the 30 sites, amounting to 157,941 tons of undressed carcasses and 31,588 tons of protein harvested (Table 2). This harvest volume corresponds to an annual consumption of 1431.8 tons of wild meat and 286.4 tons of protein for the 25,865 people inhabiting those 30 localities. This is equivalent to an average intake of 150 g of meat person$^{-1}$ day$^{-1}$, which represents a per capita annual consumption of 54.75 kg of meat and 10.9 kg of protein.

**Table 2**. Biomass of undressed carcasses and protein content of game vertebrate (total kg hunted per species) consumed by indigenous and non-indigenous forest dwellers inhabiting 30 study sites across the southwestern Amazon.

| Latin name | English name | Undressed meat biomass (kg) | Protein (kg) |
|---|---|---|---|
| **Birds** | | | |
| *Ramphastos* spp. | Toucan | 79.2 | 15.84 |
| *Pteroglossus* spp. | Araçari | 0.975 | 0.19 |
| *Ortalis guttata* | Speckled chachalaca | 154 | 30.73 |
| *Opisthocomus hoazin* | Hoatzin | 2.70 | 0.54 |
| Accipitriformes † | Kite | 9.0 | 1.8 |
| *Psophia leucoptera* | White-winged trumpeter | 199 | 39.84 |
| *Penelope jacquacu* | Spix's guan | 785 | 157 |
| *Aburria aburri* | Wattled guan | 99 | 19.80 |
| Columbidae † | Dove | 370.25 | 74.05 |
| *Aburria* spp. | Cujubi | 4.26 | 0.85 |
| *Ara macao* | Scarlet macaw | 64.8 | 12.96 |
| *Ara* spp. | Chestnut-fronted macaw | 6.46 | 1.29 |
| *Amazona* spp. | Parrot | 27 | 5.39 |
| *Mitu tuberosum* | Razor-billed curassow | 646 | 129.24 |
| Tinamidae † | Small tinamous | 1114 | 222.81 |
| *Tinamus tao* | Large tinamous | 109.8 | 21.96 |
| Anatidae † | Duck | 90 | 18 |
| Rallidae † | Common gallinule | 5 | 1.02 |
| *Tigrisoma lineatum* | Rufescent tiger-heron | 8.36 | 1.67 |
| Odontophoridae † | Wood quail | 49.79 | 10 |
| **Reptiles** | | | |
| *Chelonoidis denticulata* | Yellow-footed Tortoise | 2076 | 415 |
| *Caiman crocodilus* | Spectacled caiman | 921 | 184 |
| *Podocnemis* spp. | Turtle | 78 | 15.6 |
| **Marsupialia** | | | |
| *Didelphis marsupialis* | Common opposum | 576 | 115.2 |
| **Carnivores** | | | |
| *Leopardus pardalis* | Ocelot | 96 | 19.2 |
| *Eira barbara* | Tayra | 12 | 2.4 |
| *Potos flavus* | Kinkajou | 196.2 | 39.24 |
| *Panthera onca* | Jaguar | 432 | 86.4 |
| *Puma concolor* | Puma | 254 | 50.88 |
| *Nasua nasua* | Coati | 1075 | 215 |
| **Rodents** | | | |
| *Cuniculus paca* | Paca | 17758 | 3552 |
| *Dinomys branickii* | Pacarana | 144 | 28.8 |
| *Hydrochaeris hydrochaeris* | Capybara | 6435 | 1287 |
| *Dasyprocta fuliginosa* | Agouti | 6655 | 1331 |
| *Myoprocta pratii* | Acouchi | 333.6 | 66.72 |

| | | | |
|---|---|---|---|
| *Coendu* spp. | Porcupine | 213 | 42.60 |
| *Urosciurus* spp. | Squirel | 371.49 | 74.30 |
| **Primates** | | | |
| *Saimiri boliviensis* | Squirrel monkey | 34.21 | 6.84 |
| *Pithecia* spp. | Saki monkey | 135.6 | 27.12 |
| *Sapajus macrocephalus* | Large-headed capuchin | 469.5 | 94 |
| *Ateles chamek* | Black spider monkey | 1892 | 378.42 |
| *Callicebus* spp. | Titi monkey | 34.32 | 6.86 |
| *Lagothrix cana* | Gray woolly monkey | 861.3 | 172.26 |
| *Saguinus imperator* | Emperor tamarin | 3 | 0.6 |
| *Alouatta* spp. | Howler monkey | 4653 | 930.52 |
| *Cebus albifrons* | White-fronted capuchin | 252 | 50.40 |
| *Aotus nigriceps* | Night monkey | 84 | 16.8 |
| *Leontocebus weddelli melanoleucus* | White saddleback tamarin | 4.09 | 0.82 |
| **Ungulates** | | | |
| *Tapirus terrestris* | Lowland tapir | 11250 | 2250 |
| *Pecari tajacu* | Collared peccary | 29990 | 5998 |
| *Tayassu pecari* | White-lipped peccary | 31046 | 6209 |
| *Mazama americana* | Red brocket deer | 28770 | 5754 |
| *Mazama nemorivaga* | Brown brocket deer | 1208 | 242 |
| **Xenarthra** | | | |
| *Priodontes maximus* | Giant armadillo | 435.6 | 87.12 |
| *Dasypus kappleri* | Long-nosed armadillo | 117 | 23.40 |
| *Dasypus* spp. | Armadillo | 5195 | 1039 |
| *Tamandua tetradactyla* | Southern tamandua | 18 | 3.6 |
| *Bradypus variegatus* | Brown-throated sloth | 15.12 | 3.02 |

† Taxa containing more than one species of uncertain identification.

Medium-sized prey such as tortoise (*Chelonoidis denticulata*; 15%), paca (*Cuniculus paca*; 12%), and agouti (*Dasyprocta* spp.; 9%) were the most abundant species in the game harvest profiles. The abundance of hunted species differed considerably across vertebrate orders. Ungulates dominated hunted undressed carcasses by more than 59% (> 80 tons) and consequently the profile of protein intake (452 ± 1,130 kg protein), followed by rodents (19%; 339 ± 911 kg protein) and birds 6 (6%; 120 ± 193 kg protein) (Fig. 2). Only 15% of all individuals were threatened but provided 31% of all meat consumed (IUCN, 2018). Among the threatened species, tapir (*Tapirus terrestris*) and white-lipped peccary (*Tayassu pecari*) were the most consumed, accounting for 7% and 18% of the harvest across all sites, respectively.

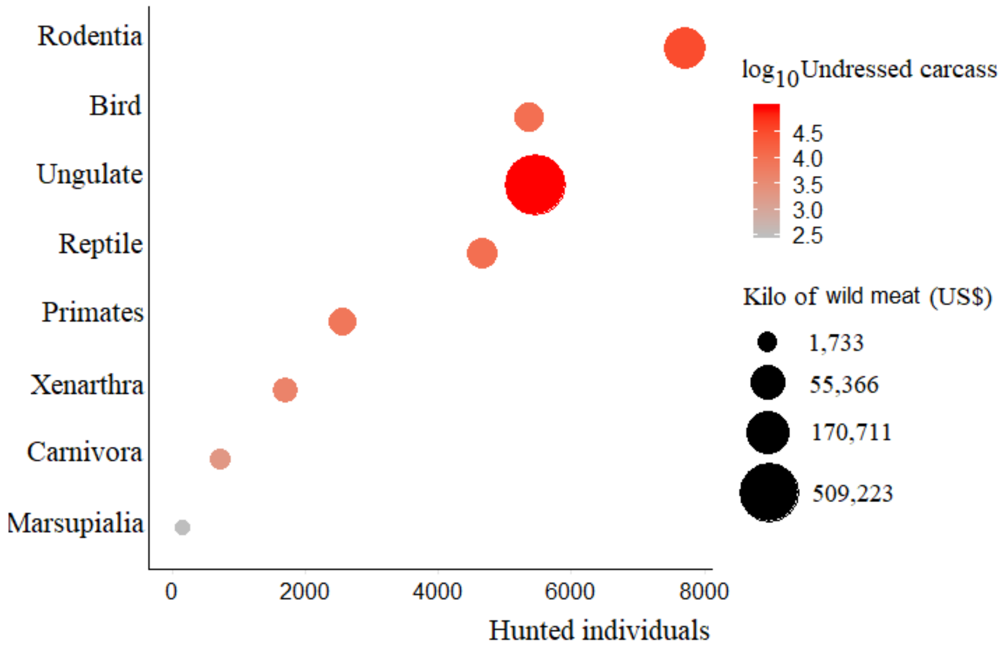
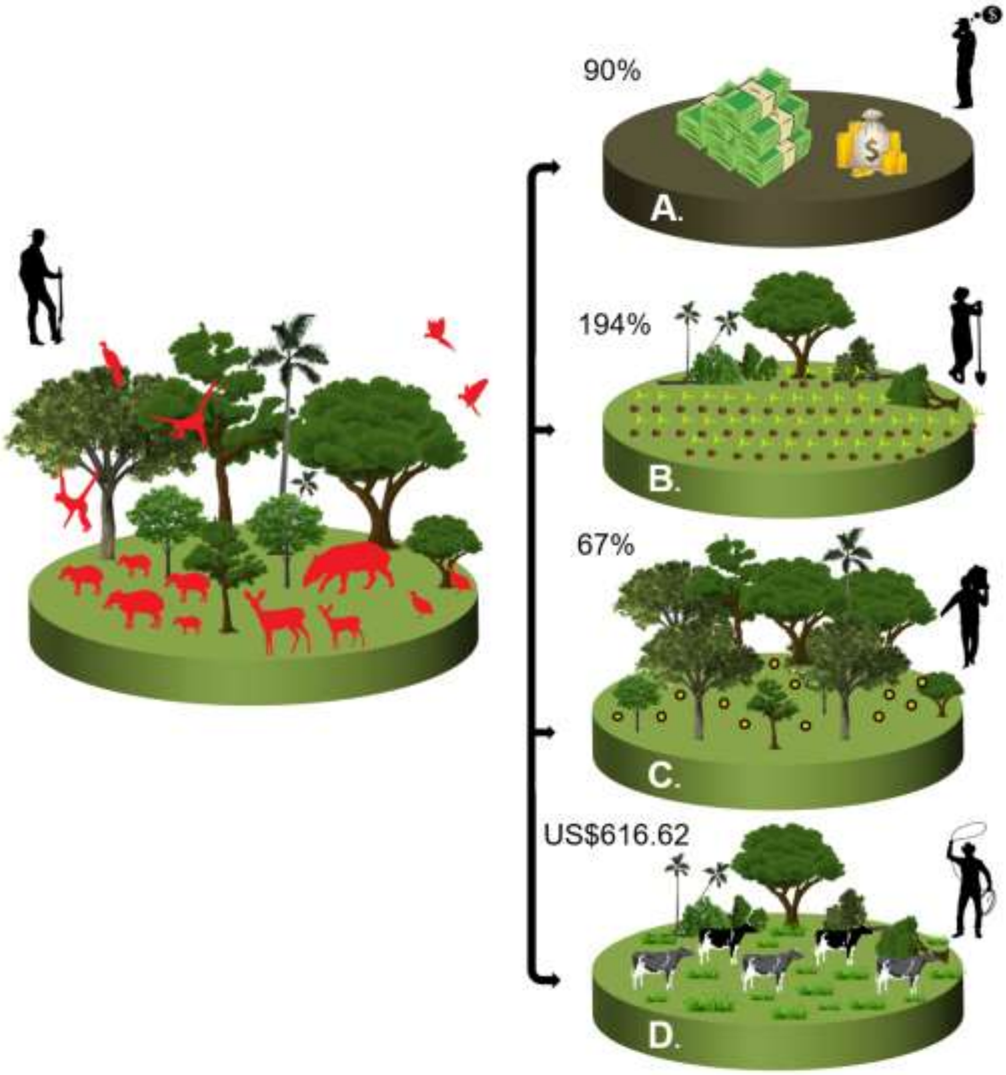



**Fig**. **2**. Contribution of each taxonomic group of game species in terms of wild meat to the extractive subsistence economy of rural populations at 30 sites in southwestern Amazonia. Substitution values are based on the average price (US$5.5 per kg) of the most frequently purchased beef in local markets. Values are calculated as the number of hunted individuals times the mean weight of an average undressed carcass, times the beef substitution price.

*3.2 Economic value of replacement of subsistence hunting*

Considering the mean market price of bovine beef (US$5.50 per kg) and an overall annual consumption of 1431.8 tons of wild meat reported here, the total terrestrial wildlife consumption value amounted to US$7.875 million per year across the study region (average rents of US$262,502 ± 5,283 $yr^{-1}$ per locality). The average consumption of wild meat per unit area was US$3.5 ± 6.0 $ha^{-1}$ $yr^{-1}$. When we considered the value of bovine beef across the region, each person would require an annual cash value of US$301 just to maintain his/her current rates of protein consumption sourced from wild meat. Each household, with an average size of six persons, would therefore require US$1,806 $yr^{-1}$ to satisfy its protein demands. Our estimates indicate that annual household wages throughout the study region is US$2,001, indicating that purchasing bovine meat to replace wild vertebrate meat would require 90% of the annual per capita income. This would therefore leave only 10% of income (US$195 ≈ US$162 per month) to cover all other essential living costs including external food supplies (e.g., rice, oil, and sugar) as well as fuel to make regular trips to local markets to purchase chilled beef and other manufactured goods (Fig. 3; Scenario A). In Scenario B, all annual income obtained from manioc flour production (US$931.26 $yr^{-1}$) would be required to purchase substitution beef. Beef purchases alone would therefore account for 194% of the overall per capita income, leaving households with an annual monetary deficit of US$875. Therefore, this would require an additional labour investment of 2 ha of manioc cropland per household to ensure the profit required for the consumption of animal protein. This is, however, a conservative estimate because it does not take into account potential price elasticities in saturating local markets, thereby both reducing the price of manioc and increasing beef prices. Considering that approximately 4,310 households inhabit our study communities, the total manioc crop production required to supply domestic protein demand, in the collapse of wild meat, would amount to approximately 9,000 ha. Under Scenario C, a Brazil-nut harvest of 4,200 tons would be required to supply the meat acquisition from domesticated livestock. In other words, 67% of the Brazil-nut extraction value would be used to purchase bovine beef. Among the total biomass consumed per mammalian order, ungulates contributed most to the economic profile of wild-meat consumption, totalling US$509,222; followed by rodents (US$170,711). At the opposite extreme, marsupials accounted for the least consumed order (US$1,732).

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To match observed intakes of wild meat protein, each household would therefore be required to accommodate exotic pasture areas to graze at least one head of cattle. Given that the carcass of an average head of cattle provides 62 kg of protein, the expected per capita annual protein consumption is 10.9 kg, and each household requires 65.4 kg of protein $yr^{-1}$, we estimated that replacing wildlife meat consumption with livestock across our study region would require 4,310 head of cattle annually. The total cost involved in expanding a regional-scale livestock sector to replace wild meat would be US$2.658 million annually. This includes the process of creating and maintaining pastures (US$1.166 million), essential veterinary care (US$58.314 thousand) and purchase of calves (US$1.433 million). These livestock husbandry costs could easily reach US$616.62 for each household. Additionally, ~4,310 ha of unflooded forest habitat would have to be converted into cattle pastures to graze this additional protein demand.

## 4. Discussion

This study highlights that wild meat extracted from tropical forests is, in practice, economically irreplaceable and an extremely important food source for the local subsistence and household economy of native and non-native Amazonian forest dwellers. We provide evidence that aggregate household revenues are insufficient to meet the substitution costs of alternative sources of farmed meat. An eventual collapse in wildlife harvesting through either chronic game depletion or a government ban on subsistence hunting would result in severe long-term problems in terms of the food security and economics of semi-extractive households. Although our scenarios — created to understand the importance of hunting for food security — comprise only some of several possible outcomes, they clearly illustrate that wild game meat is irreplaceable in safeguarding against the nutritional deficiency of animal protein, which is typically the most expensive component of human diets (Fa et al. 2015a). Next, we discuss how much this game meat is worth, and the value contributed by forest ecosystems to safeguard the food security of low-income Amazonians.

We documented very high rates of game meat consumption (54.75 kg per person $yr^{-1}$) by both indigenous and non-tribal local communities spread across the study region. This far exceeds the per capita consumption recommended by FAO (20 g of animal protein per person per day or 7.3 kg $yr^{-1}$) to preclude human malnutrition and under-nourishment. In global terms, this exceeded the average per capita consumption of animal protein (42.9 kg $yr^{-1}$; FAO 2014) by 78%. In addition, our observed rate of game meat offtake also exceeded the mean per capita consumption of bovine meat and poultry across all seven South American countries that officially record annual meat consumption, including Brazil and Peru, both of which are near the top ranking meat consuming nations (EOCD 2018). However, the general assessment provided in this study contradicts patterns of meat consumption observed in other tropical forest studies. For example, rural and indigenous populations in Afrotropical forests usually consume only 14.6 and 18.3 kg per person $yr^{-1}$, respectively. These low wild meat intake rates may result from either communities that partly rely on other sources of animal protein or a general pattern of wild-meat depletion in the aftermath of a long history of overhunting (Brashares et al., 2004; De Merode et al., 2004; Milner-Gulland et al., 2003). Our results suggest that, even following a long history of industrial-scale hunting in the 19$^{th}$ century in Southwestern Amazonia to supply the export skin trade (Antunes et al., 2016), wild meat harvesting in our study region can still ensure adequate nutrition for a large number of rural households, including high-value fats, protein and minerals.

In all meat substitution scenarios examined here, replacing wild-meat consumption with domesticated livestock would require a prohibitive reorganization of the household economy, and also lead to markedly elevated deforestation rates at either a local or regional scale and all associated consequences (O'Neill et al., 2018). These interventions can affect game vertebrate consumption in four different ways. First, elevated livestock and manioc flour production would increase local deforestation rates near settlements, impacting forest game populations due to habitat loss, which is regionally more severe than the impacts of hunting per se (Constantino, 2016; Sirén and Parvinen, 2015). Second, a possible reduction in game offtake would increase rural-urban migration as people seek new economic opportunities to ensure greater purchase power, partly to meet animal protein demands (Parry et al., 2010). Third, socioeconomic changes, such as urban wage labour, would also fuel the consumption of alternative food sources, possibly altering the search radius of urban hunters, thereby aggravating pressures on wildlife even in remote areas (Godoy et al., 2010). In other words, monetary income may exert a stronger influence on levels of wildlife mortality and consumption, as urban hunters acquire goods that enhance harvesting efficiency such as outboard motors, fuel, firearms and ammunition (Peres and Lake 2003). Fourth, elevated Brazil-nut harvesting to generate cash for commercial meat can exert further pressure on the demographic sustainability of Brazil-nut tree (*Bertholletia excelsa*) populations and other non-timber forest resources (Peres et al. 2003). Our realistic scenarios considered alternative food production to replace protein demand from hunted meat, which ultimately implies a tradeoff between food security and biodiversity conservation. Therefore, maintaining consumption of wild meat from forest vertebrates at sustainable levels remains the best possible scenario under which to continue a 'win-win' paradigm in systems characterized by socioecological dynamics (Fischer et al., 2017).

In our study, the value of forest ecosystem services provided by wildlife was much larger than the direct annual income of a household, providing a good indicator of the economic importance of provisioning services. Indeed, our estimates of the hidden economic value of hunted meat consumption largely exceeds the cost of converting forests into cattle pasture for bovine beef production. Our estimated value of wild meat in southwestern Amazonia is extremely high, and greater than that observed in northeastern Madagascar (US\$0.42 $ha^{-1}$ $yr^{-1}$; Golden et al., 2014), and higher than the market revenue estimated for non-timber forest products (e.g. fruits, seeds and latex) in a typical hectare of forest in the northern Peruvian Amazon (Peters et al., 1989). However, comparisons of the provisioning value of ecosystem services requires caution because of methodological differences between studies and differences in productivity across sites (Naidoo and Ricketts 2006). This scenario further reinforces the extremely high value of wild-meat consumption as an ecosystem service in the southwest Amazon.

From the perspective of the rural poor facing extreme social vulnerability, sources of protein are highly valuable (Golden et al. 2016). Therefore, if wild game meat is both essential and effectively irreplaceable for rural Amazonian populations, the consumption benefits of these non-timber forest resources become indisputably invaluable. This strongly suggests that environmental goods and services, which are rarely tallied in country-level statistics, should be considered priorities in national to global political arenas. Wild meat extraction should therefore be managed appropriately, in light of robust game management science (Campos-Silva et al. 2017), rather than banned indiscriminately, thereby further constraining the livelihoods of the rural poor (McShane 2003).

In summary, subsistence hunting in Amazonian hinterlands is critical for both food and economic security of rural people. Our study provides a broad geographic perspective for Amazonian populations, in which game animals can still sustain local livelihoods and provide clear provisioning benefits. Replacing wild-meat extraction with alternative sources of animal protein across the study region, for any reason, would likely lead to more predatory land-use practices, because this would incentivize deforestation to support grazelands for ruminant livestock. For rural Amazonians, wild animals are a valuable food resource that cannot be easily replaced without inducing significant environmental damage and social inequalities. Proposing dietary shifts to relatively expensive alternative sources of animal protein to a group of economically vulnerable consumers is clearly not the best strategy. Therefore, conservation scientists should take proper account of the value of wildlife in conservation planning to manage sustainable wild-meat offtake from natural ecosystems, considering the complex links between wildlife conservation and rural poverty (Brockington and Wilkie 2015). We therefore argue that wild meat is essential for rural populations in southwestern Amazonia, but game stocks will need to be managed satisfactorily to prevent wholesale resource collapse.

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