











RESEARCH ARTICLE

Neotropical mammal responses to megafires in the Brazilian Pantanal

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Abstract

The increasing frequency and severity of human-caused fires likely have deleterious effects on species distribution and persistence. In 2020, megafires in the Brazilian Pantanal burned 43% of the biome's unburned area and resulted in mass mortality of wildlife. We investigated changes in habitat use or occupancy for an assemblage of eight mammal species in Serra do Amolar, Brazil, following the 2020 fires using a pre- and post-fire camera trap dataset. Additionally, we estimated the density for two naturally marked species, jaguars *Panthera onca* and ocelots *Leopardus pardalis*. Of the eight species, six (ocelots, collared peccaries *Dicotyles tajacu*, giant armadillos *Priodontes maximus*, Azara's agouti *Dasyprocta azarae*, red brocket deer *Mazama americana*, and tapirs *Tapirus terrestris*) had declining occupancy following fires, and one had stable habitat use (pumas *Puma concolor*). Giant armadillo experienced the most precipitous decline in occupancy from 0.431 ± 0.171 to 0.077 ± 0.044 after the fires. Jaguars were the only species with increasing habitat use, from 0.393 ± 0.127 to 0.753 ± 0.085 . Jaguar density remained stable across years (2.8 ± 1.3 , 3.7 ± 1.3 , $2.6 \pm 0.85/100 \text{ km}^2$), while ocelot density increased from 13.9 ± 3.2 to $16.1 \pm 5.2/100 \text{ km}^2$. However, the low number of both jaguars and ocelots recaptured after the fire period suggests that immigration may have sustained the population. Our results indicate that the megafires will have significant consequences for species occupancy and fitness in fire-affected areas. The scale of megafires may inhibit successful recolonization, thus wider studies are needed to investigate population trends.

KEYWORDS

carnivores, extinction, forest fires, habitat use, occupancy, *Panthera onca*, *Priodontes maximus*, *Puma concolor*, *Tapirus terrestris*

1 | INTRODUCTION

Human-caused disturbances to natural ecosystems and biodiversity have led to a sixth mass extinction (Ceballos et al., 2020; Cowie et al., 2022). Habitat loss is the foremost disturbance affecting biodiversity, leading to declining species distributions, reduced abundance, and extinction (Maxwell et al., 2016). Human-induced fires are a common vehicle for land use change, whereby forests and savannahs are ignited to clear vegetation (Bowman et al., 2020) and are associated with an average 38% of annual global forest loss (van Wees et al., 2021). Droughts and heat waves linked to climate change exacerbate fire risk and lead to megafires (Marengo et al., 2021), defined as those which extend over 10,000 ha (Linley et al., 2022). Many forested ecosystems are not adapted to frequent forest fires, with intervals between fires in the hundreds if not thousands of years (Cochrane, 2003). In these ecosystems, fires disturb wildlife habitat and movement through changing vegetation structure and causing direct or indirect mortality (Barlow & Peres, 2004; Cochrane, 2003; Kelly et al., 2020; Laurance, 2003).

Understanding and quantifying wildlife responses to human-induced fires has far-reaching conservation implications (Kelly et al., 2012; Massochini Frizzo et al., 2011; Michalski & Peres, 2007). Fire-induced mortality and changes in vegetation structure, especially in non-adapted ecosystems, can shape species distributions and abundances for decades (Haslem et al., 2011; Nimmo et al., 2021). Mammals play critical roles in ecosystem functioning through seed dispersal (Pérez-Méndez et al., 2016), nutrient cycling (Peziol et al., 2023), carbon cycling (Sobral et al., 2017), and trophic regulation (Estes et al., 2011). The loss of mammals from an area is detrimental to ecosystem health, ecosystem services, and has cascading effects on species composition (Young et al., 2016).

Mammal responses to fire vary depending on their habitat and resource requirements, their dispersal ability, and other trait-based characteristics (Calhoun et al., 2023). Mammal communities in non-fire-adapted regions may lack sensory cues to detect and flee from fires. Moreover, they may not be equipped with post-fire behavioral adaptations that allow them to take advantage of resources in these modified landscapes. Theoretical models to evaluate species' responses exist, such as the habitat accommodation model which suggests that species will enter post-fire succession areas if their habitat requirements are met, and if not, they will leave or reduce in number due to a lack of sustenance (i.e., vegetation or prey) or competitive interactions make it unsuitable (Fox, 1982; Fox et al., 2003). However, trait-based models are more appropriate for medium and large mammals because of variation in home range size, diet, and behavioral ecology that will be affected by fires (Pulsford et al., 2016). For example, the critical life cycles model suggested by Whelan et al. (2002) seeks to link species' life history and local environmental characteristics with animal fire responses like direct mortality and recolonization. However, universal patterns for species' response to disturbances have not emerged (Pulsford et al., 2016). Further empirical testing of species responses will aid in the development of

models for areas experiencing increased fire frequency and severity, such as the non-fire-adapted humid tropics.

In the Neotropics, one of the most fire-affected regions in the 21st century (van Wees et al., 2021), habitat degradation from wildfires is among the main threats to medium and large mammals (Griffiths & Brook, 2014; Jolly et al., 2022; Souza et al., 2023). Establishing and quantifying the effects of fire on mammals or other tropical wildlife is difficult because of the unpredictable nature of ignitions and subsequent wildfires and the lack of studies prior to the incident, which hinder site-level comparisons. Recent studies from the region suggest that species' responses to burned areas differ beyond traits such as body size or dispersal ability (Camargo et al., 2018; González et al., 2021; Quintero et al., 2023; Souza et al., 2023). For tapirs (*Tapirus terrestris*), for example, site use in the Amazon increased further from fires (Quintero et al., 2023), and they avoid burned areas more than other large-bodied herbivores like deer (*Ozotoceros bezoarticus*, *Mazama americana*, and *Subulo gouazoubira*; Souza et al., 2023).

The Brazilian Pantanal (herein Pantanal), the world's largest continuous wetland, experienced devastating fires in 2020 (Mataveli et al., 2021). The Pantanal experienced a threefold increase in fires in 2020 compared with the previous year, caused by a combination of severe drought, high temperatures, and policy setbacks like weakened environmental institutions (Marques et al., 2021; Pletsch et al., 2021). In 2020, fires burned approximately 43% of the Pantanal that had not burned in two decades (Garcia et al., 2021)—over 17,200 km²—and over 50% of natural savannahs and forest vegetation (Kumar et al., 2022). The fires killed an estimated 17 million vertebrates in just a few months (Tomas et al., 2021). However, impacts have largely been described in individuals killed and vegetation impacts (Berlinck et al., 2021), leaving little knowledge of post-fire impacts on habitat use and species distribution.

In this study, we assessed post-fire succession of an assemblage of medium and large mammals in Brazil. Using camera traps installed annually over a three-year period (Year 1: pre-fires, Year 2: immediately after fires; Year 3: over 1 year after fires) and dynamic occupancy models (DOMs), we analyzed habitat use or occupancy (depending on home range size) of eight terrestrial mammals representing different trophic guilds: (1) Carnivores: jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), puma (*Puma concolor*), (2) Insectivores: giant armadillo (*Priodontes maximus*), and (3) Herbivores: lowland tapir (*Tapirus terrestris*), red brocket deer (*Mazama americana*), collared peccary (*Dicotyles tajacu*), and Azara's agouti (*Dasyprocta azarae*). We also estimated spatially explicit density for naturally marked species, jaguars and ocelots, for the 3 years. We hypothesized that forest fires would increase the probability of use or occupancy for large grazing herbivores like tapirs due to the availability of regrowth with high nutrient seedling concentration and high palatability (Baggio et al., 2021; Donaldson et al., 2018; Westlake et al., 2020). Contrarily, smaller browsing herbivores such as deer, peccaries, and agoutis would be negatively affected due to the decreased availability of forest resources they rely on such as roots, nuts, and seeds (Klop & Van Goethem, 2008; Prado, 2013). Burrowing species like

the giant armadillo would also be negatively affected because of their limited mobility and secondary fire effects like high soil temperature and smoke (Desbiez et al., 2020; Silva et al., 2020). Lastly, we hypothesized a weaker to no effect of fires on carnivore habitat use/occupancy and density due to their high mobility and ability to prey on a variety of species, including aquatic species in the case of jaguars (Cavalcanti & Gese, 2010; Da Silveira et al., 2010; Perilli et al., 2016), which may have been relatively safe from the fires because they reside in or near water bodies. Our study provides insight into how transformational events like megafires, which are thought to be exacerbated by climate and land use change, will affect habitat use of an assemblage of mammal species.

2 | METHODS

2.1 | Study area

The study was conducted in the Serra do Amolar area in the Brazilian Pantanal (17°57'40.7"S, 57°28'48.3"W to 18°11'53.8"S, 57°23'20.1"W), bordered to the west by Bolivia and to the east by the Paraguay River in the Brazilian states of Mato Grosso and Mato Grosso do Sul (Figure 1). The area presents an elevation gradient ranging from 80m a.s.l. to 1000m a.s.l. at the highest peaks on the western edge of the study area (Porfirio et al., 2014). Serra do Amolar has a mean temperature of 25°C (Fernandes et al., 2010; Rohli & Vega, 2008) and an annual average rainfall of 1400mm, with the rainy season between the months of November and April (Cid et al., 2015). The study area is composed of contiguous private natural heritage reserves with well-preserved primary, secondary, and gallery forests (59%), associated waterways and wetlands (35%), savannahs (6%), and scarce human productive activities, although there are large livestock operations nearby (Casagrande & Santos-Filho, 2019). The area experienced forest fires between August and September of 2020 that were ignited to clear pasture for neighborhood cattle ranching (Leal Filho et al., 2021; Marques et al., 2021; Teodoro et al., 2022) and exacerbated by the prolonged drought of 2019 and 2020 (Marengo et al., 2021). Overall, fires burned >95% of the study area, with the northern section of the study area experiencing two fires during the study period (ALARMES, 2020).

2.2 | Data collection

We used camera traps (Bushnell 119876, Panthera V4, and Cuddeback 1279) to survey the study area in December 2019 (Session 1; Year 1—pre-fires) and December 2020 (Session 2, Year 2—2months post-fires). Due to logistical constraints, we installed cameras in February 2022 (Session 3, Year 3—15months post-fires) for an average duration of 53 trap nights (range 1–136, see Table S1 for complete details). All three surveys took place in the rainy season. Thirty-five stations were active in Session 1, 43 stations in Session 2, and 31 stations in Session 3. Cameras were placed at a

distance of $1.5 \pm .5$ km between stations and were located in different land covers (primary, secondary and gallery forest, and savannah). Minimum convex polygons for each survey were 189.68 km² in Year 1, 272.26 km² in Year 2, and 245.95 km² in Year 3. We placed double stations to enable photographing both sides of each passing individual, thus enabling the identification for naturally marked species like jaguars and ocelots. Each sampling station had 24-h motion-triggered camera operation with a period of 30s between photograph triggers. Geographic coordinates, camera serial number, date and time of camera installation, canopy cover, habitat, and whether the camera was on or off trail were recorded.

Our survey design complied with methodological assumptions to estimate jaguar (Foster et al., 2020; Tobler et al., 2013) and ocelot densities (Boron et al., 2021; Satter, Augustine, Harmsen, Foster, Sanchez, et al., 2019; Wolff et al., 2019), and we kept a discrete distance between stations to obtain data for the wider mammal community (Boron et al., 2021; de Martins et al., 2006; Rovero & Ahumada, 2017; Rovero et al., 2020). Our survey was limited to less than 100 days per year and fulfills overall capture–recapture model assumptions: (a) the population needs to be considered closed and stable, and (b) all individuals should have a chance of being captured (Otis et al., 1978; White, 1982).

2.3 | Covariate selection and extraction

We selected a set of covariates to test our hypotheses related to pre- and post-fire habitat use/occupancy as well as density. Covariates were Normalized Difference Vegetation Index (NDVI), often used to assess habitat quality for mammals (Pettorelli et al., 2005; White et al., 2022), area burned (AB) derived from Differenced Normalized Burn Ratio (Δ NBR), which measures fire severity (Escuin et al., 2008), and distance from water (Boron et al., 2019). We additionally included detection covariates (p) of effort as the total of trap nights per station; year, included to account for differences related to time variation as field staff and camera type (Gutiérrez-González et al., 2015; Kotze et al., 2012); and whether the camera station was on a trail or not (Sollmann et al., 2011). Year or session was also used as a way to account for the heterogeneity of the detection probability, like seasonal activity of species and the possible loss of camera quality (Kotze et al., 2012; MacKenzie et al., 2003; Tobler et al., 2015).

NDVI was obtained for each study session from Copernicus-Sentinel-II sensors via Google Earth Engine (<https://rb.gy/r2diwi>). NDVI calculates vegetation greenness on a normalized scale with denser vegetation approaching one and barren areas or water bodies closer to a value of zero (Pettorelli et al., 2005). Annual NDVI rasters were obtained on days with less than 10% cloud cover during the period of 1 month before camera installation with a grain size of 10m. We then extracted the mean NDVI value for a 500-m buffer around each station.

We calculated AB as the area within a 500-m buffer of each camera station that presented moderate–low severity or higher

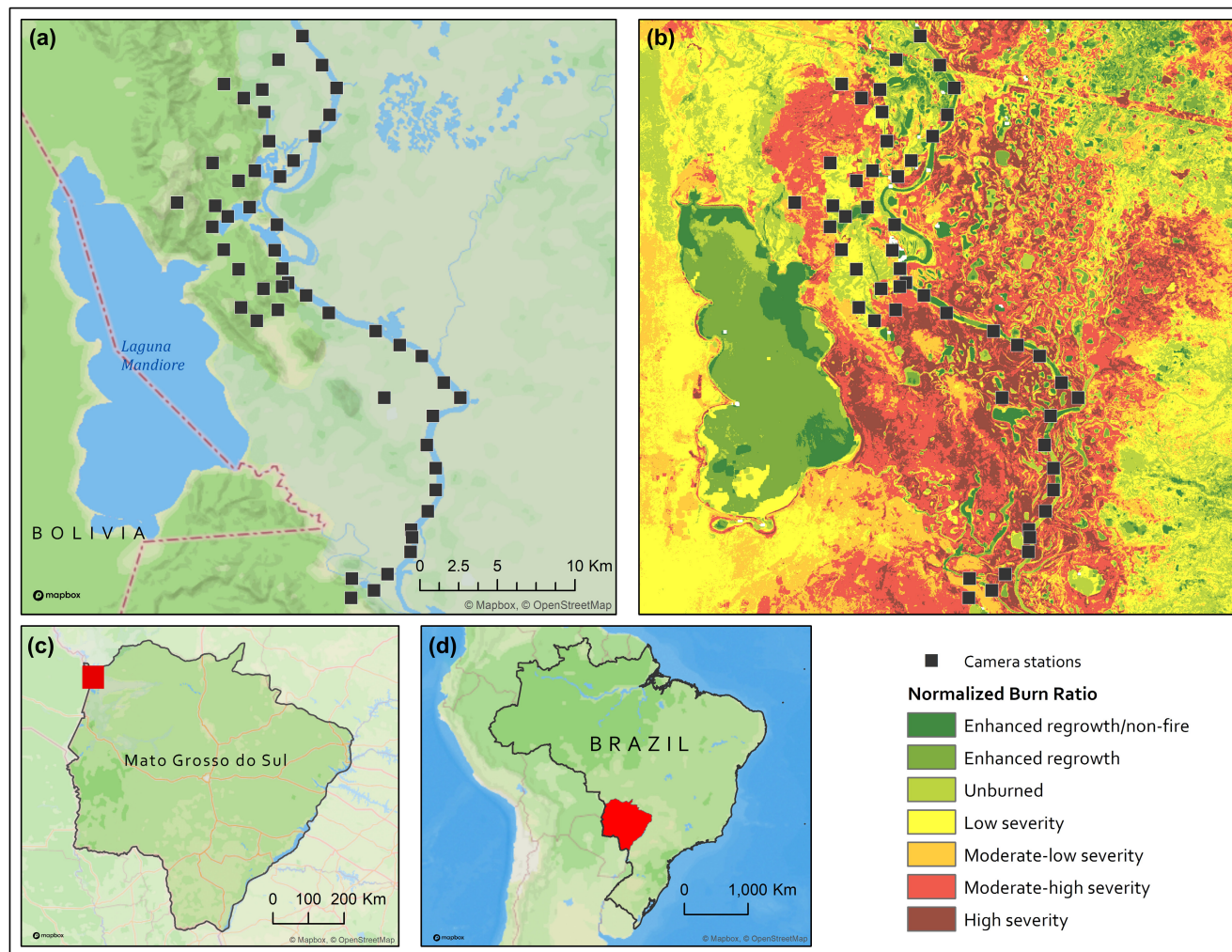


FIGURE 1 Study area in Serra do Amolar in the Brazilian state of Mato Grosso do Sul. (a) The study area and camera trap array. (b) Normalized Burn Ratio for the study area after the megafire in September and October 2020. (c) The location of the study area in the state of Mato Grosso do Sul. (d) The location of Mato Grosso do Sul in Brazil. Sources: Natural Earth, Mapbox, Google Earth Engine, Copernicus-Sentinel II images. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

according to ΔNBR . For AB, we included only ΔNBR values that represent moderate-low burn severity and higher ($\Delta\text{NBR} = 270+$) (Keeley, 2009; Key & Benson, 2006) in order to differentiate from areas that may have had low affection from the fires or that may have presented false-positive values where fires may have burned due to the lack of an NBR system for the region. We calculated the ΔNBR using Copernicus-Sentinel II images from the survey periods using images within 1 month of the fieldwork start date in Google Earth Engine (UN-SPIDER Knowledge Portal, 2023; <https://rb.gy/kw8s4e>). We obtained surface water data from MapBiomas (<https://brasil.mapbiomas.org>) and calculated the Euclidean distance of each camera station from surface water. All geoprocessing was conducted in ArcMap Desktop 10.8 (Esri, 2020). We used Spearman's correlation test to check for highly correlated covariates (>0.6) with the function `ggcorr` in the package "GGally v2.1.2" (Schloerke et al., 2022) in Program R v 4.2.2 (R Core Team, 2022). As covariates AB and ΔNBR were correlated (>0.6), we fit two global models, each including one of these covariates and selected

the best model using Akaike information criteria corrected (AICc) for small sample sizes (Burnham & Anderson, 2002; Hurvich & Tsai, 1989). The model with AB covariate performed better than ΔNBR for most species and thus was used in the analysis.

2.4 | Dynamic occupancy

We determined the habitat use or initial occupancy probability of eight mammal species in the study area: jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), pumas (*Puma concolor*), giant armadillo (*Prionomys maximus*), lowland tapir (*Tapirus terrestris*), red brocket deer (*Mazama americana*), collared peccaries (*Dicotyles tajacu*), and Azara's agouti (*Dasyprocta azarae*). We estimated initial occupancy probability when we could assume closure (individual's home range is less than the radius between camera trap stations) between camera trap locations (MacKenzie et al., 2002), for ocelots (Crawshaw & Quigley, 1989), red brocket deer (Varela et al., 2010), Azara's

agouti (Cid et al., 2013) and giant armadillo (Desbiez et al., 2020). We estimated habitat use for jaguars (Kantek et al., 2021; Soisalo & Cavalcanti, 2006), pumas (Silveira, 2004), collared peccaries (Desbiez et al., 2009), and tapirs (Medici et al., 2022), whose home range surpassed the distance (1.5 km) between stations. Detection histories were created for each species, grouping camera data into a 7–21 days survey occasions based on the results of goodness-of-fit (GOF) tests (MacKenzie & Bailey, 2004) (Tables S3 and S4). Dynamic occupancy models estimate the probability of occupancy and detection and are particularly useful for monitoring changes in occupancy status over time (MacKenzie et al., 2018), allowing us to assess what factors influence colonization (X) and extinction (E) trends. We scaled covariates before analysis for interpretability. We used “unmarked” package v 1.2.5 (Fiske & Chandler, 2011; Kellner et al., 2023) in Program R v 4.2.2 (R Core Team, 2022) for all occupancy analysis.

The parameters used in DOM were Ψ = initial probability of a site being occupied; p = probability of a species being detected if it is present, X = probability of a new area to pass from unoccupied to occupied (or to unused to used) in the next year, E = probability that a species stops occupying an area, or to pass from used to unused.

We fit models for species individually and selected models according to AICc (Burnham & Anderson, 2002). We used a stepwise method (Doherty et al., 2012) for model selection. We first fit models for detection (p) with all other parameters constant. We included survey effort, whether cameras were on a trail, and year as covariates for detection, and selected the best detection model based on AICc value. We proceeded with this best detection model and subsequently fit models using covariates describing occupancy, colonization, and, finally, extinction. We included NDVI and distance to water as covariates for occupancy, whereas AB was applied to colonization and extinction.

We considered there to be satisfactory statistical evidence for an effect if the 95% confidence interval of logit scale coefficient estimates did not include zero (Muff et al., 2022). The β estimates were back-transformed to obtain model parameter estimates (MacKenzie & Bailey, 2004). We tested model fit by using a parametric bootstrap GOF test based on Pearson's χ^2 where $p > .05$ indicates adequate model fit (Fiske & Chandler, 2011) (Table S3). Finally, we derived annual probability for each year, and calculated standard errors for the derived values using a bootstrap method (Kéry & Chandler, 2016). To assess whether differences in occupancy were statistically significant, we used a nonparametric bootstrap with 1000 iterations and calculated the difference between 95% confidence intervals between Years 1 and 3. If the difference in confidence intervals did not contain zero, we considered it significant (Kéry & Royle, 2021).

2.5 | Density

Jaguar and ocelot individuals were visually identified by their spot patterns and sex based on external genitalia (Boron et al., 2016).

Individuals of unidentified sex were classified as unknown (Table S1). We generated three files to input in “secr” in R (Efford, 2020) for density estimation (a) a capture history per species per session with trap number, individual ID, date and time occasion number of each record; (b) a trap deployment file consisting of all traps locations and a binary record file of activity per occasion (defined here as a 24-h period/day); (c) a mask file to represent the state space habitat area, at a 500 m spacing and within a buffer of 20 km using the *suggest.buffer* that corresponds to ~ 4 (Efford, 2018) that also matched the largest buffer suggested for jaguars previously (Greenspan et al., 2020; Noss et al., 2012). We used the half-normal (HN) detection function, which considers that the probability of capture (p) of any individual (i) decreases with the distance (d) from the activity center such that: $p_{ij} = g0 \exp(-d_{ij}^2 / 2\sigma^2)$, $g0$ represents the probability of capture or detection when a trap (j) is located right at the center of the home range; and sigma (σ) is a proxy parameter related to home range size (Efford, 2004). Felid species have varying home range sizes according to sex (Massara et al., 2015; Satter, Augustine, Harmsen, Foster, & Kelly, 2019); however, as sex was not identified for all individuals, this was not included in the models. Felids are also known to use unpaved roads to varying degrees and jaguars may be more detectable on them (Sollmann et al., 2011). We therefore enabled detection ($g0$) to vary by whether the station was located on a trail, while sigma (σ) varied according to the different sessions to assess whether the value is constant or varies across years. We additionally considered distance to water, NDVI, and ΔNBR as covariates for density and selected models using AICc (Burnham & Anderson, 2002).

3 | RESULTS

More than three-quarters of the study area presented a low–moderate or higher severity burn (Figure 1). During the three sessions, we obtained a total of 1132 records of the eight focal species over 6016 trap nights. Trap nights on the first session were 1665 (from 35 stations), 2692 in the second session (from 43 stations), and 1659 (from 31 stations) in the third session. Azara's agouti was the most commonly detected species (311 detections) followed by the red brocket deer (216). Giant armadillo had the fewest records (26 detections) (Table 1; Table S2).

3.1 | Dynamic occupancy

We ran 13 models for each species (Table S4). There was no statistical evidence for an effect of fire covariates on colonization and extinction for any of the species analyzed (Table 1). Habitat use or occupancy decreased for six species, remained constant for one species, and increased for one species. These overall trends presented different degrees of strength (Figure 2). Below, we describe the top model and its β coefficient estimates.

Habitat use for jaguars increased significantly from 0.393 (SE: 0.127, 95% CIs: 0.144–0.642) in Year 1 to 0.753 (SE: 0.085, 95%

TABLE 1 Top models according to Akaike information criterion corrected for small sample sizes (AICc) model for eight mammal species in Serra do Amolar, Brazilian Pantanal.

Species	n	Top model					K	ModLL	AICcWt	LL
		Ψ	p	χ	ϵ					
<i>Panthera onca</i>	91	~1	~E	~1	~AB	6	1	0.386		-181.688
<i>Puma concolor</i>	68	~NDVI	~E+T	~1	~1	7	1	0.771		-149.222
<i>Leopardus pardalis</i>	133	~1	~E+y	~1	~1	7	1	0.769		-169.710
<i>Tapirus terrestris</i>	156	~NDVI	~E+T+y	~1	~1	9	1	0.813		-165.288
<i>Maxama americana</i>	216	~1	~E+y	~1	~1	7	1	0.791		-187.728
<i>Dicotyles tajacu</i>	131	~dW	~E+T+y	~1	~1	9	1	0.842		-150.550
<i>Priodontes maximus</i>	26	~dW	~E	~1	~1	6	1	0.524		-61.697
<i>Dasyprocta azarae</i>	311	~1	~E+y	~1	~1	7	1	0.989		-133.501

Abbreviations: ~1, intercept only for the parameter; AB, area burned; AICcWt, AICc model weights; dW, distance from water; E, effort; ϵ , extinction; K, number of parameters; LL, log-likelihood; ModLL, model likelihood; n, number of independent record per species; NDVI, normalized difference vegetation index; p, detection; T, trail; y, year/session; γ , colonization; Ψ , occupancy/habitat use.

CI: 0.586–0.919) in Year 3 (Figure 2) (Table S6). The top model (Table 1; Table S4) had a GOF test p -value of .366 (Table S3). This model estimated a colonization value of 0.704 (SE: 0.143, 95% CI: 0.436–0.880), extinction intercept of 0.108 (SE: 0.243, 95% CI: 0.002–0.884) negatively influenced by AB covariate (β : -3.3, CI: -11.424–4.824) with a back-transformed value of 0.036 (SE: 0.142, 95% CI: 0.000–0.971) (Table S5).

Puma habitat use remained stable during the study period. The parameter estimate for habitat use was 0.470 (SE: 0.156, 95% CI: 0.144–0.642) for the year pre-fire and remained steady during the following years: 0.466 (SE: 0.104, 95% CI: 0.263–0.669) in Year 2 and 0.426 (SE: 0.119, 95% CI: 0.194–0.659) in Year 3, with overlapping CI (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .217 (Table S3). The model estimated a colonization value of 0.140 (SE: 0.086, 95% CI: 0.048–0.346), extinction of 0.206 (SE: 0.124, 95% CI: 0.070–0.474). Effort (β : 0.301, CI: 0.070–0.531) and NDVI (β : -1.188, CI: -2.160 to -0.217) covariates had a statistically significant effect on detection and occupancy, respectively, in the top model.

Ocelot occupancy declined significantly during the study. It decreased from 0.741 (SE: 0.114, CI: 0.518–0.965) in Year 1 to 0.661 (SE: 0.143, CI: 0.382–0.941) in Year 3 (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .042 (Table S3). The model estimated a colonization of 0.646 (SE: 0.282, CI: 0.194–0.933), and extinction of 0.323 (SE: 0.138, CI: 0.145–0.573). Year 2 (β : -1.507, CI: -2.387 to -0.626) and Year 3 (β : -1.032, CI: -2.046 to -0.017) and effort were statistically significant covariates on detection in the top model.

Lowland tapir habitat use increased immediately after the fires then declined in Year 3. The decline was significant when comparing Year 3 to Year 1. Tapir habitat use increased slightly during Year 2, from 0.366 (SE: 0.097, 95% CI: 0.176–0.557) in Year 1 to 0.389 (SE: 0.074, 95% CI: 0.244–0.534), followed by a decrease during Year 3 to 0.330 (SE: 0.093, CI: 0.147–0.514; Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .519 (Table S3). The

model's colonization estimate was 0.122 (SE: 0.056, 95% CI: 0.055–0.247), and extinction was 0.248 (SE: 0.110, 95% CI: 0.111–0.465). Covariates trail (β : 1.066, CI: 0.037–2.096), effort (β : 0.169, CI: 0.068–0.271), and year [Year 2 (β : -1.265, CI: -2.026 to -0.504), Year 3 (β : -0.182, CI: -1.108–0.745)] had statistically significant effects on detection in the top model, and NDVI (β : -0.811, CI: -1546 to -0.075) on occupancy.

Red brocket deer occupancy declined significantly after the fires, decreasing from 0.517 (SE: 0.093, CI: 0.335–0.699) in Year 1 to 0.439 (SE: 0.106, CI: 0.231–0.648) in Year 3 (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of 0.281 (Table S3). The model estimated colonization of 0.223 (SE: 0.087, CI: 0.111–0.395) and extinction of 0.291 (SE: 0.105, CI: 0.152–0.487). There was a statistically significant effect of the influence of effort (β : 0.208, CI: 0.082–0.334) and year (Year 2 (β : -1.023, CI: -1.746 to -0.299), Year 3 (β : -0.995, CI: -1.983 to -0.008)) on detection in the top model.

Collared peccary habitat use declined steadily during the study period decreasing significantly from 0.471 (SE: 0.111, CI: 0.254–0.687) in Year 1 to 0.361 (SE: 0.133, CI: 0.101–0.622) in Year 3 (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .142 (Table S3). The model estimated a colonization value of 0.116 (SE: 0.077, CI: 0.037–0.312) and extinction of 0.264 (SE: \pm 0.130, CI: 0.107–0.518). Covariates on the detection parameter trail (β : -1.152, CI: -2.45 to -0.059), effort (β : 0.136, CI: 0.013–0.260), and year [Year 2 (β : -0.996, CI: -1.803 to -0.190), Year 3 (β : -1.265, CI: -2.429 to -0.101)] had a statistically significant effect.

The giant armadillo showed significant evidence of declining occupancy after fires. Occupancy probability decreased abruptly after fires from 0.431 (SE: 0.171, CI: 0.095–0.767) in Year 1 to 0.076 (SE: 0.048, CI: -0.0118–0.170) in Year 3 (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .351 (Table S3). The model estimated a colonization value of 0.055 (SE: 0.046, CI: 0.013–0.200) and extinction of 0.816 (SE: 0.136; CI: 0.499–0.952).

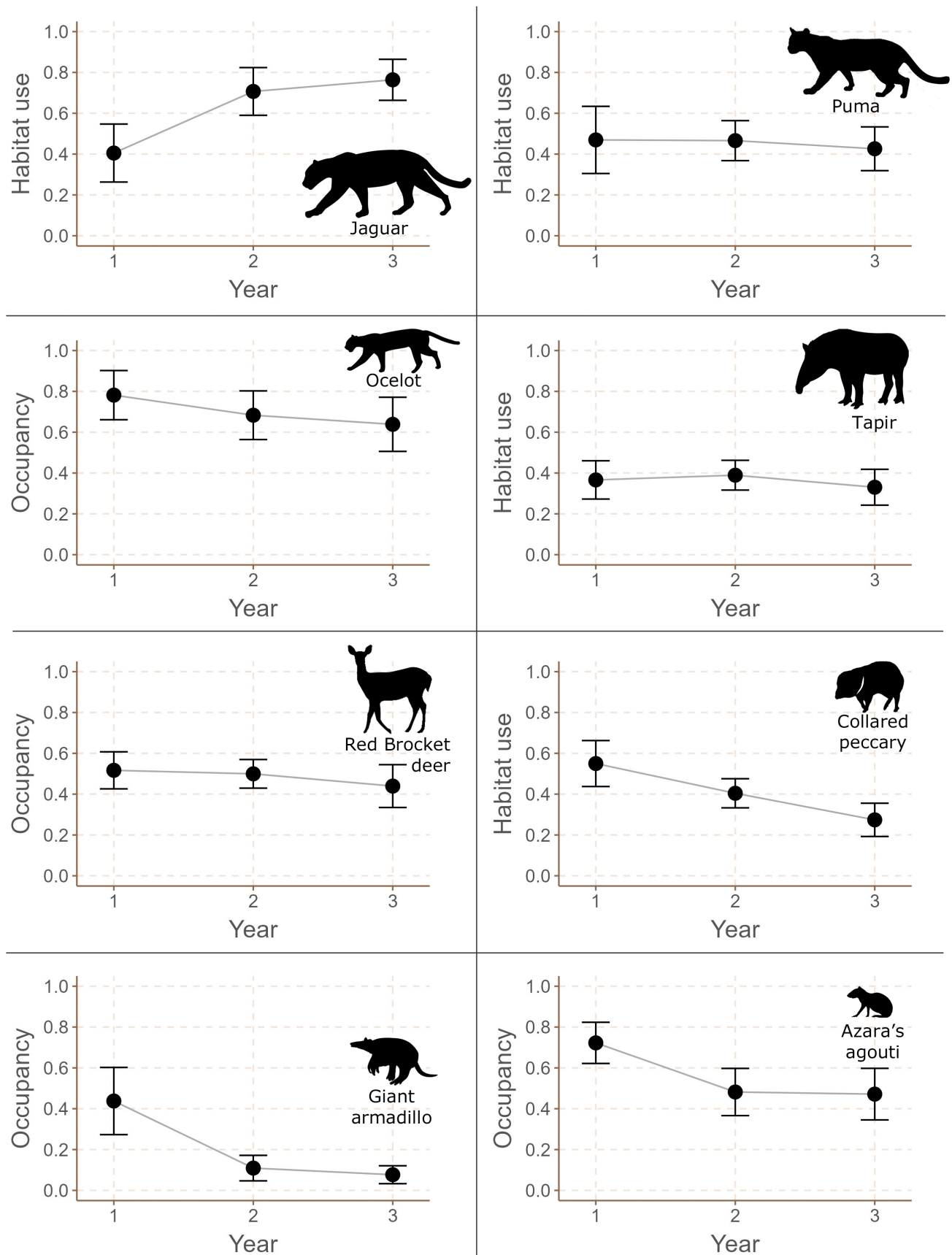


FIGURE 2 Occupancy/habitat use and standard errors for mammal species in Serra do Amolar, Brazilian Pantanal. Icon sources: Giant armadillo and agouti by [phylopic.com](https://www.phylopic.com/), others were created by RB.

Azara's agouti occupancy decreased significantly during the study. Initial occupancy was 0.734 (SE: 0.104, CIs: 0.531–0.937) in Year 1 but declined after the fires and reached 0.459 (SE: 0.130, CIs: 0.205–0.713) in Year 3 (Figure 2). The top model (Table 1; Table S4) had a GOF test p -value of .209 (Table S3). The model estimated a colonization of 0.376 (SE: 0.172, CIs: 0.153–0.670) and extinction of 0.474 (SE: 0.137, CIs: 0.268–0.689). Effort (β : 0.139, CIs: 0.080–0.198) and year [Year 2 (β : -1.678, CIs: -2.739 to -0.618), Year 3 (β : -1.813, CIs: -3.059 to -0.566)] had statistically significant effects on detection in the top model.

3.2 | Density

In total, there were seven adult jaguars recorded during Year 1 (14 events), 14 during Year 2 (27 events), and 13 (20 events) during Year 3. With the exception of Year 2, more females than males were detected (Year 1 = 4♀ vs. 3♂, Year 2 = 3♀ vs. 8♂, and Year 3 = 7♀ vs. 3♂), but recaptures for both sexes in different camera stations were scarce (3, 4, and 3 in total for each session respectively). For ocelots, we recorded 30 individuals in Year 1 (63 events), 19 in Year 2 (33 events), and 20 during Year 3 (41 events). Unlike jaguars, we recorded more males than females in all 3 years (Year 1 = 7♀ vs. 10♂, Year 2 = 3♀ vs. 11♂, and Year 3 = 3♀ vs. 6♂). However, unknown individuals (unidentifiable sex) were frequent and made up

55% of the total detections during Year 3 (Table S1). In all years, males were captured and recaptured in different stations more times than females. Notably, recapture of individuals from previous sessions was low for both felids. In Year 2, three jaguars of the 14 identified were present in the previous year, while for ocelots it was 10 in Year 2 of 19 from Year 1. Four jaguars (out of 14) from Year 2 were also present in Year 3, and only one individual was recorded in all three sessions. In the case of ocelots, no ocelot (out of 19) from Year 2 was also present in Year 3, and only four individuals were detected during the three sessions. Two additional individuals that were recorded in Year 1 were not detected in Year 2 but were present again in Year 3.

The best SECR model for jaguars was density~distance from water, $g0 \sim 1$, and $\sigma \sim$ session (Table S7). Density estimates for jaguars varied only slightly from 2.8 individuals/100km² (SE: 1.3, 95% CIs: 1.2–6.6) in Year 1, to 3.7 individuals/100km² (SE: 1.3, 95% CIs: 1.9–7.1) in Year 2, and to 2.6 individuals/100km² (SE: 0.8, 95% CIs: 1.4–4.8) in Year 3 (Figure 3a), suggesting no evidence of density change (Table 2). σ values (a proxy for home range) increased from 3.0km (SE: 0.6, 95% CIs: 2.0–4.6) in Year 1 to 4.9km (SE: 0.8, 95% CIs: 3.5–6.8) in Year 3 (Figure 3b).

The best SECR model for ocelots was density~NDVI, $g0 \sim$ trail, and $\sigma \sim$ session (Table S7). Ocelot density increased slightly from 13.8 individuals/100km² (SE: 3.2, 95% CI: 8.9–21.6) in Year 1 to 16.1 individuals/100km² (SE: 4.9, 95% CI: 8.7–30.0) in Year 3 (Table 2;

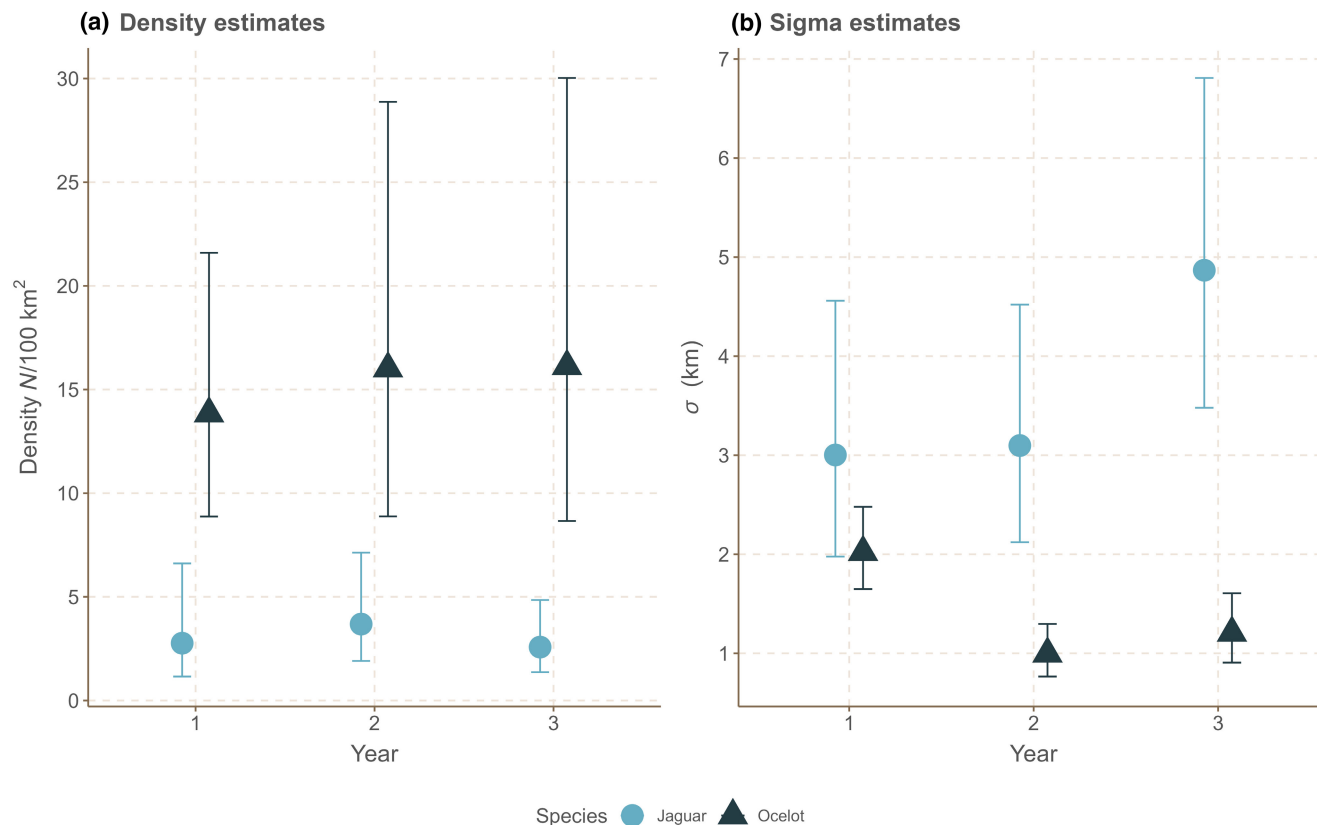


FIGURE 3 (a) Density values and 95% confidence intervals for jaguars and ocelots during the three study years in Serra do Amolar, Brazilian Pantanal. (b) Sigma (home range proxy) values and 95% confidence intervals for jaguars and ocelots during the three study years.

TABLE 2 Coefficient values for jaguar and ocelot density during the three study years in Serra do Amolar, Brazilian Pantanal. The values are taken from the top models.

	Session 1				Session 2				Session 3			
	Value	SE	95% LCL	95% UCL	Value	SE	95% LCL	95% UCL	Value	SE	95% LCL	95% UCL
Jaguars												
g0	0.005	0.001	0.003	0.008	0.005	0.001	0.003	0.008	0.005	0.001	0.003	0.008
Sigma (km)	3.003	0.647	1.977	4.560	3.098	0.603	2.123	4.521	4.868	0.840	3.480	6.809
D (N/100km ²)	2.764	1.294	1.155	6.613	3.686	1.277	1.906	7.130	2.576	0.853	1.369	4.848
Ocelots												
g0 (Y)	0.009	0.002	0.006	0.011	0.009	0.002	0.006	0.011	0.009	0.002	0.006	0.011
g0 (N)	0.016	0.003	0.011	0.022	0.016	0.003	0.011	0.022	0.016	0.003	0.011	0.022
Sigma (km)	2.022	0.211	1.649	2.480	0.996	0.134	0.766	1.297	1.207	0.177	0.907	1.607
pmix trail (Y)	0.403	0.086	0.251	0.576	0.403	0.086	0.251	0.576	0.403	0.086	0.251	0.576
pmix trail (N)	0.597	0.086	0.424	0.749	0.597	0.086	0.424	0.749	0.597	0.086	0.424	0.749
D (N/100km ²)	13.844	3.182	8.874	21.596	16.013	4.927	8.880	28.873	16.125	5.246	8.659	30.026

Abbreviations: D, density; g0, detection; LCL, lower confidence level; N, number of individuals; pmix, mixing proportion; SE, standard error; UCL, upper confidence level.

Figure 3a), though confidence intervals overlapped. Conversely, σ values showed a decrease for this species, declining from 2.0km (SE: 0.2, 95% CIs: 1.7–2.5) in the year before the fires to 1.2 (SE: 0.2, 95% CIs: 0.9–1.6) (Figure 3b).

4 | DISCUSSION

Human-caused megafires have reverberating consequences on wild-life and the ecosystems they inhabit, but few studies evaluate these impacts in the Neotropics (Geary et al., 2020; González et al., 2022). In this paper, we evaluated changes in occupancy or habitat use for an assemblage of eight species and density for two naturally marked species in the Brazilian Pantanal, where megafires destroyed much of the natural land cover (Kumar et al., 2022; Marques et al., 2021). We found that habitat use or occupancy remained constant for pumas, increased for jaguars, and decreased for ocelots, tapirs, red brocket deer, collared peccaries, giant armadillos, and Azara's agoutis. Ocelot and jaguar densities remained comparable across the years, though few individuals of both species were recaptured in Years 2 and 3, suggesting there was mortality or emigration, and that immigration may be sustaining these populations.

Only jaguars had the fire covariate of AB in the extinction parameter in their top model, despite negative trends in occupancy for many of the species post-fire and relatively high extinction values. We attribute this to the limited number of post-fire records for many species, and the entire area being affected by the high burn severity (an average of 70% of the AB for the buffer area considered each camera), thus reducing differentiation by site (Calhoun et al., 2023). Additionally, Δ NBR should be individually calibrated in each vegetation type because of the difference in their chlorophyll and density values (Kokaly et al., 2007; Miller & Quayle, 2015; Picotte & Robertson, 2011), but such measures do not exist for Brazil. Therefore, the use of values based on US ecosystems (Key & Benson, 2006) may add some uncertainty to the models. In order to improve fire severity estimates, it is necessary to calibrate burn indices for Brazilian ecosystems.

Jaguar habitat use increased from 0.0393 ± 0.127 in the year before the fires to 0.753 ± 0.085 2 years post-fire. Jaguars' colonization estimate was the highest among all eight species at 0.686 ± 0.133 . Their extinction estimate was the lowest at 0.108 ± 0.324 , though negatively correlated with the covariate of AB. This suggests that jaguars were able to expand their habitat use in response to the forest fires, likely into areas with the highest fire severity. Riparian forests in the Pantanal were found to regenerate quickly and not be highly affected by fires (de Oliveira et al., 2014). This is the habitat for two of the main prey species for jaguars: *Hydrochoerus hydrochaeris* (capybaras) and *Caiman* spp. (Cavalcanti & Gese, 2010; Da Silveira et al., 2010; Perilli et al., 2016). Additionally, lianas (e.g., *C. lanceolatum*, *A. flavum*, and *O. tamoides*) were early pioneer species post-fires (Damasceno-Junior et al., 2021; de Oliveira et al., 2014; Laurance et al., 2011), which offer cover to an ambush predator like jaguars. Therefore,

jaguars may have been attracted to these areas where they could find and hunt prey.

The estimated average density for jaguars in Serra do Amolar of 3.0 jaguars/100km² was comparable, albeit slightly lower, than previous studies in other areas of the Pantanal, such as a recent estimate in protected and unprotected areas, 4.08 ± 0.73 individuals/100km² and 3.59 ± 0.64 individuals/100km² (Devlin et al., 2023). Though jaguar density was stable after the fire, low recaptures of individuals post-fire may indicate displacement or death of individuals in a fire-induced sink effect (Menezes et al., 2021) and immigration of other individuals from surrounding areas. We found that jaguars expanded their home range following fires based on increased sigma estimates. Jaguars likely increased home ranges to find sufficient prey (Jędrzejewski et al., 2018; Nilsen et al., 2005), given that fires can decrease ecosystem productivity and therefore prey species' fitness (Rossi & Santos, 2020). The high colonization estimates for jaguars in the habitat use analysis similarly suggest that jaguars may be increasing their foraging areas. However, both seasonal and individual variation in sigma may lead to density changes over time (Harmsen et al., 2020; Jędrzejewski et al., 2017, 2018), and notably year three camera trapping took place later in the rainy season.

Contrary to our results, de Barros et al. (2022) concluded that 45% of the estimated Pantanal jaguar population had been impacted and three-quarters of their habitat destroyed in the 2020 megafires. Their study, however, did not examine post-fire habitat use or population density, and used range-wide jaguar density estimates and fire spatial layers to estimate numbers of jaguars affected. We did, however, observe that few individuals continued in the population after the fires, thus increased habitat use may be the result of displaced individuals from surrounding areas that were also burned (Rossi & Santos, 2020).

As hypothesized, the other large felid in the study, the puma, had stable habitat use during the study period. Studies from other areas within the puma's distribution documented contrasting results. For example, after a megafire in California, USA, pumas avoided burned areas and increased their diurnal activity and home range (Blakey et al., 2022). However, pumas have well-known behavioral and dietary plasticity in other regions (Karandikar et al., 2022; Magioli et al., 2014; Monroy-Vilchis et al., 2009). The reduction in vegetation heterogeneity by fires may reduce pumas' ability to stalk prey (Blakey et al., 2022). Puma habitat use may also be mediated by inter-specific competition with jaguars as the latter's habitat use expands in the area (Geary et al., 2018), which may explain a slight decrease in puma habitat use in year three. Forest recovery will be an important factor in determining the intensity of interactions between the two carnivores in the future (Boron et al., 2023).

Ocelot density increased from 13.8 ± 3.2 ocelots/100km² to 16.1 ± 5.2 ocelots/100km². We posit that changes in density were the result of immigration. Mortality from the forest fire may have been significant; ocelots were found dead in burned areas in the Chiquitania (Bolivia) and Pantanal (Pacheco et al., 2021; Tomas et al., 2021), and few individuals were recaptured in all three sessions. Ocelot occupancy declined slightly from 0.741 ± 0.114

in Year 1 to 0.661 ± 0.143 in Year 3; however, colonization was high 0.646 ± 0.282 . Moderate decreases in occupancy may be due the ability of ocelots to shift diets to larger prey due to the loss of smaller prey such as *Dasyprocta* sp. (agoutis), *Cuniculus* sp. (pacas), *Proechimys* sp. (spiny rats) on fires (Porfirio et al., 2016; Radford, 2012; Tirelli et al., 2019; Tomas et al., 2021), as well as antagonistic interactions with larger carnivores. Wildfires positively influenced jaguar habitat use in our study, which may in turn lead to competitive spatial interactions with mesopredators (Boron et al., 2023; Ritchie & Johnson, 2009), leading to decreased ocelot occupancy. Mesopredators could avoid open environments because of the risk of being attacked by apex predators (Birtsas et al., 2012; Shores et al., 2019).

Occupancy declined for all four herbivore species, of which collared peccaries had the most precipitous decline from 0.471 ± 0.111 to 0.361 ± 0.133 . Tapir habitat use increased slightly during the first year after the fires and declined in the third year. Overall, the extent and severity of the megafires depleted forest resources these species rely on such as seeds, vegetation, fruits, and roots. Browsing herbivores like red brocket deer and collared peccaries are not attracted to burned areas like grazers (Klop & Van Goethem, 2008; Prado, 2013) such as tapirs that tend to exhibit more generalist feeding behavior (Prado, 2013; Varela et al., 2019). Research from the Amazon biome points to tapirs actively using recently burned areas (Paolucci et al., 2019), while another study found they avoid them (Quintero et al., 2023). The opposing results of studies may be due to the former being a controlled study while fires in the second study were entangled with subsequent land use change. Additionally, grazers may have a strong relationship with burned areas following the "pyric herbivory model" where they can shape the regeneration of burned areas by how they graze on it (Fuhlendorf et al., 2009). This has been observed previously on grasslands in North America and Africa (Eby et al., 2014; Fuhlendorf et al., 2009); in the latter, large grazers may be attracted to burned areas for a specific period and then return to unburned areas where plant palatability is the same as in burned areas. This may explain the oscillation of lowland tapir habitat use, with this study being the first observation of this trend for the Pantanal. Red brocket deer also show restricted use of burned areas on the Brazilian Cerrado (Souza et al., 2023), a dry savannah biome. We posit that vegetation recovered quickly after the fires on riparian areas, providing regrowth but also cover for ambush predators like jaguars. Fires can have a secondary effect on populations like diminishing deer fitness which, in the long term, could affect their reproduction (Kreling et al., 2021). Importantly, many models and studies of post-fire impacts on wildlife come from temperate regions (Jolly et al., 2022), where fire adaptation of vegetation and wildlife communities are vastly different. We thus advocate for further research and model development for the impact of fires in the Neotropics.

Azara's agouti showed a decrease in occupancy after the fires; its extinction estimate was the second highest, 0.474 ± 0.137 , though colonization too was higher than other species 0.376 ± 0.172 . Mortality was likely high for agoutis due to their limited dispersal

ability, though during post-fire transects many small mammals could not be identified at the species level (Tomas et al., 2021). In another study, agoutis had significant declines in the central Amazonian forest post-fire (Barlow & Peres, 2006), which can also affect the dispersion of some plants they feed on (Cazetta & Vieira, 2021). We attribute agoutis' high extinction estimate to a population decline in 2020 immediately after the fire, followed by a stabilization of their occupancy. Agoutis can have dietary shifts according to seasons (Henry, 1999), changing their mostly frugivorous diet to eat leaves and nuts from palms (Cid et al., 2013; Silvius & Fragoso, 2003). Their plasticity may allow for survival after fires, and their higher rate of reproduction may allow for quicker colonization in the years following fire events. The ecosystem-level consequences of changes in species abundance and behavior post-fire require further research.

Giant armadillo occupancy was the most affected by wildfires, and their ecology may lead them to be the last to recover. Giant armadillo occupancy dropped sharply from 0.431 ± 0.171 in Year 1 to 0.076 ± 0.048 in Year 3. Accordingly, it was also the species that had the highest extinction probability at 0.816 ± 0.136 . Giant armadillo populations are especially susceptible to environmental disturbance because of low densities (Desbiez et al., 2020) and slow reproduction rates (Damuth, 1981), as well as in their inability to flee from fires. Giant armadillos seek refuge in burrows during forest fires, but the severity of the megafires likely caused high mortality from elevated soil temperature and smoke inhalation (Silva et al., 2020; Silveira et al., 1999). Moreover, giant armadillos may completely disappear from burned areas (Peres et al., 2003), especially if there is vegetation cover loss (Quintero et al., 2023). These same factors may prevent swift population recovery in the area, and we suggest further research to evaluate the state of the population in Pantanal, given this species is vulnerable to extinction according to the IUCN and the Brazilian legislation (Anacleto et al., 2014; ICMBio, 2023).

5 | CONCLUSIONS AND FUTURE DIRECTIONS

Our results demonstrate declining post-fire occupancy in the short-term (2 years after fire) for six of the eight species that we assessed, and comparable densities for jaguars and ocelots following fires. Jaguar habitat use may increase as a result of forest fires, but resident jaguars from the first year may have died or relocated in the blaze, and immigration from other areas maintained a stable population. Other species like giant armadillos and collared peccary had declining occupancy and habitat use, respectively, and further studies of their population post-2020 megafire are necessary to evaluate the need for further conservation interventions. Importantly, the development of models for fire impacts on Neotropical wildlife are necessary to provide a framework to assess fitness consequences, rather than relying on models developed in fire-prone regions like Australia and North America.

While occupancy and habitat use provide useful information, analyzing demographic shifts as a response to fire events through

mark-recapture techniques, particularly with genetics, may provide useful information on survival and immigration. For instance, residual populations (survivors) may be more important than recolonization for some mammals particularly if the next population source area was also affected (Banks et al., 2011). Given the increase in drought conditions and megafires as a result of human-induced climate change and agricultural practices, a spatial analysis of possible fire refugia such as drainage lines and high canopy cover, that provide ground-level shelter (Banks et al., 2011) will be important to determine how refugia influence patterns of survival, abundance, and post-fire recovery (Franklin et al., 2000; Geary et al., 2020; Lindenmayer et al., 2012). As the cost to move within suitable patches may become greater with increased fire frequency (Nimmo et al., 2019), refugia become an important source for recolonization, especially when megafires consume much of a biome, as they did in Pantanal. Identifying refugia and their fire history will help elucidate factors that will influence species persistence given frequent disturbance. This can be helpful to prioritize safeguarded areas like refugia and their connections during fire events. Finally, the combination of different techniques and the continuous monitoring of an area for several years is an invaluable tool to fully understand the natural transient dynamics of species and recovery time after fire events (Geary et al., 2020; Jolly et al., 2022).

The Pantanal has seen unprecedented devastation over the last 4 years because of ineffective and permissive legislation combined with extreme drought. This has led Mato Grosso do Sul, the state that holds the largest percentage of the Brazilian Pantanal, to temporarily suspend the licensing process for deforestation until a new state law is enacted that will specifically address the preservation and exploration of the biome. As climate change and drought continue to intensify, interventions like this are urgently needed to reduce the extent and damage of wildfires to mammals and other wildlife species. These include, but are not limited to, sound land use planning, firebreaks, improved agricultural practices, fire bans in the driest months of the year, effective early warning systems, prevention, and ensuring preparedness and resources to fire brigades on the ground.

AUTHOR CONTRIBUTIONS

Rocío Bardales: Data curation; formal analysis; investigation; methodology; visualization; writing – original draft. **Valeria Boron:** Conceptualization; formal analysis; methodology; resources; supervision; writing – review and editing. **Diego Francis Passos Viana:** Conceptualization; data curation; funding acquisition; investigation; methodology; visualization; writing – review and editing. **Lara L. Sousa:** Formal analysis; methodology; writing – review and editing. **Egil Drøge:** Formal analysis; supervision; writing – review and editing. **Grasiela Porfirio:** Data curation; investigation; validation; writing – review and editing. **Maricruz Jaramillo:** Formal analysis; methodology; writing – review and editing. **Esteban Payán:** Conceptualization; funding acquisition; methodology; resources; supervision. **Claudio Sillero-Zubiri:** Conceptualization; funding acquisition; resources; supervision; writing – review and editing. **Matthew**

Hyde: Conceptualization; formal analysis; funding acquisition; methodology; project administration; supervision; visualization; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad repository at: <https://doi.org/10.5061/dryad.p5hqbzkw>. All codes for the analysis are openly available in the GitHub repository by the authors: <https://github.com/matt-hyde-s/Amolar>.

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