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ORIGINAL ARTICLE

Responses of ground-dwelling birds and mammals to local environmental variables and human pressure in an Amazonian protected area

Carlos R. Brocardo[1,2,3] · **Dian C. P. Rosa**[1,4] · **Arlison B. Castro**[5,6] · **Clarissa Rosa**[7] · **Kelly Torralvo**[5] · **Pedro Pequeno**[8] · **William E. Magnusson**[7] · **Rodrigo F. Fadini**[1]

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Abstract

Vertebrates play key roles as seed dispersers, herbivores, and top predators in tropical ecosystems. Therefore, obtaining population estimates for these species and understanding the factors that affect them are essential for wildlife management since changes in their populations have consequences for entire ecosystems. Vertebrate abundances in tropical forest may be related to habitat characteristics, resource seasonality, and human pressure. However, how ecological variables and human pressure concurrently influence animal abundances is not well understood. We investigated the associations between the number of records of vertebrates (ground-dwelling birds and medium- and large-sized mammals) and habitat features, food availability, and human pressure in a sustainable protected area in the Brazilian Amazon of western Pará, Brazil. Our study design included the recording of animals at 38 camera trap stations, sampling of environmental variables (canopy cover, leaf area index, tree height, and local altitude) and food resources (fruit or prey biomass), and measurement of a hunting pressure proxy (distance from human settlements). Our results indicated that groups responded in different ways: omnivorous mammals were affected positively by local altitude, canopy openness, and leaf area index; game birds were affected positively by local altitude and leaf area index; ungulates were affected negatively by local altitude and positively by food resources; and large rodents were affected only by food resources (positively). In contrast, insectivorous mammals and mesopredators were not affected by any variable we tested. Surprisingly, no groups responded to distance from human access, although the low number of records of large species, such *Tapirus terrestris* and *Dicotyles tajacu*, suggests that the sampled area may suffer from significant hunting pressure.

Keywords Poaching · Resource seasonality · Tropical forest · Defaunation · Amazonian wildlife

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✉ Carlos R. Brocardo
carlosbrocardo@hotmail.com

[1] Universidade Federal do Oeste do Pará, Programa de Pós-Graduação em Biodiversidade, Rua Vera Paz, CEP 68040-255 Santarém, Pará, Brazil

[2] Instituto Neotropical: Pesquisa e Conservação, Curitiba, Paraná, Brazil

[3] Universidade Tecnológica Federal do Paraná, Estr. p/ Boa Esperança, km 04-Zona Rural, Dois Vizinhos CEP 85660-000 Paraná, Brazil

[4] Fundação Oswaldo Cruz (Fiocruz), Laboratório de Pesquisas Clínicas e Políticas Públicas de Doenças Infecciosas e Parasitárias-PPP, Belo Horizonte, Minas Gerais, Brazil

[5] Instituto Nacional de Pesquisas da Amazônia-INPA, Programa de Pós-Graduação em Ecologia, Amazonas, Manaus, Brazil

[6] Universidade Federal do Oeste do Pará, Laboratório de Ecologia e Conservação, Instituto de Biodiversidade e Florestas, Santarém, Pará, Brazil

[7] Instituto Nacional de Pesquisas da Amazônia-INPA, Coordenação da Biodiversidade, Manaus, Amazonas, Brazil

[8] Universidade Federal de Roraima, Programa de Pós-Graduação em Recursos Naturais, Boa Vista, Roraima, Brazil

Introduction

Birds and mammals are responsible for seed dispersal of more than 80% of tropical tree species (Peres and Van Roosmalen 2002; Almeida-Neto et al. 2008), which is key to plant recruitment and is a driver of vegetation structure (Schupp et al. 2010). Furthermore, mammals and birds play an essential role as seed predators and herbivores, contributing to the maintenance of forest diversity (Villar et al. 2020b). Such vertebrates occupy various trophic levels, from primary consumers to top predators, connecting complex ecological networks (Vidal et al. 2013), fostering energy flow and biochemical cycling, and returning nutrients to the soil (Villar et al. 2020a).

Additionally, tropical forest birds and mammals also provide ecosystem services. Through seed dispersal, they promote the recruitment of hardwood trees that capture more carbon and help to reduce the effects of climate change (Bello et al. 2015). Numerous plants that provide timber and non-timber forest products depend on animals for their recruitment (Haugaasen et al. 2010; Brocardo et al. 2018). Predators control the populations of species that cause damage to agriculture or are disease transmitters (O'Bryan et al. 2018). In addition, large vertebrates, mainly mammals and birds, are an important protein source for people living in tropical ecosystems throughout the world (Jerozolimski and Peres 2003; Nasi et al. 2011).

These tropical ecosystems are heterogeneous landscapes where environmental characteristics may change spatially and temporally (Alves et al. 2010; Fadini et al. 2021), creating a gradient of habitats that influences the presence and abundance of animal species. Mammals and birds may respond to vegetation type (Haugaasen and Peres 2007; Galetti et al. 2009; Tardio and Da Silveira 2015), to food and water resource (Keuroghlian et al. 2004; Tardio and Da Silveira 2015; Rabelo et al. 2019; Weiler et al. 2020), to water regime seasonality (Mamede and Alho 2006), to altitudinal gradient (Morais et al. 2019), and also to competitor and predator presence (Newsome et al. 2017).

In addition to natural features, birds and mammals in tropical ecosystems have their presence and abundance affected by human pressures such as deforestation (Kinnaird et al. 2003; Weiler et al. 2020), habitat fragmentation (Crooks et al. 2017), fires (Barlow and Peres 2006), logging (Brodie et al. 2015), roadkill (Cáceres 2011; Rosa and Bager 2012), and overhunting (Benítez-López et al. 2017; Sampaio et al. 2022). Overhunting is a particularly powerful threat because it may even affect animal populations in large continuous habitats (Peres and Palacios 2007; Galetti et al. 2017; Rosa et al. 2021c). There are many reported cases of human impacts being related to human access, notably via distance effects (Antunes et al. 2016; Prasniewski et al. 2022). Therefore, determining the factors that contribute to the presence and abundance of animals is necessary to evaluate the effects of human pressures (Jorge et al. 2013).

In this study, we investigated the effects of environmental characteristics (e.g., food source, canopy openness) and human pressure on ground-dwelling medium- and large-sized mammals and birds in a protected area of the Amazon Forest. The Amazon Forest is the world's largest tropical forest and one of the areas richest in vertebrates (Hawkins et al. 2007; Schipper et al. 2008). It has had an influence on the evolutionary history and biodiversity of the entire Neotropical region (Antonelli et al. 2018). Improving our understanding of the concurrent role of ecological variables and human pressure on animal abundances can assist in planning effective conservation and management strategies (Michalski et al. 2015).

Accordingly, we tested the following hypotheses:

H1. Response to local resources: Animals change habitat use according to resource availability; therefore, we expected the number of animal records to be higher in sites with more food resources during the survey period.
H2. Habitat structure: The occurrence of animals is related to habitat characteristics. We expected animal records to be positively or negatively related to structure, depending on the group of species studied. For example, sites with higher leaf density might have a greater abundance of birds and mammals in response to the increase in refuge availability.
H3. Human pressure: The distance from human access (e.g., roads, rivers) and settlements is related to hunting pressure in the Amazon Forest and thus to vertebrate occurrence. Therefore, we expected the number of terrestrial bird and mammal records to increase with increasing distance from roads and human settlements.

Materials and methods

Study area

This study was carried out in the Tapajós National Forest (TNF), a protected area covering 527,319 ha (IUCN category VI—protected area with sustainable use of natural resources) (ICMBio 2019), located on the right bank of the Tapajós River in the Tapajós Endemism Area of the Amazon Forest, western Pará state, Brazil (Silva et al. 2005). The altitude ranges from 8 to 330 m, with a predominance of dense and open rain forests. Mean annual temperature is 25.5 °C, mean annual rainfall is 1820 mm, and there is a 4-month dry season between August and November, although normally, there is some precipitation in all months of the year (ICMBio 2019).

Pre-Columbian settlements have been present in this region for at least 4500 years (Stenborg et al. 2012; Maezumi et al. 2018). European colonization began in the seventeenth century with the foundation of Portuguese villages (Santarém and Aveiro) (IBGE 1957), although colonization intensified in the early twentieth century with the start of the rubber boom (ICMBio 2019). The TNF was established in 1974 as a sustainable protected area for the conservation and sustainable use of natural resources. Traditional communities living within its limits were allowed to remain and exploit natural resources (ICMBio 2019). Approximately 9000 people live in the TNF in 31 communities, some of which are recognized as indigenous people (ICMBio 2019). The construction of the Cuiabá-Santarém highway (BR-163) in 1970 changed the landscape around the TNF, leading to loss of forest cover along the highway and access from unpaved roads, which increased with the expansion of soy bean culture in this region after the mid-1990s (Fearnside 2007; Garrett et al. 2013). Due to forest loss and habitat fragmentation in this landscape, the TNF is considered essential to the conservation of mammals in the region (Sampaio et al. 2010; Rosa et al. 2021c).

Currently, the TNF is managed through a reduced-impact timber-harvest system, which is restricted to areas defined by a Management Plan established by the Chico Mendes Institute for Biodiversity Conservation (ICMBio), the governmental agency responsible for the administration of federal protected areas in Brazil, with the participation of local communities living in the TNF. The TNF residents also extract non-timber products to consume and sell and practice subsistence hunting. Although subsistence hunting is only allowed for residents, the TNF suffers from poaching by outsiders (ICMBio 2019) Fig.1.

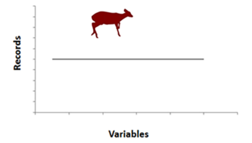
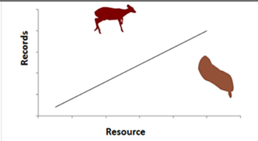
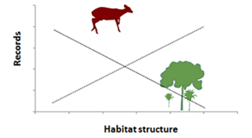
Tested hypotheses	Description of the expected response	Sketch of expected response
H0: Null hypothesis	The number of records of birds and mammals will not be affected by the tested variables	
H1: Response to resource	The number of records will increase according the resource availability in the survey period.	
H2: Habitat structure	The number of records will respond (negative or positively)to habitat characteristics	
H3: Human pressure	The number of records will increase with distance from human access (residences and roads)	

Fig. 1 Hypotheses, with their respective descriptions, and a sketch of the expected results

Study design

We sampled mammals and game birds with camera traps, a method widely used to monitor wildlife in tropical forests (Ahumada et al. 2013; Jansen et al. 2014). Our sampling design was composed of four Rapid Assessments and Long-term Ecological Research modules (RAPELD) established to monitor biodiversity in the TNF as part of the Brazilian Program for Biodiversity Research (PPBio) (Magnusson et al. 2005; Rosa et al. 2021a). Each is rectangular in shape, 1 km in width, and 5 km in length and has 10 regularly spaced plots (250-m length and variable width following the terrain contour) separated by a minimum distance of 1 km (Magnusson et al. 2013). We installed a single unbaited camera trap (Bushnell 12Mp Natureview Cam Essential HD Low Glow®, $n = 12$; Primus Proof Cam 3 Review®, $n = 5$; and Moultrie A5 Low Glow Game Camera®, $n = 3$) deployed out of the RAPELD module trail (5 to 20 m), with a total of ten camera trap stations per module (Fig. 2). The position of each camera trap was recorded with a GPS device (Garmin 62S, Garmin International Inc., Kansas, USA). We installed the cameras on trees, 30–40 cm from the ground, close to paths used by animals, and programmed them to record photographs (three photographs per trigger) or videos (10 s), with a 1-s delay, operating for 24 h/day for 34 days. Due to the number of camera traps being less than the number of stations and logistical reasons, we sequentially sampled the modules between July and December 2019 (dry season). We obtained data for only 38 stations because two camera traps failed to work.

Response variables

We used the number of records of game birds and medium- (> 1 kg) and large-sized (> 20 kg) mammals recorded per camera trap as surrogates for animal abundance (Haugaasen and Peres 2007; Galetti et al. 2009; Hawes and Peres 2014; Hong et al. 2015; Michalski et al. 2015; Alvarenga et al. 2018; Scabin and Peres 2021). Although the use of camera trap records as a measure of animal abundance does not account for imperfect and variable detection (Sollmann et al. 2013), some studies have shown that they are correlated (Rovero and Marshall 2009; Parsons et al. 2017; Palmer et al. 2018). Observations of the same species at a camera trap station were considered independent records only after an interval of 24 h between them. When more than one individual of a species was recorded in a single event, we counted them and considered the sum of individuals as the number of records. We did that because group size may

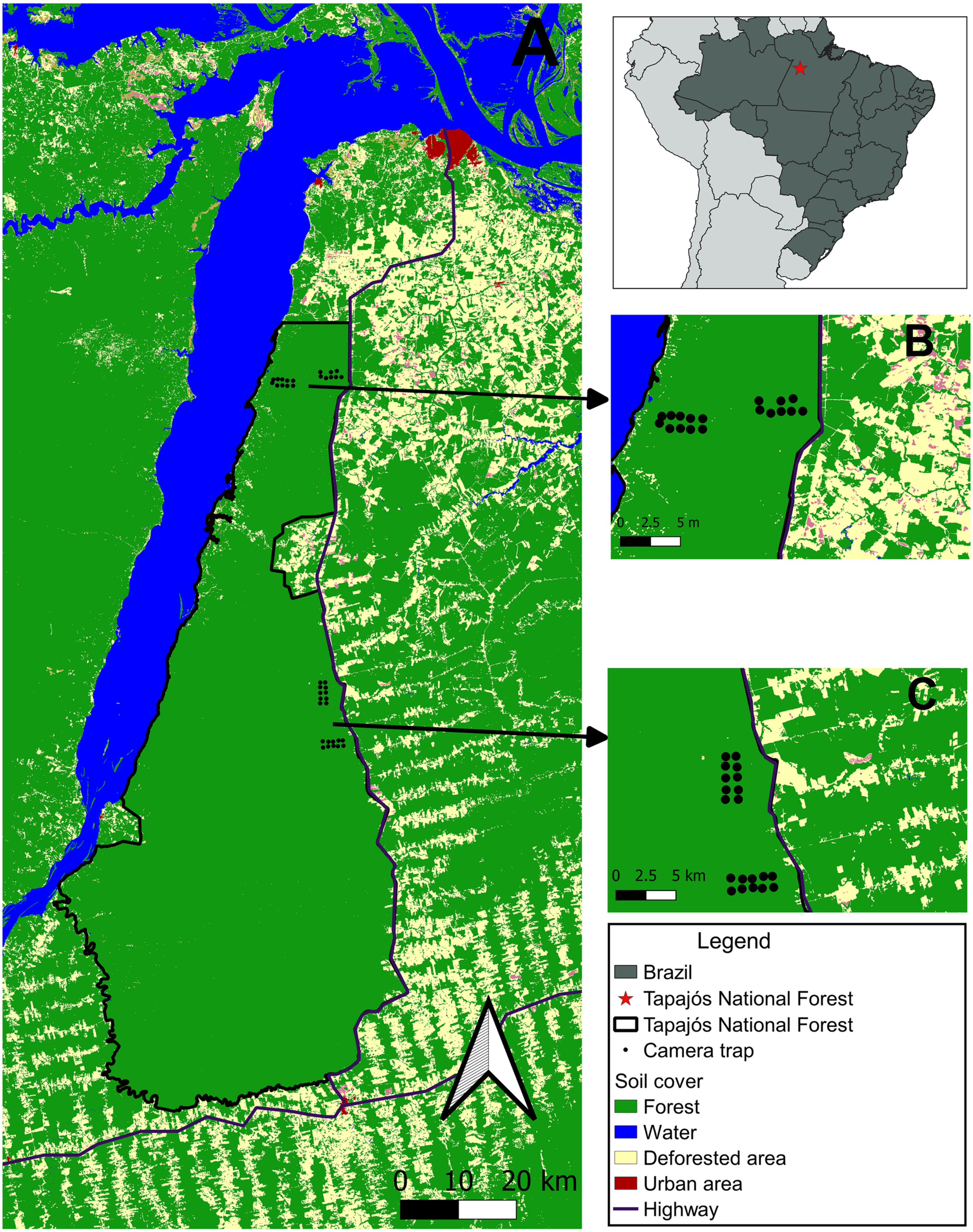


Fig. 2 Location of the Tapajós National Forest (**A**) and an enlarged images of areas around RAPELD-modules (**B, C**)

be affected by habitat characteristics and human pressure (Reyna-Hurtado et al. 2016), and so the variation in group size could be a response to environmental changes or human pressure in our study area.

Species were identified using standardized guides (Reis et al. 2010, 2015). We grouped them according to their diets and whether they were used as game by humans as follows: terrestrial game birds, omnivorous mammals, insectivorous mammals, large rodents, ungulates, mesopredators, and top predators (Ahumada et al. 2011; Kutt and Gordon 2012; Michalski et al. 2015; Paredes et al. 2017). Game birds include all large ground-dwelling birds; omnivorous mammals include mammals that have omnivorous diet and are lesser preferred by hunters in our study region (Torres et al. 2021); large rodents include two preferred rodents by hunters (Torres et al. 2021); insectivorous mammals included ant eaters and armadillos; the latter ones are a preferential hunted group (Torres et al. 2021) and, despite including other food items in their diet, have a predominant consumption of insects and other invertebrates (Sikes et al. 1990; da Silveira Anacleto 2007; Whitaker et al. 2012); ungulates included hoofed mammals, a very preferred group by hunters (Torres et al. 2021); and finally, mesopredators and top predators include, respectively, medium and large feline species found in our study area (Table 1).

Table 1 Total number of records of ground-dwelling mammals and birds

Functional group/species	Number of records	Number of stations
Large rodents		
Cuniculus paca	89	21
Dasyprocta croconota	322	37
Game birds		
Crypturellus variegatus	6	5
Crypturellus sp.	4	2
Odontophorus gujanensis	36	6
Pauxi tuberosa	12	6
Penelope pileata	1	1
Penelope superciliaris	7	6
Psophia dextralis	57	19
Tinamus guttatus	15	8
Tinamus tao	49	19
Tinamus sp.	6	5
Ungulates		
Mazama americana	9	6
Mazama nemorivaga	34	19
Mazama sp.	2	2
Dicotyles tajacu	41	6
Tapirus terrestris	3	2
Insectivores		
Cabassous unicinctus	1	1
Dasypus beniensis	20	5
Dasypus novemcinctus	24	13
Dasypus sp.	6	4
Myrmecophaga tridactyla	4	3
Priodontes maximus	1	1
Tamandua tetradactyla	6	5
Omnivores		
Atelocynus microtis	1	1
Cerdocyon thous	1	1
Didelphis marsupialis	40	15
Eira barbara	2	2
Nasua nasua	10	3
Mesopredators		
Leopardus pardalis	8	8
Leopardus wiedii	3	3
Top predators		
Panthera onca	2	2
Puma concolor	3	2

Explanatory variables

Food resources At the end of each survey, two observers collected all fruits and seeds on the ground in plots (250-m long and 1-m wide) adjacent to each camera trap (5 to 20 m). Fruits and seeds were dried in an oven at 70 °C for 48 h and weighed (Silva et al. 2019). We used dry fruit/seed biomass as an explanatory variable for game birds, omnivorous mammals, large rodents, ungulates, and insectivorous mammals. For the last group, we included fruit biomass as a proxy of insect abundance, since insects are positively related to fruit availability (Pizo and Oliveira 2000; Szinwelski et al. 2015), and *Dasypus* species consume fruits as well as invertebrates. We used the biomass of the prey (*Dasypus* spp., omnivores, large rodents, and game birds) recorded by the camera traps as food resources for mesopredators. To obtain the total biomass for each camera trap, we multiplied the mean body mass of a given species by the number of records and summed this for all species. Biomass data were log-transformed to improve model fit.

Habitat structure We chose habitat features that have been widely shown to impact ecology, density, and abundance of ground-dwelling mammals and birds, including canopy openness, mean height of trees, leaf area in the lower forest stratum (a between 0 and 15 m high), and local altitude. The first three variables were measured along each plot (250 m) using a light detection and ranging (LIDAR) ground portable device (Model LD90-3100VHS-FLP, Riegl, Horn, Austria), which scans the environment with a laser for rapid measurement of multiple variables quantifying forest structure (see Torralvo et al. 2020). Thus, the value for each plot represents a mean value obtained along its length for canopy openness (in percentage), leaf area (index), and height tree (meters). We measured the local altitude (meters, at sea level (a.s.l.))

with a hand-held GPS device (Garmin 62S) and checked it using Google Earth, which provides reliable and accurate elevation data (Wang et al. 2017).

Human pressure We used the distance (meters) of camera trap stations from human residences and roads as an index of human pressure, since hunting activities are commonly linked to distance from such access points (Peres and Lake 2003). We plotted the positions of residences and roads with the aid of Google Earth images and field inspections. Distances from camera trap stations to residences and roads were measured with Qgis 3.4.1.5 (QGIS.org 2021).

Data analysis

We undertook all analyses in R version 3.6.2 (R Core Team 2019). To investigate the influence of the explanatory variables on the number of records of each functional group, we used generalized linear models (GLM) with MASS package (Ripley et al. 2021). We also tested generalized linear mixed models (GLMM), with RAPELD modules as a random factor to account for within-module autocorrelation. However, including the random factor did not improve our models (resulting in larger values of Akaike's information criterion for small samples (AICc)); thus, we opted for simpler models. Before running the models, we tested the multicollinearity between the explanatory variables using the variance inflation factor (VIF) function (*vif.cca*) in the *vegan* package (Oksanen et al. 2019). Due to a high VIF, we excluded two variables (tree height and distance from roads) with VIF > 5 (Zuur et al. 2009). Tree height was significantly related to local altitude; therefore, we retained the latter because in addition to influences on forest structure, it may be a surrogate for other habitat characteristics, such as litter deposition, soil type, and water drainage (Costa and Magnusson 2010). Distance from roads and distance from residences were also related; we retained the latter because we considered it being more important since it represented the constant presence of people who might engage in hunting (Torres et al. 2021).

We used the negative binomial distribution with log link instead of the Poisson distribution because of overdispersion, with the exception of the data for mesopredators, for which we used the binomial distribution due to the low number of records (absence or presence). We tested the model adjustment the residual diagnostic in the *DHARMa* package (Hartig and Lohse 2020). Analysis of the spatial autocorrelation of residuals (*ncf* package; Bjornstad 2020) indicated that the game bird group was spatially autocorrelated when using a negative binomial distribution; therefore, we log-transformed the raw data to obtain an approximately normal distribution and used it in a model assuming Gaussian errors, which resulted in residuals without spatial autocorrelation. The pseudo-R^2 statistics of the models were calculated using Efron's pseudo-R^2 function available in the *performance* package (Lüdecke et al. 2021). We plotted partial regressions using the *visreg* package (Breheny et al. 2020).

Results

We recorded a total of 21 medium- and large-sized mammal species and eight game bird species (Table 1). The number of records ranged from 2 to 59 per camera trap station (mean ± SD = 21.7 ± 15.08). The functional group most recorded was large rodents with 411 records (mean = 10.8 ± 8.8; range = 0–40), present at 37 of the 38 camera trap stations, followed by game birds with 193 records (mean = 5.07 ± 6.9; range = 0–38; present at 36 stations), ungulates with 89 records (mean = 2.34 ± 4.8; range = 0–27; present at 22 stations), insectivorous mammals with 62 records (mean = 1.63 ± 2.2; range = 0–12; present at 26 stations), omnivorous mammals with 54 records (mean = 1.42 ± 2.3; range = 0–8; present at 18 stations), mesopredators with 11 records (mean = 0.28 ± 0.45; range = 0–1; present at 11 stations), and top predators with only 5 records (mean = 0.13 ± 0.41; range = 0–2; present at 4 stations).

The local altitude ranged from 83 to 209 m a.s.l. (mean = 149.9 ± 39.4 m a.s.l.), leaf area index from 1.21 to 3.09 (mean = 2.01 ± 0.43), canopy openness from 15.2 to 69.6% (mean = 42.1 ± 11.5%), distance from human residences from 1.6 to 6.4 km (mean = 3.85 ± 1.25 km), fruit biomass from 0 to 6.77 kg (mean = 0.91 ± 1.59 kg), and prey biomass (food resource for mesopredators) from 2.1 to 267.4 kg (mean = 61.7 ± 55.3 kg).

Large rodents were significantly positively affected by food resources. Game birds responded positively to local altitude and leaf area index. Ungulates were recorded more at lower altitudes and were positively affected by fruit biomass. Omnivorous mammals were positively affected by leaf area index, canopy openness, and local altitude. Insectivorous mammals and mesopredators did not respond to any variable. The low number of records of top predators did not allow the analysis for this group. Surprisingly, distance from human residences did not affect any functional group (Table 2; Fig. 3).

Discussion

Our results show different patterns in animal records in the same continuous forest according to differences in local habitat characteristics. The habitat heterogeneity of tropical ecosystems, and especially in the Amazon, is considered a key element in maintaining high levels of biodiversity and community structure (Haugaasen and Peres 2007; Ahumada et al. 2011; Rojas-Ahumada et al. 2012; Maximiano et al. 2020).

Table 2 Results of generalized linear model analysis of records of functional groups in relation to explanatory variables

Functional group			Variable					
		Intercept	Altitude	Food resource	Canopy openness	Leaf area index	Distance from settlements	Pseudo-R^2
Game birds	Coefficient	−3.793	0.011	−0.055	0.024	1.468	< 0.001	0.35
	Std. error	1.436	0.004	0.071	0.013	0.378	< 0.001	
	z-value	−2.642	2.848	−0.770	1.908	3.884	−0.398	
	$\Pr(>\lvert z\rvert)$	**0.012**	**0.008**	0.447	0.065	**< 0.001**	0.693	
Insectivores	Coefficient	1.762	−0.009	0.038	0.018	−0.079	< −0.001	0.30
	Std. error	1.939	0.005	0.097	0.016	0.495	< 0.001	
	z-value	0.909	−1.918	0.392	1.098	−0.159	−1.407	
	$\Pr(>\lvert z\rvert)$	0.363	0.055	0.695	0.272	0.873	0.159	
Large rodents	Coefficient	−0.430	0.001	0.187	0.018	0.578	< −0.001	0.23
	Std. error	1.360	0.003	0.069	0.012	0.352	< 0.001	
	z-value	−0.317	0.327	2.699	1.527	1.640	−1.106	
	$\Pr(>\lvert z\rvert)$	0.751	0.744	**0.007**	0.127	0.101	0.269	
Mesopredators	Coefficient	−5.564	0.007	0.648	0.041	0.445	< −0.001	0.15
	Std. error	4.623	0.012	0.457	0.043	1.223	< 0.001	
	z-value	−1.203	0.625	1.418	0.962	0.364	−1.237	
	$\Pr(>\lvert z\rvert)$	0.229	0.532	0.156	0.336	0.716	0.216	
Omnivores	Coefficient	−12.170	0.020	0.194	0.077	2.385	0.000	0.34
	Std. error	2.735	0.007	0.130	0.026	0.622	0.000	
	z-value	−4.451	2.859	1.500	3.007	3.832	−0.356	
	$\Pr(>\lvert z\rvert)$	**< 0.001**	**0.004**	0.134	**0.003**	**< 0.001**	0.722	
Ungulates	Coefficient	3.066	−0.020	0.414	−0.018	−0.728	< 0.001	0.23
	Std. error	2.704	0.007	0.160	0.024	0.700	< 0.001	
	z-value	1.134	−2.668	2.587	−0.778	−1.040	0.388	
	$\Pr(>\lvert z\rvert)$	0.256	**0.008**	**0.010**	0.437	0.299	0.698	

Values in bold indicate statistically significant results

The results supported our first hypothesis only for large rodents and ungulates, which were more frequent in the plots with high fruit biomass, indicating that these groups of animals may respond more intensively to changes in the availability of this resource than those in other groups. The diets of Neotropical ungulates and of large rodents are highly frugivorous (Salas and Fuller 1996; Silvius and Fragoso 2003; Keuroghlian et al. 2004), and they are the main taxa involved in the removal of fruits and seeds from the forest floor (Galetti et al. 2015; Camargo-Sanabria and Mendoza 2016; Brocardo et al. 2018; Rosa et al. 2021b). The higher records of ungulates at sites with high fruit biomass may result from the concentration of their activities near fruiting trees (Beck–King et al. 1999; Foerster and Vaughan 2002; Silvius and Fragoso 2003; Keuroghlian et al. 2004; Tardio and Da Silveira 2015). Concurrently, the absence of effect of fruit biomass on game birds and omnivorous mammals may be related to use of other food resources by these groups (Jordano 2000), such as arthropods, which could be more important than fruits for some species. In addition, the largest fruit biomass was found in plots with high incidence of *Attalea*, whose fruits on the ground are consumed mainly by large rodents and ungulates (Silvius 2002).

Although other groups did not respond to fruit biomass, they were significantly affected by habitat structure, corroborating our second hypothesis. Local altitude positively affected game birds, most likely as an indirect effect of vegetation changes along the altitudinal gradient, which may be related to the type and amount of foodstuffs. For example, Capaverde and collaborators found positive relation between altitude and the number of fruit plants and the insect biomass in Central Amazon (2018). Game birds also positively responded to higher leaf area index, a metric which correlates with high vegetation density in the understory (from zero to 15 m) and so which may provide protection from predators and opportunities for nest hiding by such species (Estrada et al. 2002; Depalma and Mermoz 2019). The protection provided by vegetation may also explain the positive relationship between omnivorous mammals and altitude and leaf area index, since they use dense vegetation to avoid predators (Dutra et al. 2011; Gorini et al. 2012). In addition, a larger net leaf area could also be linked to greater availability of foraging sites. Records of omnivores were dominated by *Didelphis marsupialis* and *Nasua nasua* (74% and 18% of the records, respectively). Both are scansorial species, able to climb and forage in understory vegetation (Beisiegel and Mantovani

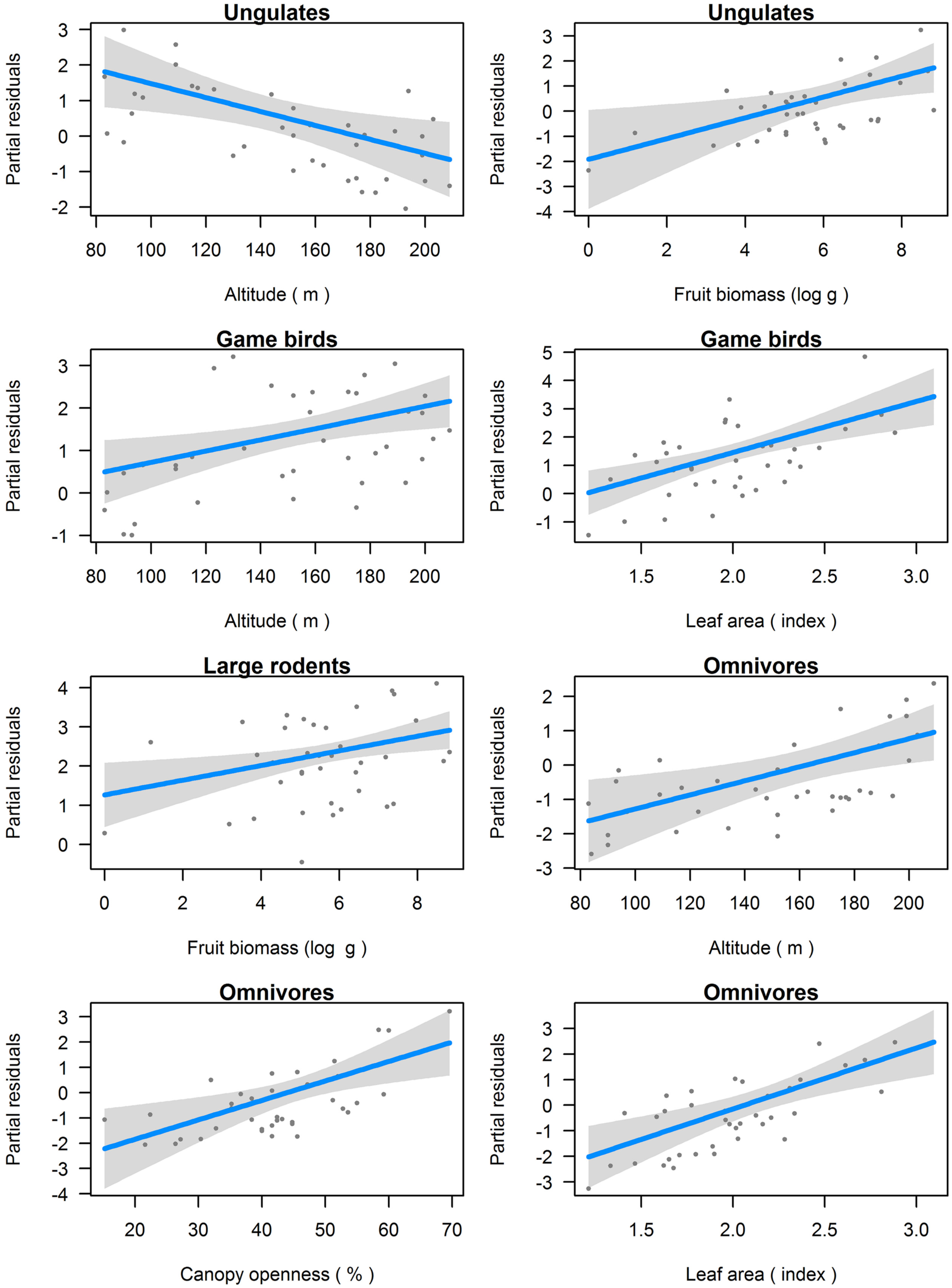


Fig. 3 Partial residuals of records (log scale) of each functional group in relation to significant predictors

2006; Rossi et al. 2010). Omnivore records were also related to canopy openness, which may be associated with increases in such food sources as fruits, small vertebrates, and arthropods (Levey 1988; Basset et al. 2001; Silveira et al. 2010; Garda et al. 2013; Tardio and Da Silveira 2015).

In contrast to game birds and omnivorous mammals, ungulates were negatively affected by local altitude, and insectivorous mammals (armadillos and ant eaters) also tended to have a negative relationship with local elevation. Since lower-altitude sites may be closer to streams (Capaverde Jr et al. 2018), they may provide greater access to water resources, a factor important for explaining the abundance of large Neotropical mammals (Michalski et al. 2015; Paredes et al. 2017; Antunes et al. 2019; Weiler et al. 2020). In addition, the lower-elevation sites also show differences in vegetation composition and soil moisture (Costa and Magnusson 2010). The quality of the understory vegetation is important for browser species, such as *Mazama* spp. and *Tapirus terrestris* (Salas and Fuller 1996; Gayot et al. 2004). Armadillos (insectivorous) and peccaries (ungulates) both forage at sites with humid soil and avoid high temperatures (Desbiez et al. 2009; Goulart et al. 2009).

Mesopredators (*Leopardus* spp.) did not respond to any measured variable. Previous studies have shown this group to be affected by forest cover (Harveson et al. 2004; Goulart et al. 2009; Wang et al. 2019); however, with our study site being a continuous area, forest cover may have varied little between sampling plots. Furthermore, these species are generalists in terms of their habitat use, with high mobility and large home ranges (Dillon and Kelly 2008; Kasper et al. 2016); therefore, micro-scale habitat features may have few effects on their presence. In addition, the greater part of the diet of *Leopardus* spp. is based on small mammals (< 1 kg) (Wang 2002), a group not investigated in our study. The different *Leopardus* species may also have different habitat requirements, and grouping them together may have masked these specificities.

No groups responded to distance from human settlements; thus, our third hypothesis (human pressure) was not supported. Several previous studies have demonstrated that human access or settlements can negatively impact animal populations and alter their habitat use in tropical forests (Peres and Lake 2003; Cruz et al. 2014; Antunes et al. 2016; Benítez-López et al. 2017; Morais et al. 2019). Hunters in the Amazon walk up to 9 km into the forest (Peres and Lake 2003); therefore, our result must be interpreted with caution, since the maximum distance between plots and human residences or road access was just over 6 km, implying that all our sampling plots may be similarly impacted by human pressure. For instance, Peres and Lake (2003) showed that some ungulates and game birds may need more than 4–5 km to be released from hunting pressure in the Amazon forest, while Prasniewski and colleagues (2022) showed that the effects of accessibility may extending up to 10 km inside the forest, in an analysis of incidence of illegal activities, including poaching, in two protected areas of the Atlantic Forest. Hunting is common in our study area region, with large rodents, ungulates, insectivorous mammals, and game birds being the main prey consumed by local people (Torres et al. 2018, 2021). The few records of the largest species (*Tapirus terrestris* and *Dicotyles tajacu*) and the absence of *Tayassu pecari* in our plots may indicate a defaunation process linked to hunting pressure (Peres and Palacios 2007; Antunes et al. 2016; Galetti et al. 2017; Rosa et al. 2021c).

Conclusion

Our results indicate that habitat features are important predictors of vertebrate presence in forested areas of the Amazon Basin, although different groups of animals respond in different ways. This finding reinforces the role of habitat heterogeneity in animal assemblage structure. Because environmental characteristics vary in their importance to different groups, conservation strategies demand the protection of a diversified range of contiguous habitats. Large reserves are widely used as a conservation tool in the Brazilian Amazon, and although they are normally large enough to include a heterogeneous landscape, 62% of the protected surface of Brazilian protected areas in Amazon is destined for sustainable use of natural resources (Veríssimo et al. 2011), as is our study site. This means that there is a likelihood of habitat quality changing over time due to human use; therefore, we recommend constant monitoring to evaluate how biodiversity responds to anthropogenic changes. Future planning must account for such eventualities. We also recommend future studies to address the distances traveled to hunt as means of better understanding the impact of humans on animal populations in this region.

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Author contribution The study conception and design were performed by Rodrigo F. Fadini, Carlos R. Brocardo, Dian P. Rosa, Clarissa Rosa, Arlison C. Bezerra, and William E. Magnusson. Data collection was performed by Dian P. Rosa, Arlison C. Bezerra, Carlos R. Brocardo, Clarissa Rosa, Kelly Torralvo, and Rodrigo F. Fadini. The analyses

were performed by Carlos R. Brocardo, Rodrigo F. Fadini, and Pedro Pequeno. The first draft of the manuscript was written by Carlos R. Brocardo and Rodrigo F. Fadini, while all authors commented on subsequent versions. All authors read and approved the final manuscript.

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Data availability The datasets generated during the current study are available as supplemental material.

Declarations

Competing interests The authors declare no competing interests.

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