

## Research Highlights

- Forest patch size and palm density predict the occurrence of *Alouatta belzebul* in Amazonian savannas.
- Flooded forests may be a keystone habitat for *A. belzebul* in small forest patches.

1 **The occurrence of the red-handed howler monkey (*Alouatta belzebul*) in Amazonian**  
2 **savannas is related to forest patch area and density of flooded area palms**

3 **Short title: Predicting the occurrence of howlers**

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5 Saulo M. Silvestre<sup>1</sup>, Joanna M. Setchell<sup>2</sup>, Bayron R. Calle-Rendón<sup>1</sup>, José J. de Toledo<sup>1</sup> and  
6 Renato R. Hilário<sup>1,3,4</sup>

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8 <sup>1</sup> Postgraduate Program in Tropical Biodiversity, Federal University of Amapá, Brazil.

9 <sup>2</sup> Department of Anthropology, Durham University, Durham, UK.

10 <sup>3</sup> Postgraduate Program in Environmental Sciences, Federal University of Amapá, Brazil.

11 <sup>4</sup> Faculty of Sciences, University of Lisbon, Portugal

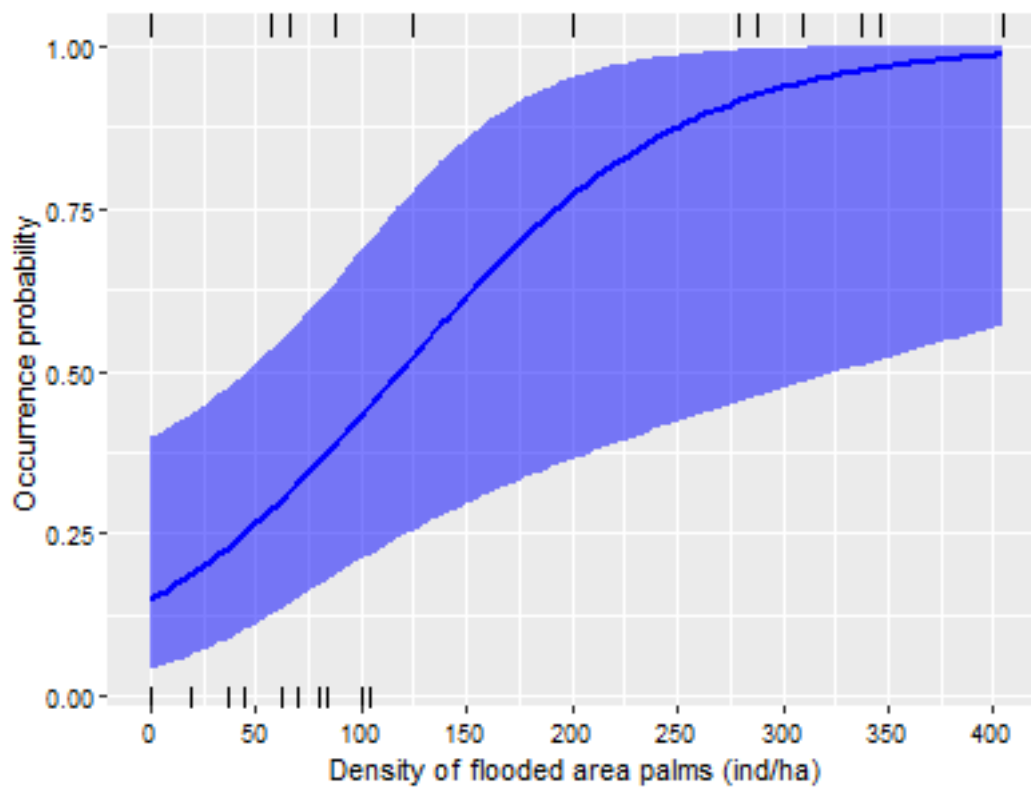
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13 Corresponding author: Saulo M. Silvestre. Programa de Pós-graduação em Biodiversidade  
14 Tropical, Universidade Federal do Amapá, Rod. Juscelino Kubitschek, S/N, Jardim Marco  
15 Zero, Macapá-AP, 68903-419, Brazil. E-mail: saulomsilvestre@gmail.com. Phone: +55 (96)  
16 99141-9930.

17

18 **Abstract**

19 All Neotropical primates are arboreal and thus depend on forests for their survival. This  
20 relationship put many Neotropical primates at risk of extinction due to the high rates of  
21 deforestation in the tropics. We assessed the influence of vegetation structure and forest patch  
22 attributes on the occurrence of the threatened red-handed howler monkey (*Alouatta belzebul*)  
23 in an Amazonian savanna. Using a sample of 38 forest patches in a region of ~2,000 km<sup>2</sup> in the  
24 state of Amapá, northern Brazil, we used logistic regression to find the best predictors of the  
25 occurrence of *A. belzebul*. We assessed patch area, patch isolation, the proportion of seasonally  
26 flooded forest in the patch, the density of flooded area palms, forest height, canopy cover, and  
27 diameter at breast height of trees. Patch area and palm density were the best predictors of the  
28 occurrence of *A. belzebul* in forest patches, both having a positive effect on the probability of  
29 occurrence. Our results indicate that areas of flooded forest in forest patches may be keystone  
30 habitats for *A. belzebul* living in Amazonian savannas. The observed effect of palm density on  
31 *A. belzebul* suggests that this variable is useful for planning conservation actions, including the  
32 selection of areas for protection and management strategies for areas inhabited by this primate.



33

34 **Keywords:** *Alouatta belzebul*, Amapá, Palms, Forest structure, Flooded forest, Patch

35 occupancy

## 36 **Introduction**

37       The factors that have the greatest influence on species occurrence are key to the selection  
38 of high-quality areas for the conservation of threatened species, and the development of  
39 management strategies to reduce their probabilities of extinction. Arboreal primates in  
40 fragmented landscapes only occasionally travel among forest fragments, mostly to migrate  
41 between groups (Mandujano, Escobedo-Morales, & Palacios-Silva, 2004; but see Pozo-Montuy  
42 & Serio-Silva, 2007). The habitat variables affecting their occurrence may help to explain their  
43 distribution in the landscape and guide the selection and management of areas for conservation  
44 that optimize the probability of long-term survival of local populations (Arroyo-Rodríguez &  
45 Dias, 2010).

46       The size of forest fragments or patches and edge effects are often major factors in  
47 determining the diversity and quantity of resources available for primates (Arroyo-Rodríguez  
48 & Mandujano, 2006; Estrada & Coates-Estrada, 1996). Habitat heterogeneity may also reduce  
49 the risk of food scarcity if different habitats have asynchronous peaks in productivity (Defler &  
50 Defler, 1996; Stevenson, 2016). For example, adjacent flooded forests can be key to the survival  
51 of primates in unflooded forest fragments during times of food scarcity, thanks to their different  
52 floristic composition and complementary phenology (Ahumada, Stevenson, & Quiñones, 1998;  
53 Carretero-Pinzon & Defler, 2019).

54       Among Neotropical primates, howlers (*Alouatta* spp.) are remarkably resilient to habitat  
55 disturbance, thanks to their ecological flexibility, and especially their flexible diet (Peres, 1997).  
56 Howlers can include exotic species in their diet (Bicca-Marques, 2003) and survive on an  
57 almost entirely folivorous diet during lean periods (Pavelka & Knopff, 2004). They may also  
58 survive in small (<5 ha) forest fragments, helping them to cope with forest fragmentation  
59 (Bicca-Marques, Chaves, & Hass, 2020; Rodriguez-Toledo, Mandujano, & García-Orduña,

60 2003). However, fragmentation has potentially negative effects on howler populations, which  
61 may include reduced food availability in the small fragments and higher levels of physiological  
62 stress, competition, parasite load, and hunting pressure (Arroyo-Rodríguez & Dias, 2010;  
63 Rimbach et al., 2013).

64 In the Amazon, floodplain (Várzea) forests have the most abundant populations of  
65 howlers, as a result of the high levels of forest heterogeneity and soil fertility found in this  
66 habitat (Peres, 1997). In fragmented landscapes, forest area is often the main determinant of  
67 howler occurrence (Arroyo-Rodríguez & Dias, 2010). Measures used as proxies for food  
68 availability, like the density of large trees and total basal area, also play a particularly important  
69 role in the occurrence and population densities of howlers in small fragments (Arroyo-  
70 Rodríguez, Mandujano, Benítez-Malvido, & Cuende-Fanton, 2007; Hue, Caubet, & Moura,  
71 2017). While vegetation parameters like canopy cover, mean size of trees, and forest height are  
72 often interpreted as positively correlated with habitat quality for howlers (*e.g.* Bolt et al. 2019),  
73 their effects may be more easily detected on population parameters (*i.e.* abundance) than  
74 occurrence (Anzures-Dadda & Manson, 2007). However, by positively affecting primate  
75 abundance, a given driver may also contribute to population persistence, thus affecting primate  
76 occurrence indirectly.

77 The red-handed howler monkey (*Alouatta belzebul*) is an endemic threatened  
78 (Vulnerable) primate from Brazil (Montenegro et al., 2019). Habitat loss and hunting are the  
79 main threats to this species and have resulted in the local extinction of several populations  
80 (Montenegro et al., 2019). *A. belzebul* faces deforestation and habitat fragmentation in most of  
81 its geographic distribution, *i.e.* in the Atlantic Forest and the arc of deforestation in the Amazon  
82 (Montenegro et al., 2019). The least degraded region of its distribution is in the southeast of the

83 state of Amapá, North of the Amazon River. However, this region has suffered increasing  
84 anthropogenic impacts in recent years (Hilário et al., 2017; Mustin et al., 2017).

85 The landscape of southeastern Amapá where *A. belzebul* occurs is predominantly  
86 composed of lowland (Várzea) forests, flooded fields, and savannas. The savannas are  
87 characterized by open formations, permeated by gallery forests and forest patches subjected to  
88 varying flooding intensity, from patches that are completely dry land to patches that are entirely  
89 floodable (IEPA, 2008). This ecosystem covers ~10,021 km<sup>2</sup> of Amapá, but over 1,000 km<sup>2</sup> has  
90 already been lost to eucalyptus plantations and it faces imminent threats mainly due to the  
91 accelerated expansion of agribusiness in the state, which is replacing remaining savannas with  
92 soybean plantations (Hilário et al., 2017). Changes in the matrix often result in changes inside  
93 forest fragments, including forest structure and food availability (Fischer & Lindenmayer,  
94 2007). In this context, understanding how variation in habitat structure influences the  
95 occurrence of *A. belzebul* is a key aspect of conservation planning.

96 In this study, we investigated the influence of patch attributes (area, isolation, the  
97 proportion of the patch that is seasonally flooded), and vegetation structure (forest height,  
98 canopy cover, tree DBH, and density of flooded area palms) on the probability of occurrence  
99 of *A. belzebul* in forest patches in the savannas of Amapá. We hypothesized that *A. belzebul*  
100 occurrence would be related to habitat availability and quality. Specifically, we predicted that  
101 patch area, forest height, canopy cover, and tree diameter would be positively associated with  
102 *A. belzebul* occurrence. Conversely, we predicted that patch isolation would be negatively  
103 associated with *A. belzebul* occurrence. We also hypothesized that seasonally flooded areas  
104 would have positive effects on *A. belzebul* occurrence because they represent potential sources  
105 of food that may complement what is available in unflooded portions of the forest patches.  
106 Because not all flooded portions of the forest patches in our study region are forest (i.e., with

107 dicot trees), we used both the proportion of the patch that is seasonally flooded, which does not  
108 take into account the type of vegetation, and the density of flooded area palms, as an indicator  
109 of flooded forests. We predicted that intermediate levels of these two variables would have  
110 positive effects on *A. belzebul* occurrence, because while smaller areas of seasonally flooded  
111 forest would be an advantage, the occurrence of howlers will start to diminish again at much  
112 larger proportions of flooded forest, due to the lack of unflooded forest.

113

## 114 **Methods**

### 115 *Ethics statement*

116 This research complied with the American Society of Primatologists' Ethical Principles  
117 for the Treatment of Non-Human Primates and with Brazilian Ethical Standards for research  
118 with animals, and adhered to all Brazilian legal requirements.

### 119 *Study region*

120 The Brazilian state of Amapá has a humid tropical climate of type Am according to  
121 Köppen and Geiger's classification system (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006).  
122 The year is characterized by two seasons: the rainy season runs from December to July, with  
123 average monthly rainfall ranging between ca. 200 and 400 mm; and the dry season, from August  
124 to November, with average monthly rainfall of less than 100 mm (IEPA, 2008). The savanna  
125 region is characterized by grasslands with sparse trees and dense herbaceous/shrub strata. In  
126 the landscape, gallery forests, stands of buritis (*Mauritia flexuosa*), and forest patches stand out  
127 amidst the predominantly open formations (IEPA, 2008).



128 In the Amapá savannas, *A. belzebul* is concentrated in the municipalities of Santana and  
129 Macapá. Park savanna and grass savanna formations predominate in this region (Mustin et al.,  
130 2017). This is also the region with the highest human population density in the state, with a  
131 metropolitan region (~646,000 inhabitants) that includes Macapá, Santana, and Mazagão  
132 (IBGE, 2017a; Mustin et al., 2017). The recent expansion of soybean plantation areas in the  
133 state is also concentrated in this region (IBGE, 2017b), making this currently the region with  
134 the greatest pressure on biodiversity in Amapá.

### 135 *Selection of forest patches*

136 We defined forest patches as areas of  $\geq 1$  ha of native forest that were not structurally  
137 connected to other forest patches (Dias, Alvarado-Serrano, Rangel-Negrín, Canales-Espinosa,  
138 & Cortés-Ortiz, 2013; Puig-Lagunes, Canales-Espinosa, Rangel-Negrín, & Dias, 2016). Given  
139 the scarcity of information on the distribution of *A. belzebul* in the region, we selected 126  
140 patches ( $\geq 1$  ha) for a preliminary survey of the occurrence of the species through interviews  
141 with residents of the region and obtained information for 58 of these forest patches in February,  
142 October and November 2017. We then selected 38 forest patches as our sample: half with  
143 indications of presence of *A. belzebul* and the other half with no indication of their presence  
144 (Figure 1). We carried out playback sampling in 22 of these patches to confirm the information  
145 from the interviews (Calle-Rendón, Toledo, Mustin, & Hilário, 2020). In the remaining 16  
146 patches, we confirmed the presence of the species via opportunistic records during vegetation  
147 sampling.

148 The playbacks were conducted using a Max Print 601205-3 speaker (frequency range: 50  
149 to 20,000 Hz, output power: 100 RMS) in points defined by transects of 800 m. We broadcast  
150 vocalizations of *A. belzebul* at the beginning and the end of each transect at 07:00 a.m. and 4:40  
151 p.m., respectively. In the meantime, the researcher walked the transect actively looking for the

152 howlers. We sampled one transect per day. The number of transects was defined by the patch  
153 area as follows:  $\leq 25$  ha: 2 transects;  $>25-50$  ha: 3 transects;  $>50-100$  ha: 4 transects; and  $>100$   
154 ha: 5 transects. If the size and/or shape of the patch did not support one transect of 800 m, the  
155 quantity and length of transects were adjusted accordingly, so the minimum distance between  
156 points was 200 m. We confirmed the presence of *A. belzebul* by direct (visual and auditory)  
157 and/or indirect (feces) signs in all 19 patches with indications of its presence. We found no  
158 evidence of howlers in any of the 19 patches where respondents said they were absent. Data  
159 collection in forest patches was carried out from July 2018 to April 2019.

160 In the study region, *A. belzebul* inhabits forest patches and gallery forests originally  
161 embedded in open savanna formations (i.e. park savannas and grass savannas), flooded fields,  
162 and lakes. Now the landscape also includes human settlements and activities that changed or  
163 replaced the matrix in some areas (i.e. soybean and eucalyptus plantations). These changes may  
164 indirectly affect the local distribution of *A. belzebul* through changes in variables like matrix  
165 permeability or hunting pressure. However, the matrix surrounding our sampled forests was  
166 predominantly composed of natural habitats, mostly open savanna formations. All forest  
167 patches had potential migration routes to/from other forested areas that did not include human-  
168 made landscape features, except for eventual dirt roads. Only one forest patch had direct contact  
169 with an urban area.

### 170 *Sampling of forest patches*

171 We evaluated patch area, patch isolation, the proportion of the patch that is seasonally  
172 flooded in the patch, the density of palms typically abundant in flooded forests (palm density),  
173 mean forest height, mean canopy cover, and mean diameter at breast height (DBH) of trees with  
174  $\geq 10$  cm DBH for each forest patch.

175 Forest patches in Amazonian savannas are often partially seasonally flooded. In our study  
176 region, we can separate the flooded portions of the forest patches into two general forms: (i)  
177 forests formed by trees and arborescent palms, and (ii) herbaceous/shrubby clearings with  
178 higher flooding intensity, dominated by dense tufts of atuíras (*Machaerium lunatum*) or arumãs  
179 (*Ischnosiphon polyphyllus*) and sparsely distributed *M. flexuosa* palms. The former presumably  
180 provide more advantages for howlers (*e.g.* support for locomotion, shelter, and food sources)  
181 than the latter. These different forms result from different flooding intensities. Areas that are  
182 flooded for longer periods tend to be more similar to flooded fields, while areas flooded for  
183 shorter periods include a higher density and richness of palms and tree species. We addressed  
184 this habitat difference by assessing the effects of flooded areas using two variables: the  
185 proportion of the patch that is seasonally flooded, and the density of flooded area palms. We  
186 used the density of palms (*E. oleracea*, *M. flexuosa*, and *M. armata*) to assess the extent of  
187 flooded forest because Arecaceae is often the most abundant plant family in flooded forests  
188 (Aquino & Bodmer, 2004), and because of the ease in identifying them in the field.

189 We calculated the patch area and the shortest distance to the nearest forest patch (*i.e.*  
190 patch isolation) based on satellite images from Google Earth Pro (version 7.3.2.5776). We  
191 calculated the mean forest height for each patch using Synthetic-Aperture Radar (SAR) images  
192 (res: 2.5 m x 2.5 m) of the vegetation height (created using pulses that are reflected by the  
193 vegetation), using all cell values  $\geq 5$  m, thus excluding clearings or imperfections in the  
194 definition of the polygons that could include the savanna matrix. We estimated the proportion  
195 of the patch that was seasonally flooded using SAR images (res: 2.5 m x 2.5 m) of the altitude  
196 (created using pulses that are reflected by the ground), by calculating the proportion of cells  
197 with altitudes  $\leq 5$  m.

198 We measured the remaining variables using 100 m x 2 m plots. We determined the  
199 number of plots per forest patch using the patch area ( $\leq 15$  ha: 4 plots;  $>15-25$  ha: 8;  $>25-50$   
200 ha: 12;  $>50-100$  ha: 16;  $> 100$  ha: 20). We chose the starting point of each plot using stratified  
201 random selection. We created a grid (200 m x 200 m) covering each of the patches using the  
202 ‘raster’ package (Hijmans, 2017) in R software (R Core Team, 2017) and randomly sampled  
203 points, conditioned to a maximum of one point per grid cell. We determined the orientation of  
204 the plot in situ, avoiding abrupt changes in altitude and preferably pointing towards the starting  
205 point of the next plot. It was not possible to sample the intended number of plots in some forest  
206 patches due to limitations in size (some patches were too small) or shape (some irregular shapes  
207 limited the number of plots that could fit inside the patch). The total area sampled per forest  
208 patch varied from 0.06 ha to 0.40 ha, and the percentage of sampled area per forest patch varied  
209 from 0.11% in the largest (228.5 ha) to 3.30% in the smallest (1.8 ha) patch.

210 To estimate canopy cover, we obtained hemispheric photographs using a fisheye lens  
211 ( $180^\circ$ ) attached to a smartphone, 1.5 m from the ground at three equidistant points, forming a  
212 triangle with sides of 5 m, every 25 m within the plots (Tichý, 2016). Using the GLAMA  
213 software (Gap Light Analysis Mobile Application), we calculated the Modified Canopy Cover  
214 index (Modif. CaCo) for each photograph. This index describes the proportion of the  
215 photograph represented by vegetation (canopy), correcting for distortion (Tichý, 2016). We  
216 measured the diameter at breast height (DBH) of trees, and counted and identified all palms at  
217 least 2 m tall within the plots. We calculated the palm density (palms/ha) by dividing the total  
218 number of *E. oleracea* clumps, *M. flexuosa*, and *M. armata* by the area sampled (ha) in the  
219 patch.

220 The number of forest patches in each size class varied, with nine patches of  $\leq 15$  ha, 10 of  
221  $>15-25$  ha, eight of  $>25-50$  ha, six of  $>50-100$  ha, and five of  $>100$  ha. The mean modified

222 canopy cover index of the sample patches varied from 75% to 84%, except for one forest patch  
223 with an exceptionally discontinuous canopy (61%) due to a large number of felled trees (Table  
224 1). Except for forest height and mean tree DBH ( $r = 0.62$ ), our variables were weakly correlated  
225 ( $r = 0.31-0.34$ ) (Table 2). Patch isolation varied from 10 m to 288 m and 84% ( $n = 32$ ) of the  
226 forest patches were less than 200 m from the nearest neighboring forest.

### 227 *Data analysis*

228 We used R software for all analyses (R Core Team, 2017). We used a logistic regression  
229 model to determine the influence of vegetation structure parameters (mean forest height, mean  
230 canopy cover, mean DBH of trees, palm density) and patch attributes (area, patch isolation, and  
231 the proportion of the patch that was seasonally flooded) on the occurrence of *A. belzebul*. We  
232 included a quadratic term for the proportion of the patch that was seasonally flooded and palm  
233 density in our model, because we predicted a non-linear relationship between those variables  
234 and the occurrence of *A. belzebul*. However, this drastically decreased the quality of the models,  
235 so we removed the quadratic terms. We used the function ‘model.avg’ in the package ‘MuMIn’  
236 (Barton, 2018) to compare the models with all possible combinations of predictors and ranked  
237 them from best to worst, based on the lowest to highest AICc (Akaike Information Criterion  
238 corrected for small samples). We used the R package ‘gam’ (Hastie, 2020) to create a  
239 Generalized Additive Model (GAM) applying a local regression smoother (LOESS) function  
240 to the palm density to assess the relationship between this variable and the occurrence of *A.*  
241 *belzebul* in the best logistic model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

242 Logistic regressions assume perfect detection, which is difficult to ensure in most field  
243 scenarios. Other, more expensive and time-consuming analytical approaches such as occupancy  
244 models could give us better results. However, by using multiple approaches to obtain  
245 occurrence data (i.e. interviews, playback, active searches, and opportunistic records), we found

246 evidence of the presence of howlers in all patches where interviewers indicated its presence and  
247 we did not find evidence of their presence in any of the patches where interviewers indicated  
248 its absence. Thus, the low probability of false absences in our dataset warrant the use of logistic  
249 regression models.

250 We tested the models for multicollinearity using the variance inflation factor (VIF –  
251 Quinn and Keough 2002), with the ‘car’ package (Fox & Weisberg, 2011). None of the  
252 variables had  $VIF > 3$ , indicating no problems of multicollinearity (Zuur et al., 2009). The  
253 ‘outlierTest’ tool in the ‘car’ package found no significant influence of outliers on the model.  
254 Finally, there was no spatial autocorrelation of the regression residuals, as indicated by  
255 variograms made with the ‘gstat’ package (Pebesma, 2004).

## 256 **Results**

257 The best model predicting the distribution of *A. belzebul* in the forest patches included  
258 only patch area and palm density, with the lowest AICc and an Akaike weight almost 3 times  
259 higher than the second-best model, which included canopy cover (Table 3). Furthermore, both  
260 patch area and palm density were included in the 15 best models. None of the other vegetation  
261 structure parameters (mean forest height, mean canopy cover, and mean DBH of trees), or patch  
262 attributes (patch isolation and proportion of the patch that is seasonally flooded) were important  
263 predictors of the probability of *A. belzebul* occurrence. Forest patch area had the strongest effect  
264 on the probability of occurrence of *A. belzebul*, which varied from  $< 10\%$  in patches below 10  
265 ha to almost 100% in patches larger than 100 ha (Figure 2). Palm density also had a positive  
266 influence on the probability of occurrence of *A. belzebul* in forest patches. Although we found  
267 howlers in forest patches with varying palm densities, the absence records were concentrated  
268 in forest patches with low palm densities and only one of the 10 patches that had over 100  
269 palms/ha was not occupied by howlers (Figure 2). The GAM using the LOESS function

270 revealed a mostly linear relationship between palm density and the occurrence of *A. belzebul* in  
271 our sample.

## 272 **Discussion**

273 We found that patch area is the best predictor for the occurrence of *A. belzebul* in forest  
274 patches of the savannas of Amapá. Additionally, while the extent of flooded forest (measured  
275 as the density of flooded area palms) increased the probability of occurrence, *A. belzebul*  
276 tolerated variation in the structural configurations of forest patches. We suggest that the effect  
277 of flooded forests on the occurrence of *A. belzebul* is related to the potential of this habitat to  
278 show peaks in fruit production during lean periods in the dry portions of small forest patches  
279 (<100 ha) (Ahumada et al., 1998; Haugaasen & Peres, 2005).

### 280 ***Vegetation structure***

281 *Alouatta belzebul* tolerated the variation in the structural configurations of forest patches  
282 we found in our sample. Howler monkeys are known to tolerate variation in the structure of the  
283 forests they occupy, including different degrees of disturbance, due to their dietary flexibility  
284 (Bicca-Marques, 2003; Bicca-Marques et al., 2020). They cope with food scarcity by adjusting  
285 their diet to the species available, and relying on the consumption of leaves, a relatively stable  
286 and abundant source of food in forests when fruits are scarce (Bicca-Marques, 2003).

287 Although most vegetation structure variables were not useful in predicting the occurrence  
288 of *A. belzebul* in our sample, we do not rule out the inherent dependence on forest structure for  
289 the survival of this arboreal primate. Such variables may have a greater influence on population  
290 parameters, such as density and demography, than on distribution. For example, the abundance  
291 of *A. palliata* in fragments is positively affected by canopy height, although canopy height does  
292 not influence the probability of occurrence (Anzures-Dadda & Manson, 2007).

293 Indicators of food availability, such as greater abundance and basal area of important food  
294 sources or the area of the patch/fragment, are important drivers of the occurrence of *Alouatta*  
295 spp. (Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2007; Cristóbal-Azkarate,  
296 Veà, Asensio, & Rodríguez-Luna, 2005). In an extreme example, *Alouatta pigra* can maintain  
297 a population structure in eucalyptus plantations similar to that of populations in native forests,  
298 thanks to the food found in vines, vegetation growing below the eucalyptus, and secondary  
299 vegetation in adjacent areas (Bonilla-Sánchez, Serio-Silva, Pozo-Montuy, & Chapman, 2012).  
300 In other words, howlers may survive in a forest with a structure very different from that of  
301 native forests if there is food available.

### 302 ***Patch attributes***

303 Forest patch area had the strongest effect on the occurrence of *A. belzebul*. Patch area is  
304 related to a series of factors that converge for a positive effect of this variable on the probability  
305 that primates occur, including resources (food, space), metapopulation dynamics (the  
306 probability of colonization and extinction), and genetic diversity. The resource limitations  
307 imposed by the reduced size of a forest patch, increase the probability of local extinctions  
308 (Rodríguez-Toledo, Mandujano, & García-Orduña, 2003; Silva et al., 2016). The probability of  
309 colonization also decreases with the size of the patch (Rodríguez-Toledo et al., 2003). Finally,  
310 the loss of genetic variability through inbreeding, genetic drift, and stochastic processes make  
311 small populations more vulnerable to environmental changes and diseases (Frankham, Ballou,  
312 Briscoe, & Ballou, 2002). Together, these processes contribute to a reduction in the probability  
313 that primates occur in smaller patches.

314 Patch isolation is bound to affect metapopulation dynamics beyond certain thresholds.  
315 However, 84% of the forest patches in our sample had isolation distances of less than 200 m,  
316 the threshold for fragment occupancy by *A. palliata* in the least fragmented of two landscapes



317 studied in Los Tuxtlas, Mexico (Mandujano & Estrada, 2005). An assessment of the overall  
318 connectivity of the landscape would be useful in determining how important patch isolation  
319 may be for the metapopulation dynamics of *A. belzebul* in the savannas of Amapá.

320 A positive effect of patch or fragment area on the occurrence of howlers is well  
321 documented (Rodriguez-Toledo et al. 2003, Cristóbal-Azkarate et al. 2005, Anzures-Dadda and  
322 Manson 2007, Puig-Lagunes et al. 2016 – *A. palliata*, Silva et al. 2017 – *A. guariba clamitans*).  
323 One factor potentially related to the higher prevalence of howlers in larger patches is protection  
324 against hunting. Howlers are highly sensitive to hunting pressure and this, in turn, is positively  
325 and directly related to human access to their area of occurrence (de Thoisy, Renoux, & Julliot,  
326 2005). Thus, larger patches where access to the interior is more difficult provide greater  
327 protection (Geldmann et al., 2013). However, this relationship is likely more evident for  
328 primates in continuous forests, as hunters often go up to 5 km into the forest (de Thoisy et al.,  
329 2005), which is enough to cross any of the forest patches in our sample (maximum length <4  
330 km). Nevertheless, mammals in larger forests may persist under higher hunting intensities  
331 because the population is larger (Silva et al., 2016). Patch area is positively correlated with  
332 plant species richness and the basal area of the main plant species that are food sources for  
333 howlers (Arroyo-Rodríguez & Mandujano, 2006). In the context of forest patches or fragments,  
334 the greater availability of resources in larger patches is probably the main factor behind the  
335 positive effect of patch area on the occurrence of primates.

### 336 ***Flooded area palms***

337 We used the density of flooded area palms (açáís, buritis, and caranãs) to quantify the  
338 amount of flooded forest in the forest patches of the savannas of Amapá and observed a positive  
339 effect of this variable on the occurrence of *A. belzebul*. Although there is little information  
340 available on how *A. belzebul* use flooded forests, a group living in Central Amazon visited the

341 flooded portions (igapó) of their home range daily during the three months of peak water level,  
342 when fruit production was intense in that habitat (Pinto, 2002).

343 Riparian and flooded forests are amongst the preferred habitats of *A. seniculus* and  
344 flooded forests dominated by palm trees are their most used habitat in some regions (Aquino,  
345 López, García, & Heymann, 2014; Carretero-Pinzon & Defler, 2019). Studies of primates using  
346 flooded forests adjacent to unflooded forests often relate this behavior to the exploitation of  
347 food sources in flooded forests, especially fruits (Ahumada et al., 1998; Carretero-Pinzon &  
348 Defler, 2019; Pinto, 2002; Stevenson, Quinones, & Ahumada, 2000).

349 Different factors regulate fruit production in flooded and unflooded forests. While rainfall  
350 and irradiance are the main factors correlated with phenological patterns in unflooded forests,  
351 seasonal flood pulses are the main factor in flooded forests (Haugaasen & Peres, 2005). These  
352 different regulatory mechanisms and differences in the floristic composition may produce  
353 divergent patterns in fruit production even in adjacent communities (Ahumada et al., 1998;  
354 Defler & Defler, 1996). Unflooded forests have a greater floristic diversity and fruit production  
355 overall, but in periods of fruit scarcity, adjacent flooded forests may produce a complementary  
356 peak in fruit production that may be key to the survival of frugivorous primates (Ahumada et  
357 al., 1998).

358 *Alouatta belzebul* is the most frugivorous species of howler monkey, with fruits generally  
359 comprising 30-70% of their diet, while other species of howlers rarely exceed 30% (Bicca-  
360 Marques, 2003; Coutinho, 2012). Portions of flooded forest in the home range of *Ateles*  
361 *belzebul* are keystone habitats that provide fruits for these highly frugivorous primates during  
362 lean periods and reduce the area they require to survive (Ahumada et al., 1998). The flooded  
363 forests in the savannas of Amapá may serve a similar purpose for *A. belzebul*. The positive  
364 effects of this habitat as a complementary source of fruits would be especially evident for

365 populations in the savannas of Amapá because of the predominantly small (<100 ha) forest  
366 patches in the landscape. However, unflooded forests tend to be the main habitat used by  
367 frugivorous primates throughout the year because of their usually greater plant diversity and  
368 fruit productivity compared to adjacent flooded forests (Ahumada et al., 1998; Pinto, 2002).

369         Although we found a linear positive relationship between palm density and the probability  
370 of occurrence of howlers, it is unlikely that the palms themselves are responsible for this pattern.  
371 Instead, we hypothesize that this variable correlates with factors that favor *A. belzebul*.  
372 Asynchronous patterns in fruit production between flooded forests and adjacent unflooded  
373 forests (Ahumada et al., 1998), and higher leaf turnover (Stevenson et al., 2000) and soil fertility  
374 (Peres, 1997) in flooded forests compared with unflooded forests are all potentially correlated  
375 with palm density in our sample. Thus, the observed relationship between palm density and *A.*  
376 *belzebul* does not imply that a forest patch composed almost entirely of flooded area palms  
377 (e.g., isolated açazais or stands of buriti), which we did not sample in this study, will have a  
378 high probability of *A. belzebul* occurrence.

### 379         ***Implications for conservation***

380         The savannas of Amapá are the least protected region of the state, with only ~9% of the  
381 area protected, mostly as areas of multiple-use (Mustin et al., 2017). However, a study has  
382 recommended that 30% of the savannas should be protected (Hilário et al., 2017). As the only  
383 threatened primate found in this ecosystem, we argue that these potential new protected areas  
384 should include areas where *A. belzebul* occurs. Our results suggest that the selection of areas  
385 for the conservation of this primate should prioritize regions with a higher mean patch size or  
386 a greater prevalence of forest patches larger than 100 ha. Additionally, the selected patches  
387 should include mostly unflooded forests but also portions of flooded forests, resulting in an  
388 overall density of over 100 flooded area palms per hectare.

389 One of the palm species we studied was the açai, *E. oleracea*, whose fruits have high  
390 socioeconomic value (Queiroz & Machado, 2007). Açai has been the focus of research and  
391 management projects because of its economic importance (Quaresma & Cunha, 2012). The  
392 reputation of this forest product can be an opportunity to promote the conservation of *A.*  
393 *belzebul* in Amapá. Community management projects for açaizais (areas with high densities of  
394 açai palms mixed with native dicot trees) where *A. belzebul* occurs could be used to disseminate  
395 information on the ecological importance of this primate, and on the threats to its survival,  
396 leading local communities to value these primates alive (*i.e.* to avoid hunting them).

397 In summary, besides showing that the probability of occurrence is higher in larger habitat  
398 patches (a well-established relationship), we found that the habitat configuration (*i.e.* palm  
399 density) is more important than some forest structure attributes in predicting the occurrence of  
400 *A. belzebul* in forest patches. Although plant composition is usually more difficult to survey  
401 than forest structure, we encourage researchers to include this parameter in future studies  
402 investigating predictors of primate occurrence in forest patches, which is important for primate  
403 conservation. Further investigations on how *A. belzebul* uses the seasonally flooded forests in  
404 the patches they inhabit should clarify the reason why palm density predicts their occurrence in  
405 the forest patches in Amazonian savannas.

406

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**Data availability statement** Data available on request from the authors.

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572

Table 1. Summary of the values of the predictor variables used in a logistic regression model to assess drivers of the probability of occurrence of *Alouatta belzebul* in forest patches (n=38).

Variable	Mean $\pm$ standard deviation	Min - Max
Patch area (ha)	46.71 $\pm$ 51.31	1.82 - 228.47
Isolation (m)	85.11 $\pm$ 86.25	10 - 288
Proportion of the patch that is seasonally flooded	0.30 $\pm$ 0.27	0.00 - 1.00
Forest height (m)	13.33 $\pm$ 2.81	8.26 - 20.62
Modified Canopy Cover index‡	0.80 $\pm$ 0.04	0.61 - 0.84
DBH (cm)	18.93 $\pm$ 2.89	13.77 - 26.11
Density of palms (n/ha)†	86.91 $\pm$ 119.08	0.00 - 404.55

573 †Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).

574 ‡Tichý (2016).

575

576

Table 2. Pearson correlation coefficients between parameters of 38\* forest patches in the savannas of Amapá. Significant (< 0.05) correlation coefficients are in bold.

Variables	Patch area	Isolation	Flood	Forest height	Canopy cover	Trees DBH	Density of palms
Patch area							
Isolation	-0.14						
Flood†	0.28	-0.26					
Forest height	0.12	-0.03	0.05				
Canopy cover	-0.08	0.17	-0.14	0.15			
Trees DBH	0.03	0.17	-0.04	<b>0.62</b>	-0.33		
Density of palms‡	0.18	0.22	0.30	0.28	-0.34	0.31	

577 \*We excluded an outlier from the correlation tests with Canopy Cover.

578 † Proportion of the patch that is seasonally flooded.

579 ‡ Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).

580

581

Table 3. Comparison of the five best (lowest AICc) models to predict the probability of occurrence of *A. belzebul* in forest patches in Amazonian savannas.

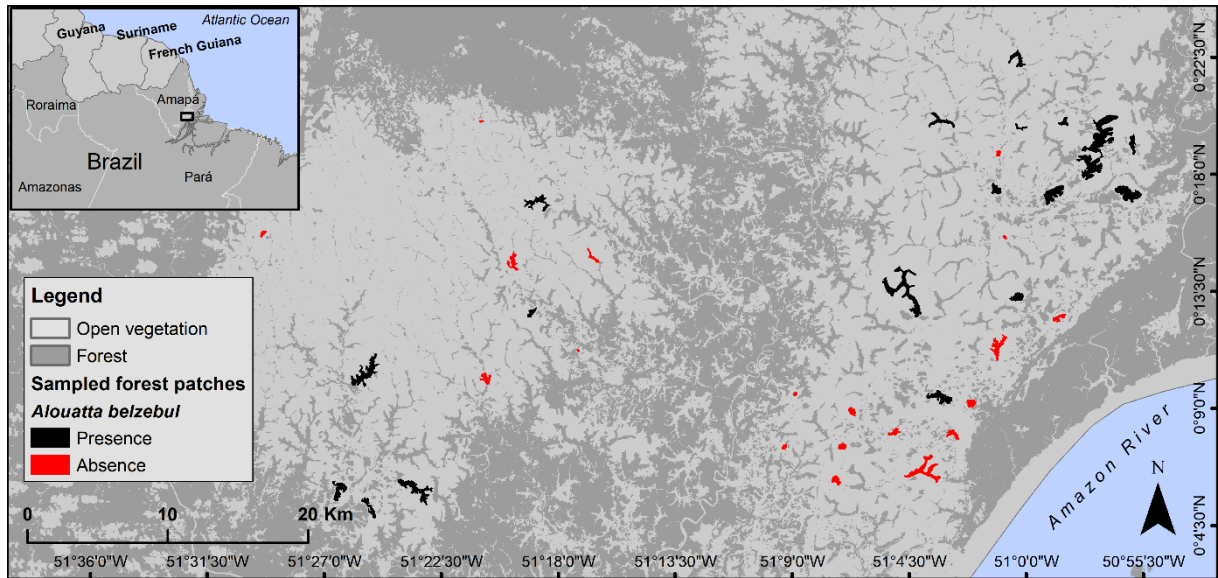
Predictors	df	logLik	AICc	Delta	Weight	R <sup>2</sup>
Patch area + Palm density †	3	-13.39	33.49	0	0.24	0.492
Patch area + Palm density + Canopy Cover	4	-13.08	35.38	1.89	0.09	0.503
Patch area + Palm density + Flood‡	4	-13.16	35.52	2.04	0.09	0.501
Patch area + Palm density + Forest height	4	-13.23	35.67	2.18	0.08	0.497
Patch area + Palm density + Isolation	4	-13.38	35.97	2.48	0.07	0.492
Patch area + Palm density + Trees DBH	4	-13.38	35.98	2.49	0.07	0.492

582 †Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).

583 ‡ Proportion of the patch that is seasonally flooded.

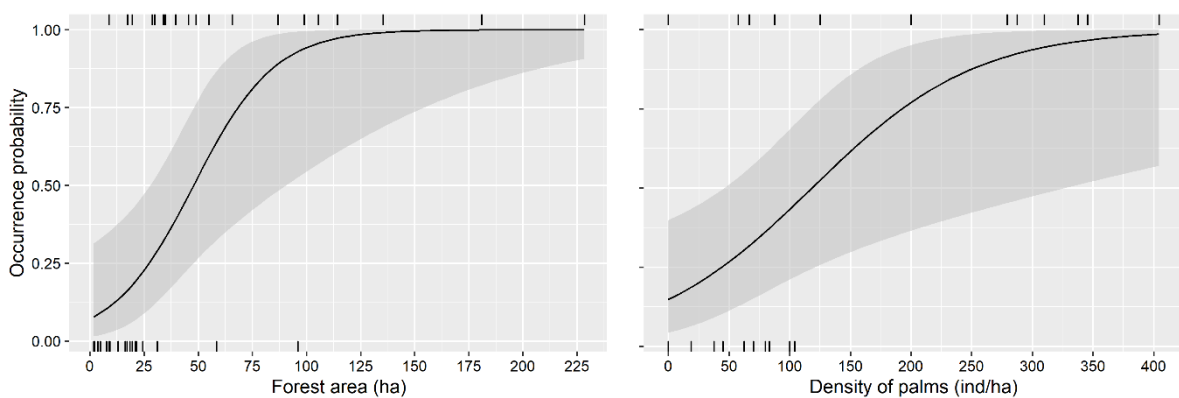
584

585 **Figure 1.** Study region and the location of 38 forest patches where potential predictors of the  
 586 occurrence of *Alouatta belzebul* were assessed, in the Southeast portion of the savannas of  
 587 Amapá, northern Brazil.



588

589 **Figure 2.** Logistic models of the effect of (a) area and (b) palm density (*Euterpe oleracea*,  
 590 *Mauritia flexuosa*, and *Mauritiella armata*) on the probability of *Alouatta belzebul* occurring  
 591 in forest patches in an Amazonian savanna.



592

593