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# 1 Landscape drivers of mammal habitat use and richness in a protected area 2 and its surrounding agricultural lands

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## 15 **Abstract**

16 Protected areas (PAs) are key to conserving biodiversity and ecosystem services globally, but  
17 their effectiveness increasingly depends on the ability of the surrounding agricultural areas to  
18 support biodiversity and secure connectivity at the landscape level. This requires monitoring the  
19 broader multi-use landscapes in which PAs exist and identifying the landscape characteristics  
20 that support rich, functional wildlife communities. Here, we investigated the species richness  
21 and habitat use patterns of a mammal community in relation to different landscape variables  
22 and land use and land cover (LULC) types in a PA and its surrounding agricultural lands in the  
23 Cerrado. We first used a hierarchical multi-species occupancy model with input camera trap

24 data and eight landscape variables (vegetation productivity, phenology, and heterogeneity,  
25 distance to water, roads and settlements, and the PA, slope, and elevation) to estimate the  
26 species richness and habitat use of 29 mammal species across the landscape. We then  
27 analyzed the relationships between the species richness and habitat use and the landscape  
28 variables at the site level, as well as the distribution of species at the landscape level in relation  
29 to the different natural and agricultural LULC types. We found that most species are present in  
30 the native forest areas across the landscape and that many species are also present in the  
31 croplands surrounding the PA. The results also showed that species' habitat use was especially  
32 determined by the productivity and heterogeneity of the vegetation cover, with a particularly  
33 strong positive relation in grasslands and pastures. These results suggest that the private  
34 properties surrounding the PA might be playing an essential role in supporting biodiversity in  
35 this region and provide insights on management practices that could largely contribute to  
36 maintaining or promoting a multifunctional landscape, such as maintaining the remaining forests  
37 or increasing the productivity and the heterogeneity (e.g., by increasing tree cover) in pastures.

## 38 **Keywords**

39 Agricultural biodiversity; Neotropical mammals; Brazilian conservation unit; Occupancy model;  
40 Remote sensing; NDVI-based landscape metrics

## 41 **1. Introduction**

42 The capacity of protected areas (PAs) to preserve some habitats and species (Coetzee et al.,  
43 2014; Geldmann et al., 2013; Gray et al., 2016) make them critical for attaining global  
44 biodiversity conservation goals (CBD, 2020, 2016). However, the effectiveness of PAs largely  
45 depends on local contexts (Coetzee et al., 2014; Laurance et al., 2012), including the complex  
46 interactions (both positive and negative) with the surrounding agricultural areas (i.e., croplands,

47 pastures) and human activities (Blanco et al., 2020; DeFries et al., 2010; Hansen and DeFries,  
48 2007).

49 Indeed, local to international policies now recognize that PAs cannot be managed as islands  
50 (Cumming et al., 2015; Palomo et al., 2014) and that PAs are not sufficient, by themselves, to  
51 curb biodiversity loss whilst meeting socio-economic development needs. This is particularly  
52 evident in tropical regions where PAs are increasingly isolated from surrounding natural habitats  
53 as a result of an increasing expansion and intensification of agriculture (Laurance et al., 2014).  
54 Recognizing that the effectiveness of PAs largely depends on the interactions with the  
55 surrounding agricultural areas demands that policies and management actions take account of  
56 the role these areas are playing in supporting or undermining biodiversity in these key  
57 conservation landscapes (Kremen and Merenlender, 2018). This requires monitoring  
58 biodiversity across the broader agricultural matrices in which PAs exist, and identifying the  
59 landscape characteristics that support biodiversity while maintaining a sustainable provision of  
60 goods and services to satisfy long-term human needs.

61 Camera traps have proven a valuable tool for obtaining occurrence data of multiple species –  
62 mostly medium to large-sized terrestrial vertebrates – across multi-use landscapes (Tobler et  
63 al., 2015). These data have been increasingly used in multi-species occupancy models  
64 (MSOMs) to provide baseline information on important state variables such as species richness  
65 and individual species responses to different environmental factors (Devarajan et al., 2020;  
66 Tingley et al., 2020; Tobler et al., 2015). Yet, most studies using these tools focus on assessing  
67 biodiversity in specific management units, such as PAs (e.g., Cavada et al., 2019; Ferreira et  
68 al., 2020), forest reserves and concessions (e.g., Easter et al., 2019; Rahman et al., 2021), or  
69 wildlife management areas (e.g., Van der Weyde et al., 2018). Moreover, the analysis of  
70 species-environment relationships is generally restricted to the camera trap sites or fixed-  
71 distance buffers around them despite the common use of wide-ranging landscape variables,

72 such as satellite remote sensing (SRS)-derived variables, as environmental predictors (Jackson  
73 and Fahrig, 2015). By doing so, the potential of camera trap surveys and MSOMs to provide  
74 critical knowledge on community and species-level habitat use across the multi-use landscapes  
75 in which PAs are embedded remains underexplored (but see Drouilly et al., 2018, Penjor et al.,  
76 2021 and Rich et al., 2016).

77 SRS-derived proxy variables for productivity, phenology (seasonal variability), or structure of  
78 natural and anthropogenic vegetation cover types can be important predictors of species  
79 distributions in these multi-use landscapes (Bellón et al., 2020). Indeed, such variables may  
80 reflect the spatial variability of ecologically relevant conditions and processes of the natural  
81 ecosystems and agroecosystems such as availability of food resources, shelter, or intensity of  
82 agricultural practices (Bégué et al., 2018; He et al., 2015; Leitão and Santos, 2019; Pettoirelli et  
83 al., 2011). These variables can therefore provide valuable information on community and  
84 species-level habitat use at spatial scales at which the underlying socio-ecological interactions  
85 operate (i.e., spatial scales that often transcend local in situ sampling sites, or specific  
86 management units). This spatial information can be of particular relevance to help identify areas  
87 of high conservation value on which to prioritize conservation efforts and to identify the surface  
88 conditions and management practices in agricultural areas that help promote or maintain  
89 biodiversity at the landscape level.

90 Here, we investigate the effects of different landscape variables on the species richness and  
91 habitat use of a neotropical mammal community in a multi-use landscape of the Cerrado  
92 biodiversity hotspot. The studied landscape comprises a National Park embedded in a mosaic  
93 of rangelands, croplands, and native vegetation remnants in privately owned rural properties.  
94 We used mammals as a focal group since they perform ecological functions and services which  
95 are crucial for many other species and are one of the most threatened groups, especially in the  
96 tropics (Ceballos et al., 2020). To this end, we deployed a camera trap network across the

97 landscape and used the collected mammal detection data to derive landscape-level estimates of  
98 species habitat use probability and richness using a MSOM and eight habitat use covariates:  
99 three Normalized Difference Vegetation Index (NDVI)-based proxy variables for vegetation  
100 productivity, phenology, and heterogeneity, distance to water, roads and settlements, and the  
101 park, slope, and elevation. We then used the model's predictive outputs to analyze the  
102 relationships between the species' habitat use patterns and the landscape variables within the  
103 different land use and land cover (LULC) types.

## 104 **2. Materials and methods**

### 105 **2.1. Study area**

106 The study area is located in the Bodoquena Plateau region, in the Brazilian State of Mato  
107 Grosso do Sul (Figure 1a). This region is characterized by a tropical savanna climate, with a  
108 rainy season between October and April (ICMBio, 2013). The study area spans 56°06'W to  
109 57°01'W and 20°25'S to 21°46'S, covering 14 215 km<sup>2</sup> with an altitude ranging from 114 to  
110 837 m. It encompasses a mountain range, that was declared a PA in 2000 (the Serra da  
111 Bodoquena National Park, hereafter, SBNP), and plains with scattered hills, with extensive  
112 pastures, localized crops in the flat areas around the park, and interspersed forest patches. It  
113 also comprises the Lalima and a portion of the Kadiwéu Indigenous Lands, two Natural  
114 Monuments, mining sites, and the urban areas of Bonito, Jardim, and Bodoquena.

115 Although the study area lies within the Cerrado savanna biome, around 70,000 ha (91%) of the  
116 SBNP are covered by sub-montane deciduous forest that includes floristic elements from the  
117 Atlantic Forest biome (ICMBio, 2013). Other predominant vegetation types in the region include  
118 alluvial semi-deciduous forest and 'Cerradão' (ICMBio, 2013). This variety of vegetation types  
119 harbors a rich diversity of species, including 61 terrestrial mammals (ICMBio, 2013), of which

120 two are currently Endangered (*Pteronura brasiliensis* and *Sylvilagus brasiliensis*) and three  
121 Vulnerable (*Myrmecophaga tridactyla*, *Tapirus terrestris*, and *Tayassu pecari*) according to the  
122 IUCN Red List of Threatened Species (IUCN, 2021).

123 Most of the land in the study area, including more than 80% of the SBNP, is privately owned.  
124 Within the park, the use of natural vegetation is, however, regulated by governmental  
125 environmental agencies. Around the SBNP, a buffer zone of around 300,000 ha further  
126 regulates the use of genetically modified crops, and the use of the native vegetation remnants  
127 must comply with the Brazilian Forest Code (i.e., all rural properties must preserve at least 20%  
128 of their land as Legal Reserves and preserve environmentally-sensitive areas as Areas of  
129 Permanent Protection) (Machado and Anderson, 2016). The dominant land use in the region is  
130 extensive livestock farming for meat production, followed by the intensive cultivation of soybean  
131 and maize as a double cropping system.

## 132 **2.2. Camera trap data**

133 The camera trap data used in this study were collected during a survey as part of the long-term  
134 ecological research program 'PELD-Planalto da Bodoquena'. 189 Reconyx Hyperfire HC500  
135 and Bushnell Trophy Cam HD cameras were deployed across a NW-SE transect over four  
136 municipalities (Municípios, in Portuguese): Bodoquena, Bonito, Jardim, and Bela Vista (Figure  
137 1b).

138 The cameras were located in 15 sites of 50 km<sup>2</sup> that represented a gradient of forest cover/open  
139 vegetation proportions, from sites with around 10% to 90% forest cover. The cameras' location  
140 within those sites was randomly set while ensuring a relative proportion of open and dense  
141 understory conditions. To do so, a '50% tree cover' threshold on the product 'Percent Tree  
142 Cover for year 2000' from the 'Global Forest Change' dataset (Hansen et al., 2013) was first  
143 used to randomly select open and dense canopy locations, and their understory conditions were

144 then verified in the field. Camera traps were positioned 40 cm above the ground, either on trees  
145 or posts, at an angle of approximately 10° relative to the ground, and were located at a  
146 minimum distance of 370 m between them.

147 Cameras were set to take a series of three shots when triggered, and delays to detect passing  
148 animals were set at an interval of 3 seconds. Cameras were active for 26 days, on average, and  
149 no bait was used. The total sampling effort (i.e., total number of days surveyed by the 189  
150 cameras) added up to 4928 days between 11/06/2016 and 16/12/2017, although around 80% of  
151 the sampling effort took place in 2017, and a relatively equal number of cameras were active  
152 during the dry season (55%) and the rainy season (45%).

153 All anthropogenic and natural vegetation cover types in the study area were sampled: 46.6% of  
154 the cameras were placed in forest areas, 7.4% in savanna, 2.1% in grassland, 40.2% in  
155 pasture, and 3.7% in cropland. These proportions are representative of the relative proportions  
156 of each vegetation cover type in the study area (vegetation cover estimates are derived from the  
157 LULC map presented in section 2.5).

158 A total of 29 terrestrial native mammal species were recorded, which represents more than 47%  
159 of the species known to be present in the region (ICMBio, 2013). Six of these species are listed  
160 as vulnerable, near threatened and endangered in the IUCN Red List of Threatened Species  
161 (IUCN, 2021) (see Appendix A). In addition, eight species are in a vulnerable situation according  
162 to the Red Book of Threatened Brazilian Fauna (ICMBio/MMA, 2018): *Tayassu pecari*,  
163 *Chrysocyon brachyurus*, *Puma concolor*, *Herpailurus yagouaroundi*, *Panthera onca*,  
164 *Myrmecophaga tridactyla*, *Sapajus cay*, and *Tapirus terrestris*. For our study, we pooled the  
165 mammal occurrence data to 1-day sampling occasions. The number of detection events per  
166 species is summarized in Figure 2, and the taxonomy, common names, and conservation status  
167 of the species are presented in Appendix A.



### 168 **2.3. Landscape variables**

169 Eight complementary landscape variables were used as environmental predictors in the MSOM:  
170 three NDVI-based proxy variables for vegetation productivity, phenology, and heterogeneity,  
171 distance to roads and settlements, water, and the SBNP, terrain slope, and elevation (see  
172 Appendix B for a detailed summary of their values' distribution).

173 The three NDVI-based variables are the static versions of the NDVI-based landscape change  
174 metrics presented in Bellón et al. (2020). NDVI has long been used in species distribution  
175 models (SDMs) as a spectral-based proxy for vegetation productivity since it can be linked to  
176 the availability or condition of different resources that drive species distribution (e.g., food  
177 availability or habitat quality) (He et al., 2015; Leitão and Santos, 2019; Pettorelli et al., 2011).  
178 Studies have used NDVI-based covariates to model species occupancy patterns and species  
179 richness of different taxa in PAs (e.g., Burton et al., 2012; Nieto et al., 2015) as well as in  
180 agricultural lands (e.g., Crego et al., 2020; Duro et al., 2014; Tyrrell et al., 2017). These studies  
181 mostly use variables that either reflect the general productivity of the natural or anthropogenic  
182 vegetation for interest (e.g., average, median, or integrated NDVI) (e.g., Crego et al., 2020), or  
183 its spatial or temporal variability (e.g., Nieto et al., 2015).

184 Similarly, we used one NDVI-based variable as a surrogate for general productivity of the  
185 vegetation types in our study area, NDVI Mean (Figure 3a), and two additional variables as  
186 surrogates for temporal and spatial variability in vegetation productivity, NDVI TempVar (Figure  
187 3b) and NDVI SpatVar (Figure 3c), respectively. Our choice was based on the hypothesis that  
188 these three variables might not only reflect the availability of important resources that may drive  
189 mammals' distribution at the landscape level (e.g., food, shelter, or habitats), but also additional  
190 relevant processes, such as fine-scale environmental heterogeneity, natural vegetation  
191 phenological cycles and development, or different levels of land degradation or land-use  
192 intensity in the agricultural areas (Bellón et al., 2020).

193 Since most of the camera trap sampling effort took place in 2017, we selected the 2017 annual  
194 time series of the MOD13Q1 v006 product, composed of 23 16-day composite NDVI images at  
195 250 m resolution. We additionally selected five extra images at both extremes of the time series  
196 for noise-reduction purposes. We preprocessed the data using a Savitzky Golay-based  
197 smoothing algorithm (Chen et al., 2004) to reduce any potential noise or atmospheric effects  
198 and used the Composite Day of Year band to generate a date-corrected time series following  
199 the method described in Testa et al. (2014). In addition, we used two Landsat 8 Operational  
200 Land Imager scenes (path 226, rows 74 and 75) of the 27th of July 2017 to compose a cloud-  
201 free high resolution (30 m) NDVI mosaic image over the study area. All the satellite imagery was  
202 acquired from the Earth Engine Data Catalog and processed in the GEE cloud-computing  
203 platform (Gorelick et al., 2017) to compute the three variables as described in Table 1.

204 We used the NDVI-based variables pixels' centroid positions to calculate the nearest neighbor  
205 distance to roads and settlements, water, and the SBNP, and to sample the slope and elevation  
206 values. The road network and settlements within an 8 km buffer around the study area (Figure  
207 3d) were extracted from the layers *Área Edificada* and *Trecho rodoviário* of the Continuous  
208 Cartographic Base of Brazil (IBGE/DGC, 2017). The SBNP extension (Figure 3e), was retrieved  
209 from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2019). The rivers,  
210 streams and lakes within a buffer of 8 km around the study area (Figure 3f) were extracted from  
211 the layers *Cursos d'Água* and *Massas d'Água* of the Brazilian National Water Agency databases  
212 (ANA, 2017a, 2017b). The slope and elevation data (Figures 3g and 3h, respectively) were  
213 extracted from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Data Version 4  
214 (Jarvis et al., 2008).

215

## 216 **2.4. Modelling framework and site-level analysis**

217 We used a hierarchical multi-species occupancy model (MSOM) with Bayesian MCMC (Markov  
218 Chain Monte Carlo)-based inference (Kéry and Royle, 2015) to derive estimates of the 29  
219 mammal species' habitat use probabilities and species richness across the study area. We  
220 assumed that the model outputs represent estimates of the species' habitat use probability  
221 rather than occupancy probability, since some detected species may have home ranges that  
222 exceed the size of the sampling units and thus the 'closure assumption', which considers no  
223 changes in site occupancy over the course of the survey, was therefore likely violated in those  
224 cases (Efford and Dawson, 2012).

225 The MSOM was implemented in the R package NIMBLE (Numerical Inference for statistical  
226 Models for Bayesian and Likelihood Estimation) (de Valpine et al., 2017; R Core Team, 2020)  
227 and was formulated to account for imperfect detection by modeling both the species' habitat use  
228 probability and the detection probability (Dorazio et al., 2006). In addition to the eight landscape  
229 variables (presented in section 2.3) used to estimate habitat use probability, we included two  
230 detection probability covariates to account for the potential effects of visibility (related to open or  
231 dense understory conditions) and season (rainy or dry) on the detection of species at the  
232 sampling sites. Site species richness was then estimated by summing the number of estimated  
233 occurring mammal species at each site. We tested for significant effects of the covariates on  
234 community-level site detection and habitat use by verifying that the 89% highest density interval  
235 (HDI) of the model parameters estimates did not overlap with zero. Additionally, we plotted the  
236 species-level habitat use probability estimates as a function of the covariates to visually assess  
237 the effect of each landscape variable on the individual species' habitat use.

238 To assess the goodness-of-fit of the model, we used the Bayesian p-value test statistic (see  
239 Broms et al. (2016) for details) and visually examined residual diagnostic plots. Further details

240 on the MSOM formulation and parameterization and the R code used to conduct the simulations  
241 are available in Appendix C.

## 242 **2.5. Landscape-level analysis**

243 To derive spatial predictions of the species' habitat use probability and the species richness  
244 across the study area, we estimated posterior distributions of the predicted habitat use  
245 probability and species richness for each pixel from 100 posterior samples of the MSOM's  
246 parameters. With the posterior mean spatial predictions, we analyzed the distribution of species  
247 at the landscape-level, in relation to the different LULC types in the study area. The LULC data  
248 used (represented in Figure 4a) was derived from the 2017 Brazilian Land Cover and Use  
249 Collection 5.0 Map Series at 30 m resolution of the MapBiomass project (Project MapBiomass,  
250 2021) and upscaled to 250 m by aggregating the 30 m pixels using the majority rule.

251 At the community level, we analyzed the species richness across the different natural and  
252 agricultural LULC types in the study area and tested for pair-wise differences in species  
253 richness with the Wilcoxon Rank Sum test with continuity correction and Benjamini-Hochberg p-  
254 value adjustment (Benjamini and Hochberg, 1995). We additionally used the Pearson's  
255 correlation coefficient to test the relationship between species richness and the different  
256 biophysical conditions and landscape characteristics represented by the eight landscape  
257 variables (presented in section 2.3) within the different vegetation cover types.

258 At the species level, we explored the links between the habitat use patterns of the different  
259 species and the LULC types. To do so, we carried out a principal component analysis (PCA)  
260 based on the posterior mean estimates of the species' habitat use probabilities over the  
261 vegetated areas (i.e., 29 variables with 230,348 observations/pixels each) using the  
262 FactoMineR package (Lê et al., 2008). To identify clusters of species based on their habitat use  
263 patterns, we performed clustering on the variables' coordinates on the principal components

264 (PC) using the k-means algorithm. We used 25 random starting assignments and the NbClust R  
265 package (Charrad et al., 2014) to choose the optimal number of clusters. To visually interpret  
266 the PC axes and the variables' vector loadings in relation to the different LULC types in the  
267 study area, we grouped the PC observations' scores by their corresponding LULC type. Finally,  
268 we selected one representative species per cluster to further explore the specificities of  
269 individual species with contrasting habitat use patterns.

270 Although this landscape-level analysis cannot incorporate the uncertainty in the posterior mean  
271 estimates of the species habitat use probability and richness, it complements the site-level  
272 analysis by allowing to get general insights into the ways species respond to the different  
273 biophysical conditions and landscape characteristics within specific natural and agricultural  
274 cover types across the landscape.

## 275 **3. Results**

### 276 **3.1. Model evaluation and site-level results**

277 Both the Bayesian p-value of the MSOM (0.49) and the residual diagnostic plots (Figure D.1 in  
278 Appendix D) indicated good model fit. The community-level posterior distributions of the  
279 parameters estimates for detection probability showed no significant effect (89% HDI  
280 overlapped zero) of the visibility and the season on the detection of species at the sampling  
281 sites. Community-level habitat use probability significantly increased with vegetation productivity  
282 and heterogeneity (as estimated by NDVI Mean and NDVI SpatVar, respectively), significantly  
283 decreased with slope, and did not show a significant response to the rest of the landscape  
284 variables (Figure D.2 in Appendix D presents the posterior distribution plots of the parameters).  
285 Vegetation productivity (NDVI Mean) showed the strongest effect on community-level habitat  
286 use probability among the eight landscape variables.

287 The estimated mean detection probabilities were lower than 0.10 for more than 70% of the  
288 species, and only four species (*Tapirus terrestris*, *Dicotyles tajacu*, *Myrmecophaga tridactyla*,  
289 and *Cerdocyon thous*) were estimated to have mean habitat use probabilities > 0.3 at the  
290 sampling sites (see Figure D.3 in Appendix D for the individual species' posterior mean habitat  
291 use and detection probabilities).

292 Individual estimated species' responses of habitat use probability to the different landscape  
293 variables were greatly diversified (see Figure D.4 in Appendix D for a detailed representation of  
294 the individual species' responses). Results show a general strong positive effect of NDVI Mean  
295 on individual species' habitat use probability, except for two species (*Cerdocyon thous* and  
296 *Myrmecophaga tridactyla*) that present a strong negative response, and some species for which  
297 no particular response is observed. NDVI SpatVar has a general positive effect on all species,  
298 and slope, a general negative effect, with individual species being more or less sensitive to  
299 these two landscape variables. Some particular species show strong responses to other  
300 landscape variables, despite these not having a significant effect at the community level. For  
301 instance, the habitat use probability of *Tapirus terrestris*, *Dicotyles tajacu*, *Euphractus*  
302 *sexcinctus*, and *Mazama gouazoubira* strongly increases with increasing seasonal variability in  
303 vegetation (as estimated by NDVI TempVar).

### 304 **3.2. Landscape-level results**

305 The species richness estimates across the study area are presented in Appendix D, Figure D.5.  
306 According to the pair-wise Wilcoxon Rank Sum test, the predicted species richness was  
307 significantly different ( $p < 0.0001$ ) between the different LULC types in the study area (forest,  
308 savanna, grassland, pasture, and cropland). The highest posterior estimates of species richness  
309 (i.e., highest median, upper quartile, and maximum values) were in forests and croplands  
310 (Figure 4b). The highest variability (highest range between the maximum and the minimum and

311 interquartile range) was also in the forests and croplands. The species richness was lowest in  
312 natural grasslands and relatively higher in pastures and savanna areas (Figure 4b).

313 The results of the correlation tests between the posterior mean species richness estimates and  
314 the landscape variables within the different LULC types are summarized in Table 2. Species  
315 richness was positively correlated with vegetation productivity (NDVI Mean), vegetation  
316 heterogeneity (NDVI SpatVar), and elevation in all LULC types (Table 2). Species richness was  
317 particularly strongly correlated ( $r > 0.5$ ) to vegetation productivity and heterogeneity in  
318 grasslands, and pastures, while moderately correlated in the rest of vegetation types (Table 2).  
319 Species richness was also positively and strongly correlated to the seasonal variability in  
320 productivity (NDVI TempVar) in grasslands (Table 2). Finally, the relationship between species  
321 richness and the other landscape variables was globally weaker ( $r < 0.4$ ) in all LULC types  
322 (Table 2).

323 The PCA on the posterior mean species' habitat use probability estimates highlighted  
324 contrasting habitat use patterns among the species (Figure 5). The total variance explained by  
325 the first two dimensions was 81.2%, with PC1 and PC2 accounting for 52.1 and 29.1%,  
326 respectively. Observations grouped by their LULC type in the scores plot and the overlapping  
327 concentration ellipses (Figure 5b) suggest that species are distributed along the first dimension  
328 (PC1) according to a gradient of tree cover density (from open pastures and grasslands to  
329 forested areas) and along the second dimension (PC2) according to the level of presence in  
330 croplands. The scores plot also suggests that the variability in the habitat use probability among  
331 species is highest in croplands and forests (largest ellipses).

332 The clustering analysis identified two optimal groups of species (represented in Figure 5a). The  
333 first cluster groups 11 species whose habitat use probabilities are strongly and positively  
334 correlated to PC2, indicating that they are quite present in croplands, except for *Dasybus*

335 *novemcinctus* whose vector is close to the origin. The second cluster groups 18 species with  
336 habitat use probabilities strongly and positively correlated to PC1, indicating that they are  
337 particularly present in forests. There is, however, a high intra-cluster variability, which suggests  
338 that species within the same cluster may have a different preference for tree cover density (for  
339 species in cluster 1) or are more or less present in croplands (for species in cluster 2).

340 We selected the Giant anteater (*Myrmecophaga tridactyla*) and the White-lipped Peccary  
341 (*Tayassu pecari*) as representative species for clusters 1 and 2, respectively. These species  
342 have contrasting spatial habitat use patterns according to their posterior mean habitat use  
343 probability estimates (Figure 6). The habitat use probability of the Giant anteater is generally  
344 higher than that of the White-lipped Peccary across all LULC types and is especially present in  
345 open areas (see radar charts in Figure 6). As the other species in their corresponding clusters,  
346 the Giant anteater is quite present in croplands and the White-lipped Peccary occupies mainly  
347 forests, with little presence in open areas (Figure 6). However, as the scatter plots in Figure 6  
348 show, their habitat use probability within croplands (for the Giant anteater) and forests (for the  
349 White-lipped Peccary) varies considerably depending on the productivity (as estimated by the  
350 NDVI Mean values) of these cover types. The White-lipped Peccary's posterior mean habitat  
351 use probability in forests increased exponentially from 0 to 0.8 over a range of NDVI Mean of  
352 0.5. As for the Giant anteater, its posterior mean habitat use probability in croplands decreased  
353 linearly with an increase of NDVI Mean.

## 354 **4. Discussion**

355 The results show that most species of the analyzed mammal community were highly present in  
356 the remaining native forest areas and that several species including *Tayassu pecari*, *Sylvilagus*  
357 *brasiliensis* (respectively Vulnerable and Endangered according to IUCN, 2021), *Panthera onca*,  
358 *Sapajus cay*, and *Tapirus terrestris* (Vulnerable according to the Red Book of Threatened



359 Brazilian Fauna (ICMBio/MMA, 2018), heavily relied on the remaining natural forest habitats.  
360 The results also revealed a high number of mammal species in the agricultural lands  
361 surrounding the SBNP, particularly in croplands. These results denote that many species have  
362 behavioral plasticity regarding transformed areas, either because they naturally use open  
363 habitats, like the Giant anteater, or because agricultural lands offer appealing resources.  
364 Considering that 75% of the remaining forest in the study area is found in private properties  
365 outside the SBNP and that agricultural areas are attractive to many species, these results stress  
366 the key conservation role of the private properties surrounding the SBNP and thus the  
367 importance of including them in policies and conservation actions (e.g., establishing incentives  
368 for the adoption of agricultural practices that support biodiversity conservation).

369 The results also show that the mammal community was particularly sensitive to the productivity  
370 and the heterogeneity of the vegetation cover (as estimated by NDVI Mean and NDVI SpatVar,  
371 respectively). Overall, the results suggest that natural and agricultural areas, and especially  
372 grasslands and pastures, that are highly productive and spatially heterogeneous host a higher  
373 number of mammal species in this multi-use landscape. Agro-ecological conservation actions in  
374 the area should therefore particularly support management practices that can contribute to  
375 maintaining healthy (as opposed to degraded), productive, and heterogeneous habitats to  
376 ensure a high abundance of resources and thus a rich mammal community at the landscape  
377 level (Benton et al., 2003; Gorczynski et al., 2021). For example, keeping trees and establishing  
378 live fence perimeters in the pasture and crop fields could be incentivized through payment for  
379 ecosystem services policies, as a way to increase heterogeneity in the agricultural areas  
380 surrounding the Park and contribute to biodiversity and carbon sequestration (Prevedello et al.,  
381 2018).

382 From a conservation perspective, it is also relevant to highlight that our results also show that  
383 individual species presented very different habitat use patterns across the different LULC types

384 and had specific responses to the different conditions of these surfaces. For instance, our  
385 results show that threatened species in our study area that were more associated with forested  
386 areas, such as *Tayassu pecari*, *Sylvilagus brasiliensis*, and *Tapirus terrestris*, had a particularly  
387 strong positive response to vegetation productivity. It is also important to note that many of the  
388 threatened species were also associated with open or transition areas (*Chrysocyon brachyurus*,  
389 *Myrmecophaga tridactyla*, *Panthera onca*, *Puma concolor*, and *Herpailurus yagouaroundi*) and  
390 that some of these species also had strong responses to particular surface conditions (e.g.,  
391 *Myrmecophaga tridactyla* shows a strong, negative response to vegetation productivity). These  
392 results claim species-focused conservation strategies. For instance, the habitat use probability  
393 of the White-lipped Peccary (*Tayassu pecari*) increased exponentially with NDVI Mean in  
394 forests, suggesting that subtle changes in tree cover density or productivity may have a big  
395 impact on the presence of this forest-dependent species. As for the Giant anteater  
396 (*Myrmecophaga tridactyla*), its habitat use probability decreased linearly with an increase of  
397 NDVI Mean in croplands, so despite this species being present in crop fields, this habitat  
398 generalist species might tend to avoid highly productive and intensive-managed crop fields.

399 Altogether, this study adds evidence to previous studies that the remaining natural habitats offer  
400 irreplaceable refuges for Brazilian mammals and hence are crucial to preserving the ecological  
401 functions and services this group provides (e.g., Rodrigues and Chiarello, 2018). Thus, from a  
402 conservation point of view, there is merit in efforts to assess the effects of natural vegetation  
403 loss and fragmentation on different species and ecological functions (Magioli et al., 2021), to  
404 monitor PA effectiveness (de O. Roque et al., 2018; Ferreira et al., 2020), and compliance with  
405 the Brazilian Forest Code in the surrounding private lands (Stefanes et al., 2018). Nonetheless,  
406 our results also stress the need for future research to assess species responses to the  
407 variability of conditions within natural habitats and in the mosaics of rangelands, croplands, and  
408 private natural vegetation reserves. Indeed, the response of species to different degrees of

409 natural habitat's ecological integrity or degradation (Grantham et al., 2020), and different  
410 agricultural and livestock systems remain largely understudied (Ferreira et al., 2012). This  
411 information is especially critical to better understand habitat use and spatial distribution of  
412 threatened wildlife for building species conservation strategies and associated practices, e.g.,  
413 for informing the Action Plans of threatened species in Brazil, which are public policies for  
414 identifying and guiding priority actions to combat threats that endanger populations of species or  
415 environments (ICMBio, 2018). Exploring these complex relationships over multi-use landscapes  
416 is also particularly important in the Cerrado biodiversity hotspot, in light of the fast intensification  
417 of agricultural systems (Arvor et al., 2012; Spera et al., 2016), and degradation of the PAs  
418 network and their surroundings (Bellón et al., 2020; de Almeida-Rocha and Peres, 2021).

419 Our MSOM highlights the potential of SRS-based variables to uncover important species-  
420 environment relationships beyond PAs boundaries or localized camera trap sites and across the  
421 broader agricultural matrix in which PAs exist. With the continuity of satellite missions, these  
422 variables can be further used to forecast and monitor changes in mammalian habitat use in PAs  
423 and their surrounding agricultural areas over time, thus opening new avenues for automated  
424 periodical and extensive monitoring. This study, therefore, contributes to the developing  
425 research on SRS-based essential biodiversity variables, and the quest for environmental  
426 predictors that are ecologically relevant, capable of generating robust, parsimonious models  
427 with minimum input data requirements, that can be easily replicated in other regions and over  
428 time (Alleaume et al., 2018; Pettorelli et al., 2016; Vihervaara et al., 2017). However, there are  
429 still many research avenues to explore to better understand the capabilities of SRS data in  
430 estimating community and species habitat use and in providing indicators on the fine-scale  
431 surface characteristics that drive species distributions (Pinto-Ledezma and Cavender-Bares,  
432 2020; Randin et al., 2020). For instance, future research is needed to explore the potential of  
433 other functionally relevant biophysical variables - such as leaf area index or fraction of absorbed

434 photosynthetically active radiation -, and fine-scale vegetation structure information from LiDAR  
435 data in estimating species distributions (Cord et al., 2013).

436 Nonetheless, SRS-based variables cannot capture other important factors that may be also be  
437 driving species occupancy patterns in and around PAs, such as human activities (e.g., hunting)  
438 or ecological processes such as metacommunity mechanisms (e.g., spillover and mass effects  
439 or source-sink dynamics). Complementary assessments with extensive local and field-based  
440 assessments are needed to capture these additional factors and to help further identify which  
441 management practices are providing key ecological functions (e.g., food, nesting sites, or  
442 dispersal routes) and thus contributing to the conservation status of focal or threatened species  
443 and to maintaining functional communities. Additional assessments are also needed to identify  
444 management practices that might be, on the contrary, threatening the conservation status of  
445 species (e.g., by increasing human-wildlife conflict or exposing wildlife to pesticides and  
446 pollution of resources). These complementary assessments are needed to fully understand the  
447 overall ecological resilience of ecosystems in these areas and are particularly necessary for  
448 fragmented neotropical areas, where the effectiveness of PAs and conservation networks  
449 increasingly depends on the ability of the surrounding agricultural areas to support biodiversity  
450 and secure functional connectivity at the landscape level.

## 451 **5. Conclusion**

452 In this study, we investigated the habitat use patterns of a mammal community over a gradient  
453 of LULC types and biophysical conditions in a National Park of the Cerrado biodiversity hotspot  
454 (Brazil) and its surrounding agricultural lands. Our research showed that most species are  
455 occupying the remaining native forests, but many of them are also present in the agricultural  
456 lands surrounding the park. These findings suggest that the private properties surrounding the  
457 park are playing a key role in this high biodiversity value area, and thus future research is

458 needed to investigate the practices that might be positively or negatively contributing to the  
459 long-term mammal community's conservation in the region. Our results show that the levels of  
460 productivity and heterogeneity of the vegetation cover, as depicted by two NDVI-based  
461 variables, largely determine the habitat use probability of the species in the different natural and  
462 agricultural LULC types. Thus, preserving the remaining natural vegetation in the private  
463 properties and adopting sustainable practices to increase the heterogeneity and productivity of  
464 the vegetation cover could greatly contribute towards the long-term effectiveness of the park in  
465 conserving a rich mammal community.

466 More globally, this research highlights the potential of improving biodiversity monitoring by 1)  
467 using MSOMs to estimate important state variables such as species richness and individual  
468 species responses to different environmental factors beyond PAs boundaries and across the  
469 whole spectrum of land uses at the landscape level, and 2) including SRS-derived biophysical  
470 variables that represent different conditions of the natural and agricultural cover types as  
471 covariates of the MSOMs. Such modeling frameworks can be used to identify key landscape  
472 characteristics that support rich communities and species' presence in multi-use landscapes  
473 and thus guide policy in establishing effective buffer zones, corridors, sustainable use areas,  
474 biosphere reserves, or other effective area-based conservation measures to increase the  
475 network of working landscapes that support both biodiversity and socio-economic development.

## 476 **Declaration of Competing Interest**

477 The authors declare that they have no known competing financial interests or personal  
478 relationships that could have appeared to influence the work reported in this paper.

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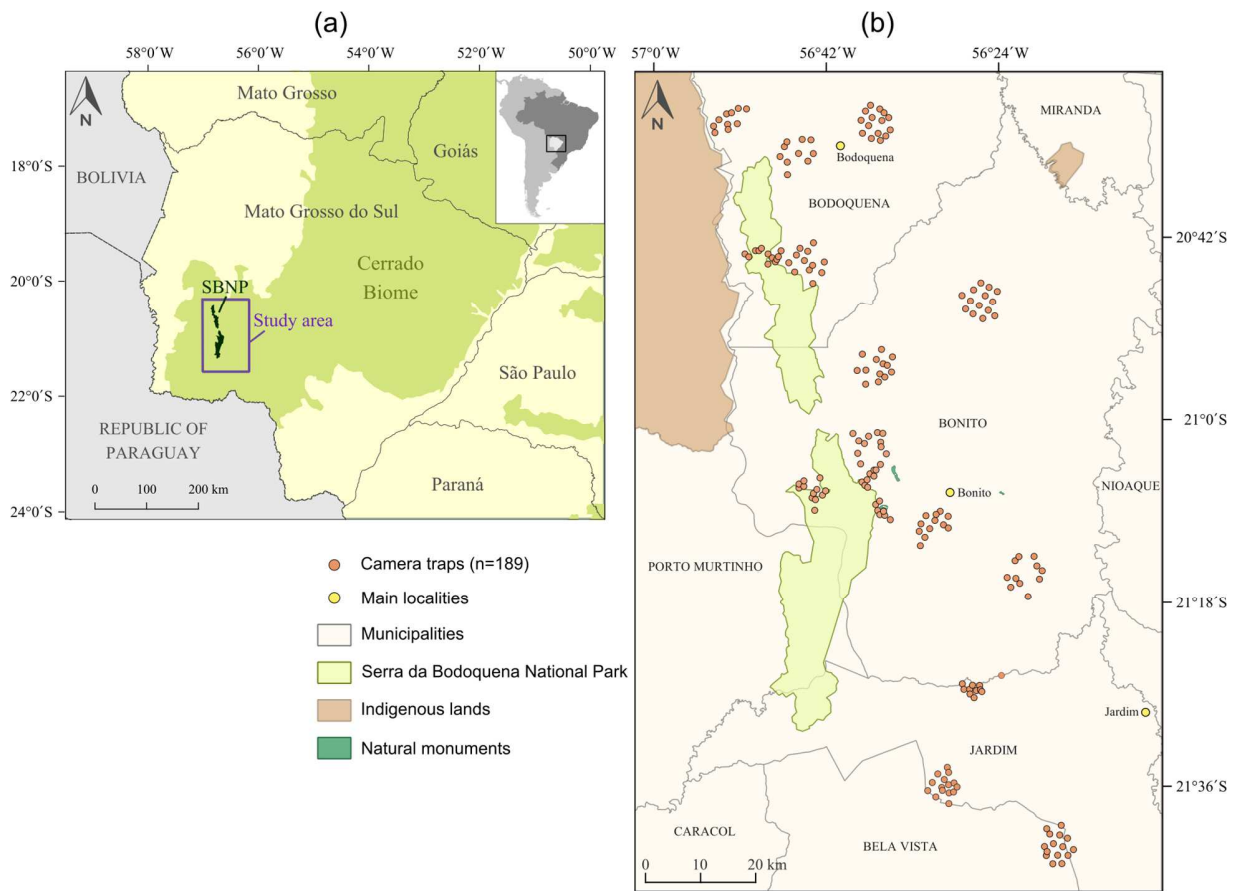
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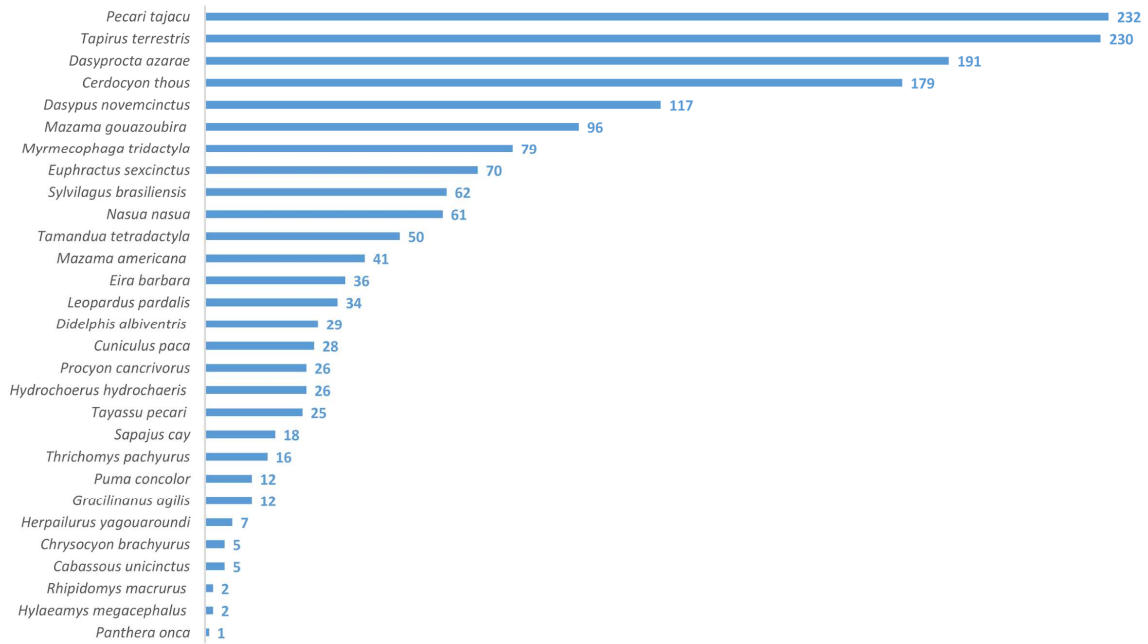
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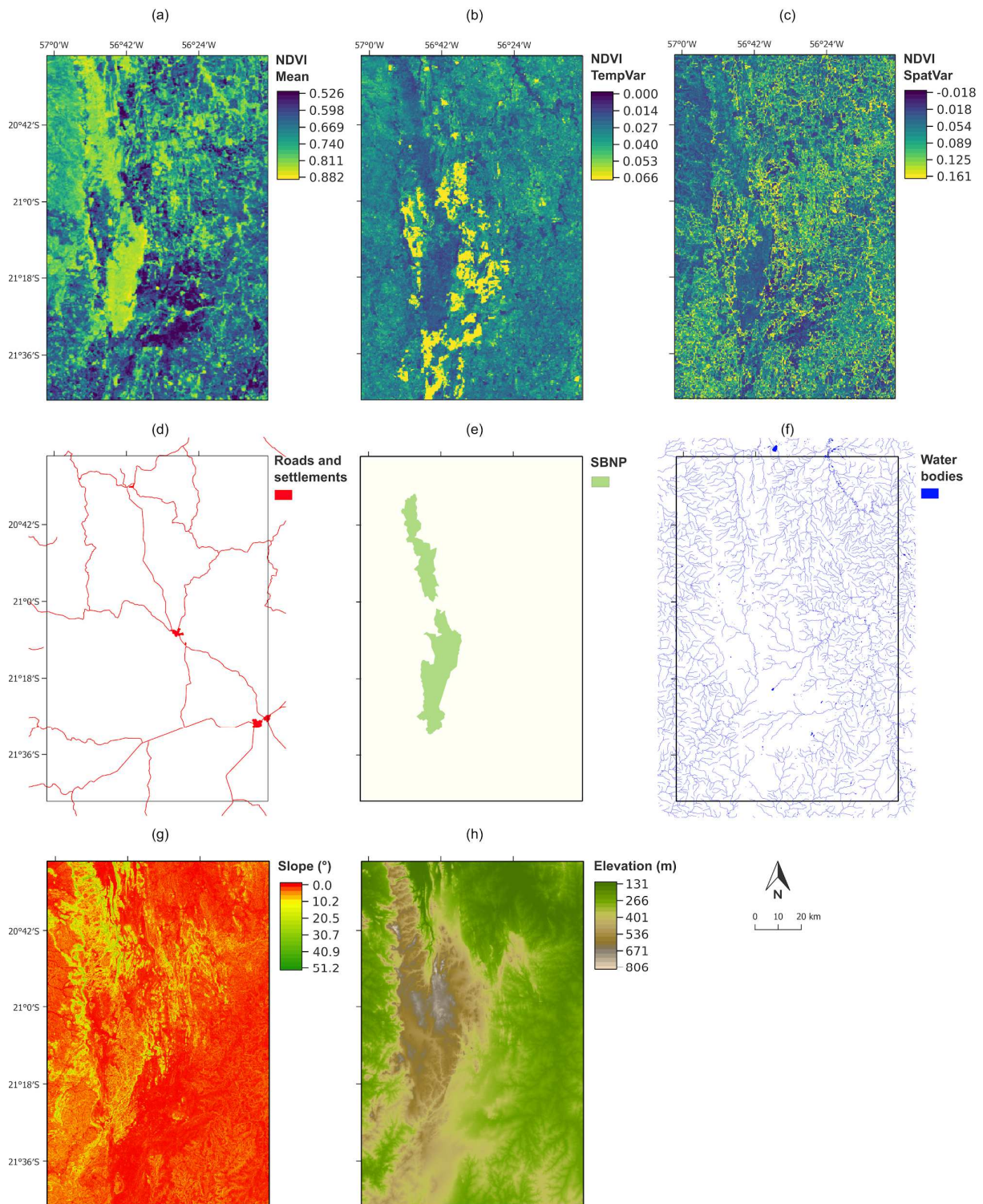




**Figure 1. (a)** Location of the study area in the eastern portion of the Cerrado Biome in Mato Grosso do Sul, Brazil. The area in dark green corresponds to the Serra da Bodoquena National Park (SBNP); **(b)** Location of the 189 camera trap sampling sites.

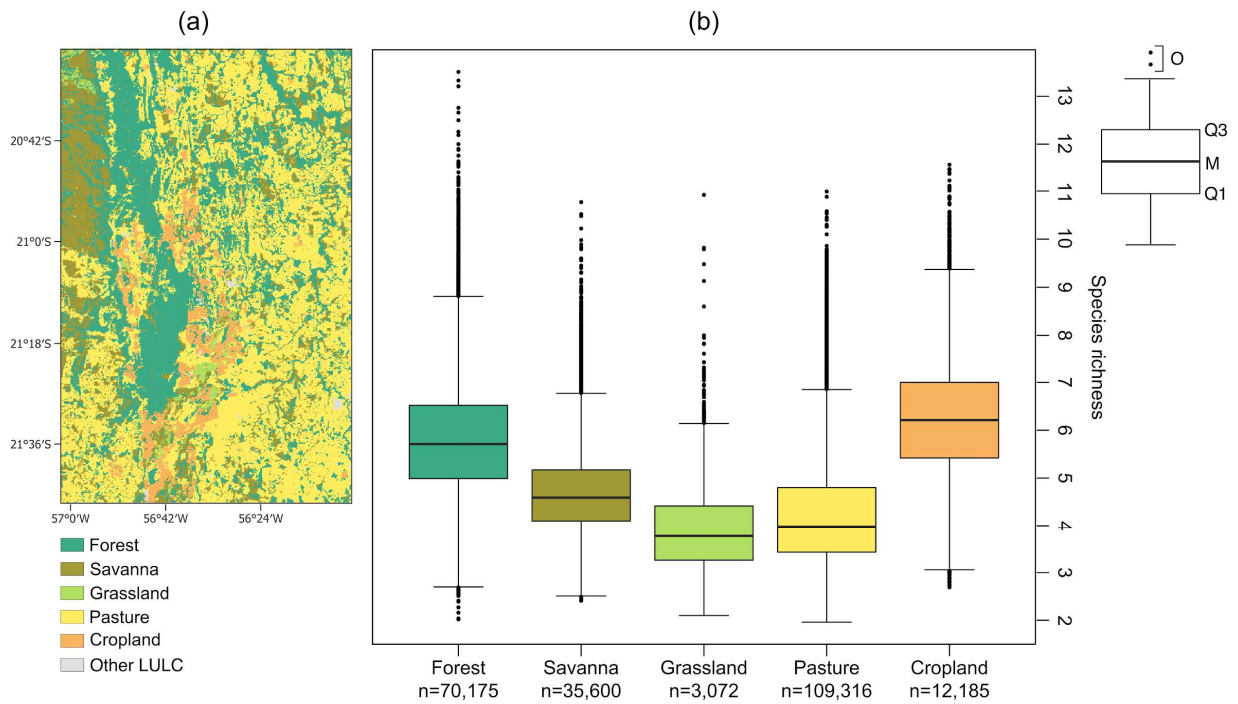


**Figure 2.** The number of detection events per mammal species from 1-day pooled camera trap data collected in and around the Serra da Bodoquena National Park in Mato Grosso do Sul. The total number of detection events is 1,692.

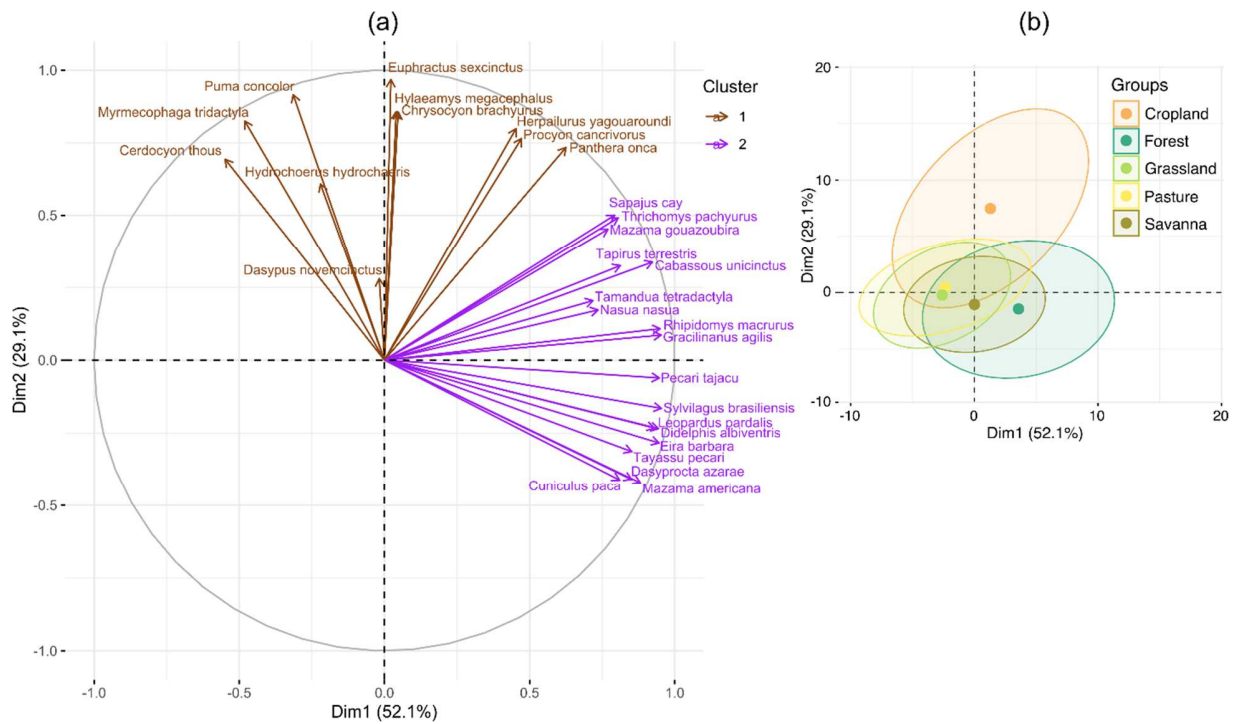


**Figure 3.** Layers used as covariates in the multi-species occupancy model: three NDVI-based variables, **(a)** NDVI Mean, **(b)** NDVI TempVar and **(c)** NDVI SpatVar, represented in a pseudocolor, using a mean  $\pm$  2 standard deviations range, for visualization purposes; **(d)** Roads network and settlements; **(e)** Serra da Bodoquena National Park (SBNP); **(f)** Inland bodies of water; **(g)** Terrain slope; and **(h)** Elevation. The black

bounding box in each figure represents the boundaries of the study area, including the Serra da Bodoquena National Park and its surroundings.

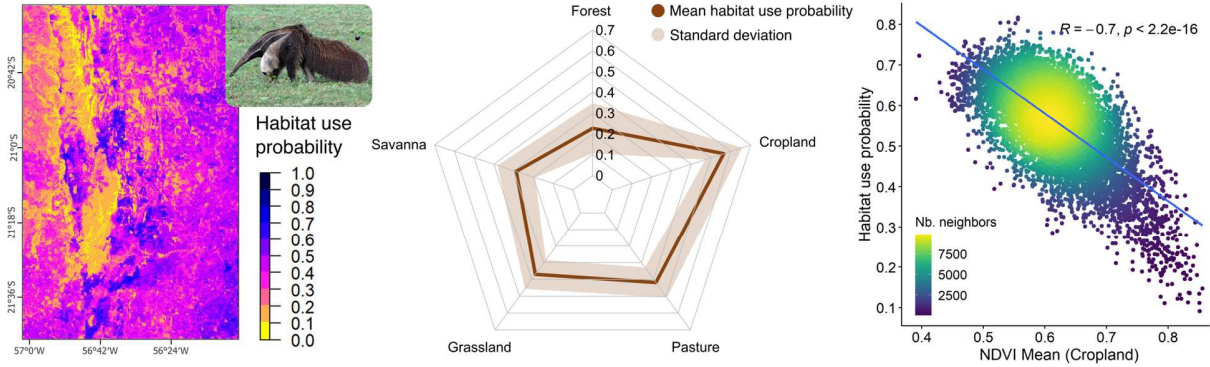


**Figure 4. (a)** Map of land use and land cover types in and around the Serra da Bodoquena National Park. The 'Cropland' class corresponds to the 'Soybean' class in the original MapBiomas nomenclature (Project MapBiomas, 2021), and the 'Other LULC' class includes the rest of LULC classes in the study area which represent < 0.7% of the total surface; **(b)** Boxplots of the posterior mean species richness estimates in the different vegetation cover types ( $n$  = number of 250 m pixels). Boxplots show medians (M), lower and upper quartiles (Q1 and Q3, respectively), and outliers (O).

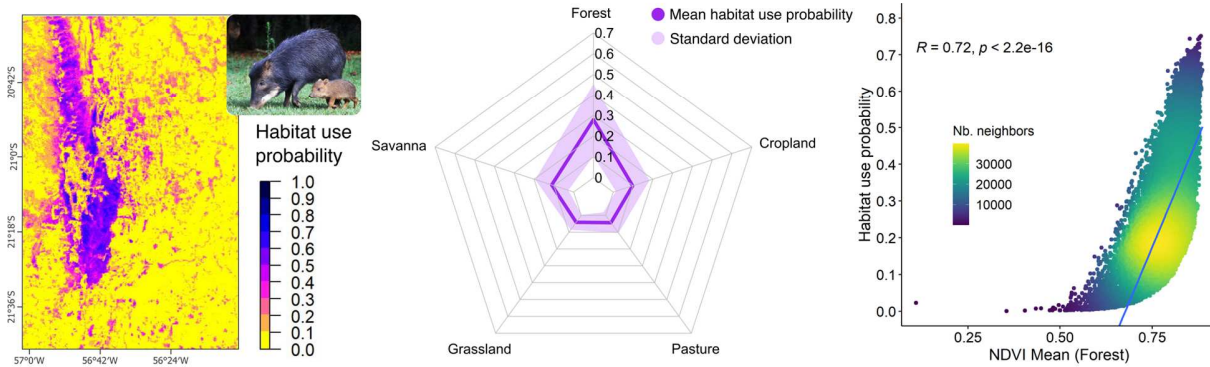


**Figure 5.** Plots of the PCA on the 29 mammal species' habitat use probability posterior mean estimates in and around the Serra da Bodoquena National Park: **(a)** PCA loadings plot with variables/species grouped by the clusters identified by k-means, and **(b)** scores plot with observations/pixels grouped by land use and land cover type, displaying 95% concentration ellipses and the group mean points (barycenters).

*Myrmecophaga tridactyla*



*Tayassu pecari*



**Figure 6.** Left: Map of the posterior mean estimates of habitat use probability for the Giant anteater (*Myrmecophaga tridactyla*) and the White-lipped Peccary (*Tayassu pecari*) in and around the Serra da Bodoquena National Park. Center: Radar charts displaying the mean habitat use probability values and standard deviation within each land use/cover type for each species (values are derived from their posterior mean estimates of habitat use probability). Right: Relationship between habitat use probability and the NDVI Mean within cropland areas for the Giant anteater (top) and forest areas for the White-lipped Peccary (bottom). Photo credits: Simone Mamede, Instituto Mamede.

**Table 1.** NDVI-based variables used as environmental predictors in the multi-species occupancy model.

Variable	Proxy for	Computation
NDVI Mean	average annual productivity	average of all NDVI values in the annual MOD13Q1 time series
NDVI TempVar	average seasonal variability of productivity (or vegetation phenology)	sum of the absolute differences between each pair of consecutive composite images in the MOD13Q1 time series divided by the number of intervals (N=22)
NDVI SpatVar	spatial variability or heterogeneity of productivity within a 250 m reference cell	standard deviation of the NDVI values of all the 30 m resolution Landsat pixels within each 250 m-cell of a regular grid matching the MOD13Q1 pixels



**Table 2.** Pearson's correlation coefficients ( $r$ ) between species richness and different landscape variables within different land use and land cover (LULC) types.

Landscape variables	Species richness within LULC types (n = no. of pixels in each type)				
	Forest (n=70,175)	Savanna (n=35,600)	Grassland (n=3,072)	Pasture (n=109,316)	Cropland (n=12,185)
NDVI Mean	0.28	0.41	<b>0.58</b>	<b>0.64</b>	0.44
NDVI TempVar	-0.06	0.01	<b>0.54</b>	0.13	0.30
NDVI SpatVar	0.34	0.42	<b>0.63</b>	<b>0.73</b>	0.46
Distance to roads and settlements	0.03	-0.17	-0.21	-0.13	-0.10
Distance to the SBNP	-0.16	-0.09	0.02*	-0.16	-0.21
Distance to water	0.26	0.24	-0.11	0.01	-0.02*
Slope	-0.35	-0.12	0.16	0.06	0.10
Elevation	0.37	0.35	0.03*	0.25	0.39

All correlations are significant at  $p < 0.001$ , except for those marked by \*, where  $p > 0.05$ . Due to the large sample sizes we, however, recommend focusing on the effect sizes reported, regardless of statistical significance. Values in bold indicate strong correlations ( $r > 0.5$ ).