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Occupancy models reveal potential of conservation prioritization for Central American jaguars

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Keywords

camera-traps; carnivore conservation; habitat suitability; human influence; jaguar conservation units; large carnivores; occupancy models; species distribution models.

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Abstract

Understanding species-environment relationships at large spatial scales is required for the prioritization of conservation areas and the preservation of landscape connectivity for large carnivores. This endeavour is challenging for jaguars (*Panthera onca)*, given their elusiveness, and the local nature of most jaguar studies, precluding extrapolation to larger areas. We developed an occupancy model using occurrence data of jaguars across five countries of Central America, collected from camera-trap studies of 2–12 months' duration, deployed over an area of 14 112 km^2 from 2005 to 2018. Our occupancy model showed that habitat use of jaguars increased with primary net productivity and distance to human settlements, and decreased with distance to rivers. Detection of the species was related to survey effort and research team identity. Within the jaguar extent of occurrence, 73% was deemed suitable for the species, with 47% of it lying within Jaguar Conservation Units (JCU) and 59% of JCU land being legally protected. Suitable areas were divided into four distinct clusters of continuous habitat shared across country borders. However, large areas of predicted low habitat suitability may constrict connectivity in the region. The reliability of these spatial predictions is indicated by the model validation using an independent dataset (AUC = 0.82; sensitivity = 0.766, specificity = 0.761), and concordance of our results with other studies conducted in the region. Across Central America, we found that human influence has the strongest impact on jaguar habitat use and JCUs are the main reservoirs of habitat. Therefore, conservation actions must focus on preventing habitat loss and mitigating human pressure, particularly within the clusters of continuous areas of high suitability, and on restoring habitat to foster connectivity. The long-term persistence of jaguars in the region will depend on strong international cooperation that secures jaguar populations and their habitat across Central American borders.

Introduction

A central task in conservation planning is identifying and prioritizing key areas for protection of endangered species and preservation of landscape connectivity. This endeavour requires a thorough understanding of the drivers of species presence, habitat associations and avoidance mechanisms. For species living in degraded landscapes and at high risk of extinction, conservation strategies must be based on integrated assessments across political boundaries, spatial scales and species' entire ranges (Wikramanayake *et al.,* 2004; Rabinowitz & Zeller, 2010). This is particularly relevant for broadly distributed species that encompass a wide range of habitat types and land uses, such as some charismatic large carnivores, like the jaguar (*Panthera onca*).

Habitat suitability models can contribute to the prioritization of protected areas and support conservation planning for several species (Cabeza *et al.,* 2004; Li *et al.,* 2020; Mukherjee *et al.,* 2020). These models relate species occurrence data to environmental conditions, using derived response curves that best reflect the set of ecological requirements of the species of concern (Guisan *et al.,* 2017). However, regional and globally comprehensive species occurrence datasets are scarce, and publicly available spatial data are often heterogeneous, discontinuous across species ranges, lack standardized study designs and are strongly biased temporally and spatially (Boitani *et al.,* 2011; Rondinini *et al.,* 2011). These limitations make the prioritization of conservation areas at the appropriate scales challenging (Ferrier, 2002).

The jaguar is a near threatened apex predator in the tropical Americas (Quigley *et al.,* 2017), whose populations are decreasing and which has been subjected to much research on their habitat relationships. The species relies mainly on habitats with forest cover, water and a sufficient prey base (Sanderson *et al.,* 2002b), although it can tolerate a variety of conditions across their geographic range (Morato *et al.,* 2018). Most studies of jaguar habitat use to date have been conducted at local scales (Foster *et al.,* 2010; Zeller *et al.,* 2011; Rabelo *et al.,* 2019), except some relying heavily on either input from experts or interviews to local people (Rabinowitz & Zeller, 2010; Jędrzejewski *et al.,* 2018; Petracca *et al.,* 2018), or with very low representation of Central American data (Thompson *et al.,* 2021). Extrapolating local and expert-witness studies to larger areas may result in spurious inferences (e.g. generalizing patterns that may be true only locally, under unique conditions), due to a lack of standardized monitoring schemes and analysis, use of different environmental predictors, and most importantly, because patterns of jaguar resource selection vary across their geographic range (Morato *et al.,* 2018).

New methods for studying distribution and habitat suitability of species have emerged over the last two decades. Occupancy modelling allows for the study of species-habitat relationships while accounting for imperfect detection of the species or 'false absences' (i.e. not always detected when present, MacKenzie *et al.,* 2005). Not accounting for imperfect detection can underestimate the distribution of the target species (i.e. modelling only the apparent distribution, Kéry *et al.,* 2010), estimate covariate relationships biased towards zero (Tyre *et al.,* 2003), and confound detectability with occurrence covariates (Guillera-Arroita *et al.,* 2014). Thus, site-occupancy models are particularly useful to study the habitat relationships of rare elusive species with low population densities, such as the jaguar in Central America.

Central America is the second largest stronghold for jaguars after the Amazon (Sanderson *et al.,* 2002a), serving as a bridge to connect populations from the northern and southern ranges of the species' distribution (Fig. 1). It holds 16 Jaguar Conservation Units (JCUs), priority areas for jaguar conservation delineated by expert opinion. JCUs are defined as areas with enough prey base and habitat quality to sustain resident jaguar populations of at least 50 breeding individuals, or less if habitat is adequate and threat reduction allows population increase (Sanderson *et al.,* 2002b). Despite this, Central America holds one of the highest deforestation rates and proportional forest degradation worldwide (Redo *et al.,* 2012). In this region, jaguar populations have been extirpated from 67% of their former range, leaving the remaining populations at small sizes, in highly degraded landscapes and exhibiting early signs of genetic isolation due to habitat loss and decreased structural connectivity (Wultsch *et al.,* 2016). Currently, the jaguar's extent of occurrence (EOO) in Central America is limited almost entirely to the Caribbean slope where much of the forest still remains (Fig. 1).

Here we study the habitat suitability of Central America for jaguars using the largest compilation to date of jaguar camera-trap data from the region, spanning five out of the six jaguar range Central American countries from 2005 to 2018 (Fig. 1). We used data from 1457 camera-traps to develop a species distribution model based on an occupancy framework accounting for imperfect detection. We used the model to: a) test *a priori* hypotheses about influences of vegetation cover, primary productivity, rivers, protected areas and human disturbance on jaguar habitat use; b) map habitat suitability for jaguars in Central America; c) refine and target areas of conservation concern across political boundaries, using entirely empirical jaguar data for the first time in the region and d) prioritize international management efforts in Central America.

Materials and methods

Study area

Central America encompasses Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica and Panama; all of which – with the exception of El Salvador – are jaguar range countries (Fig. 1). This region holds a high biological diversity and represents a hotspot of plant and animal endemism (Myers *et al.,* 2000). It is characterized by a highly diverse pattern of land uses and a high human density of 94 ind./km^2 (World Bank, 2020). Central America is covered mainly by broadleaved evergreen and deciduous trees (61%) and mosaics of natural vegetation with croplands (21%). The rest of the region is represented by a diverse matrix of land uses, including croplands (6%), secondary growth forests (4%), grasslands (3%), wetlands (1%) and urban areas

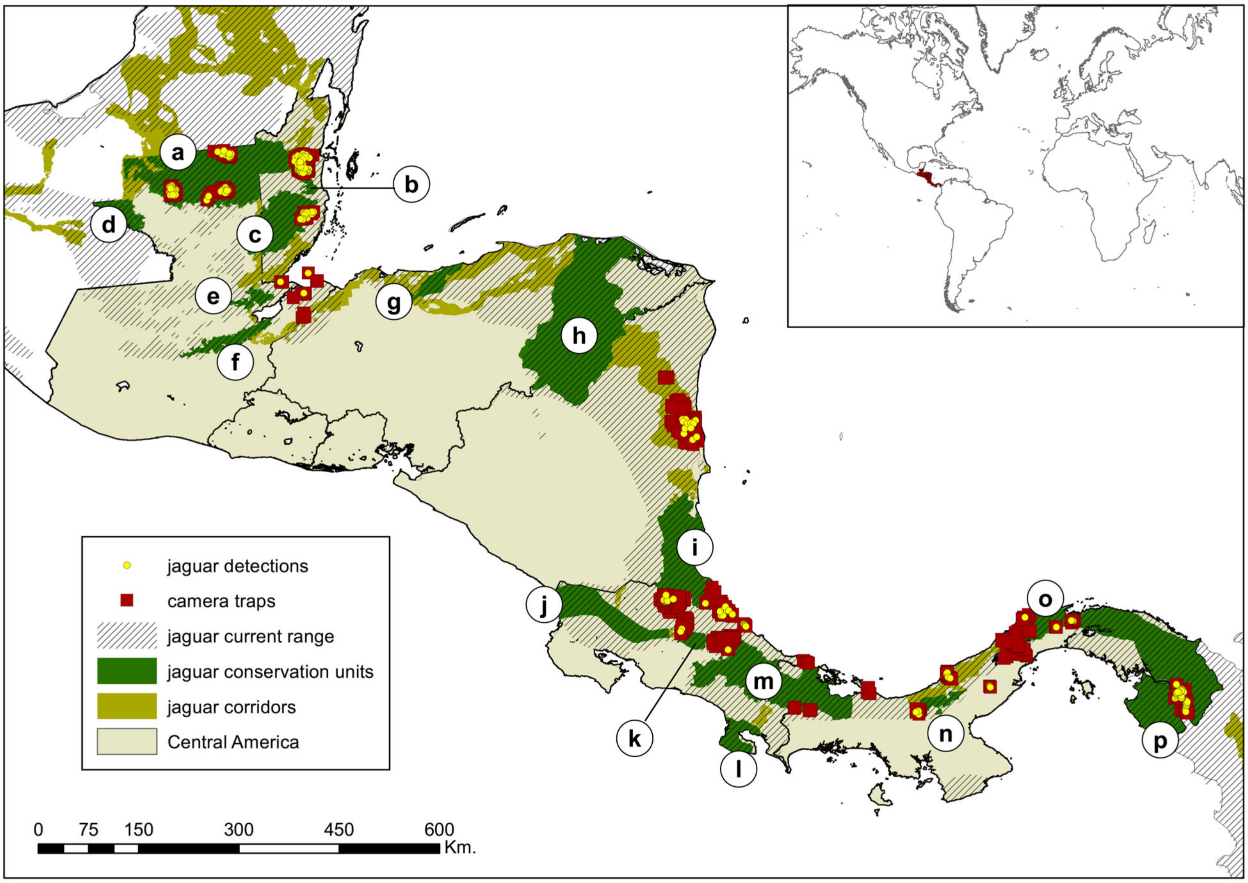

Figure 1 Central American study region, showing the camera-trap locations and the current distribution range of the species. Insert in right upper corner: Global map with Central America shaded in dark red colour. Main map: Jaguar Conservation Units and potential corridors according to Rabinowitz & Zeller (2010). Jaguar Conservation Units are identified by letters as follows: (a) Selva Maya; (b) Central Belize; (c) Maya Mountains; (d) Montes Azules/Sierra del Lacandon; (e) Sierra Santa Cruz; (f) Sierra de las Minas; (g) Cordillera Nombre de Dios; (h) Reserva de Biosfera Transfronteriza; i) Cerro Silva-Indio Maiz-Tortuguero, (j) Cordillera de Guanacaste; (k) Cordillera Volcanica Central; (l) Peninsula de Osa, (m) Talamanca-Cordillera Central; (n) Santa Fe; (o) Chagres; and (p) Chagres-Darien

(0.5%, ESA, 2015). For further details of the study region see Appendix S1.

Camera-trap data

We compiled records of jaguar detections and non-detections from camera-trap stations deployed in the study region from 2005 to 2018. The data were collected by eight well-established scientific teams working permanently with jaguars in each of these countries, as part of different research projects and jaguar conservation and monitoring activities in the region. Surveys' duration ranged from 1 to 12 months, and data recorded at each site also differed depending on project objectives (Appendix S2 and S3).

We created a study grid with a cell size of 36 km^2, to create a balance between accuracy of environmental measures, minimum estimations of jaguar home-range size (Rabinowitz & Nottingham, 1986; Salom-Pérez *et al.*, 2007) and comparability with previous studies in the region (Zeller *et al.*, 2011; Petracca *et al.*, 2018). Hence, we processed the camera-trap data by aggregating the detections-non detections of all camera-traps within 36km^2 cells. A detection was recorded whenever a jaguar was detected at a camera-trap i at grid-cell j and event k (sampling occasion: 1 month). Thus, grid-cell j obtained the value 1, regardless of how often a jaguar was detected there per event, otherwise a non-detection was noted 0.

Predictors of jaguar occupancy and detection

We compiled information on environmental and human disturbance covariates that could influence jaguar occurrence in the region. Variables for analysis were chosen based on previous research on jaguar ecology across the species range (Appendix S4) and after checking for collinearity ($|r| < 0.7$, $P > 0.05$; Appendix S5–S7). We obtained covariate values at the respective year of camera-trapping when possible, otherwise at the closest year available. For jaguar occurrence we selected the environmental variables of elevation (*elev*), tree cover per cent (*treecov%*), distance to rivers (*dist_riv*) and primary net productivity (*npp*); and variables related to human disturbance such as agricultural area (*agriculture*), distance to settlements (*dist_sett*), distance to roads (*dist_roads*), distance to protected areas (*dist_pa*), and interaction between tree cover per cent and area of agriculture (*treecov*agriculture;* details on covariate calculations in Appendix S8).

For modelling jaguar detectability we selected two additional covariates, survey effort (*eff*) and the identity of the research team (*team*) which collected the data in each grid-cell *j* and event *k*. Survey effort was calculated by summing the days each camera-trap was active within each grid-cell over the year. All covariate values for occupancy and detection were standardized (mean = 0; SD = 1) for the occupancy analysis.

Occupancy analysis

We used site-occupancy models to estimate the occurrence probability of jaguars at grid-cells *j* using the package unmarked (Fiske & Chandler, 2011) in R-4.0.4 (R Core Team, 2021). Detection histories were created using the package *camtrapR* (Niedballa *et al.,* 2016), and aggregated into monthly sample intervals (*k,* 'events') to avoid overdispersion and aid in model convergence. We designed three general *a priori* sets of hypotheses explaining occupancy probability by (1) natural habitat variables (2) human influence variables, or (3) a mixture of both (as in Jordan *et al.,* 2016). Within each of these, we developed a subset of several biologically plausible candidate models, representing different hypotheses of increasing complexity on the environmental characteristics associated with jaguar occurrence in the region. We removed from the occupancy analysis the data from one site (Appendix S2), given that it represented an outlier in distance to river, and it pulled models towards a non-logical negative association between jaguar and rivers.

We fitted single-state, single-season occupancy models treating each unique site-year combination sampled ('grid cell – year') as independent sites. We used a static approach because we were interested in the static occupancy patterns of jaguars across the region, rather than the turnover rates between years; and temporal replication was limited due to grid cells not being surveyed consistently on the same years (72% of the grid-cells had data on 1 year only, 19% on 2 years, and the rest on three to 6 years). We expected 'year' to be more related to changes in the environment across time than on the jaguar habitat use per se, and that this variability would be accounted for by matching the covariate values to the respective year of camera-trapping or the closest year available. However, we also tested for any potential year effects by running a model version with year as random effect for each of the models in the candidate set, using the R package *ubms* (Kellner, 2021; Appendix S9).

We used the most parsimonious model (i.e. top ranked) for extrapolation and evaluated it using a goodness of fit test (GOF; MacKenzie & Bailey, 2004) and checking the Dunn–Smyth residuals for both its occupancy and detection components (Warton *et al.,* 2017). We also used an independent dataset (Jędrzejewski *et al.,* 2018) to evaluate the predictive accuracy of the top model using the area under the receiver operating characteristic (AUC, details in Appendix S10). This top model was then used to predict jaguar occupancy probability in the region based on predictor values for the year 2020 (Appendix S9). We assessed model's performance using the value that minimized the difference between sensitivity and specificity as threshold (Liu *et al.,* 2005). For this we finally used a threshold value of probability of occupancy of $\Psi \geq 0.55$. We interpret here probability of occupancy as 'probability of habitat use'.

Results

Camera-trap data

We collected 409 independent jaguar detections from 1457 camera-traps and on 113 308 trapping-days. The surveyed grids ($n = 392$) covered an area of 14 112 km^2 across five countries (6% of the jaguar EOO in Central America). When aggregating the data at country level, the average number of surveyed years was 6.2 (range = 2–8 years, for Nicaragua and Panama respectively) and the average effort per year per country was 3657 camera-trap-days (range = 1547–5174 camera-trap-days, for Guatemala and Panama respectively).

Predictors of jaguar habitat use and detection

Habitat use of jaguars in Central America was best explained by models combining both natural habitat and human disturbance covariates. Out of the competing models, those including both types of covariates accounted for 99% of the cumulative AIC-weight (Appendix S11). The top model for jaguar habitat use included net primary productivity, distance to settlement, and distance to river; all with 95% confidence intervals not overlapping zero. This top model was also consistent with the model selection results performed within the Bayesian framework, in which 'year' as a random effect was evaluated but did not appear in the top ranked model (Appendix S12 and S13). Therefore, from here on we refer to the results of the analysis of this top model within the frequentist framework (Appendix S14).

Jaguar habitat use increased with net primary productivity (npp: $\beta = 0.651$, SE = 0.214) and distance to settlements (dist_sett: 3.910, SE = 0.651), and decreased with increasing distance to rivers (dist_riv: 0.981, SE = 0.245). The greatest relative impact on predicted jaguar habitat use was given by distance to settlements, evidenced by the magnitude of its β-coefficient of 3.910. One standard deviation (SD) increase in distance to settlement had an effect size 3.98 times greater than a similar increase in distance to rivers, and an effect size 6.01 times greater than a 1SD increase in net primary productivity. Jaguar detection probability was strongly influenced by survey effort, with higher detection in grid-cells with higher survey effort ($\beta = 0.629$, SE = 0.082), and research team (Table 1). The top model had a good

Table 1 Parameter estimates of the top model of jaguar habitat use in Central America. The baseline team included in the intercept was CECON

Covariate	β	SE	Lower 95%CI	Upper 95%CI	z	*P* (>|z|)
Occupancy						
Intercept[a]	2.130	0.415	1.316	2.943	5.128	<0.001
npp[a]	0.651	0.214	0.232	1.071	3.042	0.002
dist_sett[a]	3.910	0.651	2.634	5.186	6.006	<0.001
dist_river[a]	0.981	0.245	0.501	1.461	4.005	<0.001
Detection						
Intercept[a]	−1.025	0.245	−1.506	−0.545	−4.181	<0.001
Effort[a]	0.629	0.082	0.469	0.789	7.713	<0.001
Site (Team) effects						
Coastal-Jaguar-Conservation	0.772	0.280	0.223	1.321	2.758	0.006
Yaguará-Panamá	0.144	0.295	−0.434	0.723	0.489	0.625
Panthera-Costa Rica[a]	−1.081	0.497	−2.054	−0.107	−2.175	0.030
Panthera-Guatemala	−1.219	0.813	−2.813	0.375	−1.499	0.134
Panthera-Nicaragua	−0.729	0.368	−1.450	−0.008	−1.982	0.047
Panthera-Southampton-UB-ERI[a]	1.373	0.283	0.819	1.927	4.856	<0.001
WCS-Washington	0.529	0.325	−0.108	1.166	1.627	0.104

[a] Significance level of coefficients at $\alpha = 0.05$.

predictive performance (AUC = 0.821; sensitivity = 0.766, specificity = 0.761).

Spatial prediction of jaguar habitat suitability

The spatial prediction of our top model predicted habitat for jaguars in half of Central America surface ($\Psi \geq 0.55$; Fig. 2 (a)), comprising a total area of 269388 km^2, of which 33% is encompassed by JCUs. Within the EOO of the jaguar (i.e. boundary of its distribution; Quigley *et al.,* 2017), more than two thirds (73%) are suitable for the species (192 306.539 km^2), with 47% lying within JCUs and 59% of JCU land being legally protected (Fig. 3). Habitat was concentrated mainly in the Selva Maya in northern Guatemala and Belize, north-eastern Honduras, eastern Nicaragua and eastern and western Panama (Fig. 2(a)). Overall mean jaguar habitat use probabilities were lowest for El Salvador (Ψ_{mean} = 0.199, SD = 0.219) and Costa Rica (Ψ_{mean} = 0.458, SD = 0.319) and the Panamanian JCU Chagres (Ψ_{mean} = 0.454, SD = 0.340); whereas highest for Belize (Ψ_{mean} = 0.787, SD = 0.282) and the Honduran-Nicaraguan JCU Reserva de Biosfera Transfronteriza (Ψ_{mean} = 0.990, SD = 0.045). The JCU's with the highest coverage of habitat were Selva Maya, Central Belize and Peninsula de Osa (>98%, Table 2), whereas the lowest coverage is reported for Chagres and Cordillera Volcanica Central (<28%).

The largest continuous habitat was predicted in four main clusters, all of which extend across political boundaries, (1) Guatemala-Belize (62 172.861 km^2), (2) eastern Honduras-Nicaragua (128 149.928 km^2), (3) South Costa Rica-Northern Panama (29 304.690 km^2) and (4) Panamanian Darien (17 346.392 km^2, Fig. 3). In contrast, four large areas of predicted low habitat suitability within the EOO of the jaguar are located along eastern-Guatemala, western-Honduras, central-Costa Rica and north-central Panama (Fig. 2(a)).

Habitat was also predicted by our model in non-surveyed areas. Within the jaguar EOO, these areas are the east of Honduras, a country for which we had no data on jaguar occurrence; most of the Nicaraguan Atlantic-coast, and areas across central-Guatemala. Outside the jaguar EOO, small and fragmented areas of high suitability were predicted along the Pacific coast of Central America (Fig. 2(a)).

Overall the uncertainty of our habitat suitability predictions was lowest for the areas with higher habitat suitability values (Fig. 2(b)), and for the countries of Belize and Nicaragua. Uncertainty was higher for areas such as central-Guatemala, eastern-Honduras and central Costa Rica (Fig. 2 (b)).

Discussion

We conducted a broad-scale quantitative analysis of jaguar habitat use, using for the first time a comprehensive dataset of direct jaguar observation records from multiple locations and surveys across Central America, a region in which the current EOO of the species holds one of the highest deforestation rates within all Latin America and the Caribbean (Aide *et al.,* 2013). Such a broad-scale approach is required when addressing jaguar conservation (Sanderson *et al.,* 2002b), and accordingly, we identified key areas for conservation and population connectivity across international borders using a jaguar database of camera-trap records across Central America.

We found evidence that jaguar suitability at broad-scale is related to both environmental and human influence variables, however the latter impacted the species more strongly. Jaguars were positively associated with primary productivity and watercourses, supporting findings of previous studies (Jędrzejewski *et al.,* 2017; Jędrzejewski *et al.,* 2018). Primary productivity is associated with higher mammal diversity (Fritz *et al.,* 2016) and herbivore densities (Jedrzejewski

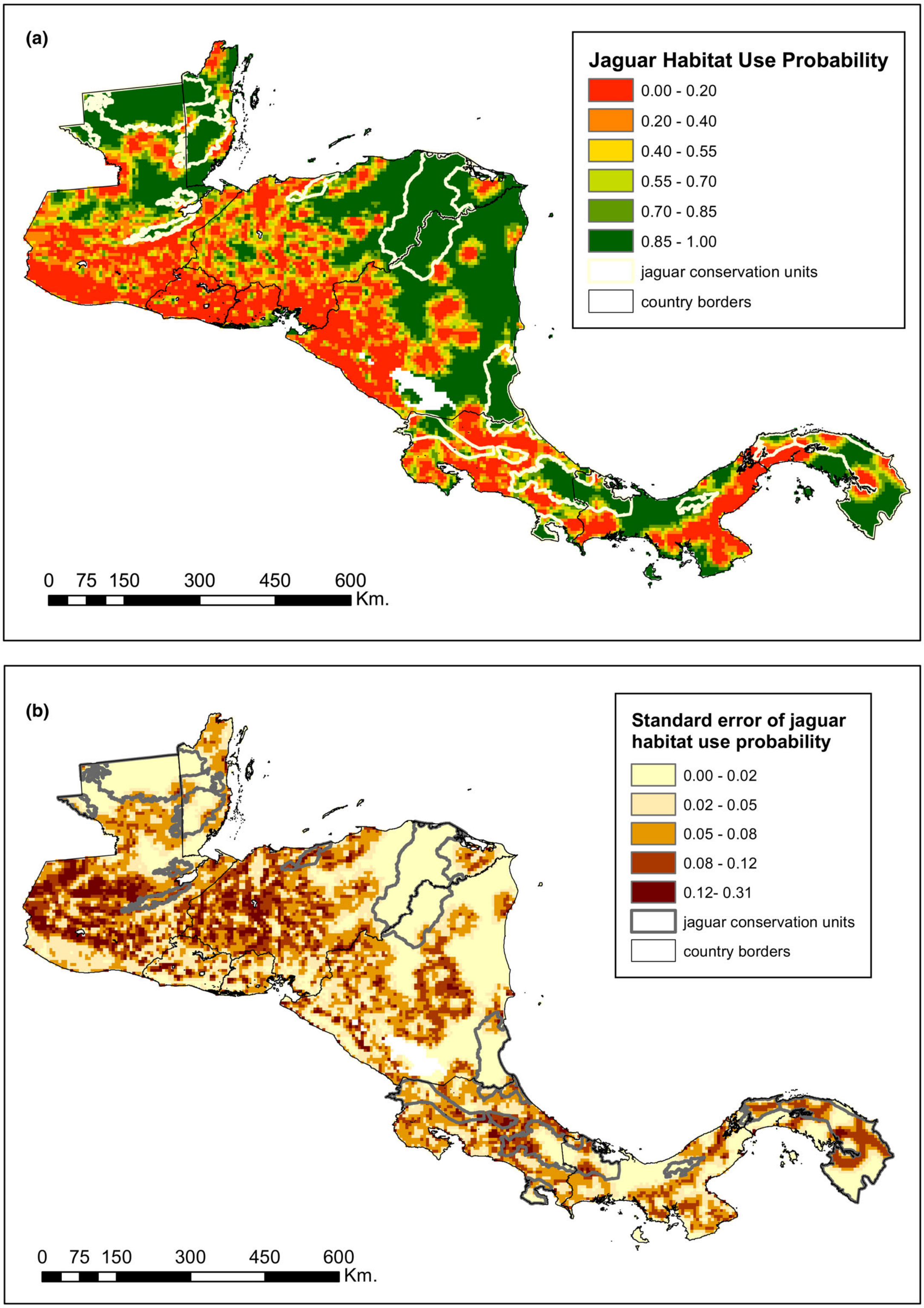

Figure 2 Prediction of jaguar habitat use in Central America, (a) Predicted probability of jaguar habitat use, (b) Standard error of the predicted probabilities of jaguar habitat use

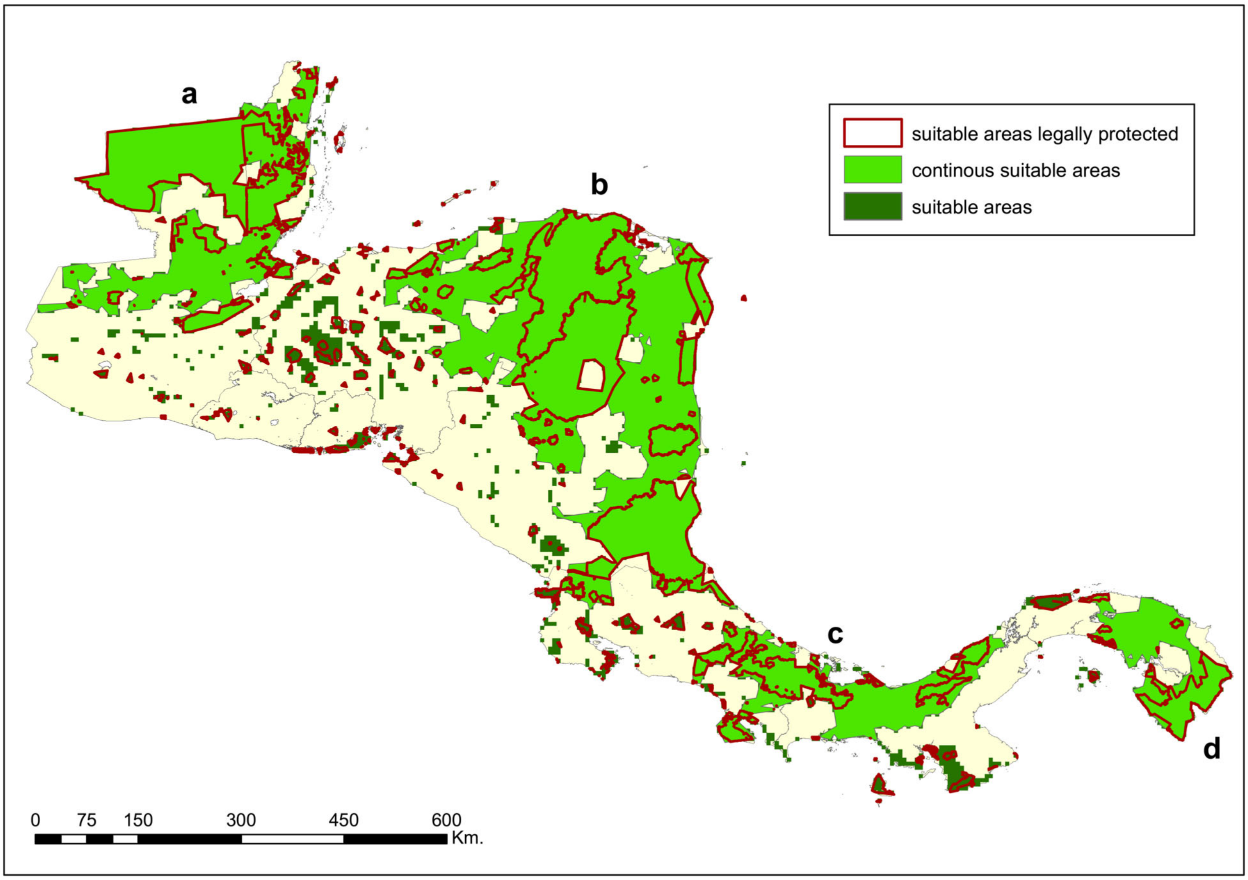

Figure 3 Continuous areas (light green) of jaguar habitat suitability ($\Psi \geq 0.55$) in Central America: (a) Guatemala-Belize, (b) eastern Honduras-Nicaragua, c) South Costa Rica-Northern Panama and d) Panamanian Darien. Dark green: remaining suitable areas. Red outline: legally protected areas registered up to January 2021 (UNEP-WCMC & IUCN, 2021)

& Jedrzejewska, 1996), thus could represent higher prey availability. Additionally, the persistence of jaguar populations is also associated with primary productivity, given that jaguar populations exhibit higher extirpation probabilities in drier areas with lower vegetation productivities than in more humid, productive areas (Jędrzejewski *et al.,* 2017). Similarly, watercourses represent areas for abundant prey (Gaitán *et al.,* 2020), and additionally, may offer protection by providing opportunities for safe movement (Foster *et al.,* 2010). The strong negative response of jaguars towards human settlements (dist_sett: $\beta = 3.910$, $SE = 0.651$) evidences an avoidance to human proximity (Petracca *et al.,* 2018; Meyer *et al.,* 2019), and compensatory mechanisms the species uses to adapt to human-dominated landscapes (Morato *et al.,* 2018). However, the effect of human presence on jaguars likely depends not only on the presence of humans *per se,* but also on human activities. In our model however, we could not consider different human activities due to the scale of our study. At local scales, we expect some variability on jaguar response to human presence, based on how humans interact with jaguars and the environment. An illustration of this is Guna Yala in Panama, an area occupied exclusively by indigenous communities where habitat suitability was underestimated by our model (Meyer *et al.,* 2019).

Overall, our predictions of habitat use suggest that there are 192 306.539 km^2 of habitat available for jaguars across the species EOO in Central America, and that JCUs represent the most important reservoirs of it. JCUs encompass almost half of all available habitat within the jaguar EOO, with >50% being protected by law. They also contribute to structural connectivity across political boundaries, especially to the four largest continuous zones of habitat in Central America (Fig. 3), all of which share bi-national borders. Notwithstanding, there are two JCUs of special conservation concern that exhibit the lowest mean habitat suitability ($\Psi_{mean} < 0.50$) and habitat coverage (<35%), namely Chagres (Panama) and Volcanica Central (Costa Rica; Table 2). The latter JCU most likely does not act as a jaguar stronghold anymore (Salom-Pérez *et al.,* 2021) and this status should be reflected in an updated list of current JCUs.

We identified four areas of low habitat suitability that could impair connectivity in the region, central-Costa Rica, central-Panama and eastern-Guatemala and western-Honduras (Fig. 2(a)), with the first two acting as potential constriction points of population connectivity from South to Central

Table 2 Mean jaguar habitat use probabilities (Ψ_{mean}), standard deviations (SD) and percentage covered by suitable areas per country and Jaguar Conservation Units in Central America

Name	Ψ_{mean}	SD	% suitable areas
Country[a]			
Guatemala	0.51	0.34	43.78
Belize	0.78	0.28	76.82
Honduras	0.60	0.34	53.97
El Salvador	0.19	0.21	7.52
Nicaragua	0.64	0.37	58.84
Costa Rica	0.45	0.31	36.96
Panama	0.59	0.37	54.75
Jaguar Conservation Unit			
Selva Maya	0.95	0.11	98.52
Central Belize	0.94	0.04	100.00
Montes Azules/Sierra del Lacandon	0.90	0.11	92.79
Maya Mountains	0.86	0.2	89.89
Cordillera Nombre de Dios	0.64	0.26	70.30
Sierra Santa Cruz	0.81	0.16	87.78
Reserva de Biosfera Transfronteriza	0.99	0.04	99.66
Sierra de las Minas	0.71	0.19	77.22
Cerro Silva-Indio Maiz-Tortuguero	0.88	0.18	90.92
Cordillera de Guanacaste	0.59	0.31	53.81
Chagres	0.45	0.34	36.05
Cordillera Volcanica Central	0.49	0.18	27.65
Chagres-Darien	0.69	0.32	70.65
Talamanca-Cordillera Central	0.80	0.21	84.64
Santa Fe	0.95	0.08	81.21
Peninsula de Osa	0.82	0.22	99.99

[a] Countries sorted by decreasing latitude.

America, which coincides with Salom-Pérez *et al*. (2021) and Meyer *et al*. (2020). Particularly concerning for the northern-Central American jaguar populations is the low habitat suitability in the Guatemala-Honduras connection, given that this area connects the Trinational-Selva Maya, the largest continuous neotropical forest north of the Amazon, and the Reserva de Biosfera Transfronteriza; two JCUs of great importance within the jaguar corridor (Rabinowitz & Zeller, 2010; Fig. 2(a)).

Our jaguar habitat use predictions seem robust despite the uncertainty of our estimates (Fig. 2(b)). They generally coincide with previous broad-scale jaguar space use studies encompassing Central America (Jędrzejewski *et al.,* 2018; Petracca *et al.,* 2018; Thompson *et al.,* 2020, 2021), and match general gene flow patterns found by Wultsch *et al*. (2016). However, our model has the advantage of being the first jaguar habitat use model that can be extrapolated to a broad-scale by including local studies' uncertainties across several Central American ecoregions, providing more precise estimates than those extrapolated from small-scale studies, for which patterns cannot be generalized. Our camera-trap data also represents reliable presence-based evidence of jaguars for Central America, a region significantly underrepresented in recent range-wide studies (Thompson *et al.,* 2021), and that in comparison to more widely available interview-derived data (Petracca *et al.,* 2018), does not require to account for false positives that can severely bias occurrence estimates (Miller *et al.,* 2011). Lastly, our occurrence estimates account for sampling biases explicitly by including jaguar detection probability, not considered in previous approaches (Jędrzejewski *et al.,* 2018).

We believe our model is general and representative enough of the Central American jaguar populations to effectively identify the drivers of the species' habitat use in our study region, as supported by our model's external validation. However, there are four potential sources contributing to uncertainty. First, even with the extensive camera-trapping effort, we were unable to cover the full gradient range of environmental variables such as forest cover and agriculture across our study region. Our data are biased towards areas occupied by the species, given that in jaguar camera-trap studies, effort is commonly maximized by placing cameras in areas known *a priori* to have jaguars. While human factors can have disproportionate effects on jaguar occurrence (Thompson *et al.,* 2020), it is possible that this spatial bias might be partially responsible for the low importance of environmental variables in our model. Using a more comprehensive dataset might show that, whereas human variables have a strong effect on jaguar-occupied areas, there is a range of environmental values that strongly limit the species' presence in jaguar-unoccupied areas. Second, there are areas predicted with a much higher habitat suitability than expected, such as the patches of high jaguar habitat use south of Selva Maya in Guatemala, central Honduras (*pers. comm.,* F. Castañeda, 12 May 2021), central and north-eastern Nicaragua (Hernández Potosme, 2019), and areas of Ngäbe-Buglé and around Darien in Panama (Meyer *et al.,* 2019); all from which jaguars have either been extirpated or remain in low numbers. This limitation would be improved, as for the first, by adding data to our model on jaguar-unoccupied areas. A third limitation is that information on sex of individuals (Foster *et al.,* 2010), prey abundance (Rabelo *et al.,* 2019), and poaching (Romero-Muñoz *et al.,* 2019) were unavailable to us and are closely related to jaguar occupancy. Therefore, predicted areas of high suitability may show smaller populations than expected due to high poaching of jaguars or their prey (Redford, 1992). And lastly, despite we aggregated occurrence accounts within sample units, given the variability of jaguar home range sizes across the region (Figueroa, 2013; Thompson *et al.,* 2020, 2021; Salom-Pérez *et al.,* 2021), there may be spatial non-independence at this spatial scale potentially affecting our standard errors.

Notwithstanding, our jaguar model usefully informs the prioritization of key areas and actions for the persistence of the species, with quantified uncertainty, and it provides the basis for future studies on connectivity between jaguar habitats in this region. Two main conservation actions supported by our results are the following. First, prevent habitat loss and mitigate human pressure within the continuous suitable areas that provide structural connectivity, as to prevent further population decrease and extirpation due to landscape fragmentation (Zanin *et al.,* 2015). Securing habitat for jaguars should therefore be focused on the largest JCUs with highest habitat coverage within: Selva Maya and Belize, Reserva de Biosfera Transfronteriza, Cerro Silva-Indio Maiz-Tortuguero, Talamanca-Cordillera Central and Chagres-Darien. In contrast, human pressure mitigation should be targeted at smaller JCU's with less remaining habitat coverage: Sierras Santa Cruz and Minas, Cordilleras Nombre de Dios and Guanacaste. Second, support habitat restoration to improve connectivity, particularly in central-Costa Rica and central Panama, where most habitat suitability has been lost. These suggested conservation targets could be supported by the implementation of conservation schemes in the buffer zones of JCUs and protected areas, such as indigenous/community managed reserves (Mena *et al.,* 2020) or forestry concessions (Tobler *et al.,* 2018), to encourage sustainable land management regimes more compatible with jaguar conservation and integrate local actors and stakeholders better.

Lastly, providing spatial requirements about the species status is crucial to assess the conservation status of the species and its evolution through time (IUCN, 2012). Some conservation works focus on population size estimates; however, they are costly, require more intense field work and produce estimates that cannot be extended to a subcontinental scale. Here, our study provides a tool that conservation managers and stakeholders may use to implement local actions but also broad-scale decisions.

We are aware that camera-trapping may not be feasible in all areas of species' environmental gradients, however, camera-trap data can be complemented with data derived from other methods in areas where the latter are more cost-effective (Petracca *et al.,* 2018). We encourage further international collaboration and coordination to secure the long-term persistence of jaguars in this region of rapid human-induced transformation, designing standardized data collection protocols, facilitating more comprehensive jaguar datasets and securing jaguar populations and their habitat across country borders.

Authors' contributions

APC, JL, AP and SKS conceived the ideas and designed methodology; APC, DA, SA, LB, JC, DC, CPD, RF, MG, RG, BH, SH, RL, DM, RM, NM, RM, RS, AS, IT, DT and YU collected the data; APC, JL and AP analysed the data; APC led the paper writing supported by SKS, JL, AP and VG. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details on study area.

Appendix S2–S3. Research teams and data (requests for data should be directed to the corresponding authors).

Appendix S4. Study species.

Appendix S5–S8. Predictor variables.

Appendix S9–S10. Occupancy analysis and model validation.

Appendix S11. Candidate model list.

Appendix S12. Candidate models list including year as random effect.

Appendix S13. Top model obtained Bayesian framework.

Appendix S14. R Scripts and anonymized data for running Occupancy modeling and evaluating the Dunn–Smyth residuals for the top model.