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

Short title: Felid habitat use in Colombia

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Abstract

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

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

Introduction

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

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

Populations of all wild felids in Neotropical forests are rapidly declining (IUCN, 2015). Jaguars - the largest Neotropical cats- have experienced a contraction of their geographical distribution to less than 50% of their historical distribution (Rabinowitz & Zeller, 2010), and are currently considered Near Threatened by the IUCN (Quigley et al., 2017), with most subpopulations at high risk of extinction (de la Torre et al., 2017). Pumas are listed as Least Concern (Nielsen et al., 2015), however their population estimates are scarce in the Neotropics (Kelly et al., 2008). Both jaguars and pumas are declining in number due to habitat loss, persecution, and decline of their prey (Caso et al., 2008; Nielsen et al., 2015), yet knowledge about their habitat use across human modified agricultural areas is limited (Foster et al., 2010; De Angelo et al., 2011, 2013). Even less is known on the ecology of smaller felid species such as ocelots *Leopardus pardalis* (Least Concern) and jaguarundis *Herpailurus yaguaorundi* (Least Concern) across agricultural landscapes (Di Bitetti et al., 2006; Kolowski & Alonso, 2010; Giordano, 2015), and both species display decreasing population trends (Caso et al. 2015; Paviolo et al., 2015)

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

Methods

Study area

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

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

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

Camera trapping

We placed 47 camera stations between April and August 2014. The set up followed a systematic sampling approach for camera trapping used in previous studies on Neotropical felids (Maffei & Noss, 2008; Davis *et al.*,2011; Tobler & Powell, 2013). We positioned the grid to include all main habitat types of the study areas: forest (10 stations), wetland (9 stations), pastures (8 stations), and oil palm (8 stations). The remaining stations were located at the edge between forest and oil palm (6) and between wetland and oil palm (6). The minimum convex polygon linking the camera stations was 154.8 km^2. We placed the cameras at regular intervals of 1.6±0.3 km (Fig. 2), since this scale of analysis is considered appropriate to investigate habitat use by felids (Davis et al., 2011; Sunarto et al., 2012; Alexander et al., 2015; Everatt et al., 2015; Strampelli, 2015). Once reached the appropriate distance, we chose the exact camera location in a radius of 200m to maximise felid encounters. When possible we placed cameras along roads and established trails to increase the probability of capturing cat species. As a result, 60% of stations were placed on trails and we took these placement differences into account in the modelling approach. We used Cuddeback Attack (model: 1149) and Ambush (model: 1170) camera traps and set them at a height of 35 cm from the forest floor.

Occupancy modelling to study habitat use

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

Land cover mapping and covariates generation

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

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

Data analysis

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

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

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

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

Results

The land cover mapping resulted in the identification of seven types: pasture (35%), wetlands (20%), oil palm (19%), forest (12%), water (10%), bare ground (3%), roads and settlements (<1%). The overall classification accuracy was 0.89 indicating an excellent performance of the classifier. We obtained a sampling effort of 3069 trap nights and grouping 14 days into one sampling occasion resulted into 25-58 species detections (Table 1). Jaguar and ocelot detections corresponded to 12 and 21 individuals respectively; whereas pumas and jaguarundis could not be individually identified. No variable correlated with others ($r<0.7$). Out of the 12 jaguars recorded four are resident as they have been in the area since 2012.

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

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

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

Discussion

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

Factors affecting species habitat use

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

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

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

Ocelots and jaguarundis are sometimes regarded as ecologically plastic and more tolerant to habitat loss and degradation than the larger felids (Nowell & Jackson, 1996; Di Bitetti et al., 2006; Michalski & Peres, 2005; Lyra-Jorge et al., 2008; Kolowski & Alonso, 2010). Accordingly, the ocelot was the only cat species recorded in oil palm plantations albeit rarely. There have been previous records of ocelots using oil palm areas (Boron & Payan, 2013; Pardo & Payan, 2015) possibly because the latter have rodent prey and are suitable for hunting due to the open visibility, as found for the leopard cat *Prionailurus bengalensis* (Rajaratnam et al., 2007). However, despite their presumed habitat plasticity, both ocelots and jaguarundis were negatively and strongly affected by pastures, which supports earlier findings showing that they favor more natural forested habitats while avoiding human disturbance (Gonzalez et al., 2003; Maffei et al., 2005; Giordano, 2015; Massara et al., 2015).

Space partitioning

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

Mesocarnivores like ocelots and jaguarundis may be negatively affected by top predators and succeed when larger predators are rare or absent through phenomena of mesopredator release (Crooks & Soulé, 1999; Moreno et al., 2006). However, ocelots can also thrive in large protected areas with better habitat quality inhabited by top predators (Massara et al., 2015), and both ocelots and jaguarundis can be positively associated with jaguars and/or pumas (Di Bitetti et al., 2010; Noss et al. 2012). Accordingly, we found that jaguarundis tend to co-occur with both ocelots and pumas. Ocelot can negatively affect jaguarundi numbers (Oliveira et al., 2010) with spatial co-occurrence being favored by temporal segregation as jaguarundis are diurnal, whereas pumas and ocelots mostly crepuscular and nocturnal (Di Bitetti et al., 2010; Harmsen et al., 2011). Overall, the lack of spatial segregation between species in the region indicates that their distributions can overlap, thus developing conservation strategies to simultaneously benefit this guild may be possible even in modified landscapes.

Methodological considerations

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

Conclusion

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

Pasture is the main land cover in Colombia (Etter et al., 2006) and holds limited conservation value for felids in the region. Further studies are needed, however our results indicate that oil palm and agricultural expansion, when inevitable, should be targeted to already modified areas such as pastures, which would minimise the loss of natural habitats (Garcia-Ulloa et al., 2012). Concurring results were documented for other taxa (Gilroy et al., 2015; Prescott et al., 2016). We did not find a clear effect of oil palm, which could be because it still covers a small proportion of the landscape (19%). Nevertheless jaguars, pumas, and jaguarundis were never detected in oil palm areas. A stronger regulatory framework could facilitate land-use planning and incentive-based approaches (e.g. tax breaks, subsidized credits, premium pieces for certified products) also encourage the preservation of natural areas within productive landscapes (Lambin et al., 2014; Boron, Payan, et al., 2016). This study can help guiding land use planning in Colombia, which is particularly timely considering the country's transition towards peace. Further research should explore the habitat requirements for felid and other priority species to identify thresholds and optimal landscape configuration.

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Authors contributions

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

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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.

Figures

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

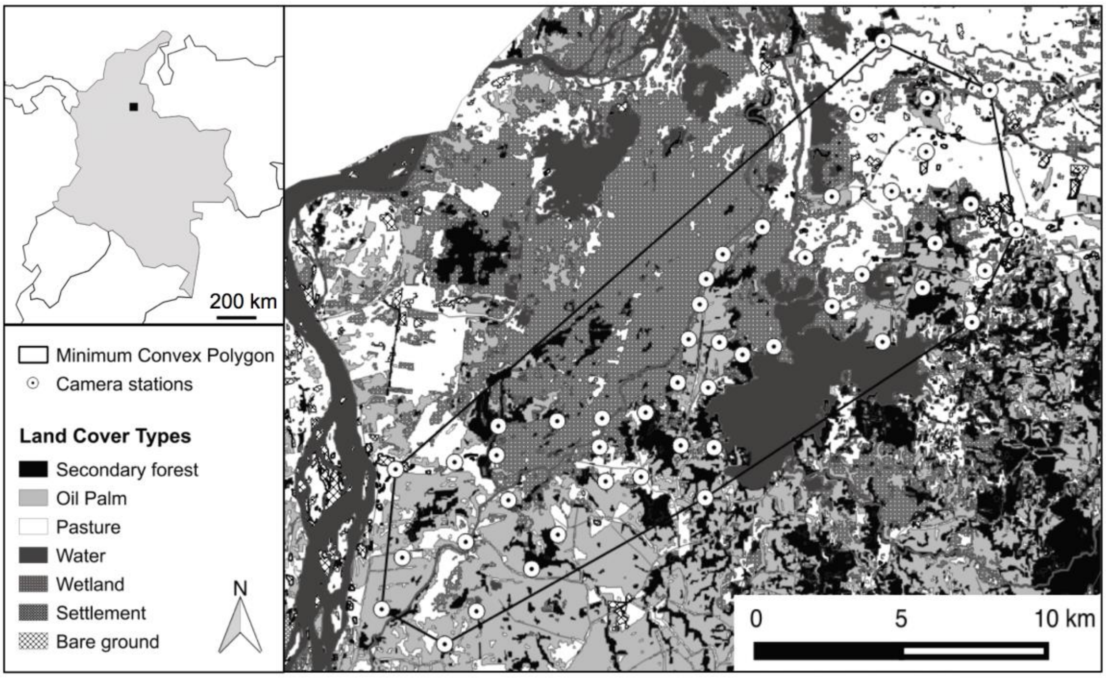

Fig. 2. Map of the study site in the Magdalena river valley of Colombia with land cover types and camera trap stations.

Tables

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

	AICc	**ΔAICc**	**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
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
Ocelot (58 detections, 23 stations)						
ψ(%pasture), p(roads)	259.74	0.00	0.28	1.00	4	251.74
ψ(%pasture, dist.settl.), p(roads)	261.05	1.31	0.15	0.52	5	251.05
ψ(%pasture, %forest), p(roads)	261.26	1.52	0.13	0.47	5	251.26
Jaguarundi (25 detections, 12 stations)						
ψ(%pasture),p(.)	153.55	0.00	0.29	1.00	3	147.55
ψ(%pasture, %wetland),p(.)	155.05	1.50	0.14	0.47	4	147.05
ψ(%pasture, %forest),p(.)	155.11	1.56	0.14	0.46	4	147.11

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

	Jaguar			**Puma**			**Ocelot**			**Jaguarundi**		
Variables	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	-	-	-

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

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

Supplementary Material

Supplementary Material 1: Land cover mapping

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

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Supplementary Table S1. Species capture rates (i.e. species capture events divided by sampling effort in each habitat), expressed per 100 trap nights. OP=Oil palm

	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

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

	AICc	**ΔAICc**	**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

ψ(%pasture, dist.settl.), p(roads)	261.05	1.31	0.15	0.52	5	251.05
ψ(%pasture, %forest), p(roads)	261.26	1.52	0.13	0.47	5	251.26
ψ(%pasture, %wetland), p(roads)	261.51	1.77	0.12	0.41	5	251.51
ψ(%pasture, %oil palm), p(roads)	261.55	1.81	0.11	0.40	5	251.55
ψ(%pasture, dist.water), p(roads)	261.71	1.97	0.10	0.37	5	251.71
ψ(%oil palm, %wetland), p(roads)	265.16	5.42	0.02	0.07	5	255.16
ψ(%forest), p(roads)	265.61	5.87	0.01	0.05	4	257.61
ψ(%forest, %oil palm), p(roads)	266.06	6.32	0.01	0.04	5	256.06
ψ(%forest, %wetland), p(roads)	266.26	6.52	0.01	0.04	5	256.26
ψ(%forest, %dist.water), p(roads)	266.69	6.95	0.01	0.03	5	256.69
Jaguarundi (25 detections, 12 stations)						
ψ(%pasture),p(.)	153.55	0	0.29	1.00	3	147.55
ψ(%pasture, %wetland),p(.)	155.05	1.5	0.14	0.47	4	147.05
ψ(%pasture, %forest),p(.)	155.11	1.56	0.14	0.46	4	147.11
ψ(%pasture, %oil palm),p(.)	155.38	1.83	0.12	0.40	4	147.38
ψ(%pasture, dist.water),p(.)	155.51	1.96	0.11	0.38	4	147.51
ψ(%pasture, dist.settl),p(.)	155.54	1.99	0.11	0.37	4	147.54
ψ(%wetland, %forest),p(.)	157.16	3.61	0.05	0.16	4	149.16