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Surviving in the Amazon Arc of Deforestation: Richness and Defaunation of Mammals in Priority-Protected Areas of the Brazilian Midwest

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ABSTRACT

The Amazon is recognised as one of the most conserved tropical rainforests in the world. However, along its peripheral agricultural frontiers, mammal assemblages are gradually being eroded due to deforestation of this large area known as the Arc of Deforestation, particularly along the Amazon's southeast. In this study, we aimed to expand on the knowledge of richness, composition, and defaunation of mammal assemblages in two priority protected areas for biodiversity in the region: Cristalino State Park (hereafter Cristalino) and Xingu State Park (hereafter Xingu). We used camera traps and line transects for data collection between 2020 and 2021. Our results demonstrated that both protected areas support rich assemblages of medium- and large-sized mammals within the south-central Amazon (Cristalino—32 species, Xingu—30 species). Due to the differing vegetation types between each park, the two mammal assemblages showed significant differences in species composition. Even with one of the highest biomasses of large ungulates (tapir and brocket deer) and apex predators (jaguar and puma) compared to other protected areas in south-central Amazon, both areas showed a high biomass defaunation index relative to these same areas. The result is largely driven by the low abundance of peccaries, especially *Tayassu pecari*. This could be one of the impacts of extensive human pressure caused by deforestation and degradation around and inside these protected areas. Both parks play an important role in the survival of threatened mammals, and in maintaining biodiversity and ecosystem functionality in the southern Amazon, helping to curb agricultural expansion into the interior of the Amazon rainforest.

RESUMO

A Amazônia é reconhecida como uma das florestas tropicais mais bem preservadas do mundo. No entanto, ao longo de suas fronteiras agrícolas, as assembleias de mamíferos estão sendo gradualmente erodidas devido ao desmatamento dessa grande região conhecida como Arco do Desmatamento, particularmente ao longo do sudeste amazônico. Neste estudo, nosso objetivo foi ampliar o conhecimento sobre a riqueza, a composição e a defaunação dos mamíferos em duas unidades de conservação prioritárias para a biodiversidade na região: o Parque Estadual do Cristalino e o Parque Estadual do Xingu. Usamos armadilhas fotográficas e transectos lineares para a coleta de dados entre 2020 e 2021. Nossos resultados demonstraram que ambas as unidades de conservação apresentam assembleias de mamíferos de médio e grande porte ricas em espécies no centro-sul da Amazônia (Cristalino – 32 espécies, Xingu – 30 espécies). Devido aos diferentes tipos de vegetação de cada parque, as duas assembleias de mamíferos apresentaram diferenças significativas na composição de espécies. Mesmo com uma das maiores biomassas de grandes ungulados (anta e veado-mateiro) e predadores de topo (onça-pintada e onça-parda) em comparação com outras unidades de conservação no centro-sul da Amazônia, ambas as áreas apresentaram um alto índice de defaunação de biomassa em relação a essas mesmas áreas. Este resultado, em grande parte, é causado pela baixa abundância de pecarídeos, especialmente *Tayassu pecari*. Esse pode ser um dos impactos da extensa pressão humana causada pelo desmatamento e pela degradação ao redor e dentro dessas unidades de conservação. Ambos os parques desempenham um papel importante na sobrevivência de mamíferos ameaçados de extinção e na manutenção da biodiversidade e funcionalidade do ecossistema no centro-sul amazônico, ajudando a conter a expansão agrícola para o interior da Floresta Amazônica.

1 | Introduction

Mammals are essential in the maintenance and regeneration of tropical rainforests, as they perform important ecological functions, such as herbivory, predation, seed dispersal, and creation of new environments for other species (i.e., ecosystem engineers), among others (Beck et al. 2013; Lacher et al. 2019). Furthermore, this group can be used as an indicator of the state of conservation of an ecological system (Soulé and Wilcox 1980; Natsukawa and Sergio 2022). Therefore, the loss of predators that regulate the lower trophic levels or even large prey that support the top predators changes the balance of trophic relationships (Finke and Denno 2004; Sandom et al. 2013).

Human actions selectively affect wildlife, which can cause severe reductions in population or local extinctions, a process known as defaunation, with medium and large herbivorous mammals being one of the most affected groups (Dirzo et al. 2014; Ripple et al. 2015; Gardner et al. 2019). The main global threats to mammals are habitat destruction and deforestation, followed by hunting and persecution, capture for illegal trade, and unofficial tourism (Schipper et al. 2008; Cardillo et al. 2023). Medium and large mammals are severely affected by habitat fragmentation and degradation, given the biological characteristics of species that, for the most part, need large areas to acquire natural resources for survival (Kinnaird et al. 2003; Galetti et al. 2021).

The Neotropics are home to 25% of the world's mammal richness, of which more than 80% are endemic (Cole et al. 1994; Burgin et al. 2018). Although Brazil is home to half of the known species in the Neotropics (Burgin et al. 2018; Quintela et al. 2020), and the Amazon has the largest number of mammal species, there are numerous gaps in the knowledge of this group when compared to other biomes in Brazil (Paglia et al. 2012). Knowledge gaps are especially worrying in the southern Amazon, where the state of Mato Grosso is located, which has suffered the highest rates of deforestation in the Amazon biome in recent decades (Fearnside et al. 2009; Zappi et al. 2016; MapBiomas 2023). This long ecotonal region between Amazon and Cerrado (Brazilian savannah) is known as the Arc of Deforestation, the largest deforestation frontier in the world (da Silva et al. 2019; Costa-Araújo et al. 2022), and is putting at risk the ecosystem functions and services, species survival and global climate regulation performed by the Amazon (Werth and Avissar 2002; Gatti et al. 2021; Feng et al. 2023).

In this scenario of rapid deforestation of the Amazon, the creation of protected areas has been one of the most efficient strategies to protect native ecosystems and associated biota (Putz et al. 2001; Killeen and Solórzano 2008; Cazalis et al. 2020). However, protected areas, whose main premise is the protection of biodiversity or socio-biodiversity (especially in the Amazon), are often created before there is adequate knowledge of the biodiversity present, as is the case of Mato Grosso. The state has 50 356.26 km^2 of federal and state-protected areas (SEMA 2021), but limited knowledge of the mammals within it.

Although the Amazon is recognised as one of the most conserved tropical rainforests in the world, its mammal assemblages are gradually being eroded along the peripheral agricultural frontiers of the biome (Bogoni et al. 2020). A recent study carried out in the state of Pará showed that even preserved areas in this biome are subject to defaunation of medium and large mammals (Rosa et al. 2021b). As such, our objective is to expand the knowledge on the richness and composition of mammal species in two protected areas of Mato Grosso: Cristalino State Park (Cristalino) and Xingu State Park (Xingu), as well as to evaluate the defaunation of mammals in these areas to assess the degree of conservation of mammal communities in one of the most deforested regions of the Amazon.

2 | Methods

2.1 | Study Area

Our study was carried out in Cristalino State Park (Cristalino – 9°25′ and 9°43′ S; 55°09′ and 56°02′ W) and Xingu State Park

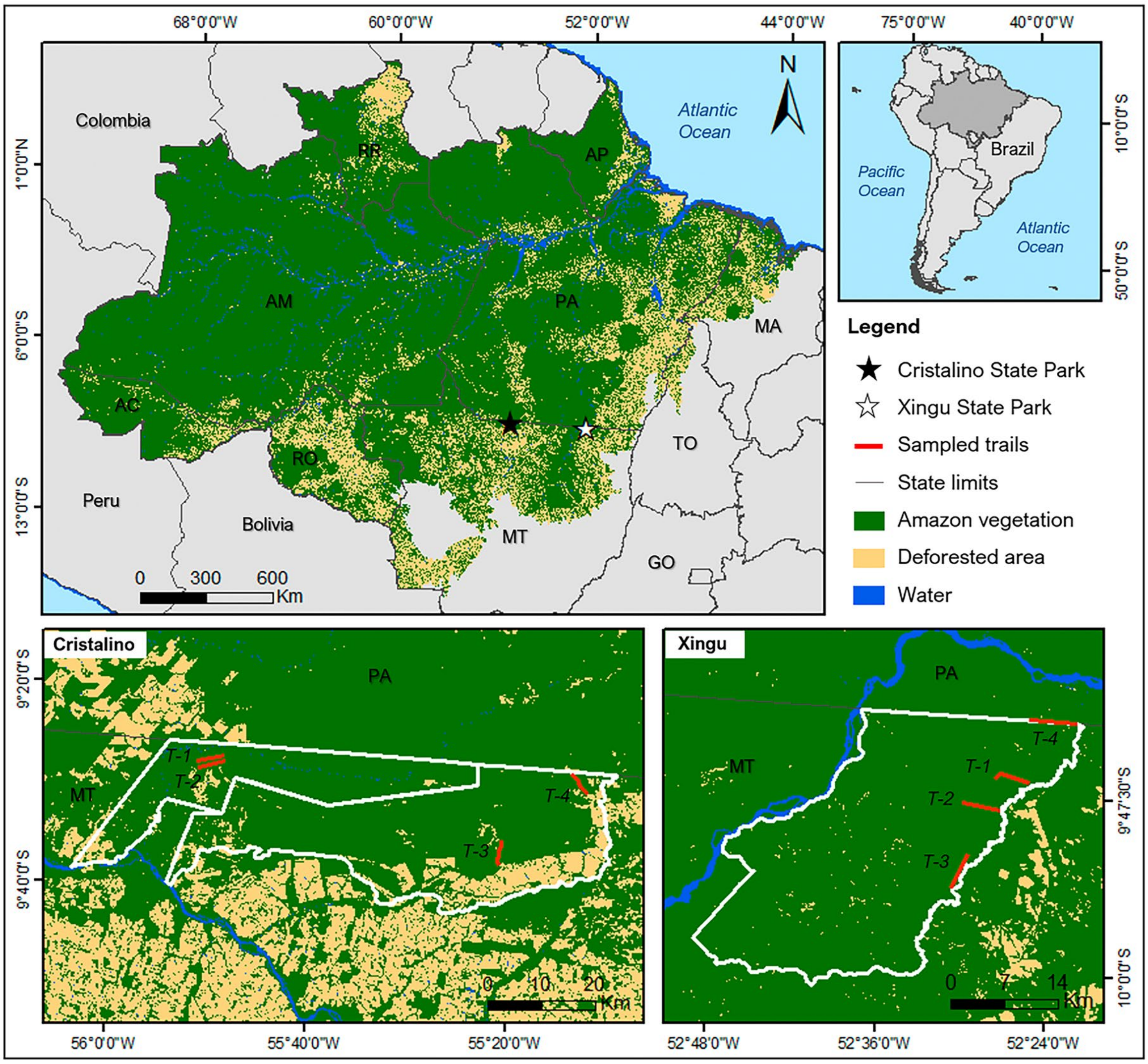

FIGURE 1 | Location of sampled trails for mammals in the Cristalino State Park and Xingu State Park in the state of Mato Grosso (MT) bordering the state of Pará (PA), southern Brazilian Amazon. Detail for the concentration of deforested areas in the south and east of the Amazon biome, characterising the Arc of Deforestation, where the study areas are located. Source imagery: Sentinel-2 L2A (Karra et al. 2021).

(Xingu – 9°40′55″ and 10°00′30″ S; 52°48′48″ and 52°21′40″ W) located in the north (municipalities of Alta Floresta and Novo Mundo) and northeast (municipality of Santa Cruz do Xingu) of the state of Mato Grosso, respectively (Figure 1). Cristalino and Xingu are located within areas of intact forest with 184 900 and 96 300 ha, respectively. The two parks lie along the state's northern border shared with Pará, are priority areas that play important roles in conserving the biodiversity of the southern Amazon (Batistella et al. 2015), and are both protected areas under the Amazon Protected Areas Program – ARPA (MMA 2007).

According to Köppen (1936) classification (Alvares et al. 2013), the climate of both areas is tropical monsoon (Am), a transition between tropical rainforest (AF) and tropical wet climate (Aw). The annual mean precipitation and temperature are similar in both areas varying between 2100 to 2400 mm and 24°C to 26°C, respectively. For Cristalino and Xingu, a dry season occurs from May to October with a wet season from November to April (Batistella et al. 2015; Zappi et al. 2016). The altitude varies between 300 to 400 m above sea level in both areas (Zappi et al. 2011, 2016; Batistella et al. 2015).

The Cristalino is characterised by Savannah, Submontane Dense Ombrophylous Forest, Submontane Seasonal Semideciduous Forest, Submontane Open Ombrophylous Forest with vines and wetland habitats (Zappi et al. 2011; Borges et al. 2014; Batistella et al. 2015), home to one of the highest proportions of threatened tree diversity in Amazon (Ter Steege et al. 2015). In Xingu, the vegetation is classified as Open Ombrophilous Submontane Forest, Dense Ombrophilous Alluvial Forest, Shrubby Floodplain and lagoons, *Campinarana*, Granitic outcrops and Savannah (Borges et al. 2014; Zappi et al. 2016). A variety of geological formations occur within Cristalino, including sedimentary rocks and sandstones, while Xingu shows a variety of soil types, including alluvial soils, sandy soils, and clay soils.

The Cristalino and Xingu are located within two large river basins in the Amazon: Tapajós and Xingu, respectively. Xingu is approximately 300 km east of Cristalino (Zappi et al. 2016). Both parks are connected and surrounded by vast areas of intact forests, such as the Campo de Prova Brigadeiro Veloso military area (located in Serra do Cachimbo), which covers over 2 million hectares and indigenous lands (e.g., Menkragnoti, Capoto/Jarina, Panará and Kayapó Indigenous Lands), which cover over 2.5 million hectares, respectively. The junction of these intact forest areas with Cristalino and especially Xingu covers an extensive area of approximately 4.8 million hectares.

In the southeastern portion of the Cristalino area, there are also agricultural areas, especially pastures and soybean crops, originating especially from illegal land grabbing and to a lesser extent rural properties established in the area in the mid-1990s, and which have not been expropriated since the creation of the park in 2001. Pressure from agricultural activities, especially agribusiness, has been growing around Cristalino, specifically in the portions of the northeast, west, and southeast (MapBiomas 2023). To a lesser extent, there are also agricultural areas in the eastern surroundings of the Xingu, but due to historical reasons and the proximity of indigenous lands, there are no pastures or crops within the park.

2.2 | Data Collection

We collected the data between October 2020 and March 2021 along eight trails, four in each park. In Cristalino we used two trails of 5 km following the Brazilian biodiversity in situ monitoring of protected areas, called *Programa Monitora* of the Institute for Biodiversity Conservation (in Portuguese, *Instituto Chico Mendes de Conservação da Biodiversidade* – ICMBio) and two additional trails, also of 5 km, in a rectangular module with the two trails separated by a distance of 1 km (Long-term Ecological Research modules – RAPELD, Magnusson et al. 2005), from the Brazilian Biodiversity Research Program (in Portuguese, *Programa de Pesquisa em Biodiversidade* – PPBio), Brazilian Ministry of Science, Technology and Innovation. In Xingu we used three trails of 5 km from the *Programa Monitora* and a fourth trail of 8 km along an old road within the park. At each trail we installed four to eight camera traps (Bushnell 12 Mp Natureview Cam Essential HD Low Glow), with 1 km spacing between each one. Disregarding malfunctioning camera traps, we sampled a total of 22 points in Cristalino and 24 in Xingu (Figure 1). The sampling system with evenly distributed plots every 1 km is widely used in the Amazon because it reduces environmental variability within the plot and captures diverse microenvironments along the main trails of 5 km or more (Rosa et al. 2021a; Bergallo et al. 2023). In addition, the RAPELD and *Programa Monitora* systems have facilitated access to remote areas, such as those sampled in the Xingu region, thanks to the periodic maintenance of the trails by ICMBio and PPBio.

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 24 h/day (Rosa et al. 2021b). The camera traps were in the field for a period ranging from 22 to 44 days. Initially, the intended deployment period for each camera trap was 30 days. However, some traps malfunctioned early due to attacks by peccaries (biting and sensor breakage) or due to memory card issues that made them unusable. Other traps were left in the field for more than 30 days due to the occurrence of torrential rains, rendering vehicle access impossible and therefore unable to remove them. In total, the sampling effort in Cristalino was 1644 camera-trap/day, and in Xingu was 970 camera-trap/day.

To complement the mammal survey for the list of species in each protected area, we also performed line transect sampling (Plumptre 2002), using the transects where the camera Putraps were installed. Six transects of 5 km each (three in each park) were sampled at least twice. In each sampling, two people walked the entire transect between 6 a.m.–12 p.m. for five consecutive days. These samplings occurred in the dry and wet seasons between August and November 2020, totaling 180 h of sampling effort in each park. All mammals found along the transects were recorded through vocalisation and direct visualisation. Where gregarious mammals were detected, we counted the number of individuals present wherever possible. The species were then identified using specialised field guides (Reis et al. 2010, 2015) and consulting specialist researchers for some groups. Species taxonomy follows the Official List of Brazilian Mammals from the Brazilian Society of Mammalogy (Abreu et al. 2024). The conservation status of species at the national level was taken from the Red Book of Threatened Fauna of Brazil (Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio] 2018; Ministério do Meio Ambiente [MMA] 2022), and at the global level from the International Union for Conservation of Nature's Red List of Threatened Species (IUCN 2024).

2.3 | Data Analysis

For the analysis, we used only the data from the camera traps. Line transect data were included only to complement the species list for each protected area (Table 1) and were not used in the analyses. For the independence of the records obtained by camera traps, we used an interval of 30 min between the photographic records of all mammals > 1 kg, as recommended by Srbek-Araujo and Chiarello (2005). To measure the sampling sufficiency of the survey for each protected area, we constructed species rarefaction curves using the Estimate S 9.1.0 program (Colwell 2013) with the Chao 2 estimator, due to the nature of presence-absence data and with many rare species (with mammals recorded only once or twice) (Gotelli and Colwell 2011).

For this purpose, we used the independent records obtained through camera traps, using monitoring days as the sampling unit (Cristalino $n = 127$; Xingu $n = 109$) and a 30 min interval between independent counts. We also calculated the relative frequency (RF) by camera traps for each taxon using the formula given in proportion: (no. records of the species/no. total records) × 100.

To compare species composition between Cristalino and Xingu, we performed two non-metric multidimensional scaling analyzes (NDMS) with the *Vegan* package in R software version

TABLE 1 | Medium and large terrestrial mammals recorded in Cristalino State Park (Cristalino) and Xingu State Park (Xingu), in the southern Brazilian Amazon, state of Mato Grosso.

		Cristalino		Xingu		Conservation status		
Taxon	**Common name**	**CT-RF**	**TR-N**	**CT-RF**	**TR-N**	**BR**	**IUCN**	**Method**
ARTIODACTYLA								
Cervidae								
Mazama americana	Red Brocket	8.75	4	9.43	8	DD	DD	CT/TR
Mazama nemorivaga	Amazonian Brown Brocket	3.82	1	1.54	—	DD	LC	CT/TR
Mazama sp.	Brocket	2.61	7	4.61	11	—	—	CT/TR
Subulo gouazoubira	Grey Brocket	—	—	0.88	—	LC	LC	CT
Tayassuidae								
Dicotyles tajacu	Collared Peccary	7.17	5	7.46	8	LC	LC	CT/TR
Tayassu pecari	White-lipped Peccary	33.61	275	1.97	5	VU	VU	CT/TR
CARNIVORA								
Canidae								
Atelocynus microtis	Short-eared Dog	0.56	—	0.22	—	VU	NT	CT
Cerdocyon thous	Crab-eating Fox	—	1	16.45	—	LC	LC	CT/TR
Speothos venaticus	Bush Dog	0.09	—	0.22	—	VU	NT	CT
Felidae								
Leopardus pardalis	Ocelot	2.05	—	2.85	—	LC	LC	CT
Leopardus wiedii	Margay	—	—	0.22	—	VU	NT	CT
Herpailurus yagouaroundi	Jaguarundi	0.28	—	1.32	—	VU	LC	CT
Panthera onca	Jaguar	0.56	—	2.85	—	VU	NT	CT
Puma concolor	Puma	1.4	—	4.39	—	VU	LC	CT
Mustelidae								
Eira barbara	Tayra	0.84	2	0.66	2	LC	LC	CT/TR
Procyonidae								
Nasua nasua	South American Coati	0.93	—	0.22	—	LC	LC	CT
Procyon cancrivorus	Crab-eating Raccoon	0.84	—	1.54	—	LC	LC	CT
CINGULATA								
Chlamyphoridae								
Priodontes maximus	Giant Armadillo	0.56	1	0.88	—	VU	VU	CT/TR
Euphractus sexcinctus	Yellow Armadillo	—	—	0.66	—	LC	LC	CT
Dasypodidae								
Dasypus kappleri	Greater Long-nosed Armadillo	4.56	3	1.54	—	LC	LC	CT/TR
Dasypus novemcinctus	Nine-banded Armadillo	0.84	1	1.1	—	LC	LC	CT/TR
Dasypus sp.	Armadillo	0.84	—	0.44	1	—	—	CT/TR
DIDELPHIMORPHIA								
Didelphidae								
Didelphis marsupialis	Common Opossum	0.65	—	—	—	LC	LC	CT

(Continues)

TABLE 1 | (Continued)

Taxon	Common name	Cristalino CT-RF	Cristalino TR-N	Xingu CT-RF	Xingu TR-N	Conservation status BR	Conservation status IUCN	Method
PERISSODACTYLA								
Tapiridae								
Tapirus terrestris	Lowland tapir	13.59	4	27.19	13	VU	VU	CT/TR
PILOSA								
Myrmecophagidae								
Myrmecophaga tridactyla	Giant Anteater	0.65	—	1.97	—	VU	VU	CT
Tamandua tetradactyla	Southern Tamandua	0.47	1	1.75	—	LC	LC	CT/TR
PRIMATES								
Aotidae								
Aotus azarae	Azara's Night Monkey	—	1	—	—	—	LC	TR
Ateliade								
Ateles marginatus	White-cheeked Spider Monkey	—	180	—	—	EN	EN	TR
Callitrichidae								
Mico emiliae	Emilia's marmoset	—	35	—	—	LC	LC	TR
Cebidae								
Sapajus apella	Black-capped Capuchin	0.09	138	—	48	LC	LC	CT/TR
Pitheciidae								
Callicebus moloch	Red-bellied Titi Monkey	—	23	—	—	LC	LC	TR
Chiropotes albinasus	White-nosed saki	—	13	—	—	NT	VU	TR
Chiropotes utahicki	Uta Hick's Bearded Saki	—	—	—	6	VU	EN	TR
RODENTIA								
Caviidae								
Hydrochoerus hydrochaeris	Capybara	0.19	—	3.51	—	LC	LC	CT
Cuniculidae								
Cuniculus paca	Lowland paca	6.52	—	2.85	—	LC	LC	CT
Dasyproctidae								
Dasyprocta azarae	Azara's agouti	7.36	7	1.32	—	LC	DD	CT/TR
Dasyprocta leporina	Red-rumped agouti	—	—	—	2	LC	LC	TR
Dasyprocta spp.	Agouti	—	—	—	2	—	—	TR
Sciuridae								
Guerlinguetus aestuans	Guianan Squirrel	0.19	5	—	—	DD	DD	CT
Guerlinguetus spp.	Squirrel	—	—	—	1	—	—	TR

Note: As well as the relative frequency (RF) of the species obtained through camera-trap (CT) and the number of individuals registered (N) through the transect methodology (TR), in addition to the conservation status of the species at the national (ICMBio 2018; MMA 2022) and global levels (IUCN 2024): Least concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Data Deficient (DD).

4.2.3 (Oksanen et al. 2019; R Development Core Team 2020). We used the Bray–Curtis distance metric that considers the number of records of species and the Jaccard distance metric that considers the presence and absence of species. Subsequently, to give statistical rigour to the clusters formed in the NMDS, we performed a PERMANOVA.

We used the defaunation index proposed by Giacomini and Galetti (2013) to estimate the defaunation of each protected area as a measure of loss of mammal richness and biomass:

$$D_{(r,f)} = \frac{\sum_{k=1}^{S} \omega_k \left(N_{k,r} - N_{k,f}\right)}{\sum_{k=1}^{S} \omega_k \left(N_{k,r} + N_{k,f}\right)}$$

where: f = the focal mammal assemblage; r = a reference mammal assemblage used to estimate defaunation at other sites; S = the total number of species comprising the mammal assemblage of all sites; k = identification of species; $N_{k,f}$ = biomass, records or presence of species k in focal assemblage f; $N_{k,r}$ = biomass, records or presence of species k in reference assemblage r; ω_k = importance of species k to defaunation; $D_{(r,f)}$ = defaunation of focal assemblage f compared to reference assemblage r.

The defaunation index represents the dissimilarity between two animal assemblages, ranging from 0 (the focal assemblage is not defaunated relative to the reference assemblage) to 1 (the focal assemblage is completely defaunated relative to the reference assemblage); however, the index can reach negative values up to −1, which means that all species in the focal assemblage are absent in the reference assemblage (Giacomini and Galetti 2013). The concept of defaunation considers the focal assemblage to be evaluated (in the present case we evaluated the Cristalino and Xingu assemblages) and the reference assemblage as a model, generally coming from pristine or less defaunated places.

We calculated the defaunation index of two study areas in two ways: species presence (Species Defaunation Index – SDI) and mammal biomass (Biomass Defaunation Index – BDI). To estimate SDI, we used as a reference assemblage (r) the Amazonia National Park (Appendix S1), which is considered one of the most preserved sites in the Amazon (Oliveira et al. 2018). We used the mean body size of species (kg by ¾ power, as indicated by Giacomini and Galetti 2013) as importance value (ω_k), since the ecology and life history of mammals can be inferred from body size (Giacomini and Galetti 2013). For the estimation of BDI, we used data from camera trap surveys conducted in the continuous forest of the Balbina Hydroelectric Reservoir Reserve as a reference assemblage (r) (Palmeirim et al. 2018), because capture rate data of species records in the Amazonia National Park were not available. The camera trap design of Palmeirim et al. (2018) was similar to ours (30 unbaited camera traps placed 30–40 cm above ground, 30 effort days per camera, using a 30-min interval for independent captures).

Balbina Reserve is situated in the central Amazon Basin (Appendix S1), in an area characterised by minimal deforestation and a higher frequency of documented appearances of large mammals like *Tayassu pecari* and *Tapirus terrestris* (Rosa et al. 2021b). These species are significant contributors to the overall biomass of non-primate mammals in Neotropical forests (Mendes Pontes 2004; Galetti et al. 2017). The selection of biomass as the parameter for N in the equation aligns with the approach of Giacomini and Galetti (2013). This choice is attributed to the inherent resilience of biomass in the face of natural fluctuations, which can result from compensatory shifts within animal population dynamics (for instance, the potential rise in the population of small species in response to a decline in larger ones).

We performed species biomass calculations for each site, both reference and focal assemblages. To avoid the bias of different sampling efforts in each study, this computation was based on the capture rate (Srbek-Araujo and Chiarello 2005), multiplied by average body mass, and by the fixed mean group size for species in literature that exhibit gregarious behaviour (Beisiegel 2001; Beisiegel and Ades 2002; Keuroghlian et al. 2004; Reyna-Hurtado et al. 2016), following the methodology outlined by Galetti et al. (2009). Given that the analysis already encompassed biomass considerations, we maintained a constant importance value (ω) of 1 for all species. We considered only terrestrial mammals with a body mass exceeding 1 kg recorded in camera trap studies (Rosa et al. 2021b). We excluded arboreal species, like primates and sloths, as well as those tightly linked to aquatic habitats (e.g., *Lontra longicaudis*, *Pteronura brasiliensis*, and *Hydrochoerus hydrochaeris*).

Finally, we compared the outcomes of our study sites and the defaunation patterns detected in areas of the Amazon characterised by *terra firme* forest ecosystems (e.g., non-flooded forests), representing a large part of the Cristalino and Xingu areas. As the *terra firme* forest is one of the least researched Amazon ecosystems and has the greatest gaps in biodiversity knowledge (among two other main ecosystems: floodplain forests and aquatic environments – *igarapés*, rivers, and lakes) (Carvalho et al. 2023), we expanded the search of comparative areas to the whole of the Brazilian Amazon. So, we selected three additional *terra firme* forest areas that have published camera-trap data on their mammal assemblages: Tapajós National Forest (northern and southern areas – Rosa et al. 2021b), Gurupi Biological Reserve (27 000 ha) (Carvalho Jr et al. 2020) and Amanã Sustainable Development Reserve (Alvarenga et al. 2018) (Appendix S1). This comparison involved the computation of SDI and BDI using presence/absence data, and the capture rates provided in the corresponding references (see Appendix S2).

3 | Results

We recorded a total of 38 medium and large mammal species, distributed in 8 orders and 21 families (Table 1). In Cristalino, we recorded 32 species, while 30 species were recorded in Xingu. In Cristalino, 27 species of mammal were recorded using camera traps (1128 independent photographic records), and 20 species from the transects (122 records and 707 individuals observed). At Xingu, 28 species were recorded using camera traps (460 independent photographic records), and 12 species of mammal were recorded from the transects (57 records and 107 individuals observed).

Our sampling effort was sufficient to register 98.1% of the species in Cristalino and 93.3% in Xingu, according to the Chao 2 richness estimator (Figure 2). There was no difference between the estimated species richness values for each protected area (Cristalino: 27.50 ± 1.29; Xingu: 29.98 ± 2.86). On the other hand, the composition of mammalian assemblage differed significantly between Cristalino and Xingu about the number of records

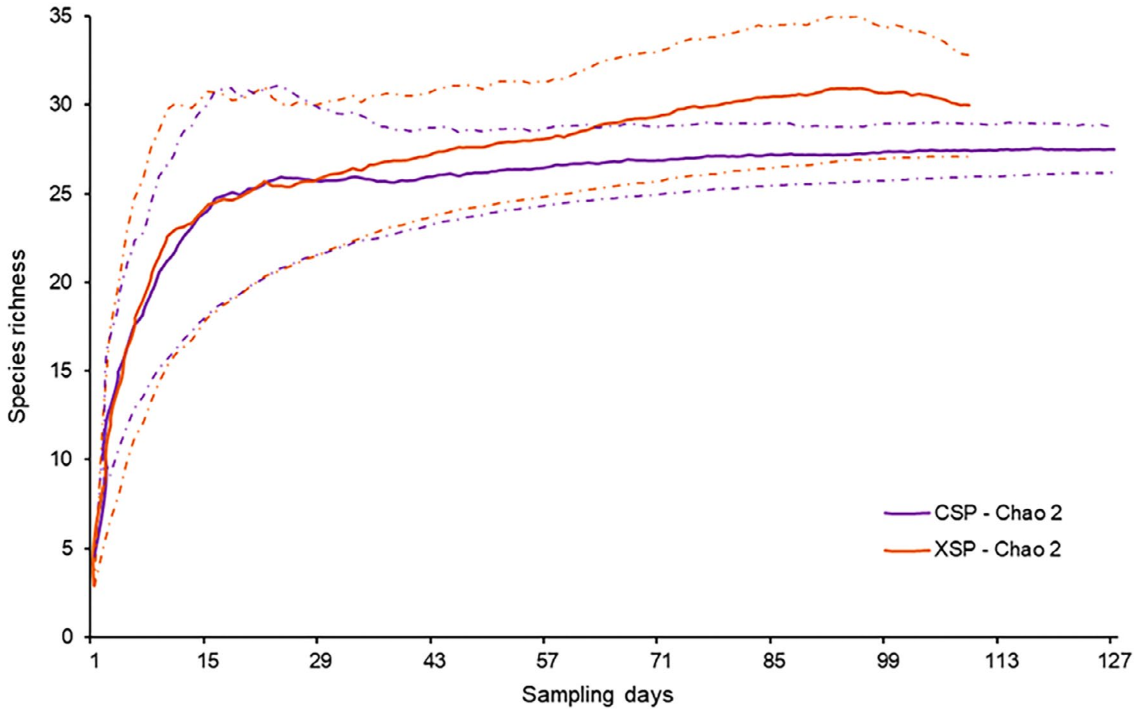

FIGURE 2 | Rarefaction curves for medium and large-sized terrestrial mammal species sampled by camera-trapping in the Cristalino State Park (CSP) and Xingu State Park (XSP), in the southern Brazilian Amazon, state of Mato Grosso (dotted lines represent the 95% confidence interval).

(PERMANOVA: $p = 0.001$; stress = 0.18) and presence–absence data (PERMANOVA: $p = 0.001$; stress = 0.18) (Figure 3). Seven species were recorded exclusively in Cristalino (*Didelphis marsupialis, Aotus azarae, Ateles marginatus, Mico emiliae, Callicebus moloch, Chiropotes albinasus,* and *Guerlinguetus aestuans*), and six other species were found only in Xingu (*Mazama gouazoubira, Leopardus wiedii, Euphractus sexcinctus, Chiropotes utahicki, Dasyprocta leporina,* and *Guerlinguetus* spp.). In addition, Cristalino showed a primate diversity three times greater than Xingu. Meanwhile, Xingu showed a higher richness of ground-dwelling mammals and a greater frequency of records of felids, especially top predators such as *Panthera onca* and *Puma concolor*. We recorded 13 threatened species in total, with 11 mammals in each park, 92% of which are threatened at a national level and 54% at a global level, with all species having Vulnerable status, except for *A. marginatus* and *C. utahicki*, which are classified as Endangered at least at some level (Table 1).

The Xingu (SDI = −0.002) was less defaunated than Cristalino (SDI = 0.005) in relation to species presence (Table 2). The negative value of the SDI obtained in Xingu indicates that the protected area is a non-defaunated site, with a greater presence of mammalian species than in the reference assemblage (Amazonia National Park). Conversely, biomass defaunation was higher in Xingu (BDI = 0.97) than in Cristalino (BDI = 0.75). The mammalian biomass in Cristalino (71 856.37 kg 100 cam.day^{-1}) and in Xingu (7648.05 kg 100 cam.day^{-1}) corresponded, respectively, to 14.1% and 1.5% of the biomass in the reference assemblage (Balbina Reserve – continuous Forest, biomass = 508 753.73 kg 100 cam.day^{-1}). Among the Amazonian reference sites, BDI ranged from −0.0008 to 0.97 (Table 2).

Although our study areas demonstrate an elevated biomass defaunation in relation to the reference assemblage, Cristalino and Xingu presented the highest biomass of *Tapirus terrestris* (Cristalino – 2309 kg 100 cam.day^{-1}, Xingu – 3323.7 kg 100 cam.day^{-1}), *Mazama americana* (Cristalino – 205.8 kg 100 cam.day^{-1}, Xingu – 159.5 kg 100 cam.day^{-1}) and *Puma concolor* (Cristalino – 41,9 kg 100 cam.day^{-1}, Xingu – 94,8 kg 100 cam.day^{-1}) in relation to four other protected Amazon reference areas (Figure 4). Xingu also features the highest biomass of *Panthera onca* (146.7 kg 100 cam.day^{-1}) compared to other sites. However, if only the biomass of *Tayassu pecari* and *Dicotyles tajacu* are analysed, our two study areas present values much lower than those found in the other reference sites in the Amazon (Table 2).

4 | Discussion

Our findings have demonstrated that Cristalino and Xingu maintain a high richness of medium and large-sized mammals that occur in other Amazonian protected areas (PA) characterised by *terra firme* forests. The connectivity of these areas with large blocks of PAs possibly ensures the high mammal diversity found. Both Cristalino and Xingu are connected to and surrounded by some areas of intact forests protected by other PAs, Indigenous Territories, and military areas, such as the Nascentes da Serra do Cachimbo Biological Reserve and the Brigadeiro Veloso Military Testing Range. Adjacent to Xingu are several indigenous reserves, such as Indigenous Territory (IT) Menkragnoti, IT Capoto/Jarina, and the Xingu Indigenous Park. The junction of these protected forest areas with Cristalino and Xingu covers an area of approximately 2.4 and 2.6 million hectares of contiguous forest, respectively, placing them among one of the largest blocks of protected area in tropical rainforest regions. This may help explain the very low rates of the Species Defaunation Index (SDI) found in Cristalino and Xingu,

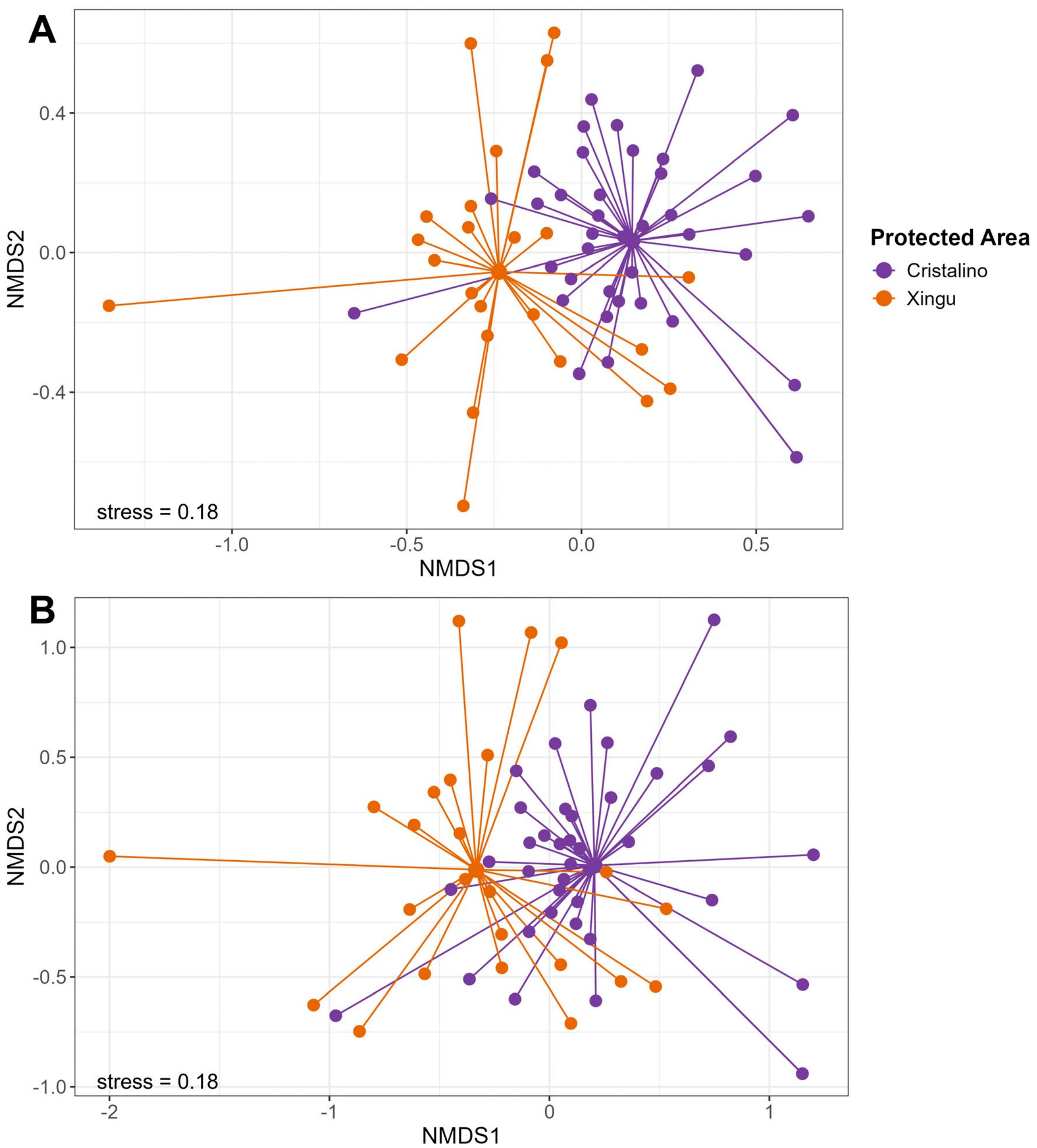

FIGURE 3 | NMDS scores of species composition of medium and large-sized terrestrial mammals in camera-trap sampling sites in the Cristalino State Park and Xingu State Park, in the southern Brazilian Amazon, Mato Grosso state. (A) independent record count data (stress = 0.18); (B) presence/absence data (stress = 0.18).

resembling the reference assemblage of the Amazon National Park, one of the most preserved and pristine sites in the Brazilian Amazon (Oliveira et al. 2016; Rosa et al. 2021b). Surprisingly, the SDI of Xingu obtained a negative rate (SDI = −0.002), indicating that the medium and large-sized mammal assemblage of Xingu has one of the lowest species richness defaunation rates of the Amazon (Giacomini and Galetti 2013). In this way, both Cristalino and Xingu were the least defaunated areas of the Amazon, until then evaluated in terms of the species defaunation index, since among the Amazonian reference sites, SDI ranged from −0.002 to 0.41 (Alvarenga et al. 2018; Carvalho Jr et al. 2020; Rosa et al. 2021b).

In addition to the high richness in both protected areas, the recorded species composition differed between sites, demonstrating the importance of complementarity between PAs to maintain biodiversity conservation in the Amazon as a whole. These differences in mammal assemblage composition between the two parks may be attributed to differences in vegetation type. Cristalino features Dense Ombrophilous and Semi-deciduous forests, *Campinarana,* and arenitic outcrops known as rupestrian fields (Zappi et al. 2011, 2016). On the other hand, the Cerrado *strict sensu* formations were found only in Xingu, together with the low-lying, riverine granitic outcrops that covered a large extension of the park (Zappi et al. 2016). These vegetation

TABLE 2 | Defaunation in the Cristalino State Park (Cristalino) and the Xingu State Park (Xingu), and in four other Brazilian Amazonian protected areas relative to reference assemblages (RA): Amazonia National Park (ANP) for the species defaunation index (SDI) and Balbina Reserve – continuous forest (BR-C) for the biomass defaunation index (BDI).

Site ID	Protected areas	SDI	BDI
Cristalino	Cristalino State Park	0.005	0.75
Xingu	Xingu State Park	−0.002	0.97
TNF-N	Tapajós National Forest – northern area	0.41	0.74
TNF-S	Tapajós National Forest – southern area	0.08	0.90
GBR	Gurupi Biological Reserve	0.02	−0.0008
ASDR	Amanã Sustainable Development Reserve	0.04	0.45
BR-I	Balbina Reserve – islands	0.03	0.44
BR-C	Balbina Reserve – continuous forest	0.03	RA
ANP	Amazonia National Park	RA	DN

Note: Data sources used to calculate defaunation index: Cristalino and Xingu – this study; TNF-S and TNF-N—Rosa et al. 2021b, Rosa et al. 2021a; GBR—Carvalho Jr et al. (2020); ASDR—Alvarenga et al. (2018); BR-I and BR-C—Palmeirim et al. (2018); ANP—Oliveira et al. (2016).
Abbreviation: DN, data not available.

characteristics help to explain the tripled richness of primates in Cristalino compared to that found in Xingu, which in turn showed a greater diversity of ground-dwelling mammals.

The importance of the two protected areas in the conservation of threatened Amazonian mammals was also confirmed by the fact that approximately 34% of the total recorded species are under some degree of threat at national and/or global levels (MMA 2022; IUCN 2024). Both parks recorded 11 threatened mammals, including some that are also rare to detect and have low population densities, such as *Atelocynus microtis, Speothos venaticus,* and *Priodontes maximus* (Oliveira et al. 2016; Pratas-Santiago et al. 2019; Rocha et al. 2020). However, the species with the highest threat level (Endangered) found in the PAs were two primates, *Ateles marginatus* recorded only in Cristalino, and *Chiropotes utahicki* found only in Xingu (Mittermeier et al. 2022). In addition, there may be the possible presence of other rare and unreported species in these areas of the Arc of Deforestation, as indicated by Castro et al. (2024), where they demonstrated the previously unknown occurrence of the Linné's two-toed sloth (*Choloepus didactylus*) in southern Amazon, especially near Cristalino. Therefore, the maintenance of the survival of this high proportion of threatened and rare mammals reinforces the role of the PAs in the conservation of Amazonian biodiversity (Walker et al. 2009; Qin et al. 2023).

In contrast, the high rates of biomass defaunation observed in Cristalino and Xingu (BDI > 0.7) compared to the reference assemblage must be analysed cautiously. The loss of mammal species is not random and is influenced by the defaunation of a specific group of ungulates in the areas, the peccaries (*Tayassu pecari* and *Dicotyles tajacu*). It is well known that the classic pattern of defaunation is characterised by the loss of larger mammal species, especially apex predators and ungulates, such as *P. onca*, *P. concolor*, *Mazama americana*, and especially *Tapirus terrestris* and *T. pecari* (Dirzo et al. 2014; Bogoni et al. 2020). However, the biomass defaunation found in Cristalino and Xingu has some peculiarities beyond this already known pattern (Galetti et al. 2017; Rosa, Brocardo, et al. 2021). For example, *T. terrestris*, the largest-bodied mammal species in South America, was the species that contributed the most to the total biomass in both parks surveyed. The biomass of *T. terrestris* found in Cristalino and Xingu was higher than that of the reference assemblage in Balbina Reserve (continuous forest) (Palmeirim et al. 2018), as well as all other compared protected areas (Alvarenga et al. 2018; Carvalho Jr et al. 2020; Rosa et al. 2021b), especially in Xingu (Figure 4). The two parks also led in biomass of *M. americana* and *P. concolor* in relation to the reference site and other protected areas, with Xingu also having the highest biomass of *P. onca*, the top predator in the Amazon. However, the biomass of *T. pecari* and *D. tajacu* in the two studied sites was much lower compared to the reference assemblage, resulting in the high BDI of both parks. Peccaries form the largest groups among Neotropical large mammals, with an average of 88.3 individuals per group for *T. pecari* (Reyna-Hurtado et al. 2016) and 9 individuals per group for *D. tajacu* (Keuroghlian et al. 2004). The formation of social groups gives these two species significant weight in biomass calculation, especially *T. pecari*, which has an influence on mammal biomass 11.8 times greater than *T. terrestris*. The latter tends to be 7.4 times heavier than an individual of *T. pecari*, but is solitary in habit.

Tayassu pecari is one of the most hunted mammals in the Amazon (Melo et al. 2015; Mesquita and Barreto 2015). Populations of this species are often locally and regionally extirpated in various locations in the Amazon, especially in areas close to human settlements (Peres 1996; Reyna-Hurtado and Tanner 2007). *Tayassu pecari* is highly sensitive to hunting pressure, which affects approximately 30% of its distribution (Ramos et al. 2016). Currently, it is categorised as Vulnerable on the Brazilian and IUCN Red Lists (Keuroghlian et al. 2013; MMA 2022). In addition to causing extensive habitat loss, the expansion of large-scale monoculture crops in the Amazon Arc of Deforestation region, where the two parks are located, may be contributing to increased hunting of *T. pecari* (Lima et al. 2019). Like in other areas of the Amazon and Cerrado, these animals are often hunted in retaliation for crop consumption and damage (Rosa et al. 2021b; Hermira and Michalski 2022). This frequent use of agricultural areas by peccary flocks may also explain the low frequency of records of the species in PAs, impacting its detectability and ecological role in its natural habitat (Fragoso 1998; Magioli et al. 2022). This paradoxical situation of the species is growing and more dramatic in the state of Mato Grosso, where it is considered a pest in certain areas, yet it has been extirpated from several places in the state (Jácomo 2004; Lima et al. 2019; Keuroghlian et al. 2023). These land use and cover changes can also interfere with the natural population cyclicity of *T. pecari*, which presents density-dependent demographic fluctuations, often with populations growing dramatically before disappearing locally (Fragoso et al. 2022). This

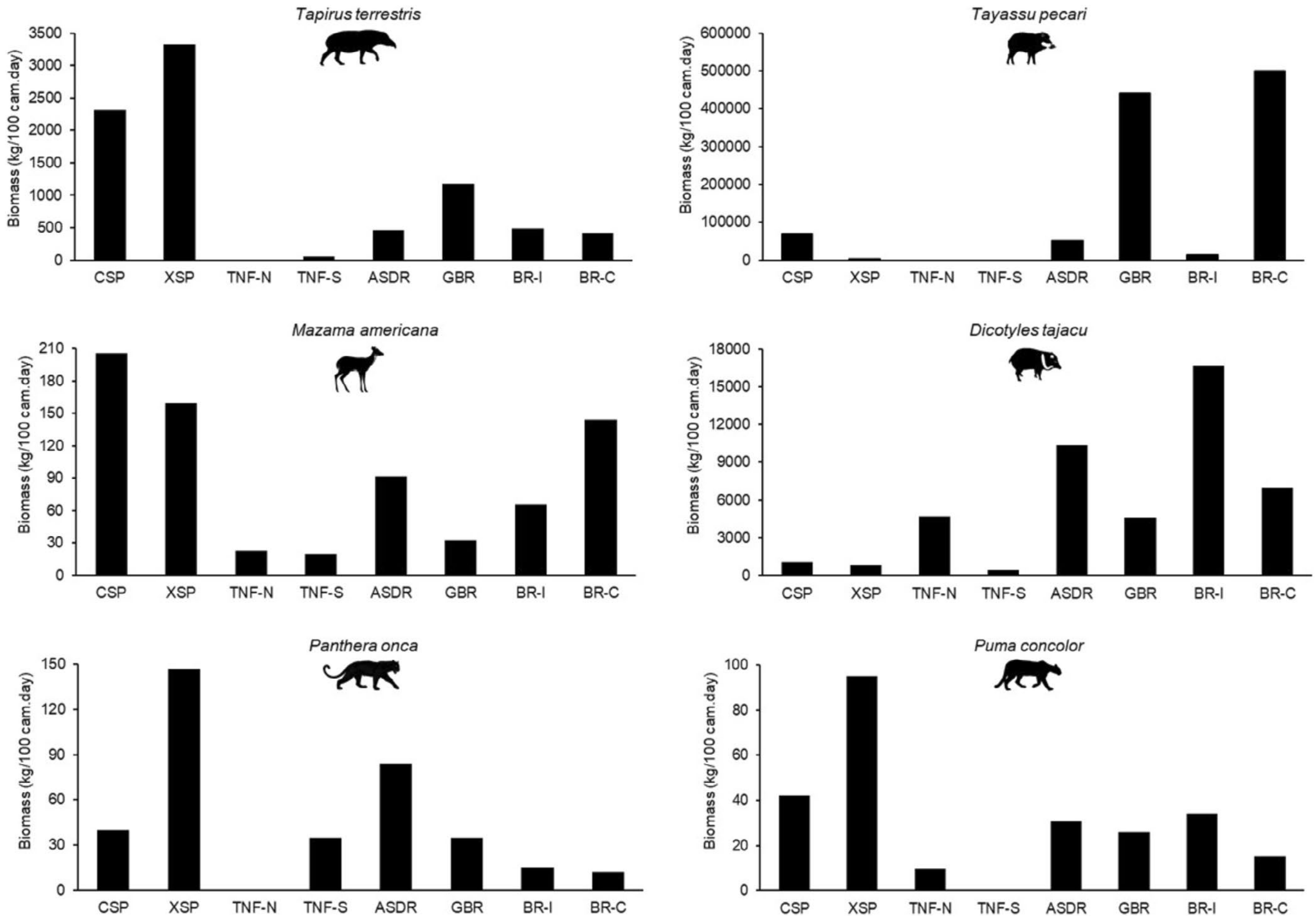

FIGURE 4 | Estimated biomass (kg/100 cam.day) of the six largest species of terrestrial mammals in our study areas, Cristalino State Park (CSP) and Xingu State Park (XSP), and four other Brazilian Amazon protected areas – Tapajós National Forest – northern area (TNF-N), Tapajós National Forest – southern area (TNF-S); Amanã Sustainable Development Reserve (ASDR); Gurupi Biological Reserve (GBR); Balbina Reserve – islands (BR-I), Balbina Reserve – continuous forest (BR-I). *Tayassu pecari* and *Dicotyles tajacu* were considered gregarious species for biomass calculation.

pattern demonstrates the importance of large and continuous fragments of Amazon forest in supporting source–sink population dynamics and the persistence of *T. pecari* populations time-locally (Fragoso et al. 2022).

Like other large ungulates, *T. pecari* plays a unique ecosystem role in tropical rainforests (Altrichter et al. 2012; Villar et al. 2020), being considered one of the most important ecosystem engineers in the Neotropics (Keuroghlian and Eaton 2009; Beck et al. 2010). The intense foraging behaviour of numerous groups of *T. pecari* (i.e., composed of about 400–1200 individuals in the Amazon – Fragoso 2004; Lima et al. 2019) disrupts live and dead plant material on the forest floor, promoting more efficient nutrient cycling, creating gaps in the forest floor, preying on and dispersing large seeds over long distances, and providing resource opportunities and conditions for other animals and plants (Silman et al. 2003; Beck 2005; Keuroghlian and Eaton 2009). The loss or simply the population reduction of this ungulate species, as our results in Cristalino and Xingu suggest, compromises both biodiversity, ecosystem functionality, and human health in Neotropical forests in the long term (Valiente-Banuet et al. 2015; Villar et al. 2020; Pires and Galetti 2023).

Both Cristalino and Xingu are located in the Amazon Arc of Deforestation, where the agricultural frontier advances towards the forest over an area of approximately 500 000 km^2 along a long ecotonal strip between the Amazon and Cerrado biomes (Garcia et al. 2019; Castro et al. 2024). The pressure from mechanised agriculture and extensive livestock farming has made this region, especially in the northern part of Mato Grosso, one of the areas with the highest deforestation rates in the Amazon (Zappi et al. 2016; Kastens et al. 2017). Thus, the existence of PAs like Cristalino and Xingu contributes to slowing down agricultural expansion and maintaining threatened and rare species in the Amazon Arc of Deforestation (Negrões et al. 2011).

Although these two parks play an important role, as we've shown, in reducing the environmental degradation happening in that region, they are still under pressure from illegal activities of mining, logging, fires, land grabbing, and deforestation due to agriculture and cattle ranching (Nobre et al. 2016; Lima et al. 2019). These activities are responsible for the intense devastation of native vegetation inside Cristalino (Zappi et al. 2011) and at the edges of Xingu (Zappi et al. 2016). Some studies have already pointed out that the increasing deforestation of the Amazon to expand agricultural areas could result in an 'agrosuicide' (Leite-Filho et al. 2021; Smith et al. 2023). The expansion of the agricultural frontier, especially in the Arc of Deforestation, has been deregulating water regimes and decreasing rainfall, which harms crops and livestock farming and could cause agricultural losses of around 1 billion dollars annually by 2050 (Leite-Filho et al. 2021; Smith et al. 2023).

An alternative to deforestation in the region is the restoration of pastures and abandoned agricultural areas (Feltran-Barbieri and Féres 2021). Estimates show that the cost of restoring these abandoned areas in the Amazon is 72% less than opening new areas through deforestation (Barreto 2021). Another measure that has proved effective in conserving biodiversity in the Amazon is payment for environmental services (Mota et al. 2023), which since 2021 has been part of a national policy of the Brazilian government (*Política Nacional de Pagamentos por Serviços Ambientais* – Law No. 14.119/2021). This legal instrument provides for financial compensation for rural landowners who conserve native vegetation on their land. In the state of Mato Grosso, the Conserv Program carried out by NGOs and research centres has proven the effectiveness of this environmental incentive (Stabile et al. 2022), adding up to 14843 ha of conserved forests by 2023, including privately preserved areas in the surrounding protected areas (https://conserv.org.br/). Still, the need for investment in community-based ecotourism in the region, which also generates revenue for local people through social and environmental policies, remains (Lebrão et al. 2021). Both parks have great potential to foment primate-watching tourism, for example, as they are home to rare and endangered monkeys (Costa-Araújo et al. 2022). The observation of other medium and large mammals should also be encouraged in these areas. Vidal et al. (2023) demonstrated that mammal-based tourism in the Brazilian Amazon has the potential to increase local income generation, ecological awareness and enhance scientific tourism.

Currently, an area of 118000 ha of Cristalino (about 64% of the PA, known as Cristalino II State Park) is in judicial dispute and has been temporarily annulled the 2001 decree that created the Cristalino II for the second time through judicial actions filed by an agribusiness company (Coelho-Junior et al. 2024). This dispute began in 2022 when the protection of this Cristalino area was judicially annulled for the first time, but in the same year, due to strong outrage and pressure from civil society and environmental organisations, the decision was overturned. But again, in April 2024 the Mato Grosso Court of Justice ruled in favour of the agribusiness company and abolished the Cristalino II area for the second time, despite evidence that the claims were illegal (Coelho-Junior et al. 2024). So far, the state government of Mato Grosso has not requested the revocation of the Cristalino II annulment due to the agribusiness lobby and the case has been referred to a conciliation centre. Meanwhile, all Cristalino's biodiversity and ecosystems are in serious jeopardy, even though it is a PA that is considered a high priority for Amazon biodiversity conservation and slowing deforestation towards the Amazon Forest central south (MMA 2018).

Our results broaden the understanding of the relevance of the biodiversity and endemism of mammals in the two parks. In particular, this study has the potential to contribute to the current judicial debate to revoke the annulment of more than half of the Cristalino area, reinforcing the importance of these PAs in the southern Amazon on the front line of deforestation and defaunation of the world's largest rainforest (Qin et al. 2023; Soares-Filho et al. 2023). In addition, both PAs also play an important role in climate change adaptation and the maintenance of ecosystem services in the Amazon Arc of Deforestation (Killeen and Solórzano 2008; Gatti et al. 2021; Csillik et al. 2024).

Author Contributions

Domingos de Jesus Rodrigues: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing – review and editing. **Clarissa Rosa:** conceptualization, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing. **Letícia G. Ribeiro:** formal analysis, methodology, visualization, writing – review and editing. **Rogério José Custódio:** conceptualization, data curation, investigation, methodology, resources, writing – review and editing. **Marcos Penhacek:** conceptualization, data curation, investigation, methodology, writing – review and editing. **Julia F. Queiroz:** data curation, methodology, writing – original draft, writing – review and editing. **Mateus Melo-Dias:** conceptualization, formal analysis, methodology, validation, visualization, writing – original draft, writing – review and editing.

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Consent

All authors have given consent to publish.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The capture rates data used to calculate the defaunation indices presented in this study are available in the Supporting Information. Other data will be made available on request to the authors.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.