



Research Paper

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Community-based monitoring reveals low anthropogenic pressure on a game vertebrate population in a sustainable-use Amazonian protected area

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Summary

Biodiversity systematic monitoring programmes have been expanding across the globe, especially in protected areas (PAs). Amongst sustainable-use PAs, medium- to large-sized mammals and birds comprise crucial groups to monitor, given their importance to forest functionality and subsistence for local residents. Here, we used 6 years of community-based monitoring data from a sustainable-use PA in the Brazilian Amazonia (Tapajós–Arapuins Extractive Reserve) to examine the influence of anthropogenic stressors and time on the density and biomass of forest mammal and bird game species. We further assessed trends in population density of target groups over the period. A total of 1915 km of line-transect surveys were completed by trained local monitors along eight established transects, providing data from 12 medium-sized and five large-sized game genera. Generalized linear mixed models of all medium-sized species, all large species and four individual taxa (Tinamidae, Dasyproctidae, primates and Cervidae) showed that some species (e.g., *Dasyprocta croconota*) exhibited great density, whereas others (e.g., *Tapirus terrestris* and *Tayassu pecari*) were rarely detected. Anthropogenic variables did not affect the density and biomass of the overall medium-sized and large vertebrates. Dasyproctidae, Tinamidae and primates were the only taxa influenced by anthropogenic stressors, with negative influence occurring only for Tinamidae. Moreover, density of groups and taxa remained stable throughout the period in the Reserve, although the frequency of some species may indicate past population losses. Continuation of this monitoring programme is required to improve understanding of population fluctuations, but over the 6 years studied, game population density and biomass were not linked to anthropogenic stressors.

Introduction

The implementation of systematic biodiversity monitoring programmes has been expanding across the globe, especially in protected areas (Schmeller et al. 2017, Reis & Benchimol 2023). As these programmes provide information on the status and trends of natural resources, including wildlife populations, they can greatly contribute to curbing the worldwide biodiversity crisis (Danielsen et al. 2022). In addition, these programmes can evaluate the impacts of a myriad of anthropogenic activities on biodiversity, including habitat destruction, climate change and wildlife overexploitation (da Veiga & Ehlers 2009). In Brazil, for instance, the federal government established a long-term and large-scale biodiversity monitoring programme across different protected areas, focused on assessing the conservation status of fauna and flora species in addition to evaluating their responses to anthropogenic pressures (Ribeiro 2018, Cronemberger et al. 2023). Implementing such initiatives is especially needed within sustainable-use protected areas, which retain high biodiversity and are home to Indigenous and other traditional human communities that rely on forest resources to survive (Lima & Pozzobon 2005).

Community-based monitoring programmes have been widely established to monitor game fauna in sustainable-use protected areas across tropical countries (Reis & Benchimol 2023). Besides providing spatiotemporal information on monitored game species and informing appropriate management actions (Danielsen et al. 2021), participatory programmes value the experiences and points of view of local people who have extensive knowledge of wildlife species. In particular, large and medium-sized forest species, including mammals and birds, are amongst the main target game fauna and represent most of the vertebrate biomass in tropical forests (Benítez-López et al. 2019). Species weighing more than 5 kg (hereafter, 'large-sized species') comprise the favourite targets of hunters (Constantino et al. 2008) due to their meat flavour and the greater return per unit of effort. In addition, large-sized vertebrate species are more vulnerable as they usually exhibit lower reproductive rates and are affected by external factors

such as anthropogenic activities (Cardillo et al. 2005). Therefore, the density of large species usually decreases in areas under pervasive anthropogenic pressure (potentially linked to hunting pressure), and this alters the structure of vertebrate communities and reduces vertebrate biomass (Peres 2000, Jerzolimski & Peres 2003). In addition, the reduction in vertebrate biomass often exceeds the changes in overall species abundance and species losses driven by anthropogenic activities, given that small species may be favoured and tend to proliferate in areas where large species were extirpated (Peres & Palacios 2007), a phenomenon termed ‘density compensation’ (MacArthur et al. 1972).

Several anthropogenic factors are highly associated with hunting pressure for forest game vertebrates, including hunter access points (e.g., communities and roads) and human population density (Beirne et al. 2019). For instance, Scabin and Peres (2021) showed that distance from villages and human population size represent good proxies of anthropogenic threats to large game vertebrates in a sustainable-use Amazonia protected area, as steep biomass declines were recorded near urban sites, indicating the greatest human pressure occurring there. Assessing the influence of anthropogenic variables on patterns of vertebrate density and overall biomass is important in sustainable-use protected areas given the potential for vertebrate populations to become depleted.

Declines in populations of large forest vertebrates driven by overhunting occur widely in tropical countries, particularly in Africa and Asia (Benítez-López et al. 2019). Thus, the diversity and relative abundance of large mammal species, such as primates and ungulates, decreased significantly near villages in Gabon due to high levels of hunting pressure (Koerner et al. 2017, Beirne et al. 2019). In Amazonian forests, heavily hunted forest sites have also experienced reductions in abundances of large mammals (Peres 2000). Nevertheless, terrestrial vertebrate populations have proved to be somewhat resilient to hunting in some Amazonian forest sites (e.g., Iwamura et al. 2014, Antunes et al. 2016), even though humans have been intensively hunting medium- and large-sized species there for many years. This is probably because many vast upland areas remain inaccessible to hunters, establishing a source-sink dynamic that can rescue over-harvested populations in heavily hunted areas (Antunes et al. 2016). Conversely, some Amazonian forest sites have experienced past population declines due to anthropogenic pressure, and currently they are recognized to be exhibiting a state of semi-defaunation (Peres et al. 2003). However, to better understand this dynamic, it is necessary to monitor game fauna over time and to generate spatiotemporal information on the monitored species.

Here, we used a comprehensive database from a 6-year community-based monitoring study in a sustainable-use protected area in the Brazilian Amazonia to evaluate: (1) how anthropogenic stressors and year modulate patterns of density and biomass of mammal and bird forest game species; and (2) how game populations fluctuate over the years (i.e., if the density of target groups and taxa are stable, increasing or decreasing over the evaluated time series). We extracted two variables related to hunting pressure (i.e., a proxy of human intensity (HI) and the distance to the nearest road) and estimated the overall density and biomass of large (≥ 5 kg) and medium-sized (0.54–5.00 kg for birds, 0.92–5.00 kg for mammals) game species pooled together, in addition to densities of the four taxa most frequently recorded within eight established linear transects per year across the Tapajós–Arapuins Extractive Reserve (hereafter, ‘RESEX-TA’). We hypothesize that the interaction between our two anthropogenic stressors would best explain the overall patterns of density

and biomass of large game taxa given the greater access of hunters and their greater preference for large species (Peres 2000). We expected to observe an increase in the overall densities and biomass of medium-sized game taxa in areas under greater human influence, caused by density compensation (MacArthur et al. 1972). We expected that Dasyproctidae and Tinamidae densities (medium-sized terrestrial taxa) would be positively influenced by anthropogenic stressors as a result of the compensatory effect, whereas for Cervidae (large-sized taxa) we expected to observe a negative influence. Similarly, because medium-sized primates such as capuchins are likely to be positively affected by human stressors due to the reductions of the large-bodied primates (i.e., Atelidae), we expected that population densities of Tinamidae, Psophiidae, Cracidae, Dasyproctidae, Procyonidae and Primates would increase over time, whereas intensive hunting would lead to decreases in Cervidae, Tayassuidae and Atelidae.

Materials and methods

Study area

This study was conducted in the RESEX-TA, a terrestrial extractive sustainable-use protected area in western Pará (Brazilian Amazonia; 02°20′–03°40′ S, 55°00′–56°00′ W; Fig. 1) created in 1998 to protect local people from the impacts of the expansion of logging companies (Oliveira et al. 2005). Covering a total area of nearly 650 000 ha, the RESEX-TA is currently the most human-populated extractive reserve in Brazil, housing c. 23 000 residents (Silva et al. 2022). It comprises the first Brazilian protected area of this category to develop a management plan, a technical document that establishes the zoning and norms that guide the use of the protected area.

The predominant vegetation is the ombrophilous forest (66.19% of the territory), characterized by large trees, with abundant woody, epiphytic and liana plants (Veloso et al. 1991, Instituto Brasileiro de Geografia e Estatística 1992) in *terra firme* (unflooded) forests. Other common plant typologies encompass secondary forest (8.88%), savannah (0.62%) and flooded forest (Carvalho-Junior 2008, Montag et al. 2012). The climate is humid tropical (Ami), with a rainy season from November to May and a dry season from August to October (Instituto Nacional de Pesquisas Espaciais & Centro de Previsão de Tempo e Estudos Climáticos 2023).

The RESEX-TA has 78 communities inhabiting areas along the Tapajós and Arapuins rivers (Silva et al. 2022), in addition to a few families living along small streams (Oliveira et al. 2005), Instituto Chico Mendes de Conservação da Biodiversidade 2014; Fig. 1). All communities are established in *terra firme* forests, in which the residents directly depend on the exploitation of natural resources (hunting, fishing and extraction of timber and non-timber forest products) and/or family farming and small-animal breeding (Saúde & Alegria 2012). Hunting is allowed for subsistence purposes, and its management depends on internal agreements signed between communities and reserve managers. In mid-2021, there was an attempt at logging through a community forest management plan, but the lack of prior popular consultation resulted in the cessation of activities.

Participatory Biodiversity Monitoring Project

In 2014, the Brazilian federal government’s Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) implemented the Brazilian Biodiversity Monitoring Program (Monitora

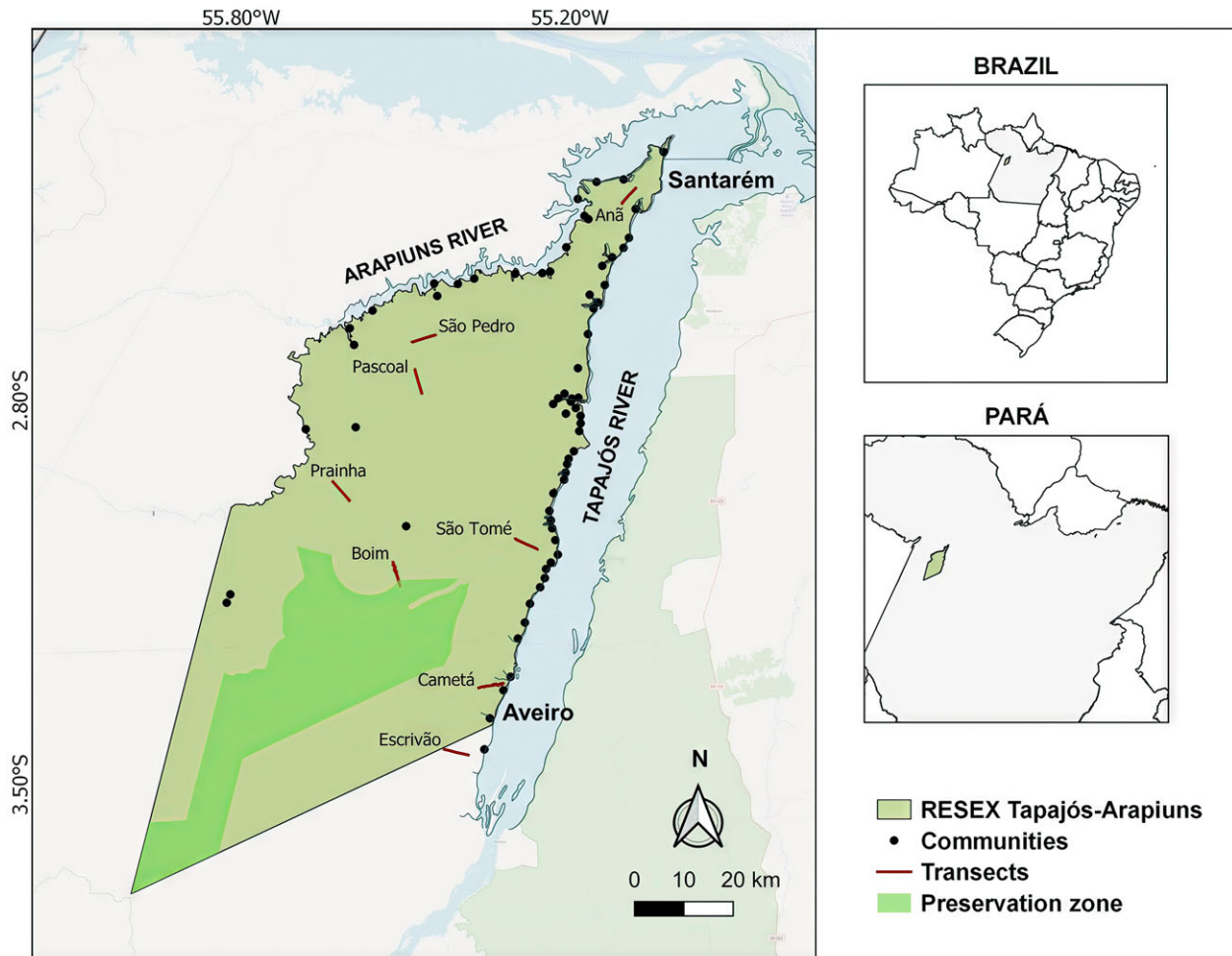


Figure 1. Location of the Tapajós–Arapiuns Extractive Reserve (RESEX) in the cities of Santarém and Aveiro (Pará), Brazil.

Program) in the RESEX-TA. Given that local residents expressed their willingness to understand the current and future population status of terrestrial game fauna (i.e., medium- to large-sized mammals and birds), the monitoring programme in the RESEX-TA focused on species belonging to these groups, as well as reptiles (total of 25 target species, carefully chosen by local people based on their hunting activities; Table S1). This programme was carried out via the Participatory Biodiversity Monitoring Project (PMPB), a partnership between ICMBio and the Instituto de Pesquisas Ecológicas (IPÊ; Ribeiro 2018).

Firstly, various meetings were conducted in the RESEX-TA to identify potential monitors belonging to these communities who would become responsible for transect establishment and data collection. In particular, transects needed to be placed in areas accessible on foot or by boat/canoe to the monitors, in areas lacking direct human impacts apart from hunting activities. Furthermore, transects were placed at various distances from the nearest community, with transects nearby being more likely to be affected by hunting pressure (Sampaio et al. 2023). Prior to effective implementation, potential areas were identified through maps, taking into account elevation profiles, obtaining coordinates from maps and on-site recognition of the areas. Finally, transects needed to be at least 5 km from each other and placed in non-flooded forests, which represent the main land cover type in the RESEX-TA; a total of nine linear transects of 5 km in length were thus

established. However, after beginning data collection in 2014, one community left the programme, leaving only eight communities/transects in the programme (Fig. 1). Each target community selected three to four monitors older than 18 years of age based on their willingness to participate combined with vast experience in walking along the forest. Subsequent training courses were provided by ICMBio and partners to all monitors, focused on providing instructions for game fauna surveys. Since 2022, data collection has been performed by 31 previously trained monitors.

Data collection

On each transect, pairs of monitors conducted linear transect surveys of the transects in their neighbourhood. The methodology widely used in tropical forests (Peres 1999, Benchimol 2016) consisted of walks at a slow and constant speed (average 1 km/h) along a linear transect, searching for both visual and acoustic records of the target species. Surveys were conducted only in the morning (06.30–11.30) by a pair of monitors and did not occur on rainy days. Whenever an individual or group of target species was observed, the following information was recorded: species name, type of record, time of encounter, location of the animal on the transect, number of individuals and perpendicular distance to the first detected individual, subgroup or group (measured with a tape measure). Given that local monitors had extensive experience of

walking in the forest and of searching for and identifying animals, and given that appropriate training courses were also provided, the data collected were consistent and robust. Surveys were conducted between 2015 and 2020, with an average of nine (SD = 2.59) survey days per transect per year, totalling 384 sampling days across the eight transects. Although initially the protocol aimed to obtain data from the dry and wet periods for 10 days per year per transect, data were collected in different months depending on the availability of the monitors, resulting in the sampling effort varying amongst transects. Furthermore, there were situations in which the linear transects extended throughout the day or rainy periods that only enabled partial sampling; such data were excluded from the analysis. The cumulative distance sampled in each transect varied from 5 to 65 km per year, with the total distance being 1915 km over the 6 years (mean ± SD = 239 ± 45 km per transect; Table S2).

Target taxa

We used data collected from nine game forest taxa (i.e., nine taxonomic orders or families of hunted medium- and large-sized forest mammals and birds) in the RESEX-TA (Reis et al. 2018, 2022; Table S1). The selected focal taxa were: those of the Monitora Program monitoring protocol, which considered the target hunting species in the region based on local people’s knowledge; and those recorded in hunting events (not covered in this study) from the Monitora Program (Reis et al. 2018, 2022). Specifically, for our study, we selected game species from those two categories that could be recorded within the RESEX-TA through the use of the linear transect technique (Table S1). A species-level analysis was not feasible due to the limited number of records for most animals. There were six taxa of medium-sized animals (0.54–5.00 kg for birds, 0.92–5.00 kg for mammals): Tinamidae (*Tinamus* spp., *Crypturellus* spp.), Psophiidae (*Psophia viridis*), Cracidae (*Penelope* spp., *Crax* sp. and *Pauxi tuberosa*), Dasyproctidae (*Dasyprocta croconota*), primates (*Cebus unicolor*, *Sapajus apella*, *Pithecia irrorata*, *Callicebus hoffmannsi*) and Procyonidae (*Nasua nasua*); and three taxa of large animals (>5 kg): Atelidae (*Alouatta nigerrima*), Cervidae (*Mazama americana* and *Mazama nemorivaga*) and Tayassuidae (*Dicotyles tajacu* and *Tayassu pecari*). Despite some species not frequently being hunted at other Amazonian sites (e.g., *P. irrorata*, *C. hoffmannsi* and *S. apella*), they were being captured for consumption in the RESEX-TA (YMS Reis, unpublished data 2023). In addition, we did not include *Ateles marginatus* as a focal species as it has been extirpated from the RESEX-TA by previous severe hunting (Peres et al. 2003).

Density and biomass

We estimated the density of each of the nine animal taxa in each transect and year using Equation 1:

$$D = \frac{N}{2 \times EW \times L} \quad (1)$$

where *D* represents the density (individuals/km²), *N* represents the total number of sightings, *EW* represents the effective width of the transect (in km) and *L* represents the total distance travelled (Bernardo & Galetti 2004). To obtain *EW*, we grouped the visualization events per taxa and constructed six competing models using the *Distance* 4.1 software: a uniform key function with either cosine or simple polynomial series expansion; a half-normal key function with either cosine or hermite polynomial series expansion; and a hazard rate key function with cosine or simple polynomial

series expansion (Thomas et al. 2010; models in Table S3). We selected the best-fit model based on the lowest Akaike information criterion (AIC) values (Burnham & Anderson 2002) and coefficient of variation and the highest goodness-of-fit χ^2 test probability values. From the estimated density per taxa, we evaluated the effect of hunting on animal densities considering (1) group (medium- and large-sized) density and biomass and (2) ‘individual’ densities of the four most frequent taxa (Tinamidae, Dasyproctidae, Primates and Cervidae) for each transect in each year. Given the low number of records, we were unable to conduct individual analyses for the other taxa. Biomass was calculated as the sum of densities of each species multiplied by the mean body mass of the species in each group (based on Robinson & Redford 1986, Ayres & Ayres 1979, Valsechi 2013).

Anthropogenic stressors

We obtained two metrics related to anthropogenic pressure. Firstly, we used a proxy of HI based on the distance to nearest community and human population size of its community (adapted from Scabin & Peres 2021), according to Equation 2:

$$HI = \sum \frac{S(\text{com})}{\sqrt{d(\text{com})}} \quad (2)$$

where *S* represents the human population size in each community (*com*; Table S4) and *d* represents the Euclidean distance from the centre of each transect to the centre of each nearby community (Table S4). For this, we considered all communities located up to 10 km from the centre of the surveyed transect. This distance was based on the evidence that hunters forage in areas located up to 10 km from their homes in the RESEX-TA (YMS Reis, unpublished data 2018). Distances were calculated in QGIS 2.18.9 (QGIS Development Team 2017) and the human population size of each community was obtained from the local ICMBio database from 2022. We assume that population size did not substantially change amongst surveyed years based on a comparison between the most current list of protected area beneficiaries (from 2022) and 2018, the previous year for which we had data (Spearman correlation, $r = 0.95$, $p = 0.001$).

We also measured the distance to the nearest road, defined as the distance from the middle of each transect to the nearest dirt road (Table S4). Because dirt roads are the main access ways in *terra firme* in the RESEX-TA, we assumed that transects closer to roads would be more accessed by humans than isolated transects (Benítez-López et al. 2017, Beirne et al. 2019).

Data analyses

We used generalized linear mixed models to relate variation in HI, distance to the nearest road and year of data collection (with the random term ‘transect’) to overall densities and biomasses of both medium-sized and large-sized groups separately and to the densities of the four selected taxa individually. We emphasize that it was only possible to analyse diurnal species that were commonly recorded (i.e., those that had greater detectability and therefore provided sufficient visual records for analysis); we excluded those game species that are rarer or more difficult to record using linear transects. Spearman tests between our predictor variables (i.e., HI, distance to the nearest road and year) showed that none was correlated at (>|0.50|) with any other, and thus we maintained all of these variables in the global model (mean,

standard deviation, minimum and maximum values of anthropogenic variables in Table S5).

For each response variable, we constructed different models: the null model, models presenting a single or two predictors, models with all possible additive combinations of them and models with the interaction effects between HI and distance to the nearest road. We selected the best model(s) based on the AIC values (Burnham & Anderson 2002), considering as parsimonious those presenting $\Delta\text{AICc} \leq 2.0$. When the null model appeared amongst the parsimonious models, we considered that no other model best explained the specific pattern than chance. We used the 95% confidence interval (CI) of the coefficient of each variable included in the best models and considered its influence when the 95% CI did not include 0. Due to convergence problems, we were unable to consider the interaction model for primates and Tinamidae. We transformed the data using log10 for groups or square root for taxa, and we confirmed data normality using the Shapiro–Wilk test. We used the Gaussian distribution family ('identity' linkage function) in all models. The analyses were performed using the package 'glmmTMB' (Brooks et al. 2022) in R 4.2.1 (R Core Development Team 2022).

To assess population trends over the years, we built state-space models that describe the stochastic and deterministic relationships between the observable and unobserved values using a Bayesian approach (Royle & Kéry 2007, Kéry 2010). We used as a response variable the annual mean density values of the medium-sized and large-sized groups and nine taxa considering all transects. The data were log transformed. The assessment was made by estimating the exponential growth rate r of density, in which the r value is a measure of change in population size that assumes positive, negative and zero values in increasing, declining and stable populations, respectively, and is calculated using Equation 3:

$$r = \frac{\log(N_t/N_0)}{t} \quad (3)$$

where N_0 is the population size at the beginning of the period and N_t is the population size after t years (Caughley & Sinclair 1994). A time-series mean r value ≥ 0 could suggest that populations are stable or growing, but values r values < 0 could be interpreted as evidence of a decline in the evaluated parameter (de Paula et al. 2022). Thus, the r value was considered as indicative of the behaviour of density over the years. If the r values over the time series were equal to 0 or positive for the medium-sized and large-sized groups or the nine 'individual' taxa, we assumed that populations were not declining; declining r values were taken to indicate otherwise. We used R version 4.2.1 (R Core Development Team 2022) and the 'R2jags' package (Su & Yajima 2012) to fit the state-space model in JAGS (Plummer 2015). Non-informative priors were used for the density, and 200 000 Markov chain Monte Carlo iterations were run in two independent chains with a burn-in of 100 000 and a thinning factor of 0.06. Furthermore, the Gelman–Rubin (Rhat) diagnosis was used to evaluate parameter convergence (Gelman & Shirley 2011), where values of 1.001 indicated a satisfactory model (the closer to 1, the better the model) and 1.1 was considered the acceptable limit. If the Bayesian 95% CI did not include 0, the r value was deemed substantially different from 0. The results are expressed as means with standard deviations.

Results

The mean density of the medium-sized group was 44.0 (± 18.97) individuals/km² (range 24.3–86.5 individuals/km²), whereas mean

biomass was 101.0 (± 63.43) kg/km² (range 51.0–258.6 kg/km²; Table S6). Within this group, the taxa with the highest mean densities were the Dasyproctidae (*D. croconota*), with 15.9 individuals/km², and the medium-sized primates (the four species grouped: *C. unicolor*, *S. apella*, *P. irrorata*, *C. hoffmannsi*), with 12.8 individuals/km², and the lowest density was 2.1 individuals/km² for Tinamidae (*Tinamus* spp. and *Crypturellus* spp.; Table S6). Some frequently hunted species, such as *T. terrestris*, were rarely recorded (Table S1).

The mean density of the large-sized group was 6.5 (± 3.01) individuals/km² (range 2.7–10.3 individuals/km²), whereas mean biomass was 121.8 (± 65.66) kg/km² (range 1.9–223.9 kg/km²; Table S6). The taxa with the highest mean densities were the Tayassuidae (*D. tajacu* and *T. pecari*), with 2.5 (± 2.37) individuals/km², and the Atelidae (*A. nigerrima*), with 2.1 (± 1.63) individuals/km². The Cervidae, with 1.9 (± 0.78) individuals/km², showed the lowest mean density amongst the large-sized group (Table S6).

Influence of anthropogenic stressors on the density and biomass of game fauna

The mean density and biomass of the medium-sized and large-sized groups were neither influenced by HI nor distance to the nearest road, and they did not vary amongst the years; the null model appeared amongst the parsimonious models in the group analyses (Table 1). However, different results were observed for the densities of individual taxa (Table 2). For Cervidae, only the null model was retained in the set of best models, whereas the predictor variables were included in the set of best models for the other three taxa. In particular, distance to the nearest road was included in the best model for both Dasyproctidae and Tinamidae, whereas HI and year were included in the best model explaining patterns of primate density (Table 2). The density of Dasyproctidae and Tinamidae decreased and increased, respectively, in transects further from roads, whereas the primate density increased in transects with high HI and also over the years (Fig. 2 & Table S7).

Population trends

The parameter convergence was satisfactory for all Bayesian models (Table S8), and the exponential growth rate r did not differ from 0 for density averages for the game group and taxa; density remained stable for both the medium-sized and large-sized groups, as well as for the nine taxa (Tinamidae, Psophiidae, Cracidae, Dasyproctidae, primates, Procyonidae, Atelidae, Cervidae and Tayassuidae) across all sampled transects in the RESEX-TA, indicating that the game populations were not declining over the years assessed (Fig. 3).

Discussion

This comprises the first study assessing the responses of vertebrate game species over a temporal series based on the Brazilian Monitora participatory monitoring programme. Contrary to our initial expectations, anthropogenic variables failed to predict overall density and biomass patterns of both medium- and large-sized groups. However, the densities of both Dasyproctidae and Tinamidae were influenced by distance to the nearest road, whereas primates were affected by year and HI. Mammal and bird populations remained stable over the 6 years considering all transects pooled together, indicating no decline or increase in the game taxa across the RESEX-TA over this period.

Table 1. Model selection table based on a candidate set of ‘best’ models ($\Delta AICc \leq 2.00$) predicting the density and biomass patterns for overall medium-sized and large-sized game species on eight transects across the Tapajós-Arapiuns Extractive Reserve. Models ranked by the AICc and $\Delta AICc$ values.

Model	df	logLik	AICc	$\Delta AICc$	Weight
<i>Medium-sized group</i>					
Density					
Null	3	-29.88	66.36	0.00	0.30
Year	4	-29.10	67.22	0.86	0.19
Distance to nearest road	4	-29.38	67.78	1.42	0.15
Biomass					
Null	3	-28.34	63.29	0.00	0.27
Distance to nearest road	4	-27.57	64.17	0.88	0.18
Year	4	-27.75	64.53	1.24	0.15
Human intensity	4	-28.10	65.23	1.95	0.10
<i>Large-sized group</i>					
Density					
Distance to nearest road	4	-61.19	131.40	0.00	0.29
Null	3	-62.51	131.62	0.22	0.26
Biomass					
Null	3	-64.18	134.95	0.00	0.42
Distance to nearest road	4	-63.93	136.88	1.93	0.16

AICc = Akaike information criterion corrected for small sample sizes; df = degrees of freedom; logLik = log likelihood.

Table 2. Model selection table based on a candidate set of ‘best’ models ($\Delta AICc \leq 2.00$) predicting density patterns for Cervidae, Dasyproctidae, Tinamidae and primates on eight transects across the Tapajós-Arapiuns Extractive Reserve. Models ranked by the AICc and $\Delta AICc$ values.

Model	df	logLik	AICc	$\Delta AICc$	weight
<i>Cervidae</i>					
Null	3	-40.58	87.76	0.00	0.36
Human intensity	4	-40.17	89.37	1.60	0.16
Year	4	-40.19	89.40	1.64	0.16
<i>Dasyproctidae</i>					
Distance to nearest road	4	-50.21	109.44	0.00	0.32
Distance to nearest road + human intensity	5	-49.32	110.21	0.77	0.22
Distance to nearest road + human intensity + distance to nearest road:human intensity	6	-48.39	111.05	1.61	0.14
Year + distance to nearest road	5	-49.91	111.40	1.96	0.12
<i>Tinamidae</i>					
Distance to nearest road	4	-44.41	97.84	0.00	0.49
<i>Primates</i>					
Year + human intensity	5	-71.72	155.03	0.00	0.48
Year + distance to nearest road + human intensity	6	-71.07	156.40	1.38	0.24
Year	4	-74.00	157.03	2.00	0.17

AICc = Akaike information criterion corrected for small sample sizes; df = degrees of freedom; logLik = log likelihood.

Our data are limited to a set of game species liable to be recorded through line transect diurnal surveys, therefore excluding other important game species such as lowland paca (*Cuniculus paca*) and armadillo (Dasyproctidae). Additionally, some species that could have been analysed had very few records (e.g., *T. terrestris* and *T. pecari*), and this could indicate past population losses. Although they have been maintained for over 6 years, our data are confined to only eight transects. Furthermore, our analyses at the taxonomic order and family levels might obscure patterns in population densities. Future studies should include camera-trapping data to better assess temporal changes over the complete vertebrate game assemblage. In addition, our 6 years

constitute a short period given the longevity and reproduction rates of vertebrate species; long-term monitoring is essential to assess overall and species-specific density patterns over generations.

Although we acknowledge these limitations to the data, we emphasize the robustness of the information gained that could help to improve our understanding of the patterns of terrestrial vertebrate densities in a populated forest reserve. We also demonstrate the value of data derived from long-term participatory monitoring programmes in Amazonian reserves.

Our study reveals that overall densities of the large- and medium-sized game vertebrates involved were unaffected by anthropogenic pressure over these years. The local people have historically and continuously hunted game fauna across the RESEX-TA; however, a previous study in this area showed that the preferred species still comprise the most frequently hunted ones (Reis et al. 2022). Preferred game species in heavily hunted areas usually exhibit low densities, become rare or even become locally extinct and therefore drop from hunting profiles (Peres & Palacios 2007). Alternative sources of animal protein – mainly fish stocks (Oliveira et al. 2005, Braga et al. 2022) and small domestic animals (e.g., pigs and chickens) – also occur in the Reserve. In addition, commercial hunting to supply urban centres is non-existent. Finally, the preservation zone, where subsistence hunting and other anthropogenic activities are prohibited, occupies more than 20% of the total area of the RESEX-TA (Instituto Chico Mendes de Conservação da Biodiversidade 2014) and can act as a ‘source’ of animals to the ‘sink’ areas (Novaro et al. 2000).

Anthropogenic stressors evidently had a substantial influence on the density of some species or taxa, but there were contrasting patterns. In particular, agoutis (*D. croconota*) were substantially affected by the distance to the nearest road, although greater densities were observed in transects near the road. In fact, agoutis can cope with disturbed forested areas, such as forest edges, which are often related to road creation (Peres 2001). For instance, forest fragmentation exerted a positive effect on agouti density in forest patches located in the Central Brazilian Amazonia, and individuals were frequently recorded in forest edges adjacent to open areas and dirt roads (Jorge 2008). Agoutis are granivorous caviomorph rodents, but despite their feeding mainly on fruits and seeds, their diet is complemented by leaves, roots, fungi and small invertebrates (Henry 1999, Silvius & Fragoso 2003, Dubost & Henry 2006). It is probable that agoutis are benefitting from a variety of food resources present at forest edges, including natural resources and anthropogenic ones, thus increasing their density. Furthermore, agoutis may be benefitting from food resources from farms (Abrahams et al. 2018) or from the absence or low presence of predators, such as jaguars, close to settlements (Carvalho & Pezzuti 2010). In addition, we noted that the density of agoutis in the RESEX-TA is substantially higher than in other Amazonian protected areas (Calouro & Marinho-Filho 2006, Rosas 2006, Endo et al. 2010, Mayor et al. 2015), further indicating that hunting is not threatening their populations in the studied protected area.

The Tinamidae, encompassing both *Tinamus* spp. and *Crypturellus* spp., were significantly influenced by anthropogenic pressure, presenting higher density estimates in transects far from roads. Although hunters prefer eating and therefore hunting large mammals (Constantino et al. 2008), large birds are also important hunting species, especially in heavily hunted forest sites (Thiollay 2005). In fact, residents in the RESEX-TA reported that tinamids can be hunted, but they are not the animals most frequently killed

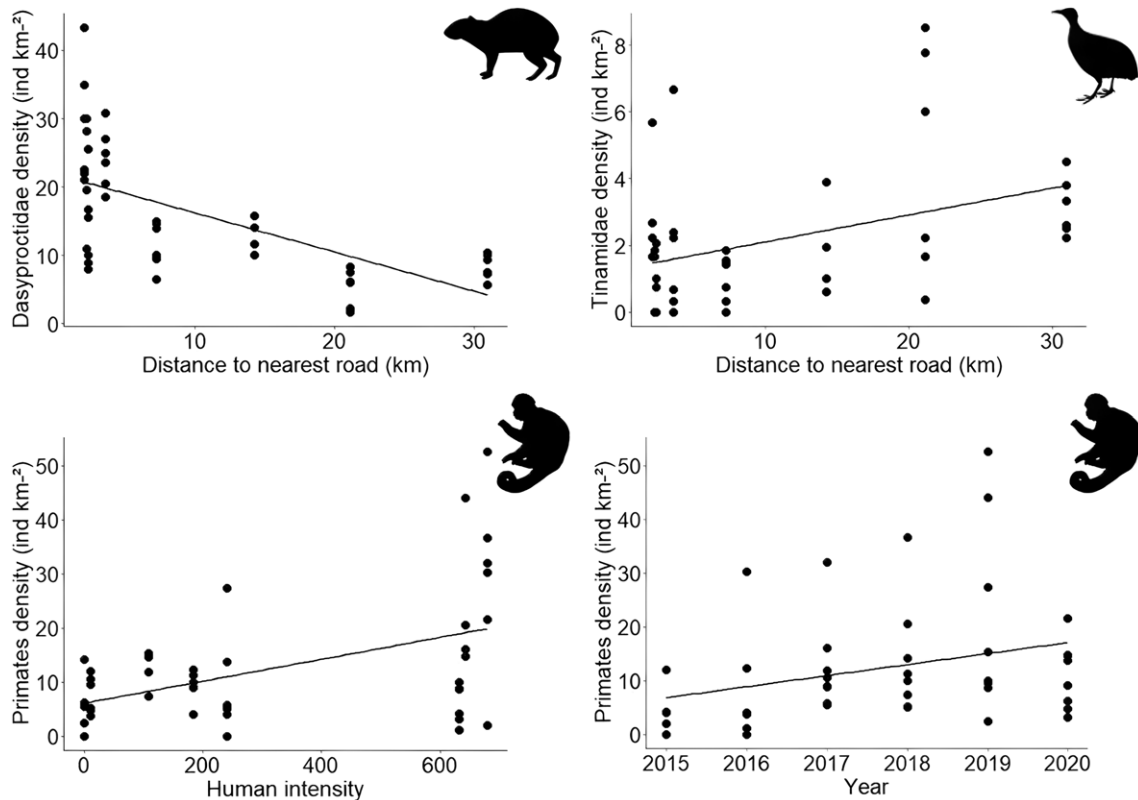


Figure 2. Mean density of Dasyproctidae and Tinamidae in relation to distance to nearest road and average density of primates in relation to human intensity proxy and year in eight transects across the Tapajós-Arapiuns Extractive Reserve.

(YMS Reis, unpublished data 2018). Furthermore, large forest-dwelling birds such as the large tinamids exhibit life-history characteristics associated with greater sensitivity to anthropogenic disturbances, such as a frugivore-granivore diet and forest dependence (Vetter et al. 2011). Two hypotheses might explain our observations regarding these animals. Firstly, easier road access of hunters might have facilitated their capture, as corroborated by the great sensitivity of large birds to hunting pressure (Peres 2001, Urquiza-Haas et al. 2009, 2011). Secondly, as tinamid species are highly dependent on forest-interior environments, they might consequently avoid transiting in regions close to open areas. No individuals were seen in two transects close to roads in some monitoring years, and we found a low density of tinamids in the RESEX-TA (mean \pm SD = 2.1 ± 1.19 individuals/km²) in contrast to other Amazonian protected areas (Peres & Nascimento 2006, Endo et al. 2010). Although our time-series analyses revealed that tinamid density did not decline in the transects over the period, ensuring the continuity of monitoring in the same transects will enable us to identify whether hunting is reducing population sizes in the transects near roads and thus whether hunting regulations might be necessary.

Our findings also revealed that the density of primates was positively related to both HI and time over the 6 years of the monitoring programme. Medium-sized primates are relatively tolerant to subsistence hunting (Peres 2000, Peres & Palacios 2007), and, in our study, the high number of sightings of capuchins was mainly responsible for this result. They are well known for their ability to adapt to disturbed environments and to exploit novel resources, such as plantations, which are common near the transects (Hill 2000). In addition, this species can replace a diet of naturally

distributed resources with anthropogenic food products (see Mikich & Liebsch 2009, Liebsch & Mikich 2015). It is possible that their high behavioural flexibility (Fragaszy et al. 2004) and proximity to cultivation areas might explain the positive influence of HI on primate density. Furthermore, the primates might be benefitting from resources that were previously exploited by larger and more vulnerable species (Peres & Dolman 2000), such as the spider monkey, which was not analysed in this study. This may be leading to an increase in their populations, whereas larger species may be declining in number. The spider monkey has probably been extirpated in many parts of the Arapiuns region by hunting (Peres et al. 2003), and only a single record was documented by experienced monitors within the Tapajós region through the Monitora Program. The increase in primate density over the period might be associated with the reduction in hunting pressure in response to increased local awareness and environmental education activities carried out through the Monitora Program. In particular, since the establishment of the monitoring programme, several educational programmes have been carried out intending to demonstrate the importance of forest species to both ecosystem functionality and the delivery of ecosystem services. We have noticed a growing awareness amongst local residents of the importance of wild fauna. Considering that primates were not favourite targets in the RESEX-TA, it is possible that the hunting pressure on this group declined over this period, therefore being reflected in their greater densities. The continuity of the monitoring in the Reserve, together with interviews of local hunters, would provide more information regarding this observed pattern.

The densities of medium- and large-sized groups and individual taxa remained stable during the 6 years of the monitoring

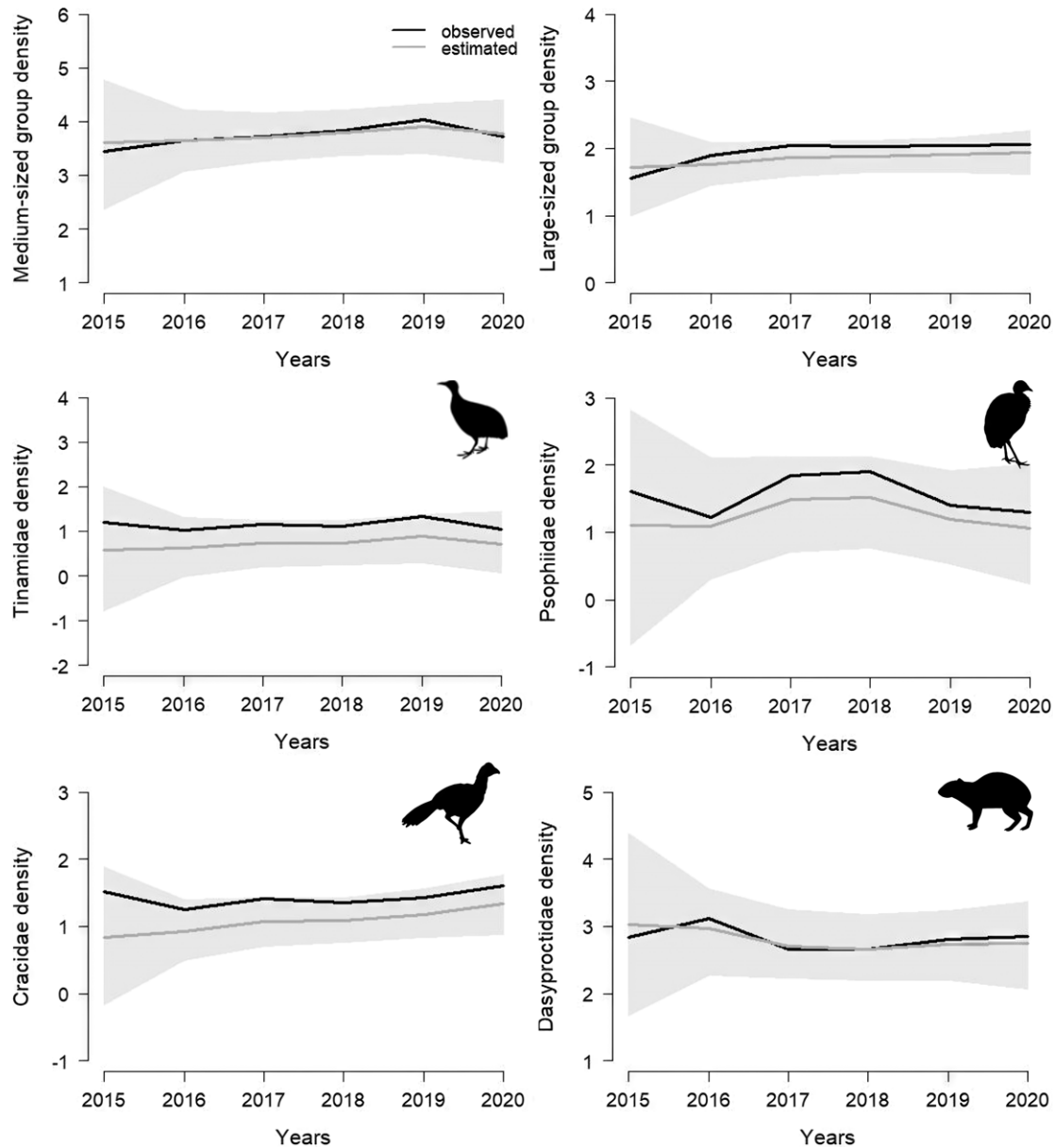


Figure 3. Annual average density, expressed as $\log(x + 1)$, of the medium-sized and large-sized game groups and nine individual taxa (Tinamidae, Psophiidae, Cracidae, Dasyproctidae, Primates, Procyonidae, Atelidae, Cervidae and Tayassuidae) in eight study transects in the Tapajós-Arapiuns Extractive Reserve from 2015 to 2020. Lines represent observed and estimated densities. The grey regions represent the confidence intervals.

programme in the RESEX-TA, suggesting that, at least within this period, hunting was not threatening diurnal, forest game species. Subsistence hunting was also not considered a severe threat to game species in two other Amazonian sustainable-use extractive reserves, even for those that are less resilient and with lower fertility rates (de Paula et al. 2022). Elsewhere across the Amazon basin, terrestrial wildlife species showed resilience to subsistence hunting due to there being large tracts of continuous forests that are virtually inaccessible to hunters (Iwamura et al. 2014, Antunes et al. 2016). The environmental and social configuration of the RESEX-TA could favour a source-sink dynamic, whereby large expanses of lightly populated, undisturbed forest might serve as population ‘sources’ that can refuel ‘sink’ areas where hunting takes place due to accessibility and proximity to local communities (Novaro et al. 2000). It seems that the high forest cover within the

RESEX-TA, comprising c. 70% of the territory, has played a crucial role in supporting the persistence of game populations. In addition, 20% of the RESEX-TA is designated as a preservation zone, where anthropogenic activities do not occur. Large tracts of forests coupled with limited human pressure may be providing the necessary conditions for game populations to thrive (Naranjo & Bodmer 2007, Ohl-Schacherer et al. 2007).

Conclusion

Our study provides new information on the status of game populations within a sustainable-use protected area in the Amazon basin for both local people and reserve managers. Moreover, although the analyses did not indicate an influence of the evaluated anthropogenic variables on the populations of medium- and large-

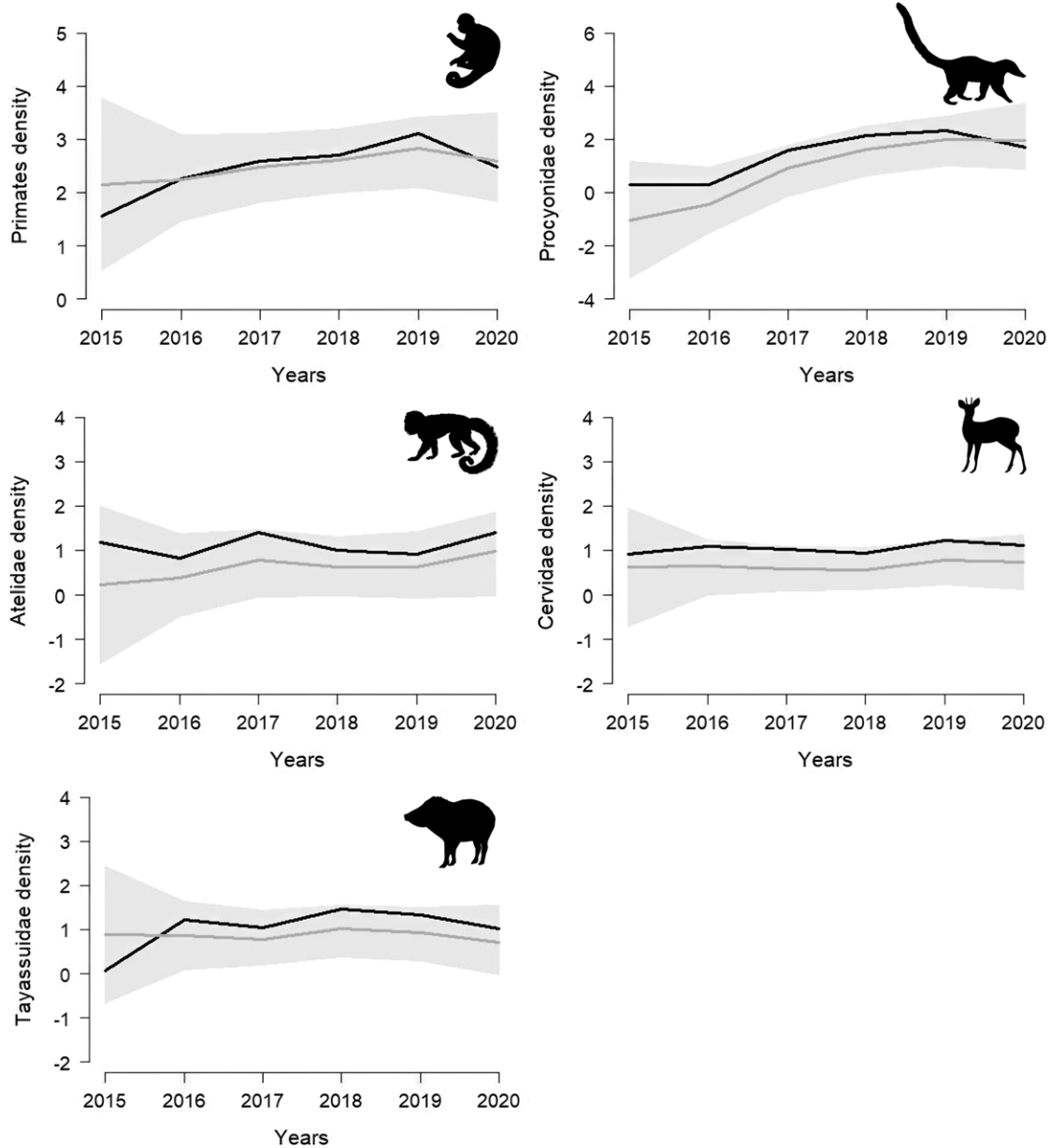


Figure 3. (Continued).

sized vertebrates considered in the evaluated time series, we recognize the importance of evaluating the RESEX-TA system within a broader context. Previous studies carried out in this same area have documented the influence of wildfires and hunting pressure on forest structure and wildlife game populations (Peres et al. 2003, Barlow & Peres 2006). The history of wildfires and hunting pressure in the region, combined with the relatively high human population density (c. 3.55 persons/km² for the entire region; Silva et al. 2022, Instituto Socioambiental 2023), might be contributing to a semi-defaunated scenario (i.e., instead of a pervasive loss of fauna, the RESEX-TA might have experienced losses of certain species prior to our study, being reflected as a low density of game species). Therefore, the stability of species population densities over the 6 years analysed might be an indicator that the system is currently in a state of fragile equilibrium, potentially maintaining stability with an altered ecological structure.

Further investigation, including continuous monitoring and interviews with hunters, could provide deeper insights that would help us to clarify these reflections.

Finally, we acknowledge the potential of community-based long-term biodiversity monitoring in tropical protected areas as a tool to evaluate species status and potentially subsidize effective management actions. However, given the small sample size in this study, we recognize the need for further research to provide more robust evidence on this matter, particularly regarding endangered large vertebrates.

In a broader context, our study could contribute to the discussion regarding the effectiveness of sustainable-use protected areas for biodiversity conservation (Terborgh & Peres 2017), demonstrating their potential for safeguarding more abundant and resilient species *in situ*. However, for large threatened species, substantial anthropogenic pressure could potentially compromise

species conservation, as indicated by past population losses. In addition to the growth of the human population and the increase in forest fires in the region, the lack of consensus regarding the legality of subsistence hunting by environmental agencies has also contributed to this situation. In the first decade of the 2000s, local residents developed a Natural Resources Use Plan for the protected area – a document containing informal agreements for wildlife use. However, this document is no longer valid. Even though hunting is illegal in Brazil, failure to comply with these agreements does not lead to fines or other forms of penalization for the hunter but can compromise the sustainability of hunting for some species. In this context, Tomas et al. (2018) highlighted the need for the world's largest tropical country to implement a comprehensive and modern environmental policy for fauna management. However, until this occurs, we recommend sharing and discussing our results with local communities in the RESEX-TA to facilitating the formation of collective decisions regarding game management. In particular, we emphasize that establishing formal rules is a key management tool that can contribute to achieving hunting sustainability over the long term, and we expressly recommend banning the hunting of endangered species such as tapirs and peccaries.

Supplementary material. For supplementary material accompanying this paper, visit <https://doi.org/10.1017/S0376892924000031>.

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Competing interests. The authors declare none.

Ethical standards. The study complies with the current laws of Brazil, with the use of the database from the Monitora biodiversity monitoring programme authorized by the Biodiversity Authorization and Information System (SISBIO) of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

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