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Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia.

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Highlights

- Agriculture reduces community diversity and evenness, while increases dominance.
- Forests and vicinity to water increase species occupancy; pastures decrease it.
- Forest areas are crucial for pumas, ocelots, raccoons, pacas, and agoutis.
- Wetlands are important for jaguars, the apex predator.
- Key to maintain forests and wetlands and target future crop expansion on pastures.

1 **Abstract**

2 As human-modified landscapes are increasing in the tropics, it becomes critical to understand
3 how they affect mammal communities to reconcile conservation and development. We
4 combined land cover information and camera-trapping data to explore the effects of
5 agricultural expansion on mammals in the Magdalena river valley of Colombia. We estimated
6 species diversity, evenness, and dominance across two agricultural landscapes, modified by
7 cattle ranching and oil palm cultivation. We further assessed which variables influence species-
8 and community-level occupancy using multi-species occupancy models. Results highlight that
9 modified landscapes display lower species richness, diversity and evenness, and higher
10 dominance than more pristine sites. Residual forest cover and distance to water had significant
11 effect on community occupancy (positive and negative respectively). Forests were particularly
12 important for pumas, ocelots, lowland pacas, Central American agoutis, and crab-eating
13 raccoons while wetlands had a positive effect on jaguars, the apex predator in the region. The
14 influence of anthropogenic pressure was not clearly evident, though pastures were not valuable
15 habitats for any mammal species, as they had a negative, yet not robust, effect on species and
16 community occupancy. In light of rapidly expanding agriculture across the tropics, our findings
17 highlight species-specific responses to disturbance that can inform land use planning and
18 conservation policies. We stress the conservation value of forest and wetland habitat to
19 mammal occupancy in heterogeneous ecosystems. Moreover, our results demonstrate that oil
20 palm and crop expansion should target existing pastures, which displayed limited conservation
21 value for Neotropical mammals but occupy vast swathes of land across Latin America.

22 **Keywords:** *Panthera onca*; camera trap; Bayesian statistics; land-use change; oil palm; pasture.

23 **1. Introduction**

24 Agricultural expansion is driving severe habitat loss and degradation, threatening biodiversity
25 worldwide (Foley et al., 2005; Green et al., 2005; Tschardt et al., 2012; Maxwell et al.,
26 2016). This is particularly concerning across tropical countries, which are extremely rich in
27 biodiversity but experiencing unprecedented land cover change (Gibbs et al., 2010; Laurance et
28 al., 2014). Therefore, there is an urgent need to understand how species respond to different
29 land cover types across modified landscapes to reconcile biodiversity conservation and
30 agricultural expansion across the tropics (Crooks et al., 2011; Rondinini et al., 2011).

31 Amongst agricultural sector, oil palm cultivation is of particular concern. These plantations
32 have a negative effect on biodiversity, including mammals, and are expanding rapidly across
33 the tropics (Fitzherbert et al., 2008; Yue et al., 2015; Wearn et al., 2017; Pardo et al., 2018a).

34 Tropical mammals are a conservation priority because they are declining due to land-use
35 change and hunting (Schipper et al., 2008; Visconti et al., 2011; Barlow et al., 2016) with
36 important consequences for ecosystem health and resilience. Mammals make significant
37 contributions to ecosystem functioning including trophic regulation, nutrient cycling, carbon
38 storage, seed dispersal and ultimately maintenance of forest structure (Brodie et al., 2009;
39 Jansen et al., 2010; Estes et al., 2011; Sobral et al., 2017). Amongst mammals, large-bodied
40 carnivores like jaguars *Panthera onca* are acutely threatened with extinction due to their slow
41 population growth rates and extensive area and dietary requirements (Crooks, 2002; Cardillo et
42 al., 2005; Carbone et al., 2011).

43 Conservation and management have largely moved away from single-species approaches to
44 sustaining ecosystems and communities (Balmford et al. 2005; Santini et al., 2017). However,
45 developing interventions to safeguard forest-dwelling mammals is hindered by their cryptic
46 nature. Statistical approaches, like occupancy modelling, that account and correct for imperfect

47 detection are, therefore, essential to provide a reliable evidence-base to support environmental
48 policies (MacKenzie et al. 2002; Brodie et al. 2014; Guillera-Aroita 2017). Multi-species
49 occupancy models (Dorazio & Royle 2005) go a step further as they enable us to
50 simultaneously explore habitat and anthropogenic variables that influence both community and
51 single species distribution, while providing robust inference for species infrequently detected
52 during ecological surveys (Ahumada et al., 2011; Ahumada et al., 2013; Tobler et al., 2015;
53 Rich et al. 2016; Wearn et al. 2017; Deere et al., 2017).

54 Colombia is the 4th largest palm oil producer (Ocampo-Penuela et al., 2018), but it is also a
55 megadiverse country, covering 0.7% of the planet and hosting 10% of known biodiversity
56 (Mittermeier et al., 1997). Yet the country's biodiversity is understudied due to a sustained
57 period of conflict that rendered much of the region inaccessible. To our knowledge, this
58 research is the first to study terrestrial mammals across agricultural landscapes in Colombia
59 using multi-species occupancy models. We combine high-resolution land cover maps and
60 camera trap data to achieve the following objectives: (1) assess how habitat availability and
61 anthropogenic pressure (pastures, oil palm cultivation, and human settlements) influence
62 community and species occupancy; (2) estimate Shannon diversity and evenness, and Berger-
63 Parker dominance across two agricultural landscapes in the Magdalena river-valley of
64 Colombia. We hypothesized that mammalian occupancy would respond positively to bottom-
65 up resources (i.e. habitat availability) and negatively to top-down anthropogenic pressures,
66 depending on species-specific habitat preferences and sensitivity to disturbance. The study sites
67 comprised the dominant land use in Latin America, cattle ranching, (Grau & Aide, 2008) and
68 oil palm cultivation. In face of a rapid land use change in the tropics, this study provides
69 valuable information to inform management, land use planning and policies that reconcile
70 agricultural expansion and mammal conservation.

71 2. Methods

72 2.1 Study sites

73 We conducted the study at two sites in the central region of the Magdalena River valley,
74 Department of Santander, Colombia (Site-1 (7.3752N -73.8842E to 7.5404N -73.7118E; Site-
75 2: 5.3450N -72.8471E to 5.4365N -72.7607E) (Fig. 1). Both sites are situated in the central
76 part of the Magdalena river valley, in between the Central and Eastern Andes, in the
77 Department of Santander, Colombia. The Euclidean distance between the two study sites is 93
78 km. The overall region is part of the tropical forest biome and is rich in wetlands with no
79 altitudinal gradient (IDEAM et al., 2007). *Mean annual temperature is 27 °C, and annual*
80 *precipitation ranges between 2100-2600 mm (IDEAM et al., 2007). Land tenure is primarily*
81 *private (different owners) and there are no national protected areas.*

82 The region is considered important for several species, including keystone mammals such as
83 the jaguar (Payan-Garrido et al., 2013; Boron et al., 2016b) and endangered endemics like the
84 brown spider monkey (*Ateles hybridus ssp. brunneus*) and white-footed tamarin (*Sanguinos*
85 *leucopus*). However, most of the region's historical forest cover has been lost due to the
86 expansion of cattle ranching and oil-palm agro-industries, while the remaining natural areas
87 facing a high risk of conversion (Etter et al., 2006; Castiblanco et al., 2013; Link et al., 2013).

88 We chose these two sites because they are modified, to a large degree, by agriculture but still
89 retained top predators like jaguars and pumas *Puma concolor* as well as other declining species
90 of conservation importance. The dominant land cover classes across our study sites
91 include: pastures (Site 1: 312 km²/35%; Site 2: 244 km²/36%), wetlands (Site-1: 182 km² Site-
92 1/20% ; Site-2: 233 km²/34% at Site-2), secondary forest (Site-1: 112 km²/12%; Site-2: 129
93 km²/19%), oil-palm plantations (Site-1: 172 km²/19% , Site-2: 17 km²/2%) , water (Site-
94 1: 190 km²/10%; Site-2: 43 km²/6%), bare ground (Site-1: 24 km²/3%; Site-2: 13

95 km²/2%), settlements <0.4%, and roads <0.6% (Fig. 1) (Boron et al., 2018). We identified
96 these land cover types and their amounts across the study sites, which we defined by adding a
97 buffer of 9.2 km around the camera stations. This reflects the maximum distance moved by the
98 species with the largest home range in the study region, (jaguars; Nowell & Jackson, 1996).

99 2.2 Camera trapping

100 We deployed 47 camera stations between April and August 2014 at Site-1 and 26 stations
101 between September and December 2014 at Site-2 using a blocked design. This included dry
102 and wet seasons at both sites (April, May, October, November, December: wet months; June,
103 July, August, September: dry months). The minimum convex polygons connecting camera
104 stations were 154.8 km² at Site-1 and 85.4 km² at Site-2. We set-up the cameras following
105 standardized survey techniques for terrestrial mammals (Ahumada et al., 2011, 2013; Rovero et
106 al., 2014), in a grid at intervals of 1.6±0.3 km, and across the main land cover types of the
107 region: forests (N=35), wetlands (N=8), pastures (N=11), and oil palm plantations (N=13). The
108 remaining cameras (N=6) were located in transitional habitat between wetland and oil palm
109 “Edge” (Fig. 1). To optimize detection, we placed the cameras so that their field of view
110 would be facing low resistance travel routes such as wildlife trails (Cusack et al., 2015).
111 Twenty-eight (60%) and 19 (73%) stations were placed on roads/trails at Site-1 and Site-2
112 respectively and we took this into account in our modelling approach. Camera traps are
113 consistently able to detect terrestrial mammals ≥ 0.5 kg, which are what we refer to in this
114 manuscript (Rovero et al., 2010). We deployed Cuddeback Attack (model 1149) and Ambush
115 (model 1170) camera traps and secured them to a tree at a height of 35 cm from the forest
116 floor. Both camera models have an identical trigger speed (0.25 seconds) and a detection zone
117 of 3-4 m due to the high temperatures characteristic of the region.

118 2.3 Species richness, diversity, and evenness

119 For each study site we produced species accumulation curves using EstimateS (Colwell, 2013).

120 Accumulation curves reach an asymptote once all detectable species have been recorded and
121 were produced using the rarefaction method with 1000 randomizations (Magurran, 2004;
122 Ahumada et al., 2011). We also calculated a) Shannon diversity index ($D_{\text{Shannon}} = -\sum p_i \ln p_i$ where
123 p_i is the proportion of abundance for species i , N_i relative to the total abundance N); b)
124 evenness index ($E_{\text{Shannon}} = D_{\text{Shannon}}/\ln(S)$, where S is the number of species observed) and c) the
125 Berger–Parker dominance index ($D = N_i/N$ where N_i is the abundance of the most abundant
126 species relative to the total abundance N) (Shannon, 1948; Berger & Parker, 1970; McCune et
127 al., 2002).

128 We defined species abundances as integer capture rates, and calculated them using the total
129 number of independent capture events of that species divided by the number of trap-nights
130 (TN) and expressed as integer records per 100 trap nights (Carbone et al., 2001; O’Brien et al.,
131 2003). Independent capture events were defined as consecutive photographs of individuals of
132 the same species taken more than 30 min apart (O’Brien et al., 2003). Capture rates may not
133 reflect real abundance, however they still provide more information than just incidence records
134 (Carbone et al., 2001; Sollmann et al., 2013).

135 **2.4 Multi-species occupancy modelling**

136 We performed statistical analysis at the scale of the camera trap station (e.g. Rovero et al.,
137 2014; Rich et al., 2016), and defined a sampling unit as the circular area with a radius of 800m
138 around each camera station, corresponding to half the average distance between neighboring
139 stations (Sollmann et al., 2012). Prior to analysis, we discarded species with fewer than five
140 detections (i.e. eastern cottontail *Sylvilagus floridanus* and grison *Galictis victata*). To reduce
141 zero inflation in the dataset, we constructed detection histories for each species grouping seven
142 consecutive camera trap nights into one sampling occasion (Alexander et al., 2016; Everatt et
143 al., 2014). This resulted in 12 sampling occasions at Site-1 and 14 at Site-2.

144 We implemented a hierarchical Bayesian multi-species model formulation (Dorazio & Royle,
 145 2005) to estimate species and community occupancy while accounting for imperfect detection
 146 (MacKenzie et al., 2006) (see Appendix 1 for model code). This class of model is composed of
 147 two components: the state process, describing the ecological system, and the observation
 148 process, defining the sampling protocol. Relative to occupancy, this distinction differentiates
 149 between non-detection and true absence.

150 We modelled the occurrence (z) of species i at site j as a realization of a Bernoulli process, $z_{i,j}$
 151 $\sim \text{Bern}(\psi_{i,j})$, where $\psi_{i,j}$ represents the latent occupancy state. To account for imperfect detection
 152 of true occupancy, detection probability was estimated as a function of temporal replicate k at
 153 site j . We denoted detection as a second Bernoulli process, $x_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where $x_{i,j,k}$
 154 represents the observed detection histories, and $p_{i,j,k}$ is the detection probability of species i for
 155 temporal replicate k at site j , conditional on species presence ($z_{i,j}=1$) (Zipkin et al., 2010).

156 We connected occurrence and detection models of observed taxa through an additional
 157 hierarchical component that modeled coefficients from a community-level distribution
 158 governed by hyper-parameters. This protocol assumes similarity in community responses to
 159 covariates. Consequently, species-specific parameter estimates are a function of individual
 160 detection histories and average community-level responses, which provides more robust
 161 estimation precision for infrequently observed species (Pacifci et al. 2014). Hyper-parameters
 162 provide insights into community level responses to covariates of interest and among species
 163 variability (Kery and Royle, 2008). We defined the linear predictor for the state process (ψ)
 164 and observation process (p) models as:

$$165 \text{logit}(\psi_{i,j}) = \mu_{(i)} \text{Site}(j) + \alpha_{1i} \text{Distance Settlement}_j + \alpha_{2i} \text{Distance Water}_j + \alpha_{3i} \% \text{Forest Cover}_j +$$

$$166 \alpha_{4i} \% \text{Pasture Cover}_j + \alpha_{5i} \% \text{Wetland Cover}_j + \alpha_{6i} \% \text{Oil Palm Cover}_j + \alpha_{7i} \text{Season}_j$$

$$167$$

$$168 \text{logit}(p_{i,j,k}) = \nu_{(i)} \text{Habitat}(j) + \beta_{1i} \text{Road}_j + \beta_{2i} \text{Season}_j$$

$$169$$

170 Occupancy and detection probabilities were defined on the logit scale, with site- and habitat-
171 specific intercepts on the state and observation processes respectively. We specify intercepts
172 and slopes as a function of individual taxa. Intercepts were specific to site (1 or 2) for
173 occupancy and land cover class for detection (i.e. forest, pasture, oil palm, wetland, and edge
174 between oil palm and wetland). We derived covariates from Landsat 8 satellite imagery using
175 Object Oriented Image Analysis (Bock et al., 2005) and eCognition Developer 9 software (see
176 Boron et al. 2018 for more details). Dominant land cover types (specified as %
177 Forest/Pasture/Wetland/Oil Palm Cover) were extracted as proportions across each sampling
178 unit with ArcMap 10.3. We measured the Euclidean distances of each camera station to water
179 and settlements, which averaged 0.60 ± 0.07 km and 4.85 ± 0.29 km respectively. We tested
180 for collinearity amongst covariates using a threshold value of $|r| = 0.7$ (Dormann et al., 2013)
181 and no covariate was highly correlated to others. As mammals can use roads and trails to
182 facilitate their movement (Cusack et al., 2015) we included a categorical covariate on detection
183 probability (0/1 representing on/off roads/trails respectively). We grouped roads and trails
184 together because the roads we refer to are not paved, ≤ 3 metres wide, not open to the public
185 (inside private lands), not used regularly and thus not very different to trails. We also tested the
186 effect of season (wet vs. dry) on both occupancy and probability of detection. To improve
187 model convergence and place covariates on a comparable scale, we centered and standardized
188 (by subtracting the mean and dividing by the standard deviation of all the sites) all continuous
189 predictor covariates prior to analysis.

190 Parameter posterior distributions were estimated using Markov chain Monte Carlo (MCMC)
191 simulation and conducted in WinBUGS version 1.4.3, called through R version 3.3.0 using the
192 package “R2WinBUGS” (Sturtz *et al.* 2005). Hierarchical models were constructed using
193 uninformative priors for all parameters. Unless stated otherwise, we present parameter
194 estimates as mean values of the posterior distribution, accompanied by 95% Bayesian Credible

195 Intervals (BCI) to express uncertainty. Parameters were considered significantly influential if
196 their 95% BCI did not overlap zero and weakly influential if their 90% BCI did not overlap
197 zero. We ran three parallel MCMC chains for 75,000 iterations each, discarding the first 25,000
198 iterations during the burn-in process and thinning posterior samples by a value of 10. To assess
199 convergence, trace plots were visually inspected for satisfactory mixing and the Gelman-Ruben
200 statistic (Gelman and Hill, 2007) was observed to ensure a value of <1.1 for all parameters. We
201 implemented a posterior predictive check to assess model fit compared to a simulated dataset,
202 extracting Bayesian P -values as a numerical overview of the predictive distribution (~ 0.5
203 indicative of good model fit; $0.05 < P < 0.95$ indicative of poor model fit).

204

205 **3. Results**

206 The total sampling effort resulted in 3069 and 1903 trap nights at Site-1 and Site-2
207 respectively. Cameras were active for an average of 66 trap nights at Site-1 and 73 at Site-2.
208 On average camera stations detected 5 species at both sites (Site 1: 5, range 0-12; Site 2: 5,
209 range 0-10). We recorded a total of 17 terrestrial mammal species at each site consisting of
210 different guilds and threat categories (Table 1) and three arboreal species (varied capuchins
211 *Cebus versicolor*, howler monkey *Alouatta seniculus* and red-tailed squirrel *Sciurus*
212 *granatensis*) that we excluded from analysis. Species accumulation curves indicate that we
213 likely recorded most species at Site-1, whereas a larger sampling effort would have been
214 required to characterise the mammal community at Site-2, as the curve does not reach an
215 asymptote (Fig. 2). Overall sites displayed identical Shannon species diversity (Site 2: 2.01 vs.
216 Site 1: 2.02) and species evenness (Site 2: 0.71 vs. Site 1: 0.71) and similar species dominance
217 (Site 2: 0.32 vs. Site 1: 0.40).

218 Species occupancy varied from 0.54 (ocelot *Leopardus pardalis*) to 0.09 (Spiny rat *Proechymis*

219 *chrysaеolus*) at Site-1 and from 0.31 (ocelot) to 0.12 (nine-banded armadillo *Dasyopus*
220 *novemcinctus*) at Site-2 (Table 1). Bayesian p values detailing model adequacy fit for single
221 species (0.08-0.78) and the full model (0.51) indicated good to optimal fit (Table A2A1).
222 Proportion of forest cover and distance to water were found to have significantly positive and
223 negative influences respectively on community-level mammalian occupancy (Fig. 3 and Table
224 2). Pumas (0.985; 95% BCI: 0.185-1.876), ocelots (0.811; 95% BCI: 0.032 - 1.618), Central
225 American agoutis *Dasyprocta punctuata* (1.008; 95% BCI: 0.222 - 1.884), lowland pacas
226 *Cuniculus paca* (0.825; 95% BCI: 0.014 - 1.668), and crab-eating racoons *Procyon*
227 *cancrivorus* (0.771; 95% BCI: 0.012 - 1.538) (Fig. 3 and Table A2) demonstrated a strong
228 preference for areas dominated by forest cover. A further nine species were positively
229 influenced by forest cover, though to a lesser extent (90% BCI non-overlapping zero) (Fig. 3
230 and Table A2). Consistent negative impacts of pasture cover on occupancy was documented
231 for all species, though this trend was not significant at the community level t (Fig. 3 and Table
232 2). The negative effect of pasture was weakly influential for lowland pacas (-0.644; 90% BCI: -
233 1.301 - -0.025), Central American agouti (-0.693; 90% BCI: -1.325 - -0.092), and jaguarundi
234 (*Herpailurus yagouaroundi*) (-0.696; 90% BCI: -1.378 - -0.045) (Fig. 3 and Table A2).
235 Wetlands increased jaguar occupancy (0.787; 90% BCI: 0.112 – 1.497); however, oil palm,
236 distance to settlements, and season had unclear effects on community occupancy driven by
237 high species variability (Tables 2 and A2, and Fig. 3).

238 Probability of detection across the community was not significantly affected by any of the
239 covariates (land cover types, season, and camera placement on roads) (Table 2), although
240 placing cameras on roads/trails significantly improved detection for jaguars (1.054; 95% BCI:
241 0.152-1.939), ocelots (0.869; 95% BCI: 0.171-1.612), crab-eating foxes *Cerdocyon thous*
242 (1.024; 95% BCI: 0.297 - 1.753) and jaguarundi detection (0.723; 90%BCI: 0.148-1.296)
243 (Table A3). We document species-specific covariate effects on occupancy and detection in

244 Tables A2-A4.

245

246 **4. Discussion**

247 As agricultural and human-modified landscapes are increasing across the tropics it becomes
248 crucial to understand how they affect species and communities to inform evidence-based
249 conservation interventions for species vulnerable to land-use change. Mammals are a key
250 component of tropical forest ecosystems yet their populations continue to decline (Schipper et
251 al., 2008; Visconti et al., 2011). We synthesized land cover information, and camera trapping
252 data using multi-species occupancy models to produce an assessment of Neotropical mammal
253 persistence in landscapes dominated by agriculture. Our results demonstrate that: a) modified
254 landscapes display lower species diversity and evenness, and higher dominance compared to
255 non-modified landscapes in the Neotropics in the literature; b) remaining forest areas and
256 distance to water significantly influenced community level occupancy confirming our
257 hypothesis; c) the effect of anthropogenic pressures was not clearly evident, although pastures
258 were not valuable habitats for any mammal species and could therefore be targeted for future
259 crop expansion.

260 4.1 Species richness and community structure

261 Species detection was commensurate with survey effort. At Site-2 the survey effort (26
262 stations) was not sufficient to detect all mammal species. At Site 1, where sampling effort was
263 higher (47 stations), the number of terrestrial mammal species (17) was similar to what
264 recorded with comparable survey efforts in an oil palm landscape in the Colombian Llanos (16
265 sp.) (Pardo & Payan, 2015) and in the Volcan Barva Transect in Costa Rica (15 sp.), which is
266 situated in a highly fragmented landscape (Ahumada et al., 2011), while lower than in pristine

267 areas such as the Peruvian Amazon (Tobler et al., 2008; Tobler et al., 2015), suggesting
268 declining mammal richness with increasing habitat modification. However, richness may not
269 be the most informative metric. The effect of habitat modification on species richness may not
270 be immediately apparent because generalist species spread and/or colonise modified
271 landscapes, as suitable niches become available (Ewers & Disham, 2006; Bogoni et al., 2016).
272 Despite detecting different guilds (e.g. carnivores, herbivores, omnivores, insectivores) we
273 recorded fewer species classified as threatened on the IUCN Red List (Vulnerable, Endangered
274 and Critically Endangered) than other studies focussing on Neotropical mammals (e.g. Tobler
275 et al. 2008; Payan, 2009; Ahumada et al. 2011), alluding to the sensitivity of vulnerable species
276 to human modification. The complete absence of browsing herbivores like tapirs *Tapirus*
277 *terrestris* and deer *Mazama* and *Odocoileus* sp. suggests that historical land transformation and
278 overhunting could have been drivers of mammal decline and local extinction (Rodriguez-
279 Mahecha et al., 2006). Deer and tapir have been the preferred quarry of hunters for centuries as
280 their significant body size yields more bushmeat per unit of hunting effort (Redford &
281 Robinson n.d.; Jerozolinski & Peres, 2003).

282 Both sites displayed lower diversity and evenness, and higher dominance than the equivalent
283 values reported by Ahumada et al. (2011) for Neotropical mammal communities (Diversity:
284 2.5-3.0; Evenness: 0.91-0.93; Dominance: 0.09-0.14). Our results discussed so far confirm that
285 while agricultural landscapes with remaining natural habitat cover still hold some potential for
286 medium-large mammal conservation (Daily et al., 2003; Cassano et al., 2012; Magioli et al.,
287 2016), habitat loss changes mammal communities, decreasing diversity and increasing
288 dominance (Ahumada et al., 2011; Bogoni et al., 2016). Top predators like jaguars and pumas
289 were still present in both study areas, however, their prey community seems impoverished as
290 armadillos, pacas, peccaries (*Pecari tajacu*), capybaras, and deer were absent or rare across
291 both sites. Therefore it is likely that puma survival depends on smaller prey such as widespread

292 agoutis, while jaguars rely on aquatic prey like caimans *Caiman crocodilus* and turtles
293 *Podocnemis* and *Trachemys* sp. (Da Silveira et al., 2010).

294 4.2 Factors influencing species and community occupancy and detection probability

295 In accordance with our hypotheses, the proportion of forest cover in each sampling unit had a

296 robust effect on mammalian occupancy, confirming that maintaining connectivity and forest

297 cover in agricultural regions is crucial to preserve functional assemblages (Magioli et al., 2016;

298 Zimbres et al., 2017; Pardo et al., 2018a;b), and wider biodiversity (Prescott et al., 2016). The

299 effect of forest cover was particularly strong for pumas, ocelots, lowland pacas, raccoons, and

300 Central American agoutis. Pumas' and ocelots' preference for forest is well documented (e.g.

301 Paviolo *et al.*, 2009; Davis *et al.*, 2011; Massara et al. 2015), reflecting higher prey occupancy

302 (e.g. agoutis and pacas) coupled with lower human presence and disturbance. Proximity to

303 water was also a strong determinant of community occupancy (distance to water had a

304 significantly negative effect meaning community occupancy increases nearer to water). Water

305 is a fundamental need of all species. Positive associations with water likely reflect the use of

306 riparian forests for movement and dispersal as thanks to legislation these forests tend to be the

307 only ones to remain in modified landscapes like our study sites (Nunez-Regueiro et al., 2015).

308 Contrary to expectation, anthropogenic pressures did not show a significant effect on

309 community or species occupancy. The presence of oil palm, for example, did not have a

310 significant effect on species, but this is likely because it only occupies a small percentage of

311 the study sites. For example, Pardo et al. (2018b) report that Neotropical mammal communities

312 drastically change when oil palm cover reaches 45–75%. Considering the documented

313 negative effect of oil palm on mammals (Fitzherbert et al., 2008; Yue et al., 2015; Wearn et al.,

314 2017; Pardo & Payan, 2015; Pardo et al., 2018a;b), the expansion of this crop in the Neotropics

315 remains a concern. Recent estimates suggest that 21.1 million hectares of land is potentially

316 suitable for oil palm expansion in Colombia (Pirker et al. 2016). Ensuring that this expansion is

317 not met at the expense of tropical forest habitat should represent a regional conservation
318 priority.

319 When unavoidable, new plantations should be established on already modified areas like
320 pastures, which displayed limited conservation value for most mammal species. We found a
321 negative (although not significant) effect of pasture on community occupancy. This was more
322 evident for jaguarundis, lowland pacas, and agoutis. The negative effect of pasture on pacas
323 and agouti could be due to lack of habitat cover and food resources. Our findings add to a
324 growing body of literature demonstrating the low conservation value of pastures for a range of
325 taxa (e.g. birds, beetles, and herpetofauna) (Gilroy et al., 2015; Prescott et al., 2016). Pastures
326 account for a large proportion of agricultural land in Latin America and generally have low
327 productivity (Grau & Aide, 2008). Thus directing oil palm expansion on pastures, albeit
328 intensifying use of land, would additionally enable to maximise food security, carbon storage,
329 and natural habitat cover (Garcia-Ulloa et al., 2012).

330 Finally, wetlands were important for jaguars, the apex predators, in agreement with previous
331 evidence (Soisalo & Cavalcanti, 2006; Quigley et al. 2017). Jaguar conservation in the study
332 region will ultimately depend on the preservation of wetlands and the aquatic prey they host
333 (Da Silveira et al., 2010).

334 In interpreting these outputs, it is important to note that covariate influences on rare species
335 occupancy may be underestimated due to the effects of shrinkage on parameter estimates.

336 Given the prevalence of generalist species, community averages are driven by the response of
337 these dominant species, thus, when statistical strength is borrowed for rare species, parameter
338 estimates are drawn towards the community mean. At the same time shrinkage allows us to
339 estimate occupancy for species that we would otherwise not be able to make reliable inferences
340 for due to data limitations. In this respect, slight bias in parameter estimates is a fair trade-off
341 (Pacifci et al., 2014).

342 Placing cameras on roads/established trails did not have an effect on community-level
343 detection. However, it was important to improve detection of jaguars, ocelots, crab-eating
344 foxes, and jaguarundis without affecting the detection of other species. Thus placing cameras
345 on trails remains the preferred option to detect multiple mammal species including carnivores,
346 which are known to use trails (Cusack et al., 2015).

347 4.3 Conclusions and management implications

348 Unprotected and increasingly human-modified areas can play a vital for species long-term
349 survival and connectivity and thus it is important to further investigate how their composition
350 and structure can affect species persistence and community composition. Furthermore, multi-
351 species approaches are particularly valuable for informing conservation strategies as they
352 enable us to move beyond single species to community impact assessments. Data on how
353 mammal assemblages respond differentially to agricultural habitats represents key information
354 to understand disturbance. Thus, similar studies to the one presented in this paper can add
355 empirical evidence to environmental decision making. More specifically this study shows that
356 species diversity tends to be low in human modified landscapes while species dominance
357 increases. We can expect similar patterns in agricultural areas around the tropics. These effects
358 may take time to unfold due to extinction debts owed to a legacy of human disturbance
359 (Tilman et al., 1994). There is clear evidence that some species were more associated with
360 natural habitats (e.g. pumas, ocelots, jaguars, pacas) than others. Therefore they are more
361 likely to decline rapidly in modified landscapes with ramifications on their historical ranges
362 and thus Red List categories (Ewers & Didham, 2006; Bogoni et al., 2016).

363
364 Overall, planning for agricultural activity needs to factor in displacement and absence of
365 species vulnerable to land-use change in areas where they naturally occur. As oil palm
366 expansion and agriculture continues across the tropics, including Colombia, it is critical to
367 minimize its negative impact on biodiversity. This study helps refine conservation strategies

368 and policy, having demonstrated that to reconcile agricultural expansion with mammal
369 conservation, it is crucial to maintain natural forest cover, since it had a robust impact on
370 community occupancy and is irreplaceable, as well as wetlands specifically for jaguars, the
371 apex predators. Furthermore, it is important to conserve natural habitat cover across
372 agricultural landscapes because no mammals displayed strong affiliation for oil palm and
373 pasture. These findings can also inform land use planning and highlight that in order to avoid
374 further negative impacts on biodiversity, future oil palm and crop expansion could be directed
375 towards existing pastures, which have low productivity (Grau & Aide, 2008), and, as we
376 attested, hold limited value for terrestrial mammals, and biodiversity in general (Gilroy et al.,
377 2015; Prescott et al., 2016). Under these conditions, oil palm has the potential to expand
378 without posing severe threat to vertebrate species in Colombia (Ocampo Penuela et al., 2018).
379 However, this presuppose the existence of both, stronger regulatory approaches (e.g. land use
380 planning that takes into account High Conservation Value forests and zero deforestation), as
381 well as incentives that could help retain vital natural habitats and thus promote mixed
382 landscapes (Lambin et al., 2014; Boron et al., 2016a).

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688 **Figure captions**

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Fig. 1 Study map of the two agricultural study sites (Site-1 and Site-2) in the Magdalena river valley of Colombia, including land cover types and camera trap stations (Site-1: $N=47$; Site-2: $N=26$).

Fig. 2 Species accumulation curves across two study sites (Site-1 and Site-2) in the Magdalena river valley of Colombia.

Fig. 3 Caterpillar plots delineating effects of covariates on single species and community-level occupancy across two sites in the Magdalena river valley of Colombia. Mean hyper-parameter values and 95% Bayesian Credible Interval (BCI) values are presented in the grey background to each plot, providing an insight to community level responses to covariates. Species-specific mean posterior summaries are denoted with points, while horizontal lines represent the associated 95% BCI. Significant species-specific associations are in blue (95% BCIs do not overlap zero). Other relevant associations are in light blue (90% BCIs do not overlap zero).

719 **Tables**

720 **Table 1.** Terrestrial mammal species recorded across two study sites (Site-1 and Site-2) in the
 721 Magdalena river valley of Colombia, their IUCN (2015) and Regional Red List (Rodriguez-
 722 Mahecha et al. 2006) categories, occupancy (ψ) estimates and 95% Bayesian Credible Intervals
 723 (95% BCIs). Site-specific estimates assume covariates are held at their average values DD= Data
 724 Deficient, LC= Least Concern, NT= Near Threatened, VU= Vulnerable, EN= Endangered. The
 725 greater grison and eastern cotton tail were excluded from the occupancy modelling due to the
 726 low number of records.

Scientific name	Common name	IUCN Red List	Regional Red List	Site-1 ψ (95% BCI)	Site-2 ψ (95% BCI)
Apex carnivores					
<i>Panthera onca</i>	Jaguar	NT	VU	0.47 (0.24-0.77)	0.13 (0.03-0.33)
<i>Puma concolor</i>	Puma	LC	NT	0.32 (0.15-0.55)	0.16 (0.05-0.39)
Meso carnivores					
<i>Cerdocyon thous</i>	Crab-eating fox	LC	/	0.26 (0.08-0.61)	0.13 (0.02-0.36)
<i>Galictis victata</i>	Greater grison	LC	/	Not recorded	Recorded once
<i>Herpailurus yagouaroundi</i>	Jaguarundi	LC	/	0.37 (0.17-0.66)	0.13 (0.02-0.35)
<i>Leopardus pardalis</i>	Ocelot	LC	NT	0.54 (0.33-0.76)	0.31 (0.12-0.66)
Omnivores					
<i>Didelphis marsupialis</i>	Common opossum	LC	/	0.24 (0.09-0.53)	0.14 (0.03-0.38)
<i>Eira barbara</i>	Tayra	LC	/	0.28 (0.12-0.57)	0.28 (0.11-0.66)
<i>Pecari tajacu</i>	Collared peccary	LC	/	0.14 (0.03-0.38)	0.20 (0.05-0.55)
<i>Proechymis chrysaеolus</i>	Spiny rat	DD	/	0.09 (0.02-0.28)	0.16 (0.04-0.43)
<i>Procyon cancrivorus</i>	Crab-eating raccoon	LC	/	0.39 (0.20-0.63)	0.20 (0.08-0.45)
Grazing herbivores					
<i>Sylvilagus floridanus</i>	Eastern cottontail	LC	/	Recorded once	Not recorded
<i>Hydrochoerus isthmius</i>	Lesser capybara	DD	/	0.26 (0.08-0.61)	0.13 (0.02-0.36)
Frugivores					
<i>Cuniculus paca</i>	Lowland paca	LC	/	0.17 (0.05-0.40)	0.17 (0.05-0.41)
<i>Dasyprocta punctata</i>	Central American agouti	LC	/	0.20 (0.08-0.41)	0.19 (0.06-0.43)

727	Insectivores					
728	<i>Dasypus novemcinctus</i>	Nine-banded armadillo	LC	/	0.19 (0.07-0.45)	0.12 (0.02-0.32)
729	<i>Myrmecophaga tridactyla</i>	Giant anteater	VU	VU	0.21 (0.06-0.51)	0.14 (0.03-0.39)
	<i>Tamandua tetradactyla</i>	Lesser anteater	LC	/	0.16 (0.05-0.38)	0.19 (0.06-0.47)
	Total N. of species				17	17

730 **Table 2.** Hyper-parameter posterior summaries denoting community-level responses to
731 covariates hypothesized to influence occupancy (ψ) and detection (p) of 16 mammal species at
732 two study sites in the Magdalena river valley, Colombia. We present mean predicted posterior
733 summary values and 95% Bayesian Credible Interval (95% BCI). Bold denotes covariates with
734 significant effects on community occupancy.

	Mean	Sigma	95% BCI	
Intercept_ψ Site-1	-1.02	0.92	-1.71	-0.36
Intercept_ψ Site-2	-1.56	0.71	-2.40	-0.76
ψ_Distance settlements	-0.11	0.38	-0.43	0.22
ψ_Distance water *	-0.39	0.32	-0.77	-0.03
ψ_Forest *	0.72	0.37	0.09	1.34
ψ_Pasture	-0.42	0.42	-1.14	0.25
ψ_Wetland	0.18	0.45	-0.51	0.86
ψ_Oil Palm	0.36	0.44	-0.33	1.07
ψ_Season	0.23	0.50	-0.45	0.89
Intercept_P_Forest	-1.66	1.07	-2.42	-0.93
Intercept_P_Wetland	-1.36	0.68	-2.17	-0.65
Intercept_P_Edge	-1.19	0.56	-1.88	-0.54
Intercept_P_Pasture	-1.29	0.68	-2.08	-0.60
Intercept_P_Oil Palm	-1.64	1.68	-2.77	-0.59
P_Roads/Trails	0.15	0.75	-0.50	0.73
P_Season	0.09	0.42	-0.29	0.47

735

736

737 **Supplementary information**

738

739 **Appendix 1. Model code used in the analysis.**

740

741 `### Hierarchical community occupancy model to assess response of neotropical mammals to`

```

742  ### habitat and anthropogenic covariates (written in BUGS language).
743  ### Based on the Dorazio-Royle Community Model (2005; J. Am. Stat. Assoc., 100, 389-398).
744  ### Implemented using code adapted from Zipkin et al. (2010; Biol. Conserv., 143, 479-484).
745  ### Species-specific slopes and intercepts.
746  ### Random intercepts on the process/occupancy model to account for sampling at
747  geographically
748  ### distinct sites ( $N=2$ ).
749  ### Random intercepts on the observation model to account for variability in detectability
750  relative ### to habitat type ( $N=5$ ).
751
752  sink("OM_Colombia_M1.txt")
753  cat("
754      model{
755
756          ### Hyperparameters for site-specific intercepts
757          ###=====
758          for (s in 1:2) {
759              a1.mean[s] ~ dunif(0,1)
760              mu.a1[s] <- log(a1.mean[s]) - log(1-a1.mean[s])
761              tau.a1[s] ~ dgamma(0.1,0.1)
762              sigma.a1[s] <- 1/sqrt(tau.a1[s])
763          }
764          ### Hyperparameters for habitat-specific intercepts
765          ###=====
766          for (h in 1:5) {
767              a2.mean[h] ~ dunif(0,1)
768              mu.a2[h] <- log(a2.mean[h]) - log(1-a2.mean[h])
769              tau.a2[h] ~ dgamma(0.1,0.1)
770              sigma.a2[h] <- 1/sqrt(tau.a2[h])
771          }
772
773          ### Hyperparameters for fixed effects on the process/occupancy model
774          ###=====
775          mu.b1 ~ dnorm(0,0.001)
776          mu.b2 ~ dnorm(0,0.001)
777          mu.b3 ~ dnorm(0,0.001)
778          mu.b4 ~ dnorm(0,0.001)
779          mu.b5 ~ dnorm(0,0.001)
780          mu.b6 ~ dnorm(0,0.001)
781          mu.b7 ~ dnorm(0,0.001)
782          tau.b1 ~ dgamma(0.1,0.1)
783          tau.b2 ~ dgamma(0.1,0.1)
784          tau.b3 ~ dgamma(0.1,0.1)
785          tau.b4 ~ dgamma(0.1,0.1)
786          tau.b5 ~ dgamma(0.1,0.1)
787          tau.b6 ~ dgamma(0.1,0.1)
788          tau.b7 ~ dgamma(0.1,0.1)
789          sigma.b1 <- 1/sqrt(tau.b1)
790          sigma.b2 <- 1/sqrt(tau.b2)
791          sigma.b3 <- 1/sqrt(tau.b3)

```

```

792 sigma.b4 <- 1/sqrt(tau.b4)
793 sigma.b5 <- 1/sqrt(tau.b5)
794 sigma.b6 <- 1/sqrt(tau.b6)
795 sigma.b7 <- 1/sqrt(tau.b7)
796
797 ### Hyperparameters for fixed effects on the observation/detection model
798 #####
799 mu.p1 ~ dnorm(0,0.001)
800 mu.p2 ~ dnorm(0,0.001)
801 tau.p1 ~ dgamma(0.1,0.1)
802 tau.p2 ~ dgamma(0.1,0.1)
803 sigma.p1 <- 1/sqrt(tau.p1)
804 sigma.p2 <- 1/sqrt(tau.p2)
805
806 ### Create priors for species i from the hyperparameters
807 #####
808 for (i in 1:(n+nzeroes)) {
809
810 ### Species and site-specific intercepts for occupancy and detection
811 #####
812   for(s in 1:2) {
813     a1[s,i] ~ dnorm(mu.a1[s], tau.a1[s])
814   }
815
816   for(h in 1:5) {
817     a2[h,i] ~ dnorm(mu.a2[h], tau.a2[h])
818   }
819
820 ### Species-specific occupancy and detection fixed effects drawn from a normal distribution
821 ### governed by community-level hyperparameters
822 #####
823   b1[i] ~ dnorm(mu.b1, tau.b1)
824   b2[i] ~ dnorm(mu.b2, tau.b2)
825   b3[i] ~ dnorm(mu.b3, tau.b3)
826   b4[i] ~ dnorm(mu.b4, tau.b4)
827   b5[i] ~ dnorm(mu.b5, tau.b5)
828   b6[i] ~ dnorm(mu.b6, tau.b6)
829   b7[i] ~ dnorm(mu.b7, tau.b7)
830
831   p1[i] ~ dnorm(mu.p1, tau.p1)
832   p2[i] ~ dnorm(mu.p2, tau.p2)
833
834 ### Process model of true occurrence
835 #####
836   for (j in 1:J) {
837     logit(psi[j,i]) <- a1[Site[j],i] + b1[i]*dist.sett[j] + b2[i]*dist.water[j] +
838       b3[i]*forest[j] + b4[i]*pasture[j] + b5[i]*wetland[j] + b6[i]*OP[j] +
839       b7[i]*Season.psi[j]
840     Z[j,i] ~ dbern(mu.psi[j,i])
841

```

```

842     ### Observation model for replicated detections
843     ###=====
844     for (k in 1:K[j]) {
845         logit(p[j,k,i]) <- a2[habitat[j],i] + p1[i]*road[j] + p2*season.det[j]
846         mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
847         y[j,k,i] ~ dbern(mu.p[j,k,i])
848
849     # Calculate Pearson's chi-squared residuals to assess goodness of fit
850     # Based on Kery and Royle: Applied hierarchical modelling in ecology, pp. 235
851     # Calculate the observed and expected residuals
852     # Add small value to prevent division by zero
853     #=====
854         y.sim[j,k,i] ~ dbern(mu.p[j,k,i])
855         chi2.actual[j,k,i] <- pow(y[j,k,i] - mu.p[j,k,i], 2)/(mu.p[j,k,i] + 0.0001)
856         chi2.sim[j,k,i] <- pow(y.sim[j,k,i] - mu.p[j,k,i], 2)/(mu.p[j,k,i] + 0.0001)
857     }
858
859     chi2.actual.sum[j,i] <- sum(chi2.actual[j,1:n.reps[j],i])
860     chi2.sim.sum[j,i] <- sum(chi2.sim[j,1:n.reps[j],i])
861 }
862 # Calculate chi-squared discrepancy for each species
863 #=====
864     fit.sp.actual[i] <- sum(chi2.actual.sum[,i])
865     fit.sp.sim[i] <- sum(chi2.sim.sum[,i])
866     c.hat.sp[i] <- fit.sp.actual[i]/fit.sp.sim[i]
867     bpv.sp[i] <- step(fit.sp.sim[i] - fit.sp.actual[i])
868 }
869
870 # Calculate overall chi-squared discrepancy measure
871 #=====
872     fit.actual <- sum(chi2.actual.sum[1:n.sites, 1:n.sp])
873     fit.sim <- sum(chi2.sim.sum[1:n.sites, 1:n.sp])
874     c.hat <- fit.actual/fit.sim
875     bpv <- step(fit.sim - fit.actual)
876
877 # Derived quantities
878 # Difference in occupancy between Sites 1 and 2
879 #=====
880     for(i in 1:n.sp){
881         effect1[i] <- a1[2,i] - a1[1,i]
882     }
883
884 # Number of occupied sites
885 #=====
886     for(i in 1:n.sp) {
887         Nocc.fs[i] <- sum(Z[,i])
888     }
889
890 # Number of species occurring at each site
891 #=====

```



```
892     for(j in 1:n.sites) {  
893       Nsite[j] <- sum(Z[j,])  
894     }  
895   }  
896   ",fill=TRUE)  
897 sink()  
898
```

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919 **Table A1.** Bayesian P values detailing model adequacy fit for single species and the full
920 model. Values between 0.025 and 0.975 indicate good fit, 0.5 is deemed optimal fit.

921

Species	Bayesian P Value
Central American agouti	0.60
Nine-banded armadillo	0.46
Capybara	0.62
Crab-eating fox	0.08
Giant anteater	0.52
Jaguar	0.53
Jaguarundi	0.59
Lesser anteater	0.46
Ocelot	0.39
Opossum	0.53
Lowland paca	0.33
Collared peccary	0.78
Puma	0.42
Crab-eating racoon	0.44
Spiny rat	0.49
Tayra	0.38
Full Model	0.51

922

923

Table A2. Posterior means and 95% Bayesian Credible Intervals (95% BCI) detailing the effect of habitat cover (Forest, Pasture, Wetland, Oil Palm), proximity covariates (Dist Settl., Dist Water) and seasonality (Season) on Neotropical mammal occupancy. Covariates are considered significant if their 95% BCIs do not overlap zero and presented here in bold with an asterisk. We additionally present in bold covariates with a weak influence (90% BCI do not overlap zero).

	Forest (95% BCI)	Pasture (95% BCI)	Dist. settl. (95% BCI)	Dist. Water (95% BCI)	Wetland (95% BCI)	Oil palm (95% BCI)	Season (95% BCI)
Capybara	0.469 (-0.580 - 1.372)	-0.347 (-1.360 - 0.629)	-0.354 (-1.211 - 0.33)	-0.596 (-1.427 - 0.071)	0.483 (-0.464 - 1.581)	-0.004 (-1.281 - 1.054)	0.283 (-0.808 - 1.405)
Central American agouti	1.008* (0.222 - 1.884)	-0.693 (-1.735 - 0.177)	0.259 (-0.263 - 0.862)	-0.484 (-1.114 - 0.083)	-0.023 (-0.912 - 0.823)	0.626 (-0.269 - 1.614)	0.395 (-0.513 - 1.351)
Collared peccary	0.820 (-0.088 - 1.780)	-0.523 (-1.627 - 0.435)	-0.068 (-0.816 - 0.702)	-0.354 (-1.049 - 0.366)	0.207 (-0.787 - 1.254)	0.366 (-0.612 - 1.37)	0.260 (-0.838 - 1.351)
Crab-eating fox	0.656 (-0.104 - 1.411)	-0.276 (-1.104 - 0.517)	-0.141 (-0.643 - 0.351)	-0.213 (-0.721 - 0.335)	0.005 (-0.806 - 0.775)	0.355 (-0.466 - 1.188)	0.432 (-0.448 - 1.372)
Crab-eating racoon	0.771* (0.012 - 1.538)	-0.075 (-0.906 - 0.774)	-0.306 (-0.865 - 0.200)	-0.355 (-0.882 - 0.178)	0.207 (-0.626 - 1.043)	0.040 (-0.951 - 0.934)	0.447 (-0.448 - 1.433)
Giant anteater	0.638 (-0.275 - 1.546)	-0.335 (-1.339 - 0.641)	0.019 (-0.674 - 0.776)	-0.288 (-0.948 - 0.423)	0.338 (-0.623 - 1.440)	0.341 (-0.679 - 1.384)	-0.122 (-1.483 - 0.972)
Jaguar	0.522 (-0.364 - 1.360)	-0.599 (-1.682 - 0.332)	0.197 (-0.396 - 0.912)	-0.529 (-1.234 - 0.098)	0.787 (-0.206 - 1.969)	0.269 (-0.757 - 1.267)	-0.130 (-1.322 - 0.879)
Jaguarundi	0.732 (-0.116 - 1.591)	-0.696 (-1.827 - 0.255)	-0.245 (-0.958 - 0.397)	-0.341 (-0.984 - 0.316)	0.230 (-0.670 - 1.137)	0.768 (-0.241 - 2.071)	-0.196 (-1.458 - 0.83)
Lesser anteater	0.681 (-0.155 - 1.515)	-0.186 (-1.087 - 0.749)	-0.278 (-0.952 - 0.336)	-0.462 (-1.123 - 0.157)	-0.191 (-1.233 - 0.725)	0.532 (-0.374 - 1.545)	0.167 (-0.872 - 1.177)

Lowland paca	0.825 * (0.014 - 1.668)	-0.644 (-1.743 - 0.278)	0.220 (-0.380 - 0.977)	-0.307 (-0.917 - 0.340)	0.279 (-0.635 - 1.237)	0.480 (-0.453 - 1.468)	0.284 (-0.695 - 1.268)
Nine-banded armadillo	0.629 (-0.238 - 1.467)	-0.120 (-0.993 - 0.795)	-0.203 (-0.880 - 0.425)	-0.405 (-1.051 - 0.216)	-0.270 (-1.361 - 0.657)	0.130 (-0.898 - 1.101)	0.101 (-0.982 - 1.109)
Ocelot	0.811 * (0.032 - 1.618)	-0.532 (-1.452 - 0.300)	-0.098 (-0.624 - 0.427)	-0.350 (-0.929 - 0.222)	0.135 (-0.693 - 0.949)	0.370 (-0.49 - 1.243)	0.504 (-0.452 - 1.581)
Opossum	0.707 (-0.149 - 1.555)	-0.317 (-1.264 - 0.598)	-0.105 (-0.786 - 0.559)	-0.457 (-1.140 - 0.171)	0.144 (-0.812 - 1.103)	0.412 (-0.521 - 1.395)	0.081 (-1.040 - 1.107)
Puma	0.985 * (0.185 - 1.876)	-0.512 (-1.450 - 0.349)	-0.182 (-0.745 - 0.340)	-0.300 (-0.842 - 0.252)	0.183 (-0.691 - 1.062)	0.143 (-0.759 - 0.983)	0.577 (-0.335 - 1.623)
Spiny rat	0.615 (-0.291 - 1.475)	-0.344 (-1.354 - 0.620)	-0.319 (-1.094 - 0.329)	-0.399 (-1.079 - 0.263)	0.225 (-0.734 - 1.218)	0.376 (-0.580 - 1.351)	0.148 (-0.960 - 1.173)
Tayra	0.712 (-0.160 - 1.621)	-0.498 (-1.505 - 0.415)	-0.100 (-0.711 - 0.556)	-0.468 (-1.139 - 0.142)	0.092 (-0.848 - 1.027)	0.534 (-0.374 - 1.535)	0.430 (-0.565 - 1.517)

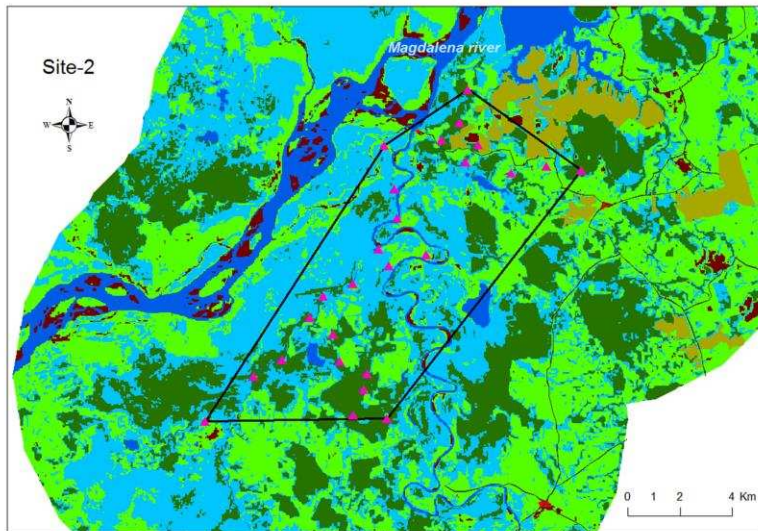
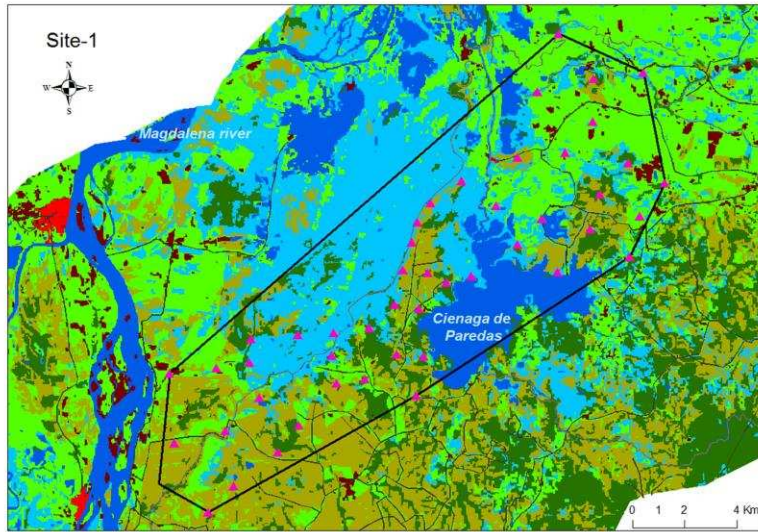
Table A3. Posterior means and 95% Bayesian Credible Intervals (95% BCI) detailing the effect of camera trap placement (Roads) and seasonality (Season) on Neotropical mammal detection probability. Covariates are considered significant if their 95% BCIs do not overlap zero and presented here in bold with an asterisk. We additionally present in bold covariates with a weak influence (90% BCIs do not overlap zero).

	Roads (95% BCI)	Season (95% BCI)
Capybara	-0.369 (-1.486 - 0.649)	0.022 (-0.784 - 0.778)
Central American agouti	0.177 (-0.741-1.070)	0.637 (-0.008 - 1.374)
Collared peccary	-0.562 (-2.039 - 0.708)	0.017 (-0.853 - 0.810)
Crab-eating fox	1.024* (0.297 - 1.753)	0.266 (-0.244 - 0.795)
Crab-eating racoon	0.286 (-0.518 - 1.083)	0.465 (-0.081 - 1.065)
Giant anteater	-0.195 (-1.578 - 1.096)	-0.114 (-1.020 - 0.677)
Jaguar	1.054 * (0.152 - 1.939)	-0.086 (-0.789 - 0.563)
Jaguarundi	0.723 (-0.159 - 1.634)	-0.031 (-0.811 - 0.698)
Lesser anteater	0.030 (-1.386 -1.346)	0.023 (-0.754 - 0.733)
Lowland paca	-0.042 (-1.117 - 0.942)	0.194 (-0.498 - 0.912)
Nine-banded armadillo	-0.071 (-1.450 - 1.185)	0.082 (-0.700 - 0.844)
Ocelot	0.869 * (0.171 - 1.612)	-0.053 (-0.599 - 0.468)
Opossum	-0.427 (-1.550 - 0.592)	0.080 (-0.711 - 0.858)
Puma	0.350 (-0.468 - 1.181)	-0.018 (-0.664 - 0.608)
Spiny rat	-0.439 (-2.034 - 0.853)	0.085 (-0.744 - 0.891)
Tayra	-0.047 (-1.044 - 0.912)	-0.203 (-0.953 - 0.445)

Table A4. Average detection probability, including 95% Bayesian Credible Interval, for Neotropical mammals in five reference habitat classes.

	Forest (95% BCI)	Pasture (95% BCI)	Edge (95% BCI)	Wetland (95% BCI)	Oil palm (95% BCI)
Capybara	0.053 (0.009 - 0.218)	0.214 (0.052 - 0.535)	0.175 (0.041 - 0.402)	0.252 (0.109 - 0.487)	0.045 (0.001 - 0.582)
Central American agouti	0.555 (0.313 - 0.779)	0.192 (0.030 - 0.540)	0.287 (0.141 - 0.516)	0.156 (0.020 - 0.490)	0.154 (0.043 - 0.435)
Collared peccary	0.038 (0.004 - 0.199)	0.171 (0.042 - 0.392)	0.197 (0.040 - 0.482)	0.178 (0.043 - 0.436)	0.388 (0.108 - 0.778)
Crab-eating fox	0.308 (0.162 - 0.514)	0.349 (0.206 - 0.537)	0.324 (0.165 - 0.572)	0.300 (0.136 - 0.567)	0.281 (0.127 - 0.499)
Crab-eating racoon	0.302 (0.144 - 0.530)	0.265 (0.134 - 0.458)	0.224 (0.100 - 0.409)	0.157 (0.047 - 0.348)	0.075 (0.012 - 0.362)
Giant anteater	0.105 (0.024 - 0.358)	0.227 (0.075 - 0.489)	0.199 (0.055 - 0.433)	0.214 (0.064 - 0.506)	0.048 (0.001 - 0.591)
Jaguar	0.086 (0.030 - 0.212)	0.239 (0.072 - 0.571)	0.285 (0.136 - 0.527)	0.334 (0.160 - 0.598)	0.026 (0.001 - 0.400)
Jaguarundi	0.077 (0.025 - 0.210)	0.194 (0.032 - 0.549)	0.263 (0.120 - 0.488)	0.210 (0.074 - 0.449)	0.057 (0.010 - 0.224)
Lesser anteater	0.174 (0.050 - 0.491)	0.170 (0.052 - 0.365)	0.204 (0.044 - 0.503)	0.177 (0.027 - 0.514)	0.099 (0.019 - 0.343)

Lowland paca	0.180 (0.066 - 0.400)	0.320 (0.134 - 0.635)	0.215 (0.077 - 0.430)	0.159 (0.035 - 0.401)	0.152 (0.023 - 0.612)
Nine-banded armadillo	0.137 (0.041 - 0.366)	0.186 (0.054 - 0.407)	0.207 (0.043 - 0.503)	0.172 (0.025 - 0.505)	0.318 (0.046 - 0.864)
Ocelot	0.179 (0.094 - 0.313)	0.166 (0.048 - 0.363)	0.305 (0.146 - 0.566)	0.190 (0.085 - 0.358)	0.285 (0.156 - 0.456)
Opossum	0.190 (0.072 - 0.413)	0.187 (0.031 - 0.525)	0.194 (0.051 - 0.431)	0.265 (0.103 - 0.561)	0.035 (0.001 - 0.397)
Puma	0.192 (0.091 - 0.357)	0.174 (0.027 - 0.496)	0.197 (0.079 - 0.381)	0.188 (0.054 - 0.438)	0.488 (0.193 - 0.790)
Spiny rat	0.105 (0.020 - 0.392)	0.191 (0.032 - 0.545)	0.240 (0.092 - 0.471)	0.176 (0.029 - 0.506)	0.688 (0.273 - 0.950)
Tayra	0.181 (0.072 - 0.398)	0.205 (0.077 - 0.406)	0.226 (0.085 - 0.450)	0.148 (0.031 - 0.375)	0.133 (0.032 - 0.409)



- ▲ Camera Stations
- Minimum Convex Polygon
- Land Cover Types
- Secondary forest
- Pasture
- Oil palm
- Bare ground
- Water
- Wetland
- Settlement
- Road

