

Fire shapes mammal abundance at the Cerrado-Pantanal ecotone: Scale of effect, species traits and land-cover interaction

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- 1 Fire shapes mammal abundance at the Cerrado-Pantanal ecotone: Scale of effect, species traits and
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- 3
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18 Abstract

19 In tropical regions, which harbour the majority of the Earth's biodiversity, land-cover change emerges 20 as the primary driver of biodiversity loss. However, despite the propensity for many tropical biomes to 21 experience fires, and the rapidly accelerating pace of intensification in fire regimes, the role of fire in 22 shaping ecological communities has largely been overlooked. We examined whether and how fire 23 regime affected the abundance of mammal species, the scale at which these putative effects operated 24 and how fire effect interacted with land cover. Using camera traps, we studied four mammal species 25 with different ecological traits in the Kadiwéu indigenous territory, a Cerrado-Pantanal ecotone. 26 Specifically, we used abundance models to analyse the response of mammal species to fire frequency, 27 spatial extent, and time since fire. Our results showed that mammals responded to fire at scales that 28 align with the scale of responses to land cover. We found that the type of response to fire, and the scale 29 at which fire effects operate, depended on species and possibly on their traits. The smallest species 30 Sylvilagus brasiliensis demonstrated a clear response to fire, as well as to the mean patch area of 31 savanna, exclusively at the smallest scale studied (i.e., within 500-m radius buffers). The abundance of 32 this species decreased with increasing proportion of land burned in the 12 months preceding the 33 monitoring. In contrast, larger species, including Mazama gouazoubira and Tapirus terrestris, showed 34 no response to fire, while Pecari tajacu would exhibit a marginal response, at the larger scale of 1000 35 m. Our results emphasize the importance of adopting trait-based approaches that consider the multiple 36 aspects of fire regimes, at multiple scales, to disentangle the mechanisms governing the effects of fire 37 on biodiversity. This should promote effective and sustainable fire management compatible with systemic conservation of species and ecological traits in fire-prone biomes. 38

39

40 Keywords: Neotropical mammals – Camera-trap monitoring – Cerrado hotspot – Tropical savanna – Fire
41 management – Biodiversity conservation

42 1. Introduction

43 Wildfires have been a natural phenomenon and fundamental ecological process in shaping landscapes for millennia (Pivello et al., 2021). In the recent years, fire has exhibited a marked increase in activity 44 45 (i.e., occurrence, size and intensity; Garcia et al., 2021; Iglesias et al., 2022; Nolan et al., 2022), largely 46 attributed to climate change (Williams et al., 2019) and additional human-induced environmental 47 changes, including land-use change, fragmentation, and inappropriate fire suppression policies 48 (Durigan, 2020; Pausas & Keeley, 2021). The emergence of megafires, defined as fire events whose 49 spatial extent exceeds 10,000 ha (Linley et al., 2022), has become commonplace (Iglesias et al., 2022), 50 and future projections further predict a global escalation of wildfire potential (Bowman et al., 2020). This situation is all the more worrying in the tropics (Liu et al., 2010) where many biomes are highly 51 52 flammable, such as the fire-prone Pampa, Cerrado or Pantanal in South America, within which intricately 53 associated fire-sensitive ecosystems, such as tropical rainforests of the Amazon and Atlantic Forest, are 54 embedded (Pivello et al., 2021). As a result, megafires kill millions of vertebrates, including in fire-55 dependent ecosystems (Tomas et al., 2021). Therefore, understanding the compound effects of the 56 dynamics of fire regimes and landscape features in space and time is not only key to anticipate the 57 effects of changing fire regimes for biodiversity conservation, but also crucial to inform sustainable fire 58 management by designing low fire risk landscapes that harmonize the coexistence of indigenous 59 communities with wildfire (Doerr & Santín, 2016; Oliveira et al., 2022; Pausas & Keeley, 2021).

60 Fire regimes can be characterized through spatial and temporal aspects, including fire 61 frequency, intensity, spatial extent (or size), and time since the last fire (Nolan et al., 2022; Pausas & 62 Keeley, 2021; Turner, 2010). In the tropics, high fire frequency over the long term maintains a marked 63 shift in plant communities at the forest-savanna interface by limiting the establishment, growth and 64 recruitment of forest species seedlings, thereby preventing the woody encroachment of savannas 65 (Hoffmann et al., 2009; Mourik et al., 2007). This results in a high degree of specialisation of plant communities, with low-diversity communities composed of fire-adapted species in open landscapes 66 67 subject to a high fire frequency, and highly diverse plant communities in closed landscapes (Costa et al.,

68 2023; Dantas et al., 2013). In turn, such variation in plant communities adversely affects vegetation structure and resource availability (Bond & Keeley, 2005) for vertebrate communities (Fontaine et al., 69 70 2009). For instance, Barlow & Peres (2006) found that fire frequency negatively affected the availability 71 of fleshy fruits in areas burned once within 10 years, causing the decline of large frugivorous vertebrates. 72 This effect was exacerbated in areas burned twice in 10 years, causing the extirpation of most forest 73 specialists. Increased fire frequency would jeopardise mammal recruitment and survival (Griffiths & 74 Brook, 2015), and population viability and persistence more than fire spatial extent (Griffiths et al., 75 2015). However, increased spatial extent of wildfires can also affect vertebrate communities (Pastro et 76 al., 2011), by reducing survival, abundances and species richness locally, particularly when the fire 77 extent exceeds the animal's home range (Lawes et al., 2015). Finally, time since the last fire, that relates 78 to post-fire regeneration of the vegetation, may affect vertebrate populations (Pastro et al., 2011). 79 Recolonisation and recovery of local populations from burned areas may occur as the vegetation 80 regenerates and becomes once again suitable to fulfill the ecological requirements of species (e.g., food, 81 shelter; Chia et al., 2016). For example, Valentin-Silva et al. (2021) found that fruiting is reduced in the 82 month following fire. Such reduction in the immediate post-fire availability of food resources could 83 explain the decrease in vertebrate abundance during the early compared to the late post-fire period 84 (Giorgis et al., 2021).

85 The effects of fire may be species dependent (Souza et al., 2023), varying with their traits 86 (Pocknee et al., 2023), such as body size (Nieman et al., 2022) and specialisation in resource use, 87 including habitat and food preferences (Barlow & Peres, 2006; Griffiths & Brook, 2014). First, although large-bodied species with large home ranges are likely to be exposed to landscape changes, their high 88 89 movement capacity could allow them to escape fire and recolonise burned areas more easily than 90 smaller species (Cardillo et al., 2005; Chia et al., 2016). Conversely, small-bodied species would be more 91 vulnerable, particularly if the extent of fire encompasses their small home ranges and their dispersal 92 distance does not allow them to reach unburned refugia (Lawes et al., 2015). Complex relationships may 93 also exist when considering the time since fire and the successional stages of post-fire vegetation 94 regeneration (Briani et al., 2004). Indeed, small grazer species would occupy recently-burned areas 95 faster than larger browsers (Nieman et al., 2022), probably because of the shorter time needed for 96 vegetation regeneration in grass than in shrub species. Second, greater flexibility in resource use, 97 including habitat and food, makes generalist species less sensitive to fire disturbance than specialists. In 98 the Brazilian Cerrado, fires favour the invasion of generalist small-mammal species from open 99 formations at the expense of more specialized forest species (Camargo et al., 2018).

100 Using camera traps, the current study aimed to investigate whether and how effects of fire 101 regimes shaped mammal abundances in addition to, or interaction with land cover in the Kadiwéu 102 Indigenous Territory, Brazil. The study region is an ecotone between the Cerrado—a biodiversity 103 hotspot and the most species-rich tropical savanna in the world (Myers et al., 2000)— and Pantanal 104 wetland. Mammals are key species providing ecosystem services in Brazil (Vale et al., 2023), and are 105 known to be sensitive to land-use/land-cover change (Harmange et al., 2023; Magioli et al., 2021) and 106 fire (Souza et al., 2023). In the Cerrado, studies demonstrated that decreasing forest cover negatively 107 affected the probability of occurrence of forest-specialist mammals (e.g., Dasyprocta azarae and Pecari 108 tajacu; Amiot et al., 2021). Land cover around forest fragments plays a key role in modulating this effect 109 and could contribute to maintain the diversity of mammal functional groups (Harmange et al., 2023). 110 While the effects of the land cover on mammal communities are well documented, the influence of fire has remained understudied, resulting in uncertainty about its effects (but see Souza et al., 2023). Here, 111 112 we examined how fire frequency, spatial extent, and time since fire, affected the abundance of mammal 113 species, and determined the scale at which the effects of fire regime on species operates. Specifically, 114 we focused on the four most abundant species in the camera-trap monitoring, which are common in the Brazilian Cerrado: Sylvilagus brasiliensis, a small generalist and charismatic endangered species that 115 116 provides cultural ecosystem services (Ruedas & Smith, 2019); Pecari tajacu, a medium-sized forest 117 specialist considered an ecosystem engineer that contributes to seed dispersal and nutrient transfer; 118 Mazama gouazoubira, a medium-sized generalist species of cultural importance that is also used as a 119 sentinel for disease prevalence, and Tapirus terrestris, a large generalist and charismatic vulnerable

species that contributes to seed dispersal and nutrient transfer (Amiot et al., 2021; Vale et al., 2023)
(Appendix A, Table A.1).

122 In the Brazilian Cerrado, previous studies showed that mammal species respond to landscape 123 processes at scales ranging from 500 to 1500 m, depending on their traits (Amiot et al., 2021; Harmange 124 et al., 2023). We therefore expect mammal species to respond to fire at scales similar to land cover, as 125 responses to fire also depend on morphological traits and ecological requirements (Pocknee et al., 2023; 126 Souza et al., 2023). While the effects of land cover on mammal communities are well documented, we 127 expected the abundance of the smallest species, S. brasiliensis, to be negatively affected by the increase 128 in fire extent, as a result of a presumed limited movement capacity compared to larger species (Lawes 129 et al., 2015). As a frugivorous forest specialist, P. tajacu is expected to be negatively affected by an 130 increased fire frequency over a short period (e.g., areas burned twice; Barlow & Peres, 2006), and 131 positively affected by time since fire, as a result of a presumed reduction in post-fire fruit availability (Valentin-Silva et al., 2021). Large generalist species, including M. gouazoubira and T. terrestris, are 132 133 expected to be not much affected by fire (Chia et al., 2016), due to their greater movement capacity 134 and flexibility in resource use (Camargo et al., 2018; Lawes et al., 2015).

135

136 2. Material and methods

137 2.1. Study area

138 The study was conducted from June to August 2021, in the Kadiwéu Indigenous Territory (from 20°10'45.59" to 21°03'10.55" S and from 56°50'52.30" to 57°50'51.27" W), Mato Grosso do Sul, Brazil 139 140 (Figure 1). The Kadiwéu IT comprises a region of about 5400 km² located in a transition area between 141 two biomes: the Pantanal (wetlands) and Cerrado (savanna) (Oliveira et al., 2022). The local vegetation 142 is mainly composed of savanna, deciduous seasonal forests, and periodically flooded mixed grasslands, 143 composed of a mix of native and exotic species (Ferreira et al., 2021; Silva et al., 2014). The study area covers 114 km² and is situated in the eastern part of the Kadiwéu IT, within the Cerrado biome, 144 145 recognized as a biodiversity hotspots (Myers et al., 2000).

146 In the Cerrado and Pantanal, fires are a common and recurring phenomenon, annually burning 147 one to several tens of thousands of square kilometres (Araújo et al., 2012; Libonati et al., 2020). In the 148 Kadiwéu IT, historically, fire has been used for hunting, agricultural and pastoral purposes, and to 149 stimulate regrowth while limiting the encroachment of woody vegetation in pastures (Damasceno-150 Junior et al., 2021; Mistry et al., 2016). Wildfires are seasonal, with the highest frequencies occurring in 151 August and September (Oliveira et al., 2022). Therefore, preventive measures, such as prescribed burning—fires deliberately set in strategic locations to reduce the likelihood of wildfires spreading—are 152 153 conducted in May–July by indigenous brigades established in 2009.

154

155 2.2. Mammal data

In the study area, we set 36 camera traps (Bushnell Trophy Cam Aggressor Brown and Reconyx Hyperfire 156 157 HC 500) (Figure 1). The monitoring was conducted in two different sessions of 30 consecutive days, from 158 24 June to 24 July 2021 (n = 15 camera traps), and from 25 July to 24 August 2021 (n = 21), respectively. 159 Camera traps were set at a height of 40 cm above the ground with a 10° inclination towards the ground. 160 They were configured to take a series of three photographs when triggered, with a 3-second delay 161 between two consecutive captures. At the end of the sampling period, photographs were downloaded 162 and analysed visually using Wild.ID, a software developed by the Tropical Ecology Assessment and 163 Monitoring Network (TEAM- <u>www.wildlifeinsights.org/team-network</u>).

To run abundance analyses from photographs of unmarked individuals, we first needed to prevent pseudo-replication by filtering out repeated captures of the same individual in consecutive photographs (Zaman et al., 2022). Following common practices in studies using camera-traps (Peral et al., 2022), we considered for each species only consecutive photographs with at least a 30-minute interval as independent instances. Then, for each of the 36 camera traps and from the 31 sampled days, we built a matrix of 5 sampling occasions of 6 consecutive days each (see Ribeiro et al., 2019; see also Amiot et al., 2021). Over the 36 camera traps, 8 camera traps (i.e., 22%) detected the common tapeti Sylvilagus brasiliensis, 8 (22%) detected the collared peccary *Pecari tajacu*, 20 (56%) detected the brown
brocket deer *Mazama gouazoubira*, and 14 (39%) detected the South American tapir *Tapirus terrestris*.

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174 2.3. Calculation of fire metrics

175 To quantify the patterns of fire regimes at camera-trap locations, we calculated fire metrics based on two MapBiomas Fire products for the year 2021 (2nd collection), derived from Landsat images (30-m 176 resolution): "Monthly burned coverage" and "Fire frequency" (Figure 1A-B and 1C-D, respectively). For 177 178 each pixel that burned during the year 2021, the "Monthly burned coverage" value corresponds to the 179 month in which fire scars were detected, ranging from 0 (no fire detected) to 12 (fire occurrence recorded in December). For each pixel, the "Fire frequency" value corresponds to the number of years 180 a fire was recorded inside the pixel, from 1985 to 2021. Therefore, values range from 0 (no fire recorded 181 182 in the period 1985–2021) to 37 (fire recorded in the pixel every year between 1985–2021).

The ability to detect effects of environmental variables (e.g., fire: Souza et al., 2023; land cover: 183 184 Jackson & Fahrig, 2012) on animal populations may depend on the spatial extent used for metric 185 calculations. Fire metrics were therefore computed at three spatial extents, defined as buffers with radii 186 of 500, 750 and 1000 m from the camera-trap locations. Given the 30-m spatial resolution of the fire 187 maps (based on Landsat images), we used a minimum radius of 500 m to ensure an adequate quantity 188 of pixels offering the necessary variation for meaningful metric assessment (see Amiot et al., 2021). 189 Since the mean distance between camera traps was 997 m (± 189 SD), we used a maximum radius of 190 1000 m to limit the overlap between neighbouring buffers (Appendix A, Table A.2) and prevent spatial autocorrelation (Amiot et al., 2021; Zuckerberg et al., 2012). Four types of fire metrics were derived 191 192 from the MapBiomas products (see Table 1). The "frequency" metrics aimed to assess the recurrence 193 of fire-induced disturbance. They include the mean and maximum frequencies recorded from 1985 to 194 2021 in a given landscape (i.e., buffer area), and the proportion of land burned at least twice within the 12 months preceding the monitoring (see Table 1 for details). The "spatial extent" metric aimed to 195 196 characterize the spreading of the fire event, and is calculated as the proportion of the area of a 197 landscape (i.e., buffer area) burned within the 12 months preceding the monitoring. Finally, the 198 "regeneration" metric aimed to quantify the delay since the last significant fire in the landscape, serving 199 as a proxy for vegetation regeneration. It classifies the landscapes into two categories: "0-4 months" for 200 those with a recorded fire within the 4 months preceding monitoring, and " \geq 11 months" for those in 201 which the last recorded fire occurred at least 11 months before monitoring (see Table 1 for details).

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3 2.4. Landscape description and calculation of land-cover metrics

204 A land-cover map was prepared to characterize the landscape of the Kadiwéu IT for the year 2021. We 205 used the 2021 annual land-cover map from MapBiomas (7th collection) (Souza et al., 2020), derived from 206 Landsat images (30-m resolution) to produce a reclassified map with four land-cover classes (see Figure 207 1E-F and Appendix A, Table A.3). 'Savanna' designated pixels categorized as savanna formation 208 according to the MapBiomas classes. Savanna represented 60.7% of the study area's land cover. 'Forest' 209 designated pixels categorized as forest formation according to the MapBiomas and represented 26.9% 210 of the study area. 'Grassland' accounted for a total of 11.4% of the study area and mainly comprised 211 natural grasslands (11.0% of the study area, while anthropogenic pastures represented 0.3%). Finally, 212 'Other' accounted for 1% of the study area and designated pixels of lesser-represented land-cover types 213 (i.e., mosaic of farming uses, wetlands, and rivers and lakes) (Appendix A, Table A.3).

214 To characterize land cover around camera traps, we calculated land-cover metrics from the 215 previously prepared land-cover map. As for fire metrics, land-cover metrics were calculated at three 216 different spatial extents, specifically within buffers with radii of 500, 750 and 1000 m from the camera-217 trap locations. The calculated land-cover metrics encompass two class-level and two landscape-level 218 metrics. First, class-level metrics include: (i) the proportion of land-cover class (composition metric), 219 representing the percentage of the landscape occupied by the given land-cover class among Savanna, 220 Forest, and Grassland; and (ii) the mean patch area (configuration metric), indicating the average size 221 of patches of a given land-cover class within a landscape (represented as the buffer area). This metric 222 was also applied to the land-cover classes Savanna, Forest, and Grassland. Secondly, landscape-level 223 metrics include: (i) the Shannon Diversity Index (composition metric) that measures landscape 224 heterogeneity by considering both the number of classes and their respective amount within a 225 landscape (i.e., a buffer area); and (ii) the edge density (configuration metric) which quantifies the total 226 length of edges of land-cover classes within a landscape, divided by the total area of the given landscape 227 (i.e., buffer area). Both landscape-level metrics were calculated considering the four land-cover classes 228 of the map previously prepared, i.e., Savanna, Forest, Grassland and Other. All metrics were calculated 229 using the R package landscapemetrics (Hesselbarth et al., 2019). All these metrics were used as 230 covariates in the models described in the statistical analyses (see below), with the exception of Shannon 231 Diversity Index (SHDI) which was strongly correlated, at each buffer extent, with savanna proportion (Pearson's correlation at 500-m buffer extent: r = -0.74; p < 0.0001), mean patch area of savanna (r = -232 233 0.81; p < 0.0001) and edge density (r = 0.87; p < 0.0001) (see Appendix B for details).

234

235 2.5. Statistical analyses

236 2.5.1. Scale of effects of fire and land-cover metrics on mammal abundance

To analyse the effects of fire and land cover on mammal species, we applied abundance modelling using the "*pcount*" function (N-mixture models) of the *unmarked* R package (Fiske & Chandler, 2011; see Harmange et al., 2023 for details). The modelling process can be described as follows: the abundance λ of a mammal species (i.e., the number of filtered photographs of the given species taken by the camera traps aggregated into 6-day occasions) at each camera-trap location and the detection probability p_d were modelled as a function of the covariates x_i and z_i using log and logit link functions, respectively (see Fiske & Chandler, 2011 for details).

First, for each species, the detection probability p_d was estimated using a stepwise process starting with model $\lambda(.)p_d(.)$ (hereafter referred as the "null model"), where the abundance and detection probabilities are constant. The probability of an individual being captured at the sampling site can be influenced by several factors, including the visibility in front of the camera trap (i.e., depending on the openness of the vegetation), or the technical characteristics of the camera-trap model (e.g., 249 sensitivity or format of the sensor). We therefore computed two covariates z_i: visibility (open vs. dense vegetation) and *camera-trap model* (Bushnell[®] and RECONYX[®]). The effect of detection covariates was 250 251 estimated by running three models $\lambda(.)p_d(z_i)$ for each species, to test whether z_i covariates including 252 visibility, camera-trap model, or both, affected the detection probability p_d , when the abundance λ was 253 constant. These four models [i.e., $\lambda(.)p_d(.)$, $\lambda(.)p_d(visibility)$, $\lambda(.)p_d(camera-trap model)$, and 254 $\lambda(.)p_d(visibility, camera-trap model)]$ were compared using Akaike Information Criterion (AIC) (Burnham 255 & Anderson, 2002). For each species, we selected as the "null detection model" the model with (i) the 256 lowest AIC value (i.e., the strongest statistical support), and (ii) a difference in AIC (Δ AIC) > 2 with the 257 null model.

258 Finally, we tested the effect of fire and land cover on the abundance λ of the four mammal 259 species, and identified the most appropriate scale at which study species response to fire and land 260 cover. To do so, we ran models $\lambda(x_i)p_d(z_i)$, including as a single covariate x_i each of the five fire metrics and the seven land-cover metrics, calculated at each of the three buffer extents (i.e., 500, 750 and 1000 261 262 m). For each metric, three models were thus run (i.e., one per buffer extent) and compared with the 263 null detection model using AIC. A metric was considered significant when the AIC value of the respective 264 univariate model was lower than the AIC of the null detection model, with an AIC difference (Δ AIC) > 2. Competing models with a $\Delta AIC < 2$ were considered with equivalent statistical support. For each 265 266 significant metric, the buffer extent that yields the lowest AIC value among the three candidate models 267 indicates the best scale for studying the effect of the given metric on the given mammal species.

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269 2.5.2. Testing for additive and interactive effect of fire and land-cover metrics

For each species for which fire and land cover showed significant effects, we tested the additive or interactive effects of fire and land-cover metrics on relative abundance. This implied integrating several variables into a single model, which required inspection of correlations between predictors to avoid multicollinearity (see Appendix B for Pearson correlation matrices between all fire and land-cover metrics, prepared at each buffer extent).

275 For each species and based on the results of the previous analysis, we selected the species' main 276 responsive scale (i.e., the scale for which the best statistical support from univariate fire and land-cover 277 models converged). At this scale, due to the high correlation among most of the predictors, we 278 separately compared fire metrics and land-cover metrics using AIC, to identify the metric within each 279 category (i.e., fire and land cover) that best predicts the relative abundance of the mammal species. 280 Finally, five models were compared using AIC: the model incorporating the interaction between 281 fire and land cover [i.e., λ (*fire*land cover*)p_d(z_i)], the model with additive effect of fire and land cover 282 [i.e., λ (*fire*+*land cover*)p_d(z_i)], the two univariate models [i.e., λ (*fire*)p_d(z_i) and λ (*land cover*)p_d(z_i)], and the 283 null detection model $[\lambda(.)p_d(z_i)]$. Abundance estimates (±SE) were extracted from the best candidate 284 models and predicted relative abundances (±95% CI) were represented as a function of the covariate x_i 285 using the *predict* function for the *unmarked* package objects.

286

All statistical analyses were conducted using R (R Core Team, 2022).

287

288 3. Results

289 3.1. Scales of effects

290 Fire metrics demonstrated scale-dependent effects on the relative abundance of Sylvilagus brasiliensis and Pecari tajacu (Figure 2A; Appendix C, Table C.1). We detected a significant effect of the proportion 291 292 of land burned in the 12 months preceding monitoring on the relative abundance of the small species 293 S. brasiliensis, exclusively at the smallest spatial extent (500 m) (Figure 2A, Table 2). For P. tajacu, a 294 medium-sized forest specialist, the strongest statistical support was obtained at the largest scale (1000 295 m), regarding the proportion of land burned twice in the 12 months preceding monitoring (Figure 2A, 296 Table 2). However, this species was also affected by time since fire, but only at the spatial extent of 750 297 m (Figure 2A; Table 2).

298 We also found scale of effects of land-cover metrics on the relative abundance of S. brasiliensis, 299 P. tajacu and M. gouazoubira (Figure 2B; Appendix C, Table C.2). Consistently with the scale of the fire 300 metric effects, we detected a significant effect of the mean patch area of savanna on the relative 301 abundance of *S. brasiliensis*, again exclusively at the smallest spatial extent (500 m) (Figure 2B; Table 3). 302 Similarly, for P. tajacu, the strongest statistical support aligned with the scale of fire metric effects, i.e., 303 the largest scale of 1000 m for all significant land-cover metrics, including mean patch area of savanna, 304 savanna proportion, mean patch area of grassland and grassland proportion (Figure 2B; Appendix C, 305 Table C.2). At this scale, the mean patch area of savanna provided the best statistical support for 306 explaining the relative abundance of the species (Table 3). Finally, the relative abundance of M. 307 gouazoubira, a medium-sized generalist, was affected by land-cover metrics mainly at the largest scale 308 of 1000 m (Figure 2B; Appendix C, Table C.2). At this scale, savanna proportion obtained the strongest 309 statistical support for explaining the relative abundance of the species (Table 3). Finally, we did not 310 detect any effect of fire (Figure 2A; Appendix C, Table C.1) and land cover (Figure 2B; Appendix C, Table 311 C.2) on the large generalist species, Tapirus terrestris. Overall, there was no evidence of an effect of 312 forest proportion, mean patch area of forest, edge density, and fire frequency (mean and max) on the 313 species studied at any of the scales examined (Appendix C, Tables C.1 and C.2).

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315

5 3.2. Interactive effects of fire and land cover on mammals

316 Model selection indicates that the univariate model that includes the fire metric proportion of land 317 burned in the 12 months preceding monitoring had similar statistical support for explaining the relative 318 abundance of S. brasiliensis, as the model incorporating the land-cover metric mean patch of savanna 319 (Table 4). The additive model incorporating both metrics also received equivalent support (Table 4). 320 According to the model predictions, the relative abundance of S. brasiliensis decreased with an 321 increasing proportion of land burned within the same radius in 12 months preceding monitoring—a 322 proxy for the fire spatial extent — (Figure 3B), while it increased with the mean patch area of savanna 323 within a 500-m radius of camera-trap locations (Figure 3A).

At the most responsive scale of 1000 m, the relative abundance of *P. tajacu* was influenced by the additive effects of fire (proportion of land burned twice in the 12 months preceding monitoring) and land cover (mean patch area of savanna) (Table 4). The model which incorporates the interactive effect

between these metrics was not retained for reasons of parsimony, as it introduces complexity without significantly enhancing explanatory power (Table 4). The relative abundance of *P. tajacu* decreased with increasing proportion of land burned twice within the same radius in the 12 months preceding monitoring—a proxy for the frequency of fire-induced disturbance—, and increased with the mean patch area of savanna within a 1000-m radius of camera-trap locations. However, these results should be interpreted with caution, as the standard error values of the model estimates were high.

No combined effect of fire and land cover was detected on *M. gouazoubira*, the relative abundance of which was only positively affected by the proportion of savanna within the 1000-m-radius buffer of camera-trap locations (Figure 3C).

336

337 4. Discussion

338 Our study revealed scale-dependent effects of fire on the relative abundance of mammal species, 339 consistent with the scale of mammal responses to land cover. Our study further demonstrated that the 340 response to fire was species-dependent, with no detected fire effect on the largest, habitat and 341 herbivorous generalist species, *Mazama gouazoubira* and *Tapirus terrestris*.

342

343 4.1. Scales of fire effects on mammal abundance

The effect of fire on the abundance of mammal species was found to be scale-dependent. Specifically, 344 345 Sylvilagus brasiliensis and Pecari tajacu responded to fire at scales that align with the scale of responses 346 to land cover. This result was expected due to two main mechanisms. Firstly, the Cerrado and Pantanal are fire-prone biomes that have adapted to, and been shaped by fire over millions of years (Pivello et 347 al., 2021; Simon et al., 2009). For instance, fire regimes in the Cerrado are more intense and more 348 349 frequent in savannas than in adjacent, less fire-prone forests (Hoffmann et al., 2009). Consequently, in 350 these fire-adapted landscapes, landscape processes are linked to fire dynamics. It is therefore not 351 surprising that the scales of wildlife responses to fire are closely related to those of responses to 352 vegetation cover.

353 Secondly, similar scales of animal response to fire and land cover were expected, based on the 354 hypothesis that these responses are determined by the ecological requirements and morphological 355 traits of mammal species. Our results support this hypothesis, as we found (1) consistent response 356 scales within species, and (2) variations between species with differing ecological and/or morphological 357 traits. Indeed, the small species S. brasiliensis responded at the smallest scale of 500 m to both fire and 358 land cover, while larger species such as P. tajacu and Mazama gouazoubira responded at a larger scale 359 of 1000 m to fire and/or land cover. This is consistent with our predictions and previous studies 360 indicating that body size and correlated movement capacity are key factors determining the scale of 361 effects (Holland et al., 2005; Jackson & Fahrig, 2012). However, it is worth noting that the scales of 362 effects of 1000 m identified for *P. tajacu* and *M. gouazoubira* in our current study are slightly larger than 363 those found in the Bodoquena Plateau which ranges from about 15 to 150 km away from to our study 364 area (i.e., respectively 500 m and 750 m for those species in Amiot et al., 2021). Three main mechanisms can explain the difference. First, increased fire regimes and associated disturbance in our study area 365 366 (pristine environment) may contribute to an increase in the movement and home-range size of mammal 367 species (Merrick et al., 2021), thereby expanding the scale at which they are influenced by landscape 368 processes (including fire and land cover). Second, in human-modified landscapes, such as the surroundings of the Bodoquena Park studied in Amiot et al. (2021) which consist of a mixture native 369 370 forest, savanna, pastures and crops (see Harmange et al., 2023), mammals may be less active and mobile 371 due to increased human disturbance (Tucker et al., 2018, 2023), potentially leading to a reduction in 372 the scale of effects. Additionally, in Amiot et al. (2021), the mountainous topography of the Bodoquena 373 Plateau may have contributed to increased costs of terrestrial movement (Shepard et al., 2013), 374 potentially resulting in constrained mammal movements.

Finally, our study found no effect of fire and land cover on the largest species, *Tapirus terrestris*, at any of the scales studied. This result is consistent with that of Amiot et al. (2021), who also found no effect of landscape features on this species in the Brazilian Cerrado, at scales ranging from 500 m to 10 km. This result also confirms our predictions that larger species, including *M. gouazoubira* and *T*.

terrestris, would not be greatly affected by fire (Chia et al., 2016), due to their capacity to move over 379 380 longer distances than small-sized terrestrial species (Cardillo et al., 2005). They might therefore escape 381 fire, reach unburned refugia and recolonise burned areas after fire more easily than smaller species 382 (Chia et al., 2016; Lawes et al., 2015). This is particularly relevant in our study area, where prescribed 383 burning conducted by indigenous brigades has increased landscape pyrodiversity (in terms of fire 384 frequency and time since last fire) and reduced the average and maximum extent of fires (Oliveira et al., 2022), likely decreasing the distance required to reach the nearest unburned refugia. Previous 385 386 studies also found that Mazama spp. were not much affected by fire, supposedly because of their 387 generalist herbivorous feeding habits, which make them less sensitive to fire disturbance (Souza et al., 388 2023). Camargo et al. (2018) also showed that fire facilitated the invasion of generalist small-mammal 389 species from open habitats of the Cerrado, such as grassland and savanna.

390 It should be noted, however, that mammals may also respond to fire at scales smaller and/or larger than those studied, although our data did not allow us to test this hypothesis. Indeed, we focused 391 392 on the landscape scale (i.e., using buffers with radius ranging from 500 to 1000 m, which equates to 393 78.5 to 314.2 ha), while mammal species have also been documented to respond to fire at a more local 394 scale (e.g., from 0.8 to 78.5 ha in Souza et al., 2023), and potentially at larger scales, as suggested by 395 the reduced occupancy of Mazama americana observed after megafires (Bardales et al., 2024). Overall, 396 our results demonstrate that the scale at which mammals best responded to fire is species-specific. This 397 emphasizes the importance of systematically considering multiple scales when studying the effects of 398 fire dynamics on biodiversity, as is common in analyses of landscape dynamics.

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4.2. Effect of fire regime on mammal abundance

401 Consistent with Souza et al. (2023), our results revealed species-specific responses of mammals to fire 402 regimes. We found that the spatial extent of fire provided equivalent statistical support to that of mean 403 patch size of savanna in explaining *Sylvilagus brasiliensis* abundance. This suggests that fire plays a key 404 role in shaping mammal abundances and distribution, as important as land cover. Indeed, the relative

405 abundance of the small species S. brasiliensis decreased with increasing proportion of land that burned 406 in 12 months preceding the camera-trap monitoring, within a 500-m radius. Specifically, 30% of the land 407 burned in the 12 months preceding monitoring (i.e., 23.5 ha burned per 78.5 ha of land) reduced the 408 population abundance by 50%. This result aligns with our expectations that smaller species are 409 disproportionately affected by fire, particularly when fire extent exceed their home range (Lawes et al., 410 2015). S. brasiliensis, being a small species (i.e., 0.95–1.2 kg; Reis et al., 2006; Ruedas et al., 2017), is 411 likely to have limited dispersal abilities. While data on its home range size are lacking (Pasqualotto et 412 al., 2021), S. brasiliensis is likely to have a small home range, as observed in most Sylvilagus spp. species, 413 characterized by home ranges \leq 3 ha (Jones et al., 2009), equivalent to a buffer with a radius of 100 m. 414 This result is corroborated by Lawes et al. (2015) who found that increased proportion of surrounding 415 land burned and, to a lesser extent, mean distance to unburned vegetation-two proxies for fire extent-416 decreased the species richness and abundance of small mammals.

417 Furthermore, the increase in mean size of savanna patches (or savanna proportion in the 418 landscape for Mazama gouazoubira) has contributed to an increase in the abundance of S. brasiliensis 419 and Pecari tajacu. Considering that savannas in the Brazilian Cerrado are subject to frequent and intense 420 fire regimes (Hoffmann et al., 2009), a combined effect of fire and land cover could potentially 421 exacerbate the impact of fire and play a significant role in regulating the population dynamics of 422 mammal species. Indeed, Griffith & Brook (2014) found that the reduction in small-mammal 423 abundances and demographic parameters in burned compared to unburned areas was particularly 424 pronounced for small-bodied species (101–1000 g) and those with fire-sensitive habitat preferences. 425 Further studies are needed to quantify the combined effects of fire and land cover on mammal 426 population growth rates and viability analysis in fire-prone landscapes. This is particular relevant for 427 decreasing or low-density populations of long-lived, low reproductive rate species (de Silva & 428 Leimgruber, 2019), as it can allow identify the return interval of perturbation they can cope with, and 429 the time and extent to which populations recover after perturbation (Gerber & Hilborn, 2001).

430 Although the strength of the effect seems debatable, the frequency of fires within the 12 431 months preceding monitoring may also affect mammal abundance. Indeed, although we detected, as 432 expected, a negative effect of the proportion of the land burned twice in the 12 months preceding 433 monitoring on the abundance of the frugivorous forest specialist P. tajacu, the high variability of 434 coefficient estimates necessitates this result to be considered carefully. Previous studies indicate that 435 short return intervals of fires may have negative impact on mammals (Pocknee et al., 2023). This result, if confirmed, would be consistent with Deus et al. (2023) who found a reduction in the occurrence of P. 436 437 tajacu after fires in Pantanal, and with Barlow & Peres (2006) showing that a frequency of 1-2 fire events 438 in 10 years contributed to the extirpation of most frugivorous and forest-specialist vertebrates.

439 In summary, our results suggest that fire, in addition to land cover, may exert selection pressure 440 on mammals by selecting species based on specific ecological traits (see also Culhane et al., 2022). In 441 particular, the effect of fire on species involved in key ecological functions and services, such as seed 442 dispersal and nutrient transfer (e.g., the forest specialist P. tajacu), may raise concerns about the 443 ecosystem integrity. However, other species that share similar ecological traits and in which no effect 444 of fire has been detected (e.g., T. terrestris) also contribute to ecosystem functioning. Further studies 445 at the community level are therefore needed to assess whether and how fire might affect the 446 assemblage of species, ecological traits and functions available in landscapes. Adopting integrated fire 447 and land-cover management strategies implemented at the landscape scale (Oliveira et al., 2022) would 448 be necessary to reduce megafires, maintain landscape heterogeneity and effectively conserve the 449 diversity of species and ecological functions in fire-prone landscapes.

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1 4.3. Conservation implications and perspectives for fire management

Faced with the rapidly accelerating changes in fire regimes (Iglesias et al., 2022; Nolan et al., 2022),
identifying strategies that promote the coexistence of both human and biodiversity with fire has become
an urgent challenge (Doerr & Santín, 2016; Garcia et al., 2021). Worldwide, fire management strategies
and policies have increasingly moved towards prescribed burning (Costa & Thomaz, 2021; Hunter &

456 Robles, 2020), incorporating indigenous and local knowledge for increased efficiency (Bowman et al., 457 2020). Although our study did not specifically test the effects of prescribed burning on the abundance 458 of mammals, previous research in the region has shown that prescribed burning reduced fire frequency 459 by 80% and the size of the area burned by 53% (Oliveira et al., 2022), reducing the loss of species 460 diversity to imperceptible levels in Cerrado and Pantanal (Durigan, 2020). However, some studies 461 suggest that the outcomes of prescribed burning for biodiversity conservation could be more complex due to taxon-dependent and difficult-to-predict responses of species (Pastro et al., 2011). Further 462 463 research would therefore be needed to confirm whether our results apply to mammal responses to 464 prescribed burns, which would help refine fire management strategies.

465 Our study reveals that in mammals, the type of response to fire, and the scale at which it operates, are species-specific and possibly driven by trait-related processes (see also Pocknee et al., 466 467 2023; Souza et al., 2023). Fire management aimed at designing low fire risk landscapes for biodiversity conservation should carefully consider the scale used to determine the proportion of land targeted by 468 469 prescribed burning, particularly within scales ranging from 500 to ≥1000 (78.5–314.1 ha) for mammals 470 ≥ 1 kg. We believe that finding a trade-off between the extent of land burned and return interval of fire, 471 allowing for balanced proportions of recently burned to long-unburned areas (Souza et al., 2023), would 472 create conditions favourable to the coexistence of biodiversity with fire. Further studies integrating 473 analyses of multiple fire metrics to test different aspects of fire regimes, at multiple scales, and using 474 trait-based approaches for all taxa, are critically needed to disentangle the mechanisms governing the 475 effects of fire regimes on biodiversity. This research should inform sustainable fire management practices, compatible with the conservation of species, ecological traits and functions, particularly in 476 477 protected areas and indigenous territories which constitutes biodiversity-rich, pristine environments. 478 Faced with the unprecedent and rapid intensification of fire regimes, implementing such integrated 479 management has become an urgent challenge to promote more sustainable coexistence between 480 wildfire, indigenous communities and biodiversity, on which they depend for food security (Doerr & 481 Santín, 2016; Oliveira et al., 2022).

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486

487 CRediT authorship contribution statement

488 Clément Harmange: Conceptualization, Investigation, Data curation, Methodology, Formal Analysis, 489 Writing – original draft, Writing – review & editing. Thiago Silva Teles: Conceptualization, Investigation, 490 Data curation, Methodology, Writing - review & editing. Danilo Bandini Ribeiro: Funding acquisition, 491 Project administration, Supervision, Conceptualization, Methodology, Writing – review & editing. Anny 492 M. Costa: Investigation, Data curation, Writing - review & editing. Mauricio N. Godoi: Investigation, 493 Data curation, Writing – review & editing. Fabio de Oliveira Roque: Funding acquisition, Writing – review 494 & editing. Franco Leandro Souza: Funding acquisition, Project administration, Conceptualization, 495 Methodology, Writing - review & editing. Olivier Pays: Funding acquisition, Project administration, 496 Supervision, Conceptualization, Methodology, Writing – review & editing.

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504

505 Appendix A. Supplementary information

506 Appendix B. Correlation matrix of fire and land-cover metrics calculated at varying spatial extents

507 Appendix C. Supporting information and statistical details for the scale of effect analysis and the
508 selection of fire and land-cover metrics in explaining mammal abundances

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- r59 ecological data. *The Journal of Wildlife Management*, 76(5), 1072-1080.

- 760 Table 1 Comprehensive description of the calculation of fire metrics, along with the primary data
- 761 source (i.e., MapBiomas products).
- 762

Metric type	Metric name	Calculation	Source					
Fire frequency	Fire frequency (mean)) Mean of the fire frequency values of all pixels Fire frequency 1985						
	Fine free success (man)	Contained within a given buller	ZUZI					
	Fire frequency (max)	across all pixels contained within a given buffer	2021					
	Proportion burned	Proportion of pixels contained within the	Months burned					
	twice	buffer (i.e., proportion of the buffer area) that burned twice during the 12 months preceding the monitoring: once within the	coverage 2020, 2021					
		period July/August 2020–December 2020, and once within the period January 2021–						
		July/August 2021 (depending on the						
		monitoring session)						
Fire spatial extent	Proportion burned	Proportion of pixels contained within the buffer (i.e., proportion of the buffer area)	Months burned coverage 2020, 2021					
		that burned during the 12 months preceding						
		and hulv/August 2021						
Regeneration	Time since fire	First the delay (in months) between the	Months burned					
hebeneration		monitoring period and the month since the	coverage 2020, 2021					
		largest fire recorded within the buffer in	θ ,					
		2021, was calculated. If no fire was recorded						
		in 2021, the same process was applied						
		considering the data of 2020. Secondly the						
		distribution of months since fire identified						
		two distinct groups: buffers for which fire						
		was recorded within the 4 months preceding						
		monitoring ("0-4 months"), and buffers for						
		which the last recorded fire occurred at least						
		11 months before monitoring (" \geq 11						
		months")						

764	Table 2 Statistical support for univariate models testing the effects of fire metrics on the relative
765	abundance of the four mammal species. The scale used for metrics calculation is indicated. The
766	selection process was based on the Akaike's information criterion (AIC). The number of parameters (K)
767	is presented together with model weights (ω i), log likelihood values (LL) and differences in AIC (Δ AIC)
768	in respect of the model with the highest statistical support (i.e., the lowest AIC value). Grey envelops
769	within the table indicate the candidate models with a Δ AIC < 2 compared with the null detection
770	model (NULL). Only the best candidate models (i.e., those with a Δ AIC < 2 with the candidate model
771	with the lowest AIC value) and the null detection model are indicated (see Appendix C, Table C.3 in for
772	statistical details on all candidate models). Models selected are represented in bold. Estimates ± SE are
773	indicated for significant metrics. Estimate of the categorical variable Time since fire are provided using
774	as reference the level "≤4 months".

Species	Scale	Candidate models	К	AIC	Δ AIC	ω	LL	Evidence	Estimate ± SE
								ratio	
S. brasiliensis	500 m	Proportion burned	4	111.53	0.00	0.47	-51.76		-0.021 ± 0.010
		Time since fire	4	113.21	1.68	0.20	-52.60	2.31	
		NULL	3	114.54	3.01	0.10	-54.27	4.50	
P. tajacu	1000 m 750 m	Proportion burned twice	3	106.95	0.00	0.66	-50.48		-1.577 ± 1.477
		NULL	2	111.21	4.26	0.08	-53.60	8.41	
		Proportion burned twice	3	107.43	0.00	0.44	-50.71		-1.613 ± 1.726
		Time since fire	3	108.03	0.61	0.33	-51.02	1.35	1.381 ± 0.594
		NULL	2	111.21	3.78	0.07	-53.60	6.62	

777	Table 3 Statistical support for univariate models testing the effects of land-cover metrics on the
778	relative abundance of the four mammal species. The scale used for metrics calculation is mentioned.
779	The selection process was based on the Akaike's information criterion (AIC). The number of
780	parameters (K) is presented together with model weights (ω i), log likelihood values (LL) and
781	differences in AIC (Δ AIC) in respect of the model with the highest statistical support (i.e., the lowest
782	AIC value). Grey envelops within the table indicate the candidate models with a Δ AIC < 2 compared
783	with the null detection model (NULL). Only the best candidate models (i.e., those with a Δ AlC < 2 with
784	the candidate model with the lowest AIC value) and the null detection model are indicated (see
785	Appendix C, Table C.4 in for statistical details on all candidate models). Models selected are
786	represented in bold. Estimates ± SE are indicated for significant metrics.

787									
Species	Scale	Candidate models	Κ	AIC	ΔAIC	ω	LL	Evidence	Estimate ± SE
								ratio	
S. brasiliensis	500 m	Savanna patch area	4	112.21	0.00	0.32	-52.11		0.021 ± 0.010
		Grassland patch area	4	112.79	0.58	0.24	-52.40	1.34	
		NULL	3	114.54	2.33	0.10	-54.27	3.20	
P. tajacu	1000 m	Savanna patch area	3	101.69	0.00	0.75	-47.85		0.009 ± 0.002
		NULL	2	111.21	9.52	0.01	-53.60	116.48	
M.	1000 m	Savanna proportion							0.032 ± 0.011
gouazoubira			5	234.45	0.00	0.60	-112.23		
		NULL	4	241.21	6.76	0.02	-116.60	29.33	

789	Table 4 Statistical support for models testing univariate, additive and interactive effect of land-cover
790	and fire metrics on the relative abundance of Sylvilagus brasiliensis and Pecari tajacu. The scale used
791	for metrics calculation is indicated. The selection process was based on the Akaike's information
792	criterion (AIC). The number of parameters (K) is presented together with model weights (ω i), log
793	likelihood values (LL) and differences in AIC (Δ AIC) in respect of the model with the highest statistical
794	support (i.e., the lowest AIC value). Grey envelops within the table indicate the candidate models with
795	a Δ AIC < 2 compared with the null detection model (NULL). Models selected are represented in bold.
796	Estimates \pm SE are indicated for significant effects. Models with Δ AIC < 2 are considered statistically
797	equivalent.

Species	Scale	Candidate models	К	AIC	Δ AIC	ω	LL	Evidence	Estimate ± SE
								ratio	
S. brasiliensis	500 m	Proportion burned	4	111.53	0.00	0.38	-51.76		-0.021 ± 0.010
		Savanna patch area	4	112.21	0.68	0.27	-52.11	1.41	0.021 ± 0.010
		Proportion burned +	5	112.22	0.69	0.27	-51.11	1.41	-0.014 ± 0.012
		Savanna patch area							0.014 ± 0.011
		NULL	3	114.54	3.01	0.08	-54.27	4.50	
		Proportion burned *	6	126.49	14.96	0.00	-57.24	1771.38	
		Savanna patch area							
P. tajacu	1000 m	Proportion burned twice	5	06.45	0.00	0 5 2	12 22		
		* Savanna patch area	J	90.45	0.00	0.55	-43.23		
		Proportion burned twice	Л	06.00	0.42	0.42		1 7 2	-2.54 ± 2.15
		+ Savanna patch area	4	90.00	0.42	0.45	-44.44	1.25	0.009 ± 0.002
		Savanna patch area	3	101.69	5.24	0.04	-47.85	13.74	
		Proportion burned twice	3	106.95	10.50	0.00	-50.48	190.57	
		NULL	2	111.21	14.76	0.00	-53.60	1603.59	

800 Figure caption

801

Figure 1 Characterization of the Kadiwéu Indigenous Territory (Mato Grosso do Sul, Brazil; left-side
panels) and the study area (right-side panels) in terms of: (A, B) monthly burned coverage in 2021; (C,
D) fire frequency expressed as the number of years with fire from 1985 to 2021 (MapBiomas, 2nd fire
collection); and (E, F) land cover in 2021 (MapBiomas, 7th land-cover collection). Blue dots indicate the
locations of the camera traps (n = 36).

807

808 Figure 2 Statistical support of univariate models testing the effects of fire metrics (A) and land-cover 809 metrics (B) calculated at three buffer extent (i.e., within 500-m, 750-m, and 1000-m-radius buffers) on 810 the relative abundance of the four mammal species. The dashed line indicates the AIC value of the null 811 detection model. The grey envelope materializes the difference in AIC (Δ AIC) \leq 2 relative to the null 812 detection model. White dots refer to models with $\Delta AIC \leq 2$ relative to the null detection model, 813 therefore considered as equivalent in terms of statistical support. Black dots indicate significant 814 models, i.e., models whose AIC value was lower than the AIC value of the null detection model, with a 815 Δ AIC > 2. See Appendix C, Figures C.1 and C.2, and Tables C.1 and C.2 for statistical details on all the metrics analysed. Mammal silhouettes were extracted using the R package rphylopic (Gearty & Jones, 816 817 2023).

818

Figure 3 Predicted relationships (solid lines) with 95% confidence interval (grey envelope) between fire
or land-cover metrics and the relative abundances of *Sylvilagus brasiliensis* (A, B) and *Mazama gouazoubira* (C). Metrics were calculated within buffers of 500-m radius (*S. brasiliensis*) or 1000-m
radius (*M. gouazoubira*) from camera-trap locations. Values of fire and land-cover metrics of each
buffer are shown as vertical lines on the x-axes. See Table 4 for statistical details.

Kadiwéu Indigenous Territory

Study area



824 825 Figure 1



827 Figure 2

