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1 **Conserving predators across agricultural landscapes in Colombia:**
2 **habitat use and space partitioning by jaguars, pumas, ocelots, and**
3 **jaguarundis**

4

5 **Short title: Felid habitat use in Colombia**

6

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8

9

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29 **Abstract**

30 Habitat loss and degradation continue to increase across the tropics. Consequently there is an urgent
31 need to understand their effects, as well as species' habitat requirements and distribution within
32 human-modified landscapes, in order to reconcile agricultural expansion with the conservation of
33 endangered and keystone species, like the felids. We combined camera trapping and remote
34 sensing-generated data into occupancy modelling to study the habitat use and space partitioning by
35 four sympatric felids across an agricultural landscape in Colombia. The area includes cattle
36 ranching and oil palm cultivation, an emerging land use in the Neotropics. Strong determinants of
37 species occupancy were wetlands for jaguars (positive effect); water proximity (positive effect) for
38 pumas; and pasture (negative effect) for ocelots and jaguarundis. Felid species except ocelots were
39 never recorded in oil palm areas. Our results suggest that to align development with the
40 conservation of top predators it is key to maintain areas of forest and wetland across agricultural
41 landscapes and targeting agricultural and oil palm expansion to already-modified areas like pastures,
42 which showed limited conservation value in the region. Lastly, as there was no spatial segregation
43 between the studied felid species, conservation strategies to simultaneously benefit this guild seem
44 possible even in modified landscapes.

45

46 **Keywords:** camera trap; Object Oriented Image Analysis; occupancy; oil palm; *Panthera onca*;
47 *Puma concolor*.

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51

52 **Introduction**

53 Habitat loss and degradation, largely driven by agricultural expansion, are the main threats to
54 biodiversity worldwide (Foley et al., 2005; Maxwell et al., 2016). Consequently, there is an urgent
55 need to reconcile agricultural expansion with the conservation of endangered and keystone species,
56 such as the felids. This is especially true across tropical countries, which are experiencing
57 considerable land cover change and are a priority for carnivore conservation (Gibbs et al., 2010;
58 Laurance et al., 2014; Di Minin et al., 2016). Wild cats, as other carnivores, exert important
59 functions in the ecosystems they inhabit: by limiting herbivore populations growth, they help
60 retaining the structure and composition of complex biological communities and ecosystems (Estes
61 et al., 2011; Ripple et al., 2014).

62 Protected areas are crucial to conserve high quality source habitats, however, on average, 90% of
63 the geographical distribution of wild carnivores falls outside protected areas (Di Minin et al., 2016),
64 implying that the latter are not able to guarantee carnivore long-term survival. Consequently, there
65 is an urgent need to understand species distribution and habitat use in unprotected and modified
66 landscapes. Exploring the role of human dominated landscapes for large-scale conservation
67 strategies is especially important for wide-ranging carnivores. Species like jaguars (*Panthera onca*)
68 and pumas (*Puma concolor*) require large areas to survive, have slow reproductive rates, and live at
69 low densities, making them particularly vulnerable to extinction (Cardillo et al., 2005; Carbone et
70 al., 2011).

71 Populations of all wild felids in Neotropical forests are rapidly declining (IUCN, 2015). Jaguars -
72 the largest Neotropical cats- have experienced a contraction of their geographical distribution to less
73 than 50% of their historical distribution (Rabinowitz & Zeller, 2010), and are currently considered
74 Near Threatened by the IUCN (Quigley et al., 2017), with most subpopulations at high risk of
75 extinction (de la Torre et al., 2017). Pumas are listed as Least Concern (Nielsen et al., 2015),
76 however their population estimates are scarce in the Neotropics (Kelly et al., 2008). Both jaguars

77 and pumas are declining in number due to habitat loss, persecution, and decline of their prey (Caso
78 et al., 2008; Nielsen et al., 2015), yet knowledge about their habitat use across human modified
79 agricultural areas is limited (Foster et al., 2010; De Angelo et al., 2011, 2013). Even less is known
80 on the ecology of smaller felid species such as ocelots *Leopardus pardalis* (Least Concern) and
81 jaguarundis *Herpailurus yagouaroundi* (Least Concern) across agricultural landscapes (Di Bitetti et
82 al., 2006; Kolowski & Alonso, 2010; Giordano, 2015), and both species display decreasing
83 population trends (Caso et al. 2015; Paviolo et al., 2015)

84 We combine high-resolution land cover maps and camera trapping data into occupancy models to
85 investigate the habitat use of four sympatric Neotropical felids: jaguars, pumas, ocelots, and
86 jaguarundis (Fig. 1) across an agricultural landscape in Colombia. The area included cattle ranching,
87 the main land use in the country (Etter et al., 2006), and oil palm plantations, an emerging land use
88 in the Neotropics (Pacheco, 2012). The latter is particularly worrying for conservation because it
89 constitutes poor habitat for many species (Fitzherbert et al., 2008; Yue et al., 2015) and has an
90 unknown effect on Neotropical felids. Finally we also investigate patterns of spatial co-occurrence
91 or avoidance between the four species. The data will help inform strategies to align regional
92 development with conservation actions for these predators and the diverse ecosystems they live in.
93 This is particularly timely in Colombia, because the end of the armed conflict represents an
94 opportunity for new developments and investments (Baptiste et al., 2017).

95

96 **Methods**

97 **Study area**

98 We conducted the study in the central part of the Magdalena River valley, in between the Central
99 and Eastern Andes and in the Department of Santander, Colombia (7.3752N -73.8842E to 7.5404N
100 -73.7118E) (Fig. 2). The region is part of the tropical forest biome and it is rich in wetlands
101 (IDEAM et al., 2007). The mean annual temperature is 27°C, and rainfall ranges between 2100 and

102 2600 mm annually (IDEAM et al., 2007). The area is considered an important genetic corridor for
103 several species including jaguars, and hosts other endangered and endemic species (Payan-Garrido
104 et al., 2013). However, the majority of its historical forest cover has now been transformed into
105 cattle ranches and oil-palm plantations, and the remaining natural areas are fragmented and at risk
106 of further conversion (Etter et al., 2006; Link et al., 2013; Castiblanco et al., 2013).

107 Within the region we specifically chose our study area because it is an agricultural area, which
108 includes cattle ranching and oil palm plantations, but still hosts top predators like jaguars and
109 pumas. Hence it offers opportunities to study these predators in an anthropogenic landscape.
110 Regionally land tenure consists principally of private properties and there are no national protected
111 areas. Main land cover types comprise secondary forest, wetlands, pastures, crops, and oil-palm
112 plantations (Fig. 2).

113

114 **Camera trapping**

115 We placed 47 camera stations between April and August 2014. The set up followed a systematic
116 sampling approach for camera trapping used in previous studies on Neotropical felids (Maffei &
117 Noss, 2008; Davis *et al.*, 2011; Tobler & Powell, 2013). We positioned the grid to include all main
118 habitat types of the study areas: forest (10 stations), wetland (9 stations), pastures (8 stations), and
119 oil palm (8 stations). The remaining stations were located at the edge between forest and oil palm
120 (6) and between wetland and oil palm (6). The minimum convex polygon linking the camera
121 stations was 154.8 km². We placed the cameras at regular intervals of 1.6±0.3 km (Fig. 2), since this
122 scale of analysis is considered appropriate to investigate habitat use by felids (Davis et al., 2011;
123 Sunarto et al., 2012; Alexander et al., 2015; Everatt et al., 2015; Strampelli, 2015). Once reached
124 the appropriate distance, we chose the exact camera location in a radius of 200m to maximise felid
125 encounters. When possible we placed cameras along roads and established trails to increase the
126 probability of capturing cat species. As a result, 60% of stations were placed on trails and we took

127 these placement differences into account in the modelling approach. We used Cuddeback Attack
128 (model: 1149) and Ambush (model: 1170) camera traps and set them at a height of 35 cm from the
129 forest floor.

130

131 **Occupancy modelling to study habitat use**

132 We used occupancy models in order to investigate the potential effects of different variables on
133 species habitat use. Such models take into account imperfect detection and use repeated presence-
134 absence surveys (detection histories) at multiple sampling units to estimate a detection probability
135 (p) and the true proportion of area occupied by a species (ψ) (MacKenzie et al., 2006). The
136 following assumptions are made: 1) sampling units are closed to changes in occupancy (i.e. they are
137 either occupied or not by the species for the duration of the survey); 2) species are correctly
138 identified; 3) detections are independent; and 4) heterogeneity in occupancy or detection probability
139 are modeled using covariates (MacKenzie et al., 2006). We conducted our analyses at the scale of
140 the camera trap station rather than at the home range scale and we were evaluating habitat use rather
141 than the proportion of study area occupied by each species. We defined a sampling unit as the
142 circular area with a radius of 800m around each camera station. 800 m corresponds to half the
143 average distance between neighboring camera stations (Sollmann et al., 2012). Therefore we
144 interpreted ψ as the intensity of use of the various sampling units and modeled both ψ and p using
145 predictor variables (covariates). Under these circumstances assumption 1 can be relaxed and even
146 extensive survey lengths do not represent an issue (MacKenzie et al., 2006). We included in our
147 analyses covariates that have been proposed to explain habitat use (ψ) by felids (Di Bitetti et al.,
148 2006; Foster et al., 2010; Zeller et al., 2011; De Angelo et al., 2011; Petracca et al., 2014; Giordano,
149 2015) considering (1) bottom up resources (hypothesized positive effect): proportion of the area
150 covered by forests and wetlands in the sampling units, water, and amount of prey, as well as (2) top-
151 down anthropogenic pressures (hypothesized negative effect): settlements, and the proportion of

152 sampling units covered by pastures and oil palm plantations.

153

154 **Land cover mapping and covariates generation**

155 We identified land cover types and their proportions across the study area. We defined such area
156 adding a buffer of 9.2 km to the camera stations. 9.2 km corresponds to the maximum distance
157 moved by jaguars, the species with the largest home range. We used Object Oriented Image
158 Analysis (OBIA) on three Landsat 8 images, captured on 4/1/2015, 9/3/2015, and 12/7/2015 (for
159 more details on land cover mapping refer to Supplementary Material 1). We then extracted the
160 proportion of the land cover types in each sampling unit, and measured the distance of each camera
161 station from water and settlements in ArcMap 10.3. For jaguars and pumas we also considered prey
162 availability. These species have wide dietary breadth but tend to favor larger prey species (Polisar et
163 al., 2003; Foster et al., 2010). Consequently we built two indices: one considering all prey species
164 and another considering only prey species with body mass > 10kg, which consisted of capybaras
165 (*Hydrochoerus isthmius*), white-collared peccaries (*Pecari tajacu*), and giant anteaters
166 (*Myrmecophaga tridactyla*). Our index of prey presence was calculated as the sum of the number of
167 days on which a prey species was captured at each camera station, divided by the active trap days at
168 that station (Alexander et al., 2015). We could not test prey availability for ocelots and jaguarundis
169 because they predate also on small prey such as rodents and small reptiles (Abreua et al., 2008;
170 Giordano, 2015), which are under-detected by our camera trap methodology.

171 As wild felids tend to use roads and trails to facilitate their movement (Schaller & Crawshaw Jr,
172 1980; Cusack et al., 2015) we included a categorical covariate on p (1 for cameras on roads/trails vs.
173 0). Both camera models have the same trigger speed (0.25 seconds) and due to high temperatures
174 they were triggered only at distances < 3-4 m. Therefore we did not include camera model as a
175 covariate on p and assumed constant detection probability across habitats.

176

177 **Data analysis**

178 We constructed detection histories for each species and each sampling unit using unambiguously
179 identified species photographs and grouping 14 camera trap nights into one sampling occasion. We
180 then deployed single season single species models in PRESENCE v.10.3 (Hines, 2006). Before
181 running the models we standardized continuous covariates to z scores and tested for collinearity
182 using a cut-off value of $r = 0.7$ (Dormann et al., 2013). In the first stage we defined a global model
183 for ψ and assessed whether including the covariate on p improved the Akaike Information Criteria
184 adjusted for small sample size (AICc) (Royle & Nichols, 2003). Following we used the best
185 detection model and modeled all combinations of covariates for ψ for each species. We included a
186 maximum of two covariates per model, given the amount of samples to avoid over fitting
187 (MacKenzie et al., 2006).

188 We ranked models based on AICc and if there was no single model possessing a weight ≥ 0.95 we
189 considered models whose combined weight was ≥ 0.95 . Following, we summed AICc weights for
190 each covariate in the 95% confidence set to evaluate their relative importance. We determined
191 whether the influence of a covariate was positive or negative by the sign of the β coefficient
192 (MacKenzie et al., 2006) and employed weighted model averaging to calculate overall estimates of
193 β coefficients, ψ , and p (Burnham & Anderson, 2002). We considered covariates to have a robust
194 effect on ψ if the 95% confidence intervals of their β coefficients or averaged β coefficients did not
195 overlap zero (Burnham & Anderson, 2002; Zuur et al., 2010; Everatt et al., 2015). We assessed
196 model fit for the global standard occupancy model by running goodness-of-fit tests using 10,000
197 bootstrap samples and obtaining the overdispersion parameter \hat{c} (MacKenzie & Bailey, 2004).
198 We repeated this process for each species.

199 Finally, to test for space partitioning between species we used two-species single season occupancy
200 models (MacKenzie et al., 2006; Sollmann et al., 2012; Sunarto et al., 2015). If two species, namely
201 A and B, occur independently then the probability of occurrence of both species $\psi(A \text{ and } B) =$

202 $\psi(A) \times \psi(B)$. Consequently, we determined whether A and B, co-occurred more or less often than
203 expected using $\phi = \psi(A \text{ and } B) / (\psi(A) \times \psi(B))$. If $\phi > 1$ species co-occur more often than expected
204 whereas if $\phi < 1$, species co-occur less often than expected, provided ϕ 's 95% confidence intervals
205 do not overlap 1 (MacKenzie et al., 2006).

206

207 **Results**

208 The land cover mapping resulted in the identification of seven types: pasture (35%), wetlands
209 (20%), oil palm (19%), forest (12%), water (10%), bare ground (3%), roads and settlements (<1%).

210 The overall classification accuracy was 0.89 indicating an excellent performance of the classifier.

211 We obtained a sampling effort of 3069 trap nights and grouping 14 days into one sampling occasion
212 resulted into 25-58 species detections (Table 1). Jaguar and ocelot detections corresponded to 12
213 and 21 individuals respectively; whereas pumas and jaguarundis could not be individually identified.

214 No variable correlated with others ($r < 0.7$). Out of the 12 jaguars recorded four are resident as they
215 have been in the area since 2012.

216 Jaguar occupancy was strongly favoured by the proportion of wetlands available (Table 1 and 2).

217 Pumas occupancy was best explained by the distance to water (robust negative effect), availability
218 of prey > 10kg (positive effect), proportion of pasture habitats (negative effect), and forest (positive
219 effect) (Table 1 and 2). Lastly, ocelots and jaguarundis were strongly and negatively affected by
220 pastures (Table 1 and 2). With the exception of ocelots, no other species was recorded in oil palm
221 areas (Table S1).

222 Cameras placed on roads/established trails were more likely to detect jaguars, pumas, and ocelots
223 (Table 2) and including this covariate for p improved models for these species. These cameras were
224 also the only ones to detect jaguarundis. However, for the latter, we could not include it as a
225 covariate on p due to lack of convergence. Full model selection results for the four species are
226 available in Table S2.

227 The goodness of fit test for global standard occupancy models for all species indicated no
228 overdispersion, with c values close to 1 and p values > 0.05 (jaguar: c=0.90, p=0.77; puma: c=1.10,
229 p=0.24; ocelot: c=1.18, p=0.19; jaguarundi: c=1.08, p=0.29). Species average ψ and p values ranged
230 between 0.27 and 0.55 for ψ ; and between 0.25 and 0.35 for p (Table 3). Analyses on space
231 partitioning indicate co-occurrence (ϕ 95% CI > 1) between jaguars and pumas, pumas and
232 jaguarundis, and ocelots and jaguarundis (Table 4).

233

234 **Discussion**

235 As agriculture continues to expand causing habitat loss and degradation across the tropics, there is
236 an urgent need to understand how to achieve conservation of keystone species like the felids across
237 increasingly human-dominated landscapes, as the latter are key to ensure felid connectivity beyond
238 protected areas (Karanth & Chellam, 2009; Rabinowitz & Zeller, 2010; Boron et al., 2016; Di
239 Minin et al., 2016). Neotropical felid populations are declining with important ecological
240 consequences (Estes et al., 2011; Galetti & Dirzo, 2013). Results can inform strategies to reconcile
241 development with their conservation and highlight that (1) it is key to maintain wetland and forest
242 areas to conserve these cats across agricultural landscapes, (2) the expansion of oil palm plantations
243 and agriculture is a growing threat for felids (3) pastures have limited conservation value for felids
244 in the region and should be targeted for future agricultural expansion, (4) the four felids did not
245 display any spatial segregation, thus conservation strategies aimed to simultaneously benefit this
246 guild are possible even in modified landscapes.

247

248 **Factors affecting species habitat use**

249 Wetlands emerged as a key habitat for jaguars and the only variable that strongly influenced their
250 occupancy. Jaguars inhabit a variety of ecosystems but generally prefer forests and water-
251 dominated habitats (Crawshaw Jr & Quigley, 1991; Nowell & Jackson, 1996; Foster et al., 2010;

252 Zeller et al., 2011; De Angelo et al., 2011, 2013). The expansion of the cattle ranching and oil palm
253 agro-industries restricted forests to only 12% of the study area and increased human disturbance.
254 Consequently, important jaguar prey such as capybaras, peccaries, tapirs (*Tapirus terrestris*), and
255 deer (*Mazama sp.*) (Foster et al., 2010; Polisar et al., 2003), has been largely depleted due to both
256 habitat loss and hunting (Rodríguez-Mahecha et al., 2006). Indeed prey exerted no effect on jaguar
257 occupancy. Hence it is likely that jaguars use wetlands to complement their diet with aquatic prey
258 such as caimans (*Caiman crocodilus*) and turtles (*Podocnemis* and *Trachemys sp.*) (Da Silveira et
259 al., 2010), since predation on livestock is rare in the area (V. Boron *personal observation*).
260 Preserving wetlands is therefore crucial for jaguar survival in the region.

261 Pumas were strongly associated to water bodies (i.e. streams, ponds, and cienegas), avoided
262 pastures, and their occupancy was positively affected by forest and remaining larger prey. Pumas'
263 association with water may be related to the use of riparian forests for their movements (De Angelo
264 *et al.*, 2011), as these forests are usually the last to remain in heavily modified regions like our
265 study area. These findings suggest that to conserve the species it is key to maintain forest habitat in
266 modified landscapes for both pumas and to guarantee the survival of its prey. Pumas tend to be
267 considered more habitat generalist than jaguars and are able to live in close proximity with humans
268 (Dickinson & Beier, 2006; De Angelo et al., 2011; Sollmann et al., 2012). However, pumas can also
269 avoid modified areas and prefer forests when they are present (Paviolo *et al.*, 2009; Di Bitetti *et al.*,
270 2010; Foster *et al.*, 2010a; Negrões *et al.*, 2010; Davis *et al.*, 2011; De Angelo *et al.*, 2011), which
271 concurs with our findings. This is possibly due to higher prey availability in this habitat.

272 Ocelots and jaguarundis are sometimes regarded as ecologically plastic and more tolerant to habitat
273 loss and degradation than the larger felids (Nowell & Jackson, 1996; Di Bitetti et al., 2006;
274 Michalski & Peres, 2005; Lyra-Jorge et al., 2008; Kolowski & Alonso, 2010). Accordingly, the
275 ocelot was the only cat species recorded in oil palm plantations albeit rarely. There have been
276 previous records of ocelots using oil palm areas (Boron & Payan, 2013; Pardo & Payan, 2015)

277 possibly because the latter have rodent prey and are suitable for hunting due to the open visibility,
278 as found for the leopard cat *Prionailurus bengalensis* (Rajaratnam et al., 2007). However, despite
279 their presumed habitat plasticity, both ocelots and jaguarundis were negatively and strongly affected
280 by pastures, which supports earlier findings showing that they favor more natural forested habitats
281 while avoiding human disturbance (Gonzalez et al., 2003; Maffei et al., 2005; Giordano, 2015;
282 Massara et al., 2015).

283

284 **Space partitioning**

285 Interspecies interactions are stronger between species of similar body mass and overlapping prey
286 preferences; and spatial, temporal, and/or diet segregation can improve co-existence (Donadio &
287 Buskirk, 2006). At the continental scale, puma population sizes seem low where jaguars are
288 abundant and vice versa (Kelly et al., 2008; Noss et al. 2012). However, when the two cats are
289 sympatric, their habitat use is similar and segregation tends to be temporal or dietary, rather than
290 spatial (Scognamillo et al., 2003; Harmsen et al., 2009; Foster et al., 2010; Di Bitetti et al., 2010).
291 This agrees with our findings of spatial co-occurrence and it is possible that segregation occurs at
292 the diet level with jaguars preying mainly on aquatic prey, and pumas on terrestrial prey.

293 Mesocarnivores like ocelots and jaguarundis may be negatively affected by top predators and
294 succeed when larger predators are rare or absent through phenomena of mesopredator release
295 (Crooks & Soulé, 1999; Moreno et al., 2006). However, ocelots can also thrive in large protected
296 areas with better habitat quality inhabited by top predators (Massara et al., 2015), and both ocelots
297 and jaguarundis can be positively associated with jaguars and/or pumas (Di Bitetti et al., 2010; Noss
298 et al. 2012). Accordingly, we found that jaguarundis tend to co-occur with both ocelots and pumas.
299 Ocelot can negatively affect jaguarundi numbers (Oliveira et al., 2010) with spatial co-occurrence
300 being favored by temporal segregation as jaguarundis are diurnal, whereas pumas and ocelots
301 mostly crepuscular and nocturnal (Di Bitetti et al., 2010; Harmsen et al., 2011). Overall, the lack of

302 spatial segregation between species in the region indicates that their distributions can overlap, thus
303 developing conservation strategies to simultaneously benefit this guild may be possible even in
304 modified landscapes.

305

306 **Methodological considerations**

307 We adopted an appropriate survey design to investigate felid habitat use (Davis et al., 2011; Sunarto
308 et al., 2012; Alexander et al., 2015; Everatt et al., 2015; Strampelli, 2015). Despite felids being
309 wide-ranging, our models showed no over dispersion, suggesting that our data was not affected by
310 spatial autocorrelation. Furthermore, the identification of individual jaguars and ocelots shows that
311 adjacent cameras never recorded the same assemblage of individuals. Habitat selection takes place
312 at a variety of spatial and temporal scales ranging from distribution and home range selection to
313 habitat use within home range (Johnson, 1980; Sunarto et al., 2012; Strampelli, 2015), thus
314 conducting more studies to explore these differences in modified landscapes is important. Finally,
315 using OBIA produced highly accurate land cover maps and covariates, and occupancy models
316 reduced bias by taking into account imperfect detection, which is especially important for elusive
317 species like the felids.

318

319 **Conclusion**

320 Unprotected and increasingly human modified areas are crucial for wide-ranging carnivores, thus it
321 is important to understand how to achieve conservation there. This study focused on habitat use.
322 However, it is also important to bear in mind that to conserve predator species across human-use
323 areas, habitat preservation needs to be complemented by hunting limitations, and conflict
324 management (Inskip & Zimmermann, 2009).

325 Pasture is the main land cover in Colombia (Etter et al., 2006) and holds limited conservation value
326 for felids in the region. Further studies are needed, however our results indicate that oil palm and

327 agricultural expansion, when inevitable, should be targeted to already modified areas such as
328 pastures, which would minimise the loss of natural habitats (Garcia-Ulloa et al., 2012). Concurring
329 results were documented for other taxa (Gilroy et al., 2015; Prescott et al., 2016). We did not find a
330 clear effect of oil palm, which could be because it still covers a small proportion of the landscape
331 (19%). Nevertheless jaguars, pumas, and jaguarundis were never detected in oil palm areas. A
332 stronger regulatory framework could facilitate land-use planning and incentive-based approaches
333 (e.g. tax breaks, subsidized credits, premium pieces for certified products) also encourage the
334 preservation of natural areas within productive landscapes (Lambin et al., 2014; Boron, Payan, et al.,
335 2016). This study can help guiding land use planning in Colombia, which is particularly timely
336 considering the country's transition towards peace. Further research should explore the habitat
337 requirements for felid and other priority species to identify thresholds and optimal landscape
338 configuration.

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373

374 **Authors contributions**

375 VB collected field data. VB and PX processed and analysed the data. All authors provided guidance
376 on data analysis, and contributed to study design and writing the article.

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397 **References**

- 398 ABREUA, K.C., MORO-RIOS, RODRIGO F. SILVA-PEREIRA, J.E. & MIRANDA, JOAO M.D.
 399 JABLONSKIB, ESTEFANO F. PASSOSA, F.C. (2008) Feeding habits of ocelot (*Leopardus pardalis*)
 400 in Southern Brazil. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 73, 407–411.
 401 ALEXANDER, J.S., SHI, K., TALLENTS, L. & RIORDAN, P. (2015) On the high trail: examining
 402 determinants of site use by the Endangered snow leopard *Panthera uncia* in Qilianshan, China.
 403 *Oryx*, 1–8.
 404 DE ANGELO, C., PAVIOLO, A. & DI BITETTI, M. (2011) Differential impact of landscape
 405 transformation on pumas (*Puma concolor*) and jaguars (*Panthera onca*) in the Upper Paraná
 406 Atlantic Forest. *Diversity and Distributions*, 17, 422–436.
 407 DE ANGELO, C., PAVIOLO, A., WIEGAND, T., KANAGARAJ, R. & DI BITETTI, M.S. (2013)
 408 Understanding species persistence for defining conservation actions: A management landscape
 409 for jaguars in the Atlantic Forest. *Biological Conservation*, 159, 422–433.
 410 BAPTISTE, B., PINEDO-VASQUEZ, M., GUTIERREZ-VELEZ, V.H., ANDRADE, G.I., VIEIRA, P.,
 411 ESTUPIÑÁN-SUÁREZ, L.M., ET AL. (2017) Greening peace in Colombia. *Nature Ecology &*
 412 *Evolution*, 1, 102.
 413 DI BITETTI, M.S., DE ANGELO, C.D., DI BLANCO, Y.E. & PAVIOLO, A. (2010) Niche partitioning
 414 and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36, 403–412.
 415 DI BITETTI, M.S., PAVIOLO, A. & ANGELO, C. DE (2006) Density, habitat use and activity patterns
 416 of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of*
 417 *Zoology*, 270, 153–163.
 418 BORON, V. & PAYAN, E. (2013) Abundancia de carnívoros en el agro-paisaje de las plantaciones de
 419 palma de aceite del valle medio del río Magdalena, Colombia. In *Plan de Conservación de*
 420 *Felinos para el Caribe Colombiano 2007-2012: Logros y proyecciones*. pp. 165–176.
 421 Conservation International, Procat, and Fundación Herencia Ambiental Caribe, Santa Marta.
 422 BORON, V., PAYAN, E., MACMILLAN, D. & TZANOPOULOS, J. (2016) Achieving sustainable
 423 development in rural areas in Colombia: future scenarios for biodiversity conservation under
 424 land use change. *Land Use Policy*, 59, 27–37.
 425 BORON, V., TZANOPOULOS, J., GALLO, J., BARRAGAN, J., JAIMES-RODRIGUEZ, L., SCHALLER, G. &
 426 PAYÁN, E. (2016) Jaguar Densities across Human-Dominated Landscapes in Colombia: The
 427 Contribution of Unprotected Areas to Long Term Conservation. *PLoS ONE*, 11, e0153973.
 428 BURNHAM, K.P. & ANDERSON, D.R. (2002) Model Selection and Multimodel Inference: A Practical
 429 Information-theoretic Approach, 2nd edition. Springer, New York.
 430 CARBONE, C., PETTORELLI, N. & STEPHENS, P. (2011) The bigger they come, the harder they fall:
 431 body size and prey abundance influence predator-prey ratios. *Biology letters*, 7, 312–315.
 432 CARDILLO, M., MACE, G.M., JONES, K.E., BIELBY, J., BININDA-EMONDS, O.R.P., SECHREST, W., ET
 433 AL. (2005) Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, 1067,
 434 1239–1241.
 435 CASO, A., de OLIVEIRA, T., & CARVAJAL, S.V. (2015) *Herpailurus yagouaroundi*. The IUCN Red
 436 List of Threatened Species 2015: e.T9948A50653167.
 437 CASTIBLANCO, C., ETTER, A. & AIDE, T.M. (2013) Oil palm plantations in Colombia: a model of
 438 future expansion. *Environmental Science & Policy*, 27, 172–183.
 439 CRAWSHAW JR, P. & QUIGLEY, H. (1991) Jaguar spacing, activity and habitat use in a seasonally
 440 flooded environment in Brazil. *Journal of Zoology*, 222, 357–370.
 441 CROOKS, K. & SOULÉ, M. (1999) Mesopredator release and avifaunal extinctions in a fragmented
 442 system. *Nature*, 400, 563–566.
 443 CUSACK, J.J., DICKMAN, A.J., ROWCLIFFE, J.M. & CARBONE, C. (2015) Random versus Game Trail-
 444 Based Camera Trap Placement Strategy for Monitoring Terrestrial Mammal Communities.
 445 *PLoS ONE*, 10, e0126373.

- 446 DAVIS, M.L., KELLY, M.J. & STAUFFER, D.F. (2011) Carnivore co-existence and habitat use in the
447 Mountain Pine Ridge Forest Reserve, Belize. *Animal Conservation*, 14, 56–65.
- 448 DE LA TORRE, J.A., GONZALEZ-MAYA, J.F., ZARZA, H., CEBALLOS, G. & MEDELLIN, R.A.,
449 (2017) The jaguar's spots are darker than they appear: assessing the global conservation status of
450 the jaguar *Panthera onca*. *Oryx*, 1-16.
- 451 DICKSON, B.G. & BEIER, P. (2007) Quantifying the influence of topographic position on cougar
452 (*Puma concolor*) movement in southern California, USA. *Journal of Zoology*, 271, 270-277.
- 453 DONADIO, E. & BUSKIRK, S.W. (2006) Diet, morphology, and interspecific killing in carnivora. *The*
454 *American naturalist*, 167, 524–536.
- 455 DORMANN, C.F., ELITH, J., BACHER, S., BUCHMANN, C., CARL, G., CARRÉ, G., ET AL. (2013)
456 Collinearity: A review of methods to deal with it and a simulation study evaluating their
457 performance. *Ecography*, 36, 027–046.
- 458 ESTES, J., TERBORGH, J., BRASHARES, J., POWER, M., BERGER, J., BOND, W., ET AL. (2011) Trophic
459 downgrading of planet Earth. *Science*, 333, 301–306. American Association for the
460 Advancement of Science, Washington, D.C.
- 461 ETTER, A., MCALPINE, C., WILSON, K., PHINN, S. & POSSINGHAM, H. (2006) Regional patterns of
462 agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems & Environment*,
463 114, 369–386.
- 464 EVERATT, K.T., ANDRESEN, L., SOMERS, M.J., EVERATT, K.T., ANDRESEN, L. & SOMERS, M.J.
465 (2015) The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an
466 apex predator. *African Journal of Wildlife Research*, 45, 187–196.
- 467 FITZHERBERT, E.B., STRUEBIG, M.J., MOREL, A., DANIELSEN, F., DONALD, P.F. & PHALAN, B.
468 (2008) How will oil palm expansion affect biodiversity? *Trends in ecology & evolution*, 23,
469 538–545.
- 470 FOLEY, J., DEFRIES, R., ASNER, G.P., BARFORD, C., BONAN, G., CARPENTER, S.R., ET AL. (2005)
471 Global consequences of land use. *Science*, 309, 570–574.
- 472 FOSTER, R.J., HARMSSEN, B.J. & DONCASTER, C.P. (2010) Habitat Use by Sympatric Jaguars and
473 Pumas Across a Gradient of Human Disturbance in Belize, 42, 724–731.
- 474 FOSTER, R.J., HARMSSEN, B.J., VALDES, B., POMILLA, C. & DONCASTER, C.P. (2010) Food habits of
475 sympatric jaguars and pumas across a gradient of human disturbance. *Journal of Zoology*, 280,
476 309–318.
- 477 GALETTI, M. & DIRZO, R. (2013) Ecological and evolutionary consequences of living in a
478 defaunated world. *Biological Conservation*, 163, 1–6.
- 479 GARCIA-ULLOA, J., SLOAN, S., PACHECO, P., GHAZOUL, J. & KOH, L.P. (2012) Lowering
480 environmental costs of oil-palm expansion in Colombia. *Conservation Letters*, 5, 366–375.
- 481 GIBBS, H.K., RUESCH, A.S., ACHARD, F., CLAYTON, M.K., HOLMGREN, P., RAMANKUTTY, N. &
482 FOLEY, J.A. (2010) Tropical forests were the primary sources of new agricultural land in the
483 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of*
484 *America*, 107, 16732–16737.
- 485 GILROY, J.J., PRESCOTT, G.W., CARDENAS, J.S., CASTAÑEDA, P.G.D.P., SÁNCHEZ, A., ROJAS-
486 MURCIA, L.E., ET AL. (2015) Minimizing the biodiversity impact of Neotropical oil palm
487 development. *Global Change Biology*, 21, 1531–1540.
- 488 GIORDANO, A.J. (2015) Ecology and status of the jaguarundi *Puma yagouaroundi*: A synthesis of
489 existing knowledge. *Mammal Review*, 46, 30–43.
- 490 GONZALEZ, C.A.L., BROWN, D.E. & GALLO-REYNOSO, J.P. (2003) The ocelot *Leopardus*
491 *pardalis* in north-western Mexico: ecology, distribution and conservation status. *Oryx*, 37, 358-364.
- 492 HARMSSEN, B., FOSTER, R., SILVER, S. & DONCASTER, C.P. (2011) Jaguar and puma activity patterns
493 in relation to their main prey. *Mammalian biology*, 76, 320–324. Urban Fischer, Jena.
- 494 HARMSSEN, B.J., FOSTER, R.J., SILVER, S.C., OSTRO, L.E.T. & DONCASTER, P. (2009) Spatial and
495 temporal interactions of sympatric jaguars and pumas in a neotropical forest. *Journal of*

- 496 *mammalogy*, 90, 612–620.
- 497 HINES (2006) Presence. Software to estimate patch occupancy and related parameters.
- 498 IDEAM, IGAC, IAVH, INVEMAR, SINCHI & IIAP (2007) Ecosistemas continentales, costeros y
499 marinos de Colombia. Imprenta Nacional de Colombia, Bogota.
- 500 INSKIP, C. & ZIMMERMANN, A. (2009) Human-felid conflict: a review of patterns and priorities
501 worldwide. *Oryx*, 43, 18–34.
- 502 JOHNSON, D. (1980) The comparison of usage and availability measurements for evaluating
503 resource preference. *Ecology*, 61, 65–71.
- 504 KARANTH, U. & CHELLAM, R. (2009) Carnivore conservation at the cross roads. *Oryx*, 43, 1–2.
- 505 KELLY, M.J., NOSS, A.J., DI BITETTI, M.S., MAFFEI, L., ARISPE, R.L., PAVIOLO, A., ET AL. (2008)
506 Estimating Puma Densities From Camera Trapping Across Three Study Sites : Bolivia ,
507 Argentina , and Belize. *Journal of Mammalogy*, 89, 408–418.
- 508 KOLOWSKI, J.M. & ALONSO, A. (2010) Density and activity patterns of ocelots (*Leopardus pardalis*)
509 in northern Peru and the impact of oil exploration activities. *Biological Conservation*, 143,
510 917–925. Elsevier Ltd.
- 511 LAMBIN, E.F., MEYFROIDT, P., RUEDA, X., BLACKMAN, A., BÖRNER, J., CERUTTI, P.O., ET AL. (2014)
512 Effectiveness and synergies of policy instruments for land use governance in tropical regions.
513 *Global Environmental Change*, 28, 129–140.
- 514 LAURANCE, W.F., SAYER, J. & CASSMAN, K.G. (2014) Agricultural expansion and its impacts on
515 tropical nature. *Trends in Ecology and Evolution*, 29, 107–116.
- 516 LINK, A., DE LUNA, A. & BURBANO, J. (2013) Estado de conservación de uno de los primates más
517 amenazados con la extinción: El mono araña café (*Ateles hybridus*). In *Primates Colombianos*
518 *en Peligro de Extinción* (eds T. Defler, P. Stevenson, M. Bueno & D. Guzman), pp. 90–117.
519 Asociacion Primatologica Colombiana, Bogota.
- 520 LYRA-JORGE, M.C., CIOCHETI, G. & PIVELLO, V.R. (2008) Carnivore mammals in a fragmented
521 landscape in northeast of São Paulo State, Brazil. *Biodiversity and Conservation*, 17, 1573–
522 1580.
- 523 MACKENZIE, D.I. & BAILEY, L.L. (2004) Assessing the fit of site-occupancy models. *Journal of*
524 *Agricultural, Biological, and Environmental Statistics*, 9, 300–318.
- 525 MACKENZIE, D.I., NICHOLS, J.D., ROYLE, J.A., POLLOCK, K.H., BAILEY, L.L. & HINES, J.E. (2006)
526 Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence.
527 Academic Press, San Diego.
- 528 MAFFEI, L. & NOSS, A.J. (2008) How small is too small? Camera trap survey areas and density
529 estimates for ocelots in the Bolivian Chaco. *Biotropica*, 40, 71–75.
- 530 MASSARA, R.L., MARIA, A., PASCHOAL, D.O. & DOHERTY, P.F. (2015) Ocelot Population Status in
531 Protected Brazilian Atlantic Forest. *PLoS ONE*, 10, 1–17.
- 532 MAXWELL, S.L., FULLER, R.A., BROOKS, T.M. & WATSON, J.E.M. (2016) The ravages of guns, nets
533 and bulldozers. *Nature*, 536, 146–145.
- 534 MICHALSKI, F. & PERES, C. (2005) Anthropogenic determinants of primate and carnivore local
535 extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*,
536 124, 383–396.
- 537 DI MININ, E., SLOTOW, R., HUNTER, L.T.B., MONTESINO POUZOLS, F., TOIVONEN, T., VERBURG,
538 P.H., ET AL. (2016) Global priorities for national carnivore conservation under land use change.
539 *Scientific Reports*, 6, 23814.
- 540 MORENO, R.S., KAYS, R.W. & SAMUDIO JR, R. (2006) Competitive release in diets of ocelot
541 (*Leopardus Pardalis*) and puma (*Puma Concolor*) after jaguar (*Panthera Onca*) decline.
542 *Journal of Mammalogy*, 87, 808–816.
- 543 NEGRÕES, N., SARMENTO, P., CRUZ, J., EIRA, C., REVILLA, E., FONSECA, C., ET AL. (2010) Use of
544 Camera-Trapping to Estimate Puma Density and Influencing Factors in Central Brazil. *Journal*
545 *of Wildlife Management*, 74, 1195–1203.

- 546 NIELSEN, C., THOMPSON, D., KELLY, M. & LOPEZ-GONZALEZ, C.A. (2015) *Puma concolor*
547 (errata version published in 2016). The IUCN Red List of Threatened Species 2015:
548 e.T18868A97216466.
- 549 NOWELL, K. & JACKSON, P. (1996) Wild Cats: Status Survey and Conservation Action Plan. IUCN,
550 Gland.
- 551 NOSS, A.J., GARDNER, B., MAFFEI, L., CUELLAR, E., MONTANO, R., ROMERO-MUNOZ, R, ET
552 AL. (2012) Comparison of density estimation methods for mammal populations with camera traps
553 in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation* 15, 527–535.
- 554 OLIVEIRA, T.G., TORTATO, M.A., SILVEIRA, L., KASPER, C.B., MAZIM, F.D., LUCHERINI, M.,
555 ET AL. (2010) Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. In
556 *Biology and Conservation of Wild Felids* (eds D.W. Macdonald & A.J. Loveridge), pp. 563–574.
557 Oxford University Press, Oxford..
- 558 PACHECO, P. (2012) Soybean and oil palm expansion in South America: a review of main trends
559 and implications. Working paper 90. Bogor.
- 560 PARDO, L. & PAYAN, E. (2015) Mamíferos de un agropaisaje de palma de aceite en las sabanas
561 inundables de Orocué, Casanare, Colombia. *Biota colombiana*, 16, 54–66.
- 562 PAVIOLO, A., BLANCO, Y.E. DI, ANGELO, C.D. DE & DI BITETTI, M.S. (2009) Protection Affects the
563 Abundance and Activity Patterns of Pumas in the Atlantic Forest. *Journal of Mammalogy*, 90,
564 926–934.
- 565 PAVIOLO, A., CRAWSHAW, P., CASO, A., de OLIVEIRA, T., LOPEZ-GONZALES, C.A., KELLY,
566 M., ET AL. (2015) *Leopardus pardalis*. (errata version published in 2016) The IUCN Red List of
567 Threatened Species 2015: e.T11509A97212355.
- 568 PAYAN-GARRIDO, E., CASTANO-URIBE, C., GONZALEZ-MAYA, J.F., VALDERRAMA-VASQUEZ, C.,
569 RUIZ-GARCIA, C.M. & SOTO, C. (2013) Distribución y estado de conservación del jaguar en
570 Colombia. In *Grandes Felinos de Colombia* (eds E. Payan & C. Castano-Uribe), pp. 23–26.
571 Panthera Colombia, Conservación Internacional Colombia, Fundación Herencia Ambiental
572 Caribe y Cat Specialist Group UICN/SSC, Bogota.
- 573 PETRACCA, L.S., RAMIREZ-BRAVO, O.E. & HERNANDEZ-SANTIN, L. (2014) Occupancy
574 estimation of jaguar *Panthera onca* to assess the value of east-central Mexico as a jaguar
575 corridor. *Oryx*, 48, 133–140.
- 576 QUIGLEY, H., FOSTER, R., PETRACCA, L., PAYAN, E., SALOM, R. & HARMSSEN, B. (2017)
577 *Panthera onca*. The IUCN Red List of Threatened Species 2017: e.T15953A50658693.
- 578 POLISAR, J., MAXIT, I., SCOGNAMILLO, D., FARRELL, L., SUNQUIST, M.E. & EISENBERG, J.F. (2003)
579 Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a
580 management problem. *Biological Conservation*, 109, 297–310.
- 581 PRESCOTT, G.W., GILROY, J.J., HAUGAASEN, T., MEDINA URIBE, C., FOSTER, W. & EDWARDS, D.P.
582 (2016) Managing Neotropical oil palm expansion to retain phylogenetic diversity. *Journal of*
583 *Applied Ecology*, 53, 150–158.
- 584 RABINOWITZ, A. & ZELLER, K. (2010) A range-wide model of landscape connectivity and
585 conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143, 939–945.
- 586 RAJARATNAM, R., SUNQUIST, M., RAJARATNAM, L. & AMBU, L. (2007) Diet and habitat selection of
587 the leopard cat (*Prionailurus bengalensis borneoensis*) in an agricultural landscape in Sabah,
588 Malaysian Borneo. *Journal of Tropical Ecology*, 23, 209–217.
- 589 RIPPLE, W.J., ESTES, J.A., BESCHTA, R.L., WILMERS, C.C., RITCHIE, E.G., HEBBLEWHITE, M., ET AL.
590 (2014) Status and Ecological Effects of the World’s Largest Carnivores. *Science*, 343,
591 1241484.
- 592 RODRÍGUEZ-MAHECHA, J.V., ALBERICO, M., TRUJILLO, F. & JORGENSON, J. (2006) Libro Rojo de
593 los Mamíferos de Colombia. Serie Libros Rojos de Especies Amenazadas de Colombia.
594 Conservación Internacional Colombia, Ministerio de Ambiente, Vivienda y desarrollo
595 Territorial, Bogota.
- 596 ROYLE, J. & NICHOLS, J. (2003) Estimating abundance from repeated presence–absence data or

597 point counts. *Ecology*, 84, 777–790.

598 SCHALLER, G.B. & CRAWSHAW JR, P.G. (1980) Movement patterns of jaguar. *Biotropica*, 161–168.

599 SILVA-PEREIRA, J.E., MORO-RIOS, R.F., BILSKI, D.R. & PASSOS, F.C. (2011) Diets of three
600 sympatric Neotropical small cats: Food niche overlap and interspecies differences in prey
601 consumption. *Mammalian Biology*, 76, 308–312.

602 DA SILVEIRA, R., RAMALHO, E.E., THORBJARNARSON, J.B. & MAGNUSSON, W.E. (2010)
603 Depredation by Jaguars on Caimans and Importance of Reptiles in the Diet of Jaguar. *Journal*
604 *of Herpetology*, 44, 418–424.

605 SOLLMANN, R., FURTADO, M.M., HOFER, H., JÁCOMO, A.T.A., TÔRRES, N.M. & SILVEIRA, L.
606 (2012) Using occupancy models to investigate space partitioning between two sympatric large
607 predators, the jaguar and puma in central Brazil. *Mammalian Biology - Zeitschrift für*
608 *Säugetierkunde*, 77, 41–46.

609 STRAMPELLI, P. (2015) Status and habitat use responses of leopard (*Panthera pardus*) in a human
610 impacted region of rural Mozambique. Imperial College London.

611 SUNARTO, S., KELLY, M.J., PARAKKASI, K. & HUTAJULU, M.B. (2015) Cat coexistence in central
612 Sumatra: ecological characteristics, spatial and temporal overlap, and implications for
613 management. *Journal of Zoology*, 296, 104–115.

614 SUNARTO, S., KELLY, M.J., PARAKKASI, K., KLENZENDORF, S., SEPTAYUDA, E. & KURNIAWAN, H.
615 (2012) Tigers need cover: multi-scale occupancy study of the big cat in Sumatran forest and
616 plantation landscapes. *PLoS ONE*, 7, e30859.

617 TOBLER, M.W. & POWELL, G.V.N. (2013) Estimating jaguar densities with camera traps: Problems
618 with current designs and recommendations for future studies. *Biological Conservation*, 159,
619 109–118. Elsevier Ltd.

620 YUE, S., BRODIE, J.F., ZIPKIN, E.F. & BERNARD, H. (2015) Oil palm plantations fail to support
621 mammal diversity. *Ecological Applications*, 25, 2285–2292.

622 ZELLER, K.A., NIJHAWAN, S., SALOM-PÉREZ, R., POTOSME, S.H. & HINES, J.E. (2011) Integrating
623 occupancy modeling and interview data for corridor identification: A case study for jaguars in
624 Nicaragua. *Biological Conservation*, 144, 892–901. Elsevier Ltd.

625 ZUUR, A.F., IENO, E.N. & ELPHICK, C.S. (2010) A protocol for data exploration to avoid common
626 statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

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Biographical sketches

Valeria Boron’s research focuses on large carnivores, unprotected areas, and achieving conservation and sustainability across agricultural landscapes in South America. Panteleimon Xofis is a vegetation and landscape ecologist and his main research interests are the post disturbance landscape dynamics and the use of remote sensing for monitoring landscape change. Andres Link’s research is centred on understanding the ecological and social factors that influence primate sociality and evaluating how changes in land use influence the composition and conservation status of vertebrate communities. Esteban Payan is interested in the contribution of unprotected areas to large carnivore conservation, sustainable wild meat hunting, road ecology, jaguar-human conflict, and reducing the impact from productive practices. Joseph Tzanopoulos is a landscape ecologist working on impacts of land-use change on mountains and islands and reconciling biodiversity conservation and sustainable development on rural areas.

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Figures

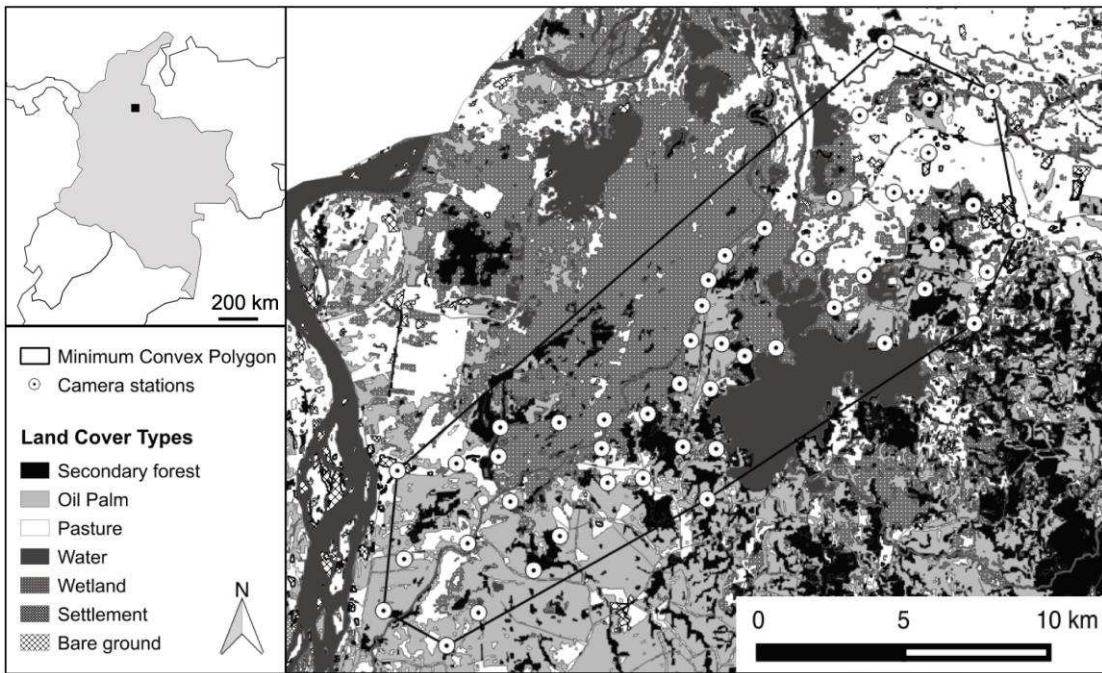


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689 **Fig. 1.** Felid species recorded by camera traps across the study site in the Magdalena river valley of
690 Colombia: Jaguar (a), Puma (b), Ocelot (c), Jaguarundi (d).

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713 **Fig. 2.** Map of the study site in the Magdalena river valley of Colombia with land cover types and
714 camera trap stations.

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Tables

739 **Table 1.** Best models for variables influencing occupancy (ψ) and probability of detection (p) of
740 jaguars, pumas, ocelots, and jaguarundis across the study site in the Magdalena river valley of
741 Colombia. AICc= Akaike’s information criterion adjusted for small sample size; Δ AICc difference
742 in AICc between each model and the best one; ML=Model Likelihood; k= no. of parameters, LL=
743 2log-likelihood (LL); dist.=distance; and settl.=settlements; prey10=prey>10kg. See Table S1 for
744 full model selection results (combined weight ≥ 0.95).

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	AICc	Δ AICc	AICc weight	ML	k	LL 746 747 748
Jaguar (46 detections, 15 stations)						
ψ (%wetland), p(roads)	172.06	0.00	0.38	1.00	4	164.96 749
ψ (%wetland, dist.settl), p(roads)	173.84	1.78	0.16	0.41	5	163.84 750
ψ (%wetland, %pasture), p(roads)	173.95	1.89	0.15	0.39	5	163.95 751
Puma (28 detections, 14 stations)						
ψ (dist.water, prey10), p(roads)	158.54	0.00	0.20	1.00	5	148.54 752
ψ (dist.water, %forest), p(roads)	158.93	0.39	0.17	0.82	5	148.93 753
ψ (dist.water, %pasture), p(roads)	159.82	1.28	0.11	0.53	5	149.82 754
Ocelot (58 detections, 23 stations)						
ψ (%pasture), p(roads)	259.74	0.00	0.28	1.00	4	251.74 755
ψ (%pasture, dist.settl.), p(roads)	261.05	1.31	0.15	0.52	5	251.05 756
ψ (%pasture, %forest), p(roads)	261.26	1.52	0.13	0.47	5	251.26 757
Jaguarundi (25 detections, 12 stations)						
ψ (%pasture),p(.)	153.55	0.00	0.29	1.00	3	147.55 758
ψ (%pasture, %wetland),p(.)	155.05	1.50	0.14	0.47	4	147.05 759
ψ (%pasture, %forest),p(.)	155.11	1.56	0.14	0.46	4	147.11 760 761 762 763 764 765

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772 **Table 2.** Estimates of β coefficient values, their associated standard errors (SE), and summed
 773 Akaike weights (W) for covariates that influenced occupancy (ψ) and probability of detection (p) of
 774 jaguars, pumas, ocelots and jaguarundis across the study site in the Magdalena river valley of
 775 Colombia. Dist.=Distance; Settl.=Settlements; NT=Not tested. *Denotes covariates with robust
 776 impact ($\beta \pm 1.96 \times SE$ not overlapping 0)

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Variables	Jaguar			Puma			Ocelot			Jaguarundi		
	β	SE	W	β	SE	W	β	SE	W	β	SE	W
ψ .%Wetland	2.91*	1.25	0.97	0.02	0.45	0.11	-0.02	0.40	0.15	0.45	0.40	0.19
ψ .%Pasture	-0.31	0.99	0.15	-0.97	0.58	0.27	-1.24*	0.50	0.89	-1.96*	0.64	0.91
ψ .%Oil palm	-	-	-	0.34	0.54	0.08	0.31	0.44	0.14	-0.17	0.41	0.14
ψ .%Forest	-	-	-	0.81	0.53	0.19	0.39	0.42	0.18	0.43	0.39	0.18
ψ .Dist. Water	-0.15	0.74	0.14	-1.20*	0.60	0.64	0.02	0.39	0.11	0.09	0.44	0.11
ψ .Dist. Settl.	0.57	0.61	0.16	-	-	-	0.34	0.43	0.15	0.04	0.39	0.11
ψ .Prey>10kg	0.02	0.55	0.14	0.80	0.51	0.30	NT	NT	NT	NT	NT	NT
ψ .Prey	-	-	-	0.53	0.47	0.10	NT	NT	NT	NT	NT	NT
p. roads	3.14*	1.12	0.97	2.27*	0.76	0.95	0.87*	0.43	0.96	-	-	-

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Table 3. Model-averaged estimates of probability of site use (ψ), probability of detection (p), and associated standard errors (SE) for jaguars, ocelots, pumas, and jaguarundis across the study site in the Magdalena river valley of Colombia.

	ψ	SE	p	SE
Jaguar	0.42	0.10	0.26	0.04
Ocelot	0.55	0.11	0.32	0.06
Puma	0.45	0.14	0.25	0.05
Jaguarundi	0.27	0.09	0.35	0.06

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Table 4. Species interaction factors (ϕ) between pairs of cat species across the study site in the Magdalena river valley of Colombia. SE=Standard error, CI=Confidence interval. * denotes strong interactions as the confidence intervals do not overlap 1.

	ϕ	SE	95% CI
Jaguar & Puma	1.93*	0.33	1.38-2.69
Jaguar & Ocelot	0.93	0.27	0.53-1.63
Jaguar & Jaguarundi	0.91	0.58	0.26-3.21
Puma & Ocelot	1.01	0.36	0.50-2.03
Puma & Jaguarundi	2.05*	0.72	1.03-4.07
Ocelot & Jaguarundi	1.47*	0.27	1.02-2.12

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865 **Supplementary Material**

866 **Supplementary Material 1: Land cover mapping**

867 We identified land cover types using Object Oriented Image Analysis (OBIA) on three Landsat 8
868 images, captured on 4/1/2015, 9/3/2015, and 12/7/2015 (downloaded from www.usgs.gov). We
869 increased the spatial resolution of the multispectral image bands by pansharpening, employing the
870 High Pass Filter technique and five as Kernel size. The pansharpened multispectral bands had more
871 than 90% correlation to the original ones in all cases, resulting in limited loss of spectral
872 information. We applied Tasseled Cap Transformation on all images using the coefficients
873 suggested by Liu *et al.* (2015) for Landsat 8 data, after converting the DN to TOA reflectance
874 values. The classification was further assisted by two vegetation indices, namely: the Normalized
875 Difference Vegetation Index (NDVI) and the Normalized Difference Moisture Index (NDMI). We
876 employed a step-wise Object Based Image Analysis (OBIA, in eCognition Developer 9) for the
877 image classification. In OBIA, spectrally similar adjacent pixels are grouped into meaningful
878 objects, which are then classified into one of the possible classes, using spectral as well as spatial,
879 neighborhood and other characteristics (Bock et al., 2005). For training the classifier and testing the
880 result we collected 343 ground truth validation points. We used two thirds of the ground-truth
881 dataset for training and one third for testing. Finally we performed an overall accuracy assessment
882 using an error confusion matrix method and calculated classification accuracy and kappa statistics.

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884 **References**

- 885 BOCK, M., XOFIS, P., MITCHLEY, J., ROSSNER, G. & M., W. (2005) Object-Oriented Methods for
886 Habitat Mapping at Multiple Scales – Case Studies from Northern Germany and Wye Downs,
887 UK. *Journal for Nature Conservation*, 13, 75 – 89.
- 888 LIU, Q., LIU, G., HUANG, G. & XIE, C. (2015) Comparison of tasseled cap transformations based on
889 the selective bands of Landsat 8 OLI TOA reflectance images. *International Journal of*
890 *Remote Sensing*, 36, 417–441.

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893 **Supplementary Table S1.** Species capture rates (i.e. species capture events divided by sampling

894 effort in each habitat), expressed per 100 trap nights. OP=Oil palm

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	Wetland	Wetland edge OP	Forest	Forest edge OP	Pasture	OP
Jaguar	11.11	8.55	2.53	0	0	0
Puma	0.59	1.39	1.85	4.98	0	0
Ocelot	4.89	2.58	1.69	3.32	0.25	1.97
Jaguarundi	1.63	5.17	0.17	0.95	0.25	0

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916 **Supplementary Table S2.** Model selection results (combined weight ≥ 0.95) for variables
 917 influencing occupancy (ψ) and probability of detection (p) of jaguars, pumas, ocelots, and
 918 jaguarundis across the study site in the Magdalena river valley of Colombia. AICc= Akaike's
 919 information criterion adjusted for small sample size; Δ AICc difference in AICc between each
 920 model and the best one; ML=Model Likelihood; k= no. of parameters, LL= 2log-likelihood (LL);
 921 dist.=distance; and settl.=settlements; prey10=prey>10kg.

	AICc	Δ AICc	AICc weight	ML	k	LL
Jaguar (46 detections, 15 stations)						
ψ (%wetland), p(roads)	172.06	0.00	0.38	1.00	4	164.06
ψ (%wetland, dist.settl), p(roads)	173.84	1.78	0.16	0.41	5	163.84
ψ (%wetland, %pasture), p(roads)	173.95	1.89	0.15	0.39	5	163.95
ψ (%wetland, dist.water), p(roads)	174.02	1.96	0.14	0.38	5	164.02
ψ (%wetland, prey10), p(roads)	174.06	2.00	0.14	0.37	5	164.06
Puma (28 detections, 14 stations)						
ψ (dist.water, prey10), p(roads)	158.54	0.00	0.20	1.00	5	148.54
ψ (dist.water, %forest), p(roads)	158.93	0.39	0.17	0.82	5	148.93
ψ (dist.water, %pasture), p(roads)	159.82	1.28	0.11	0.53	5	149.82
ψ (dist.water), p(roads)	160.61	2.07	0.07	0.36	4	152.61
ψ (all prey, %wetland), p(roads)	161.15	2.61	0.05	0.27	5	151.15
ψ (%pasture), p(roads)	161.31	2.77	0.05	0.25	4	153.31
ψ (dist.water, %oil palm), p(roads)	161.74	3.20	0.04	0.20	5	151.74
ψ (%pasture, prey10), p(roads)	161.78	3.24	0.04	0.20	5	151.78
ψ (dist.water, %wetland), p(roads)	162.43	3.89	0.03	0.14	5	152.43
ψ (dist.water, all prey), p(roads)	162.6	4.06	0.03	0.13	5	152.6
ψ (prey10), p(roads)	162.64	4.10	0.03	0.13	4	154.64
ψ (.), p(roads)	163.07	4.53	0.02	0.10	3	157.07
ψ (%pasture, all prey), p(roads)	163.26	4.72	0.02	0.09	5	153.26
ψ (%pasture, %oil palm), p(roads)	163.27	4.73	0.02	0.09	5	153.27
ψ (%pasture, %wetland), p(roads)	163.3	4.76	0.02	0.09	5	153.3
ψ (%pasture, %forest), p(roads)	163.31	4.77	0.02	0.09	5	153.31
ψ (prey10, %oil palm), p(roads)	163.99	5.45	0.01	0.07	5	153.99
ψ (prey10, %wetland), p(roads)	164.45	5.91	0.01	0.05	5	154.45
ψ (prey10, %forest), p(roads)	164.49	5.95	0.01	0.05	5	154.49
Ocelot (58 detections, 23 stations)						
ψ (%pasture), p(roads)	259.74	0.00	0.28	1.00	4	251.74

$\psi(\% \text{pasture, dist.settl.}), p(\text{roads})$	261.05	1.31	0.15	0.52	5	259.02
$\psi(\% \text{pasture, \%forest}), p(\text{roads})$	261.26	1.52	0.13	0.47	5	259.23
$\psi(\% \text{pasture, \%wetland}), p(\text{roads})$	261.51	1.77	0.12	0.41	5	259.24
$\psi(\% \text{pasture, \%oil palm}), p(\text{roads})$	261.55	1.81	0.11	0.40	5	259.25
$\psi(\% \text{pasture, dist.water}), p(\text{roads})$	261.71	1.97	0.10	0.37	5	259.26
$\psi(\% \text{oil palm, \%wetland}), p(\text{roads})$	265.16	5.42	0.02	0.07	5	259.27
$\psi(\% \text{forest}), p(\text{roads})$	265.61	5.87	0.01	0.05	4	259.28
$\psi(\% \text{forest, \%oil palm}), p(\text{roads})$	266.06	6.32	0.01	0.04	5	259.29
$\psi(\% \text{forest, \%wetland}), p(\text{roads})$	266.26	6.52	0.01	0.04	5	259.30
$\psi(\% \text{forest, \%dist.water}), p(\text{roads})$	266.69	6.95	0.01	0.03	5	259.31
Jaguarundi (25 detections, 12 stations)						934
$\psi(\% \text{pasture}), p(.)$	153.55	0	0.29	1.00	3	149.35
$\psi(\% \text{pasture, \%wetland}), p(.)$	155.05	1.5	0.14	0.47	4	147.05
$\psi(\% \text{pasture, \%forest}), p(.)$	155.11	1.56	0.14	0.46	4	147.11
$\psi(\% \text{pasture, \%oil palm}), p(.)$	155.38	1.83	0.12	0.40	4	147.38
$\psi(\% \text{pasture, dist.water}), p(.)$	155.51	1.96	0.11	0.38	4	147.51
$\psi(\% \text{pasture, dist.settl.}), p(.)$	155.54	1.99	0.11	0.37	4	147.38
$\psi(\% \text{wetland, \%forest}), p(.)$	157.16	3.61	0.05	0.16	4	149.16
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