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Terrestrial mammal assemblages in protected and human impacted areas in Northern Brazilian Amazonia

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Abstract

Mammal communities in the vicinity of human settlements are often subject to subsistence hunting and retaliatory killings. We used fourteen digital camera traps equipped with infrared triggers to sample the medium-sized and large mammal communities for ca. 34 (±1.64) days per site. Diversity was measured as both Shannon entropy and Fager´s number of moves (NMS), and dominance was quantified using the Berger-Parker index. We used Kruskall-Wallis tests to investigate if there were statistically significant differences in richness, diversity and dominance among the sites. At an overall sampling effort of 1,946 trap days we recorded 216 independent observations of a total of 20 species belonging to 17 genera and 15 families. Richness and diversity appeared to be determined by forest structure, since, independent of the level of human impact, the richest areas were those closest to the ombrophilous forests of southern Guyana shield, closest to central Amazonia, whereas the poorest were at those sites closest to the vegetation mosaics of central Guyana shield. The disappearance of *Tayassu pecari* from the impacted areas as well as higher relative abundances in the protected areas, albeit not significant, foresees a possible bleak future for the mammalian assemblages in the near future.

Keywords
Medium-sized and large terrestrial mammals, Amazonia, Richness, Relative abundance, Fishbone human settlements

Introduction

Studies in South America, India, and Africa (Hill et al. 1997, Naughton-Treves et al. 2003, Rist et al. 2009, Levi et al. 2009, 2011, Pillay et al. 2011, Rovero et al. 2012) have shown that deforestation and hunting have been the major drivers of mammalian assemblages decline and ultimately mass extinction (Mendes Pontes et al. 2016). This can change the overall composition of the assemblage, but can be attenuated by the presence of a continuous forest matrix, which allows an efficient source-sink balance with recolonization of the depleted areas, such as in southeastern Peru (Ohl-Schacherer et al. 2007), and Ecuadorian Amazonia (Zapata-Rios et al. 2009).

Richness and diversity of terrestrial large mammals in the Neotropics is higher in strictly protected areas that are surrounded by other undisturbed forests than in those subject to deforestation and hunting in its surroundings, and is lowest in highly impacted areas (Tobler et al. 2008, Ahumada et al. 2011, Pickles et al. 2011, Botelho et al. 2012, Santos and Oliveira 2012, Carvalho et al. 2014, Melo et al. 2015, Meyer et al. 2015). In strictly protected areas that are surrounded by other undisturbed forests, Carnivora and Artiodactyla are among the richest mammalian orders (Santos and Oliveira 2012, Carvalho et al. 2014), whereas in protected areas that are subjected to anthropogenic impacts in its surroundings, although Carnivora may still be the most speciose order, Rodentia and Xenarthra may replace Artiodactyla and become the most species-rich orders (Ahumada et al. 2013, Michalski et al. 2015, Lizcano et al. 2016). This could be the result of a time-lag between deforestation and/or hunting, and species extirpation, or result from location, resources availability, species resilience and proximate benefits of secondary vegetation (Tobler et al. 2008, Pickles et al. 2011, Botelho et al. 2012, Bovendorp and Guevara 2015, Galetti et al. 2015, Melo et al. 2015, Meyer et al. 2015).

The first to become rare or extinct from the impacted areas are the large-bodied, terrestrial mammals such as white-lipped peccary, *Tayassu pecari*, jaguar, *Panthera onca*, giant ant-eater, *Myrmecophaga tridactyla*, tapir, *Tapirus terrestris*, and puma, *Puma concolor*, with *T. pecari* being one of the most sensitive, and therefore, the first to go locally or, regionally, extinct (Azevedo and Conforti 2008, Peres 1996, Reyna-Hurtado and Tanner 2007, Naranjo and Bodmer 2007, Richard-Hansen et al. 2014, Melo et al. 2015, Meyer et al. 2015). This is due to their higher energetic demands, larger home ranges, slower reproductive rates, and densities (Peres 2000, Brown and Brown 1992, Grelle et al. 2006).

The impacts of hunting, nevertheless, may also depend on the ethnic origin and dietary preferences of the local assemblages of hunters (e.g. indigenous; *caboclos*, which are descendants of Indigenous peoples with Europeans, among others) (Peres 2000).

In the northern Brazilian Amazonia, where the Government provides incentives for non-Amazonians of European and African ancestry to immigrate to the newly created human settlements (as in this study), long-term monitoring of their taboos and hunting practices is critical for assessing the impacts of hunting on primate assemblages (see Levi et al 2009, 2011).

Studies of medium-sized and large mammals in the Neotropics with the use of camera-traps has become increasingly popular in the last decades. It has been used to determine richness and diversity, abundance, habitat preferences and activity patterns, and has been suggested to be among the best methods for conducting minimally invasive mammal surveys (van Schaik and Griffiths 1996, Maffei et al. 2005, Goulart et al. 2009, Ahumada et al. 2011, Harmsen et al. 2011, Munari et al. 2011, Gonçalves 2013, Michalski et al. 2015, Lizcano et al. 2016).

Camera-trap studies have also shown that the most abundant species in strictly protected areas that are surrounded by undisturbed forests in Central Amazonia is normally a large mammal, such as *Tapirus terrestris* or *Tayassu pecari* (Santos and Oliveira 2012, Reyes 2013), whereas in protected areas that are subjected to anthropogenic impacts in its surroundings and in those highly impacted areas throughout the Amazonia *Dasyprocta* spp. is normally the most abundant (Tobler et al. 2008, Botelho et al. 2012, Michalski et al. 2015, Lizcano et al. 2016). Studies of medium-sized and large mammals in the State of Roraima are relatively recent and the focus has been mainly on the mammals of protected areas, such as Maracá Ecological Station (Mendes Pontes 1997, 1999, Fragoso 1998, Mendes Pontes et al. 2007), and the Waimiri-Atroari (Mazurek et al. 2000), Yanomami and Macuxi Indian reserves (Fragoso 2004). Studies around the fishbone human settlements are almost completely absent, with the only exception of our previous study (Melo et al. 2015). Thus, the diversity of mammals, the impact of hunting and the types of wildlife used in these settlements of Roraima remain almost completely unknown.

In this study we aimed at determining richness, diversity and abundance of medium-sized and large mammals in the Guyana shield of the Brazilian Amazonia, in protected areas and also in fishbone human settlements surrounded by undisturbed forests where no previous camera-trap studies were available.

Methods

Study area

The study was carried out in the Guyana shield of the Brazilian Amazonia, in two protected areas (PA) and two impacted areas (IA), as follows: (1) PA Maracá Ecological Station (3°25'28"N; 61°39'21"W) (Figure 1): an area of 104,000 ha, located in the centre of the Guyana shield, in Brazililan Amazonia, with a typical vegetation comprised of a mosaic of seasonally-dry terra firme forest, campinarana forest, campina and savannas. Mean annual temperatures range between 24°C and 31.6°C (Mendes Pontes 2004, ICMBio 2010, SEPLAN 2010a).

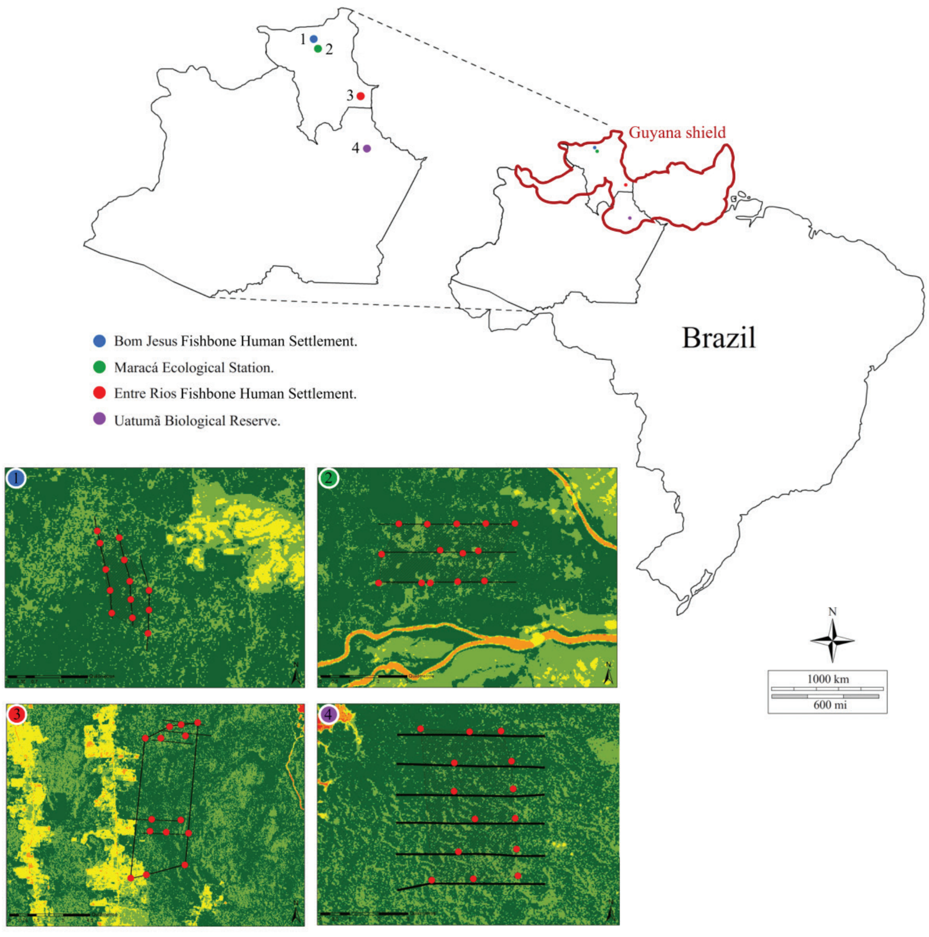

Figure 1. The study area in Northern Brazilian Amazonia showing the four study sites with the study transects and trapping stations. Guyana shield is according to Hoorn et al. (2010).

(2) PA Uatumã Biological Reserve (1°48'24"S; 59°14'16"W) (Figure 1): It has an area of 9,500 ha, is located in southern Guyana shield, and has a vegetation typical of southern Guyana shield, central Amazonia, comprised of dense ombrophilous terra firme forests (ICMBio 2013). Mean annual temperature is around 28.5°C (Governo do Estado do Amazonas 2013).

The impacted areas are formed by two fishbone human settlements, which are forest clearings that appear in satellite images in a fishbone pattern, with forest clearance extending along secondary roads from the main road (Figure 1). The settlements were founded in the 1990's by the Government of the State of Roraima in what was once undisturbed forests (Governo do Estado de Roraima 2005). It is primarily populated by non-indigenous settlers (and their descendants) of European and African ancestry who came from regions outside the Amazonia (mostly north and northeast of Brazil) attracted by free land offered by the Federal Government as part of an Amazonian colonization program initiated under the initiative ‚Cut it or Lose it'.

The settler families have a low income, and frequently practice deforestation and forest burning both inside and outside their plots to clear the land for pasture and to plant crops. Because these plots are located within the forest, this is easily accessed and this facilitates a form of hunting which is practiced indiscriminately and without any control by the local government (as in Melo et al. 2015; R.B.L. personal observation). Additionally, settlers are entitled to ‚subsistence hunter permits' granted on request by the local office of the Federal Police (Melo et al. 2015; A.R.M.P. personal communication). The settlements are:

(3) IA Bom Jesus human settlement (3°37'53"N; 61°42'29"W) (Figure 1): It covers 15,000 ha, and is located in the centre of the Guyana shield. Natural vegetation is a mosaic of seasonally-dry terra firme forest, campinarana forest, campina and savannas (ICMBio 2010). Mean annual temperature is around 26°C (SEPLAN 2010a). Population is approximately 900 non-indigenous settlers whose main activities are livestock and smallholder farming, but they also practice subsistence agriculture.

(4) IA Entre Rios human settlement (0°48'1"N; 59°25'41"W) (Figure 1): It covers 1,206 ha, and is located in the south of the Guyana shield. Natural vegetation is seasonally-dry to dense ombrophilous terra firme forests (IBGE 2005). Mean annual temperature is around 27°C (Governo do Estado de Roraima 2005, SEPLAN 2010b). Population is 1,100 non-indigenous settlers whose main activities are livestock and smallholder farming, but they also practice subsistence agriculture.

Vegetation types present at the study sites and recognisable on RADAM Project (RADAMBRASIL 1975, IBGE 2005) satellite images, are classified as:

(1) Dense ombrophilous terra firme forest: continuous closed-canopy forests with trees of up to 50 m tall that occur in alluvial soils, which are or have been subjected to seasonal flooding. In this study they occurred in southern Guyana shield;

(2) Seasonally-dry terra firme forest: closed- and open-canopy forests with trees of up to 40 m tall that occur on flat terrain that is not subjected to flooding. In these forests many trees lose their leaves seasonally due to water stress which can last for up to six months. In this study they occurred in central and northern Guyana shield;

(3) Campinarana forest: open canopy forests with thin-trunked trees of up to 15 m tall on hydromorphic soils with many shallow pools that flood during the wet season. In this study they occurred in central and northern Guyana shield;

(4) Campina: Sparse short trees of up to 5 m tall on sandy oligotrophic soils. Occasional stands of palms occur along streams, and some areas are covered by grasses and sedges. In this study they occurred in central and northern Guyana shield;

(5) Savannas: open field formed mainly by grasses, an herbaceous layer and widely spaced contorted trees. In this study they occurred in central and northern Guyana shield.

Experimental design

Fieldwork in all areas was carried out during the dry season (Figure 2). In PA Maracá field work was carried out between 3rd November and 7th December 2012. In PA Uatumã, between 21st August and 25th September 2012. In IA Bom Jesus, between 9th March and 9th April 2013. In IA Entre Rios, between 15th February and 21th March 2012. We sampled the medium-sized (≤5 kg, excluding mice and marsupials) and large (>5 kg) terrestrial mammals of the selected areas via digital camera traps (Tigrinus Digital 6.5D, Timbó, Santa Catarina, Brazil), equipped with infrared triggers. Fourteen cameras were placed in each of the 14 pre-established trapping stations, fixed 30 to 40 cm from forest ground, and maintained working uninterruptedly for 24 hours a day for a mean of 34 (±1.64) days. We set cameras to take one picture at every 3 min., and each picture was considered an independent record of the same species in the same camera after a period of one hour from the previous one. We visited the cameras every eight days when to conduct maintenance, replace memory cards and download data.

In the PAs, surveys were carried out in the 25-km^2 RAPELD grids of the PPBio program of the Brazilian government (www.ppbio.inpa.gov.br), which consists of six north-south and six east-west 5-km trails alphanumerically marked every 100 m. We aimed to place the 14 camera-traps within the grid in the most homogeneously order possible so as to cover the greatest part of the 25-km^2 PPBio grid. In the IAs the surveys were carried out in freshly opened parallel trails, each one located behind and perpendicular to one of the inhabited plots of the fishbone human settlements.

Field constraints (locals denying permission to access their plots, camera traps thefts, and threats to the lives of the researchers) determined the size, location and number of trails, and camera trap points in the IA (six 4-km trails in IA Entre Rios; three 3-km trails IA Bom Jesus). Following Ahumada et al. (2011), Munari et al. (2011) and Botelho et al. (2012), once we determined the camera trap points in the four areas, we subsequently searched for spots close to animal trails, footprints and mud holes to maximize image capture. Additionally, we also had to avoid those trails that were seasonally or eventually flooded to prevent camera damage. Mean distance between camera traps in Maracá Ecological Station was 1,033 m (±463), in Uatumã Biological Reserve it was 1,820 m (±249), in Bom Jesus fishbone human settlement it was 529 m (±121), and in Entre Rios fishbone human settlement it was 1,338 (±197).

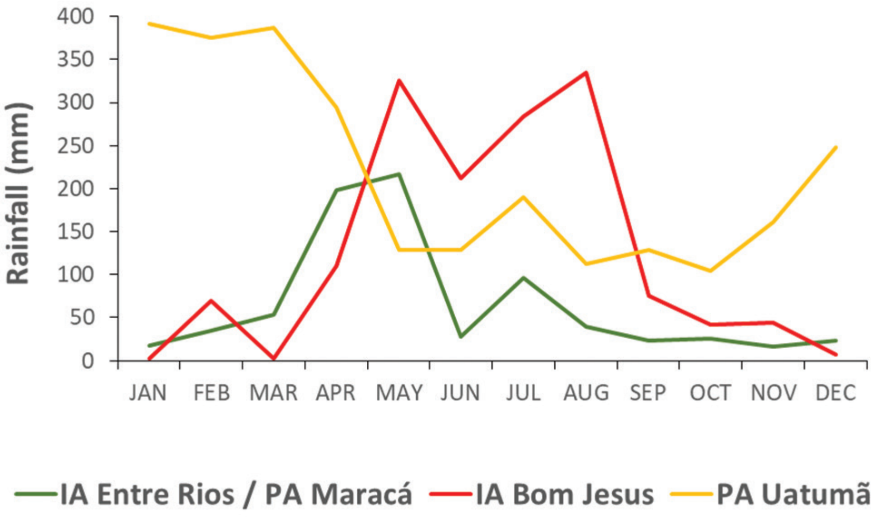

Figure 2. Rainfall in the study areas during the study.

Data analysis

Sample effort for each area was calculated as number of trapping stations per area multiplied by number of sampling days and trapping success was calculated as number of records per area divided by sample effort, multiplied by 100 (Srbek-Araújo and Chiarello 2007). We used Shapiro-Wilk (*W*) test of data normality. Diversity was measured as Shannon entropy (*H)* and Fager´s number of moves (*NMS*), dominance was quantified using Berger-Parker index (*d*) (Hubálek 2000). We used Kruskall-Wallis tests (*K*) to detect statistically significant differences between sites. Moreover, we report effect sizes to facilitate both interpretation and inclusion of our results in meta-analysis (Morris and DeShon 2002).

Relative abundance was calculated as number of species individual records multiplied by 100, and divided by sample effort (Jenks et al. 2011). Kruskall-Wallis test was used in order to verify it there was any statistically significant difference in mean relative abundance among the areas, and Mann-Whitney to verify if there was any statistically significant difference in mean relative abundance between protected and impacted areas. All statistical tests were performed using the software R (R Core Team 2012), version 3.2.

Results

Species richness and diversity

Overall total sample effort was 1,946 trap-days, and total sample effort per study area varied between 448 trap-days in IA Bom Jesus and 504 trap-days in IA Entre Rios

Table 1. Sample size in the protected areas and in the fishbone human settlements in northern Brazilian Amazonia.

Areas	Sample (days)	Camera traps per area	Number of independent records	Camera traps per day	Capture success (%)
IA Bom Jesus	32	14	19	448	4.24
PA Maracá	35	14	86	490	17.55
IA Entre Rios	36	14	27	504	5.36
PA Uatumã	36	14	54	504	10.71

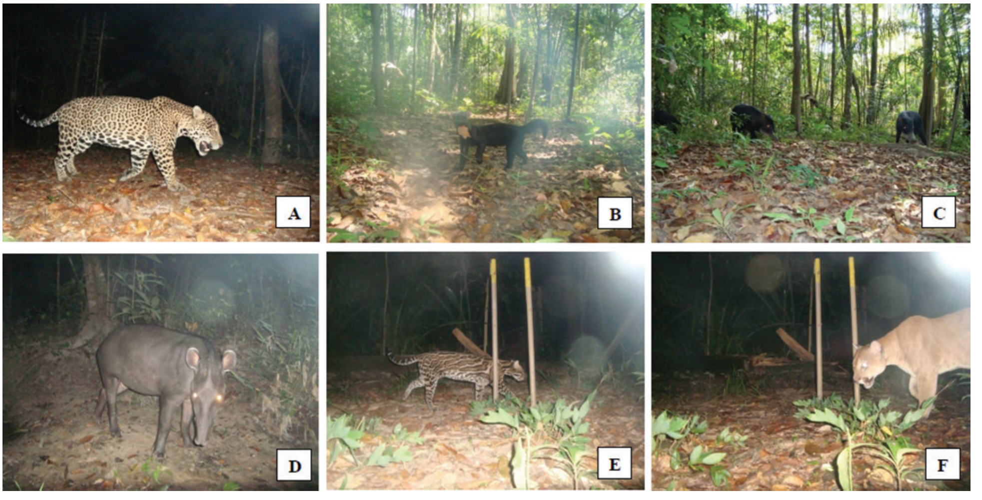

Figure 3. Medium-sized and large terrestrial mammals recorded during this study in the Northern Brazilian Amazonia. **a** *Panthera onca* **b** *Eira barbara* **c** *Tayassu pecari* **d** *Tapirus terrestris* **e** *Leopardus pardalis* **f** *Puma concolor.*

and PA Uatumã (Table 1). This resulted in an overall total of 216 independent species records (11.1% capture success), with a minimum of 19 records (4.24% capture success) in IA Bom Jesus and a maximum of 86 records in PA Maracá (17.55% capture success) (Table 1).

During this study 20 species were recorded, from 17 genera and 15 families (Table 2; Figure 3). PA Uatumã had the highest number of species (n = 15), followed by PA Maracá and IA Entre Rios (n = 10), and IA Bom Jesus (n = 9) (Table 2). No significant difference were detected in species richness ($\chi^2 = 3.68$, df = 3, $p = 0.298$) among the areas.

The most speciose orders in PA Uatumã and PA Maracá were Carnivora (n = 6 and n = 4), Artiodactyla (n = 3 and n = 2), and Xenarthra (n = 3 and n = 2). In IA Entre Rios and IA Bom Jesus most species belonged to Carnivora (n = 5), Artiodactyla (n = 3), and Rodentia (n = 3).

The highest Shannon diversity was registered in PA Uatumã (*H* = 2.4*; NMS* = 41.31), and the lowest in PA Maracá (*H* = 1.2*; NMS* = 13.06) (Figure 4). PA Uatumã

Table 2. Medium-sized and large terrestrial mammals relative abundance in the study areas in northern Brazilian Amazonia.

Species	PA Uatumã	PA Maracá	IA Entre Rios	IA Bom Jesus
Artiodactyla				
Cervidae				
Mazama americana	0.4	0.41	1.39	0.67
Mazama nemorivaga	–	–	0.2	–
Tayassuidae				
Pecari tajacu	2.38	–	0.79	–
Tayassu pecari	0.2	12.04	–	–
Carnivora				
Felidae				
Leopardus wiedii	0.4	–	–	–
Leopardus pardalis	1.39	0.41	0.4	0.22
Panthera onca	1.98	1.02	0.2	
Puma concolor	0.6	0.2	–	0.22
Procyonidae				
Nasua nasua	0.4	–	–	0.22
Procyon cancrivorus	–	–	–	0.22
Mustelidae				
Eira barbara	0.2	0.41	–	–
Cingulata				
Dasypodidae				
Dasypus novemcinctus	1.19	–	–	–
Priodontes maximus	0.2	0.2	–	–
Perissodactyla				
Tapiridae				
Tapirus terrestris	0.6	2.45	2.58	0.22
Pilosa				
Myrmecophagidae				
Myrmecophaga tridactyla	0.4	–	0.2	–
Tamandua tetradactyla	–	0.2	–	–
Rodentia				
Cuniculidae				
Cuniculus paca	–	0.2	0.2	0.45
Dasyproctidae				
Dasyprocta leporina	1.59	–	3.17	1.12
Myoprocta acouchy	–	–	–	0.89
Didelphimorphia				
Didelphidae				
Didelphis sp.	0.79	–	0.2	–
Total	12.72	17.54	9.33	4.23

had the lowest Berger-Parker index (d = 0.2), and PA Maracá, the highest (d = 0.7) (Figure 4). No significant differences, however, were detected in Shannon entropy (χ^2 = 5.82, df = 3, p = 0.121), or dominance (χ^2 = 5.53, df = 3, p = 0.137).

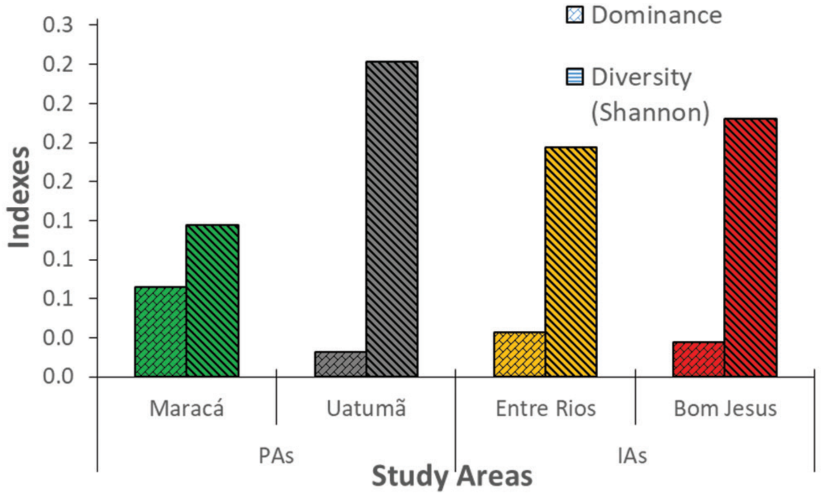

Figure 4. Diversity and dominance indexes for the four study sites in the Northern Brazilian Amazonia.

Relative abundance

No statistically significant differences were detected in mean relative abundance among the areas (χ^2 = 5.32, df = 3, p = 0.150) (Table 2). At PA Maracá the overall relative abundance was 17.55 ind./trap-days, with *Tayassu pecari* as the most abundant species (12.04 ind./trap-days), followed by *Tapirus terrestris* (2.45 ind./trap-days), and *Panthera onca* (1.02 ind./trap-days) (Table 3). At PA Uatumã the overall relative abundance was 12.7 ind./trap-days, with *Pecari tajacu* as the most abundant species (2.38 ind./trap-days), followed by *Panthera onca* (1.98 ind./trap-days), and *Dasyprocta leporina* (1.59 ind./trap-days (Table 3).

At IA Entre Rios the overall relative abundance was 9.33 ind./trap-days, with *Dasyprocta leporina* as the most abundant species (3.17 ind./trap-days), followed by *Tapirus terrestris* (2.58 ind./trap-days), and *Mazama americana* (1.39 ind./trap-days) (Table 3). At IA Bom Jesus the overall relative abundance was 4.24 ind./trap-days, with *Dasyprocta leporina* as the most abundant species (1.12 ind./trap-days), followed by *Myoprocta acouchy* (0.89 ind./trap-days), and *Mazama americana* (0.67 ind./trap-days) (Table 3).

No statistically significant differences were detected in mean relative abundance between protected and impacted areas (U = 142, p = 0.121). Overall relative abundance, however, appeared to be higher in the PAs (15.09 ind./trap-days) than in the IAs (6.93 ind./trap-days) (Table 4). In the PAs the most abundant species in this study was *Tayassu pecari* (6.04 ind./trap-days), followed by *Tapirus terrestris* (1.51 ind./trap-days), and *Panthera onca* (1.51 ind./trap-days), whereas in the IAs the most abundant species was *Dasyprocta leporina* (2.21 ind./trap-days), followed by *Tapirus terrestris* (1.47 ind./trap-days), and *Mazama americana* (1.05 ind./trap-days) (Table 4). Failing to detect any statistically significant results should most probably be due to sample size, which, nevertheless, is a common problem with large terrestrial mammals, many of which are rare and highly secretive.

Table 3. The three most abundant medium- and large-sized terrestrial mammals in the study areas in Northern Brazilian Amazonia.

Study areas	Total relative abundace (ind./trap-days)	Species	Relative abundance (ind./trap-days)
PA Maracá	17.55	*Tayassu pecari*	12.04
		Tapirus terrestris	2.45
		Panthera onca	1.02
PA Uatumã	12.7	*Pecari tajacu*	2.38
		Panthera onca	1.98
		Dasyprocta leporina	1.59
IA Entre Rios	9.33	*Dasyprocta leporina*	3.17
		Tapirus terrestris	2.58
		Mazama americana	1.39
IA Bom Jesus	4.24	*Dasyprocta leporina*	1.12
		Myoprocta acouchy	0.89
		Mazama americana	0.67

Table 4. Overall relative abundance of the medium- and large-sized terrestrial mammals in protected *vs*. fishbone human settlements in northern Brazilian Amazonia.

Species	IAs	PAs
Artiodactyla		
Mazama americana	0.74	0.4
Mazama nemorivaga	0.11	0
Pecari tajacu	0.42	0.7
Tayassu pecari	0	6.54
Carnivora		
Eira barbara	0	0.3
Leopardus pardalis	0.21	1.01
Leopardus wiedii	0	0.1
Nasua nasua	0.11	0.1
Procyon cancrivorus	0.11	0
Panthera onca	0.11	1.11
Puma concolor	0.11	0.3
Cingulata		
Dasypus novemcinctus	0	0.6
Priodontes maximus	0	0.3
Perissodactyla		
Tapirus terrestris	0.95	1.61
Pilosa		
Myrmecophaga tridactyla	0.11	0
Tamandua tetradactyla	0	0.1
Rodentia		
Dasyprocta leporina	1.37	0.3
Cuniculus paca	0.32	0.2
Myoprocta acouchy	0.42	0.1
Didelphimorphia		
Didelphis sp	0.11	0.3
Total	**5.15**	**14.08**

Discussion

Determinants of the structure of the mammalian assemblages

The number of species recorded during this study, between nine and 15 terrestrial species, is higher than expected. Literature has shown that mammal species richness in the Guyana Shield has been recognized as one of the poorest in the Brazilian Amazonia, and is poorest in its central zone (between two and 10) where this study took place (Eisenberg and Redford 1979, Emmons 1984, Janson and Emmons 1990, Hoorn et al. 2010, Mendes Pontes et al. 2010). As shown by Zuquim et al. (2014) and Tuomisto et al. (2014), this should be a result of poor soil quality and comparatively drier climates, with longer dry season, which is positively correlated with plant diversity, and ultimately, with the availability of food resources for the mammalian assemblage. Regarding only our study areas, Maracá and IA Bom Jesus, with the poorest soils (Thompson et al. 1992) were the ones with the lowest richness, whereas Uatumã, with the richest soils (Zuquim et al. 2014, Tuomisto et al. 2014), was the one with the highest.

In this study Carnivora was the most speciose order, followed by Artiodactyla, in both PAs and IAs, suggesting that the structure of the mammalian community is preserved, although some of the species are generalist and matrix/fragmented tolerant species, such as *Eira barbara*. Studies in the Neotropics have shown that Carnivora is the most speciose order of large terrestrial mammals in protected areas, followed by Artiodactyla (Tobler et al. 2008, Munari et al. 2011, Springer et al. 2012, Santos and Oliveira 2012, Ahumada et al. 2013, Burton et al. 2015, Michalski et al. 2015), whereas in protected areas that are surrounded by human disturbances, Carnivora was followed by Rodentia and Xenarthra, which could represent an intermediate conservation status (Pickles et al. 2011, Carvalho et al. 2014, Lizcano et al. 2016), or Rodentia could even be the most speciose order (Michalski et al. 2015). In impacted areas, however, the most speciose order seems to be Xenarthra, followed by Rodentia (Michalski and Peres 2007, Botelho et al. 2012). Different patterns, however, may be found in highly impacted areas, in which most medium-sized and large mammals are extirpated or driven to such low numbers that the most abundant species becomes the smaller-bodied rodent, *Dasyprocta* spp. (Tobler et al. 2008, Botelho et al. 2012, Michalski et al. 2015, Lizcano et al. 2016).

In this study in the Guyana shield of the Brazilian Amazonia no statistically significant differences were detected between PAs and IAs. In our previous studies (Mendes Pontes 2004, Mendes Pontes et al. 2007, Mendes Pontes et al. 2012, Melo et al. 2015), we showed that in the highly heterogeneous vegetation mosaics of the northernmost Guyana shield the structure of the terrestrial mammalian assemblages was shaped by forest type and heterogeneity, which, in turn, is directly connected with resource availability. Species richness and diversity may vary between protected and impacted areas, with the latter in most studies presenting a lower number of species due to hunting (Lopes and Ferrari 2000, Peres and Nascimento 2006, Michalski and Peres 2007, Sampaio et al. 2010, Ahumada et al. 2011, Melo et al. 2015, Meyer et al. 2015).

Accordingly, the richest area was PA Uatumã, located south of the Guyana shield, closest to central Amazonia, the natural vegetation cover for which is dense ombrophilous forests, followed by IA Entre Rios, which is located in the transition between the dense ombrophilous terra firme forests of the south of the Guyana shield, and the seasonally-dry forest mosaics of central Guyana shield, and the poorest areas were PA Maracá and IA Bom Jesus, in the northernmost Guyana shield, where the vegetation is mainly seasonally-dry forest mosaics interspersed with extensive areas of savannas (See Hoorn et al. (2010)). The highest NMS value in Uatumã (41.31) could be related to the fact that this is one of the most ombrophilous and productive forests, besides being a protected area, whereas the lowest NMS (5.49) in Bom Jesus settlement could be related to the fact that it is a highly degraded, impacted area, besides having a very open, discontinuous forest.

Our previous studies (Mendes Pontes 2004, Mendes Pontes et al. 2007, Mendes Pontes et al. 2012, Melo et al. 2015), also showed that the more heterogeneous and shorter the vegetation types (e.g., the mosaics of terra firme forest, campinaranas, campinas, and savannas of northernmost Guyana shield), the higher the abundance of *Tayassu pecari*, which decreases considerably the diversity of the mammal assemblage. PA Maracá, in the northernmost Guyana shield, therefore, had the lowest species diversity due to the very high dominance of *Tayassu pecari*, whereas PA Uatumã, in the south of the Guyana shield, closest to central Amazonia, had the lowest dominance, and therefore, the highest species diversity. At the fishbone human settlements IA Bom Jesus and IA Entre Rios, due to the fact that *Tayassu pecari* has been extirpated, dominance was lower than in PA Maracá (and diversity higher), but was higher still than PA Uatumã (and diversity lower). In these impacted areas the medium-sized *Dasyprocta leporina* had the highest dominance, possibly replacing *Tayassu pecari*, as seems also to be the case in Meyer et al. (2015) where agoutis, (*Dasyprocta leporina*) were the most abundant, causing a decline in evenness and dominance.

Hunting has been shown to be the major driver of the decline and extirpation of the mammalian abundance in human impacted areas around the world (Hill et al. 1997, Naughton-Treves et al. 2003, Rist et al. 2009, Levi et al. 2009, 2011, Pillay et al. 2011, Rovero et al. 2012). In the neotropics, *T. pecari* was one of the first to disappear due to its extreme sensitivity to hunting in areas close to human settlements (Peres 1996, Reyna-Hurtado and Tunner 2007, Naranjo and Bodmer 2007, Meyer et al. 2015, Reina-Hurtado et al. 2015).

In some cases, however, no differences were detected in the structure of the mammalian assemblages between protected and impacted areas, in which case, hunting was considered sustainable (Peres and Nascimento 2006, Ohl-Schachereret al. 2007, Zapata-Rios et al. 2009), because large contiguous tracts of surrounding primary forests allowed an efficient source-sink balance and recolonization of the depleted areas. Hunting may be sustainable also if the forest is remote and the assemblages have very low human population density, if settlements are relatively young, small, and have a low consumer population (De Thoisy et al. 2005, Demmer et al. 2002, Mazurek et al. 2000, Alvard et al. 1997).

In this study, relative overall abundance of medium-sized and large mammals did not present any statistically significant differences between PAs and IAs. When we considered the areas separately, PA Maracá was the area with the highest overall relative abundance, mainly due to the very high abundance of *Tayassu pecari*, which, in these highly seasonal forests of the Guyana shield, are among the most abundant terrestrial mammals. For instance, its relative abundance in PA Maracá is ~70% of the overall abundance of the area, and is almost the total relative abundance of the second most abundant area, PA Uatumã. As expected, the latter does not have such a high *Tayassu pecari* abundance as most areas of the Guyana shield (Munari et al. 2011, Negrões et al. 2011, Botelho et al. 2012, Santos and Oliveira 2012).

The scenario of this study comprises PAs and IAs that are surrounded by large tracts of undisturbed forests that although not legally protected and totally accessible, are protected from human presence by remoteness. Additionally, the IAs are comparatively younger (~25 years since decreed), are among the smallest in the state of Roraima (around 4,000 and 15,000 ha, compared to 220,000 of the largest), and, consequently, have fewer families (around 200, compared to a maximum of around 2,000 in the largest settlement) (Governo do Estado de Roraima 2017).

Additionally, the settlers normally obtain their necessary animal protein intake from domestic livestock (cattle, pig, goat, chicken, duck, turkey) (R.B.L., pers. comm.), and these IAs are only a few miles from the nearest town where they can obtain additional food supplies from the market, especially that most of them have their own means of motorized transport. As in Melo et al. (2015) in Novo Paraíso, a similar fishbone human settlement also in the Guyana shield, subsistence hunting does not play a significant role in the diet of the settlers in these fishbone human settlements in the Guyana shield of the Brazilian Amazonia.

Thus, the structure of the mammalian assemblages here studied were determined by the structure of the vegetation, whether it was the highly heterogeneous vegetation mosaics of the northern part of the Guyana shield, the ombrophilous forests of the southern part, or a transition between them, and in the case of the IAs, the integrity of the mammalian assemblages were also maintained by the large tracts of surrounding undisturbed forests that allowed an efficient source-sink balance and recolonization of the depleted areas.

How sustainable were the hunted-mediated impacts of these fishbone human settlements (IAs)?

Despite the fact that the structure of the mammalian assemblages did not present any statistically significant differences between PAs and IAs, one major change, the local extirpation of *Tayassu pecari* from the IAs, predicts their bleak future. The structure of the mammal assemblage also appears to be changing in these settlements because in the protected areas the most abundant species are the three largest mammals, namely, *Tayassu pecari*, *Panthera onca*, and *Tapirus terrestris*, whereas in the impacted areas the most abundant species are smaller: a rodent, *Dasyprocta leporina*, followed by *Tapirus terrestris*, and *Mazama americana*. *D. leporina* was also the most abundant mammalian species in the nearby Novo Paraíso human settlement (Melo et al. 2015).

Deforestation and hunting are among the main causes of species extirpation in the tropics, and have been responsible for what is considered the sixth major extinction event of the planet (Brook et al. 2003; Thomas et al. 2004; Asfora and Mendes Pontes 2009; Mendes Pontes et al. 2016). Some species may even be driven to extinction before they are known by scientists, or described, such as was the case of a primate and a deer in northeastern Brazil (Mendes Pontes et al. 2016). The only alternative to avoid such catastrophic extinctions is to prevent the first stages of the anthropogenic impacts in the environment, such as those that are occurring in the impacted areas of this study. It should be a matter of time until we can witness its devastating impacts on the mammalian assemblages.

Conclusion

This study confirmed that the northernmost Brazilian Amazonia, in the Guyana shield, is one of the poorest regions in mammal species, and is poorest in those sites that are drier and that have a longer dry season, such as Maracá Ecological Station. No significant differences were detected between protected and impacted areas, possibly because the fishbone human settlements are relatively young and surrounded by vast tracts of source forests, allowing the structure of the mammalian assemblage to be maintained even under the human pressure exerted by these settlements. The local extirpation of *Tayassu pecari* in these impacted areas, however, and lower abundances of other large mammals such as *Panthera onca*, suggest imminent changes to the mammalian assemblage structure.

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