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The jaguar in South America – status review and strategy

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Estimating species distribution changes due to human impacts: the 2020's status of the jaguar in South America

Monitoring species distribution over time and understanding factors and mechanisms that determine it is crucial for effective conservation planning. We estimated the current jaguar *Panthera onca* distribution in South America based on a large set of records (2,557) from 2000–2020 and a set of absence points (both field collected and randomly selected from known jaguar absence areas) using a combination of kriging interpolation and logistic regression models. The current jaguar range in South America is estimated at 7.9 million km^2 which is 14% less than the estimate for 2015 and 25% less than for 2000. The reduction of the jaguar's South American range has been continuous and relatively rapid. Our logistic regression models show that the decrease in jaguar distribution across South America was mainly driven by increasing deforestation, road density, pasture and farmland area, and human population density. During the last 20 years, negative changes in the jaguar habitat suitability (ranging from minor to major) occurred over various parts of the jaguar's range, including core areas in the Amazon basin, covering 9.3% of the area of the jaguar range. We also show that different ecological factors drive the distribution of jaguar populations in different eco-regions. Based on this work, we propose a stronger international collaboration in monitoring jaguar populations and conservation efforts and a new approach for estimating species distribution for IUCN Red List assessments.

The natural distribution of a species depends on its evolutionary adaptations to habitats and available resources, the current distribution of those habitats, and a set of limiting factors, for example, competition with other species (Krebs 2001). However, the distribution of many species today is progressively shaped by human activities (Ripple et al. 2014). Therefore, estimating the current distribution and understanding factors and mechanisms that determine it is crucial for effective conservation planning and actions, including the IUCN Red List assessments and subsequent action plans (IUCN 1994, Baillie et al. 2004).

There are two main approaches for determining species distributions: (1) mapping presence records and delimiting distribution patches in strict relation to the distribution of species records, for example, as a minimum convex or concave polygon encompassing all data points, often supplemented with expert opinions where data are not available (IUCN Red List Technical Working Group. 2019); and (2) modelling the occurrence and distribution of a species based on the association between known presence or presence/absence data and a set of predictive variables, generally referred to as species distribution modelling (Guisan & Thuiller 2005, Elith & Leathwick 2009, Phillips et al. 2017). The advantage of the first mapping approach is that it is simple and directly related to data points. The main shortcoming is that often data are limited and do not cover the entire area where a species may be present, leading

to underestimation in some areas or uncertainty when supplemented by expert opinions. On the other hand, presence points can also be spatially mixed with absence, which are usually not evaluated, leading to an overestimation when using presence points only. An advantage of the habitat suitability or species distribution modelling (henceforth referred to as 'SDM') is that the models are capable of predicting the probability of species presence or absence in areas where data may be limited or completely lacking. Another important advantage of SDM is that it helps to identify factors determining species distributions and driving declines, critical information for planning conservation efforts. However, SDMs may also suffer from small datasets or inadequate predictive variables, leading to unsatisfactory predictions, such as presence predicted in areas where the species is absent or vice versa (Hirzel et at. 2006). Additionally, populations of animal species are often not homogenous, they may consist of genetically unique sub-populations that have adapted to specific local habitats and prey communities and may respond differently to environmental factors over space and time (Pilot et al. 2006, 2012, Jędrzejewski et al. 2012). Such differences must be accounted for to predict species distribution across large geographic regions accurately.

Here, we estimate the current distribution of the jaguar in South America. Earlier assessments of the jaguar's range in South America in 2000 and 2015, prepared for the IUCN Red List assessment, resulted in estimated total areas of 10.2 and 8.4 million km^2, respectively (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018). However, recent high deforestation rates driven by increasing demands for beef, soybeans and other commodities, extensive fires, mining expansion, human population growth, as well as political instability in several parts of South America may have changed the jaguar's status (Romero-Muñoz et al. 2020) requiring a re-assessment of the distribution of jaguar populations across South America. Additionally, those earlier estimates were largely based on expert opinions, especially for areas where data were limited, likely resulting in high prediction uncertainty.

In this paper, we compiled the most up-to-date dataset of jaguar presence and absence records from across South America, as well as new data on forest cover, human population density, road density, changes in agriculture areas, and other predictive variables

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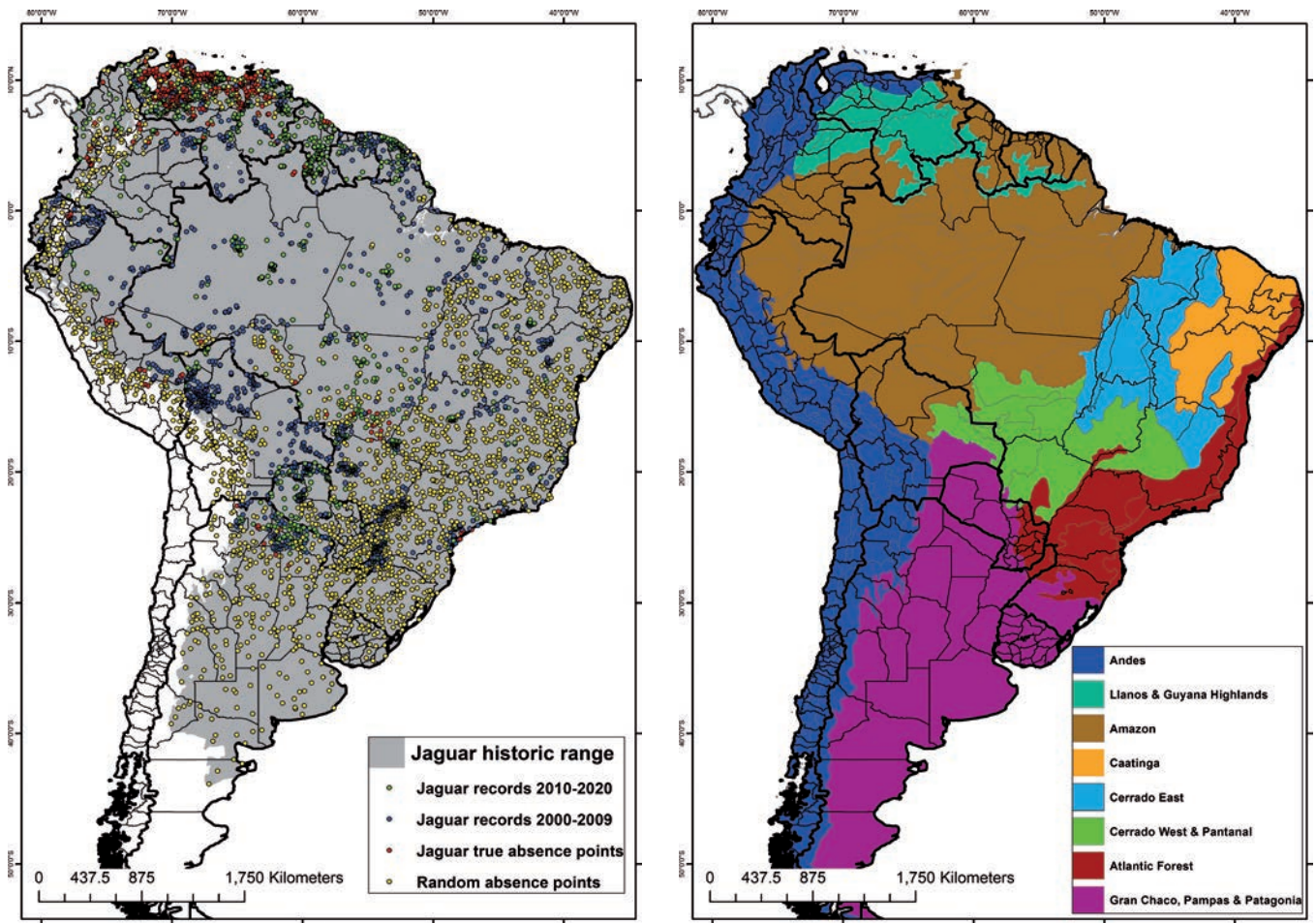
Fig. 1. Left: the historic jaguar range in South America (after Sanderson et al. 2002) and jaguar records (from 2000–2010 and from 2011–2020), jaguar true absence points, and randomly selected points from the known jaguar absence areas used to analyse current jaguar distribution. Right: the division of eco-regions of South America, used in our analysis (based on Griffith et al. 1998). We distinguished the following eco-regions: 1 – Andes, 2 – Los Llanos and Guiana Highlands; 3 – Amazon, 4 – Caatinga, 5 – Cerrado East, 6 – Cerrado West and Pantanal, 7 – Atlantic Forest, 8 – Gran Chaco, Patagonia, and Pampas. Country and administrative borders after Porto Tapiquen (2020).

known to affect jaguar distribution including any recent changes. We combined the records' mapping and SDM approaches to estimate the actual jaguar distribution better while still fulfilling the requirements of the IUCN Red List mapping standards (IUCN Red List Technical Working Group 2019). We also considered the recently discovered genetic differences between jaguar populations inhabiting different eco-regions (Roques et al. 2016, Lorenzana et al. 2020) and the fact that each of these populations may have different adaptations to ecological factors.

Finally, we compared our estimate of jaguar distribution in 2020 with earlier IUCN Red List assessments of jaguar populations for 2000 and 2015 (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018) to identify changes in the jaguar's range over the last twenty years, as well as to make inferences about the effect of different methodological approaches on estimates of species distribution.

Methods

We compiled a large set of records of jaguar presence and a smaller set of records of jaguar absence from each of the twelve countries of South America, including data from published sources and ongoing monitoring projects collected primarily with camera trapping, radiotracking, recording of tracks, and field interviews (see Supporting Online Material SOM Table T1 and Data Set D1 for the complete list of data records and their sources). Absence points came mostly from interviews and a smaller number of long-term camera trapping studies. As the presence of jaguars is fairly easily recorded by hunters, ranchers, or researchers through distinctive tracks, attacks on livestock, prey remains, roaring, and also direct observations, we assumed that a declared absence of jaguar records in the interviews is a reliable indicator of a true jaguar absence in an area (Zeller et al. 2011). The reliability of presence/absence data obtained with interviews was earlier

verified by comparisons with data obtained independently by other methods and by spatial autocorrelation tests (Jędrzejewski et al. 2017a). To ensure equal numbers of jaguar presence and absence points for the subsequent logistic regression analysis (see below), we randomly selected the balance of the absence points from the areas within the historic jaguar range where jaguars were identified as locally extinct by the IUCN 2000 (Sanderson et al. 2002, Caso et al. 2008) or 2015 assessments (Quigley et al. 2018) and where no new jaguar records were collected (see SOM Text T1 for more information).

To estimate the current distribution of jaguar populations and identify factors driving changes over the last 20 years, we combined kriging interpolation technique (corresponding to the records' mapping/IUCN approach) with logistic regression (species distribution modelling SDM approach), following the procedure in Jędrzejewski et al. (2017a). We applied kriging interpolation to our dataset

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Fig. 2. Jaguar presence probability based on kriging interpolation of jaguar presence-absence (left) and kriging variance (right). High kriging variance (> 0.218, pink) corresponds to the areas with low data point density and indicates low confidence in kriging prediction.
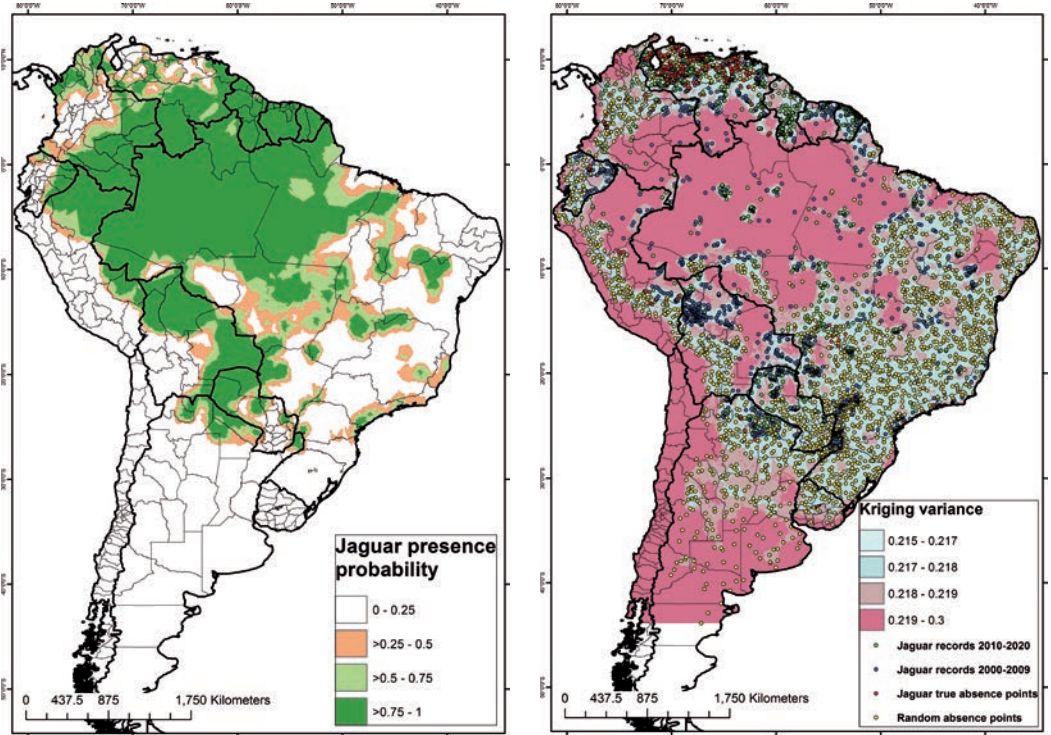
of jaguar presence-absence. We calculated a spatial prediction of the probability of jaguar presence (values from 0 to 1) by interpolating all jaguar presence (value 1) and absence (value 0) records using the kriging interpolation function within ArcGIS 10.3 (see further information in SOM Text T1).

In the case of logistic regression, we fitted a general model to presence-absence data for the whole of South America but also produced individual models for each of the eight eco-regions of South America (Fig. 1).

In the case of the latter, the data has been divided into eight appropriate subsets to take into account possible different responses to environmental variability resulting from documented or potentially possible genetic differences between jaguar populations. We distinguished eco-regions following the classification proposed by Griffith et al. (1998), adjusted to the genetic variation between jaguar populations of the Amazon, Pantanal, western and eastern Cerrado, Caatinga, and Atlantic Forest identified by Roques et al.

(2016) and Lorenzana et al. (2020). We also distinguished the ecologically unique Gran Chaco and Andes regions, which were not included in genetic studies. Additionally, jaguars from the Llanos region have shown morphological (and thus possibly genetic) dissimilarity from jaguars in adjacent areas (Hoogesteijn & Mondolfi 1996). Finally, eco-region divisions were adjusted to the distribution of our data points to ensure that we could fit models with sufficient data). For this reason, we combined Gran Chaco with

Fig. 3. Probabilities of jaguar occurrence in 2000 (left) and 2020 (right), resulting from the composition of predictions of logistic regression models fit separately to data in each of eight Eco-regions (as in Fig. 1 and Table 1). Both predictions are based on a total set of 21 predictive variables (SOM Table T2); however, for the 2000 and 2020 predictions we used different (respective) data for four variables: human population density, pastures, croplands, and forest cover. Prediction for 2000 is compared with the IUCN estimate of jaguar range in 2000 (Caso et al. 2008).

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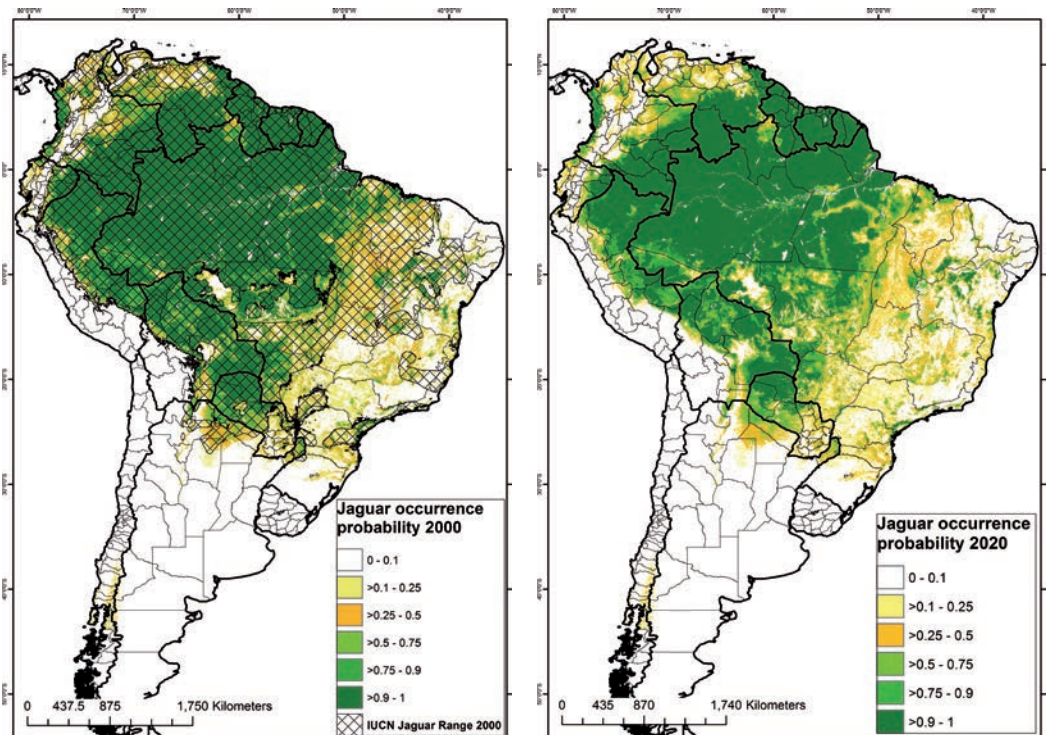
Patagonia and Pampas, western Cerrado with Pantanal, and Los Llanos with adjacent Guiana Highlands (Fig. 1).

Variables used to fit the logistic regression models included % forest cover, annual precipitation, mean annual temperature, mean and standard deviation of vegetation indices obtained from satellite images related to vegetation abundance and primary productivity (NPP, GPP, NDVI, EVI) as well as with water content in leaves and the ground (NDWI), human population density, human footprint index, indicators of protected areas and indigenous territories, proportions of croplands and pastures in an area, and road density index (SOM Table T2, SOM Fig. F1, SOM Dataset D2). We used climatic and vegetation productivity indices (mean values) because they are related to the density and productivity of herbivores, the jaguar food base, and thus indirectly, they affect jaguar populations (Polisar et al. 2003, Karanth et al. 2004, Melis et al. 2009, Pettorelli et al. 2011). Standard deviations of vegetation indices are measures of the seasonality of vegetation development and also may be related to densities of herbivores and carnivores. We converted the logit values from the best regional models to the probability of jaguar occurrence and made spatial predictions at the same resolution (1 km^2) for each eco-region. We then combined the regional maps into a single map for South America. Predictions for 2000 and 2020 were based on the relevant data for each period for four variables: forest cover, croplands, pastures, and human population density; for the other independent variables we used the same data for both predictions (see further information in SOM Text T1).

All model fitting was conducted using SYSTAT 13.2 (Systat Software, Inc. 2017, San Jose, CA, USA).

To estimate the current (2020) jaguar distribution in the areas with a high density of data points and low kriging variance (high certainty of kriging prediction), we averaged probability values obtained with both models (kriging interpolation and logistic regression with data for 2020) for each 1 km^2 raster cell. We did so because each type of model carries partly different information. Combining them allowed us to evaluate conservation status better (see below) and to reduce the probability of wrong classification of any area as presence or absence. We produced a confusion matrix and calculated the proportion of correctly classified presence and absence points ("sensitivity" and "specificity", respec-

tively) to verify if this combined method fits better to data points than single models. However, we could not use interpolation results and calculate average probabilities for areas with low confidence in kriging prediction (low density of data points and high kriging variance). Instead, we chose to use probabilities from predictions based on the logistic regression models alone for these areas. We used the same classification criteria as for the areas with averaged probabilities. We then classified the estimated probability values into four classes that refer to the categories of distribution mapping standards for the IUCN Red List (Technical Working Group, 2019): (1) Extinct (mean probability values between 0 and 0.25), (2) Possibly Extinct (>0.25–0.49), Possibly Extant (>0.49–0.75), and Extant (>0.75–1). See further information in SOM Text T1.

We assumed that the combined areas classified as "Extant" and "Possibly Extant" represent South America's current 2020 jaguar distribution. Therefore, we compared this area with the estimates developed for the IUCN 2000 and 2015 Red List assessments (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018). However, as those assessments were partly incomplete due to the lack of data from some areas (e.g. from Mato Grosso state in Brazil), we filled these knowledge gaps by inputting the results for 2020, assuming that areas inhabited by jaguars in 2020 likely also hosted jaguar populations in 2000 and 2015.

In preparing the maps, we used country and administrative borders (after Porto Tapiquén, 2020) to help locate data and results; however, they do not include any disputed boundaries and do not pretend to represent any political opinions.

Results

The total number of collected jaguar records from South America, after reducing densely distributed points to only one per 100 km^2, was 2,557. This included 1,305 records from 2000–2010 and 1,252 from 2011–2020. We also collected 426 verified jaguar absence points from South America (SOM Table T1), and we selected 2,136 random points from the area of known jaguar absences (Fig. 1, SOM Dataset D1).

Spatial kriging interpolation of jaguar records (value 1) and all absence points (value 0) produced an estimation of the distribution of jaguar populations, with probability of presence (Fig. 2). However, an analysis of

kriging variance indicated which areas have higher or lower certainty of this prediction (Fig. 2). Areas with a kriging variance <0.218 corresponded to a relatively high density of data points (mean 15.0/10,000 km^2, SD = 13.2) and predictions from these areas were used for further analyses. On the other hand, areas with the kriging variance > 0.218 (prevailing in our study area; Fig. 2) had a lower density of data points (mean 2.2/10,000 km^2, SD = 1.1). For these areas, we excluded predictions based on kriging interpolation from the subsequent analysis of the jaguar range.

The highest performing logistic regression model of jaguar occurrence based on the entire dataset included 12 variables (Table 1). Five of them (mean annual temperature, water index, forest cover, protected areas, and indigenous territories) had a positive effect on jaguar occurrence across the continent. In contrast, six (human population density, road density, croplands, pastures, and standard deviations of NDVI and NPP) had negative effects. This model also included the division of eco-regions as a categorical variable (Table 1 and SOM Table T3). Mean annual temperature, protected areas, human population density, croplands, road density, and forest cover had the strongest impact on jaguar probability of occurrence, as indicated by Z values (SOM Table T3). This general model had good predictive power (p < 0.001, AUC = 0.911, Nagelkerke's R^2 = 0.62, sensitivity = 0.83, specificity = 0.85) and performed well in cross-validation (mean AUC value for the smaller subsamples = 0.902, range 0.897 to 0.909). However, individual models for eight eco-regions had high predictive performance (AUC from 0.89 to 0.97) except for the eastern Cerrado (AUC = 0.84). These models included various sets of predictive variables. Protected areas, human population density, and pastures were included in seven models, temperature and road density in six, and croplands and NPP_SD in five models (Table 1 and SOM Table T3). Interestingly, temperature, which had a positive effect in the general model, had a negative effect in Caatinga and Cerrado (very dry and hot areas). Similarly, pastures had a negative effect in the general model but positively affected jaguar occurrence in the Andes and Caatinga. We used the mosaic composition of these individual models for each eco-region to predict jaguar occurrence probability across South America in 2000 and 2020 (Fig. 3, SOM Dataset D3). The overall prediction for 2020 (Fig. 3 right) improved predictive performance (sen-

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Table 1. The best logistic regression models of jaguar occurrence for the whole of South America (based on the whole data set) and for each Eco-region (based on the split data), selected with the Akaike Information Criterion (AIC), as well as information on predictive performance of all models used to estimate the current (2020) jaguar distribution in South America. See SOM Table T2 for information on predictive variables and SOM Table T3 for detailed parameters of each model. Sign in front of a variable indicates if its impact on jaguar occurrence was positive or negative.

Eco-region	Variables	N presence points	N absence points	Sensi-tivity	Speci-ficity	AUC	Nagle-kerke's R²
All South America (general model)	+TEMP, -NDVI_SD, -NPP_SD, +NDWImean, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -CROPLAND, -PASTURE, +INDTER, +PROT_AR, ECOREG (8 cat)	2,478	2,492	0.83	0.85	0.911	0.624
Andes	+PRECIP, +TEMP, -NPP_SD, +EVImean, +EVI_SD, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -HFOOTP2004,+PASTURE, +PROT_AR	241	596	0.64	0.91	0.891	0.532
Los Llanos & Guiana Highlands	+PRECIP, +TEMP, +EVImean, -HPDEN_LN, -ROAD_DENSITY, -HFOOTP2004, -PASTURE, -CROPLAND	374	185	0.89	0.69	0.893	0.560
Amazon	+TEMP, +GPP_SD, -NPP_SD, -HPDEN_LN, -ROAD_DENSITY, -PASTURE, -CROPLAND, +INDTER, +PROT_AR	947	158	0.96	0.58	0.925	0.575
Caatinga	-TEMP, +GPP_SD, -NDVI_SD, -HPDEN_LN, -ROAD_DENSITY, +PASTURE, +PROT_AR	60	179	0.83	0.96	0.968	0.786
Cerrado East	-EVI_SD, -HPDEN_LN, -PASTURE, +PROT_AR	85	227	0.51	0.95	0.838	0.415
Cerrado West & Pantanal	+PRECIP, -TEMP, +NPP_SD, -NDVI_SD, +NDWImean, +CANOPY, -ROAD_DENSITY, -PASTURE, -CROPLAND, +PROT_AR	267	262	0.82	0.86	0.912	0.625
Atlantic Forest	-GPP_SD, +NPP_SD, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -PASTURE, -CROPLAND, +PROT_AR	219	489	0.73	0.95	0.892	0.590
Gran Chaco, Pampas, Patagonia	+TEMP, -GPP_SD, +NPP_SD, +EVI_SD, -NDWI_SD, -HPDEN_LN, -CROPLAND, +PROT_AR	316	409	0.92	0.90	0.968	0.806
Mozaic composition of logistic regression models for each eco-region	According to the models for each region	2,509	2,505	0.83	0.88	0.932	-
Final classification: combined kriging interpolation and mosaic composition of logistic regression models	-	2,501	2,304	0.91	0.92	0.969	-

*V*ariables' abbreviations: TEMP – mean annual temperature, PRECIP – annual precipitation, CANOPY – forest cover, HPDEN_LN - human population density, ROAD_DENSITY – index approximating road density, CROPLAND – proportion of croplands in 1 km² area, PASTURE – proportion of pastures in 1 km² area, PROT_AR – protected areas, INDTER - Indigenous territories, HFOOTP2004 - Human footprint index 2004, NDVI_SD - Standard deviation of normalised difference vegetation index, EVImean – enhanced vegetation index (mean value), EVI_SD - Standard deviation of enhanced vegetation index, NDWImean - Mean annual value of normalised difference water index, NDWI_SD - Standard deviation of normalised difference water index, NPP_SD - Standard deviation of net primary productivity, GPP_SD - Standard deviation of gross primary productivity ECOREG (8 cat) - respective ecoregion number.

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sitivity 0.83, specificity 0.88) compared to the general model. It reveals that the most optimal habitats for the jaguar are generally in the great Amazon Basin, up to the Orinoco River in the north, and south to the Pantanal - Gran Chaco region. However, it also identifies the destruction of large portions of jaguar habitat even inside the core of the jaguar's current distribution and a high degree of fragmentation on the edges of its range, especially in eastern Brazil, Argentina, Colombia, and Venezuela (Fig. 3 right). Predictions for 2000 and 2020 (based on different data for four variables: human population density, pastures, croplands, and forest cover; see SOM Table T2) were only slightly different (Fig. 3). A comparison of our model prediction for 2000 with the IUCN estimate of jaguar range in 2000 (Caso et al. 2008) indicates that already by 2000 several areas inside the predicted jaguar range were of low suitability for jaguars (e.g in Brazil, Colombia, and Venezuela, Fig. 3 left). However, our models identified some areas as highly suitable in 2000 that were not included in the IUCN 2000 jaguar estimate, e.g. central parts of Mato Grosso in Brazil (Fig. 3 left). We subtracted both predictions (2020 and 2000) to estimate changes in jaguar occurrence probability across the continent during the last 20 years (Fig. 4). About 9% of the total area inside the 2000 jaguar range has experienced major or minor negative change, about 3% slight positive change, while 87.6% showed no change (Table 2, Fig. 4). The highest proportion of areas with a negative change was in Ecuador (25.8%). At the same time, all other countries, except Suriname, Guyana, and French Guiana, ex-
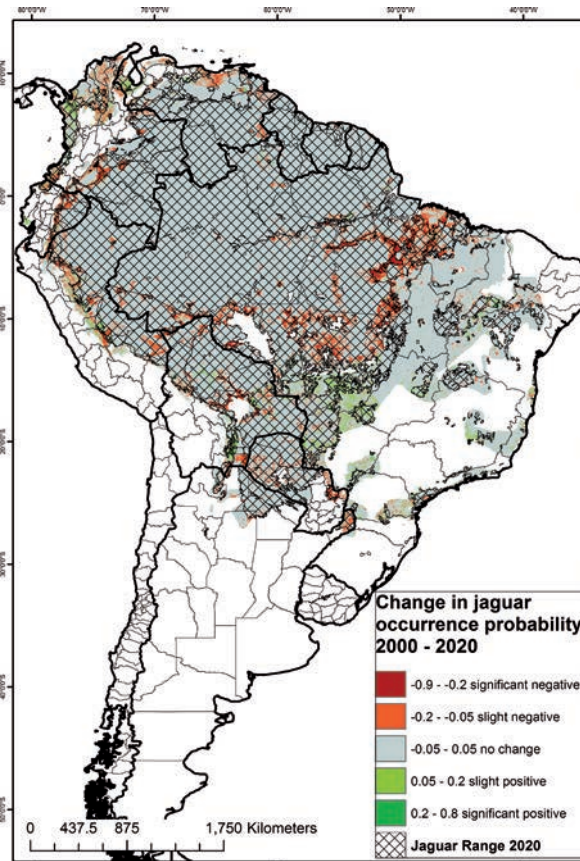
Fig. 4. Changes in the probability of jaguar occurrence during the last 20 years due to human impacts (red - negative change, green - positive change), inside the IUCN 2000 jaguar range (Caso et al. 2008), compared to the current (2020) jaguar range (this work). Probability changes were calculated as difference between predictions of our logistic regression models for 2020 and 2000, based on respective data for four predictive variables: human population density, cropland, pasture, and forest cover.

perienced a deterioration of jaguar habitats over some parts (7%–13%) of the jaguar range inside their territories (Table 2). These changes in the jaguar occurrence probability were driven by an increase in human population density, increase in areas of croplands and pastures, decrease in forest cover, or the combined effects of these factors.

We combined the results of kriging interpolation with the composed prediction of logistic regression models for eight eco-regions (see Methods) to estimate the current

(2020) jaguar status across South America (Fig. 5, SOM Dataset D4). This estimate combines a good fit to the data points (sensitivity 0.91, specificity 0.92, AUC 0.969; Table 1, Fig. 5, right) with the information on habitat suitability. It is in line with the independent estimates obtained by national censuses at the country levels (SOM Fig. F1). Following our reclassification of occurrence probabilities to the jaguar status categories, jaguars are Extinct or Possibly Extinct from 47% of their historic range in South America. They

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Table. 2. Percentage of area with changes in jaguar occurrence probability during the last 20 years due to human impacts (approximated by changes in human population density, area of croplands and pastures, and forest cover). The changes are calculated within the IUCN 2000 jaguar range (Caso et al. 2008) extended by the areas detected as occupied by jaguars in the 2020 estimate (compare Figs 4 and 5).

Country	Area of the 2000 Jaguar range (thousands km²)	% of the 2000 jaguar range with a probability change				
		Signif. neg. change (-0.9 – -0.2)	Slight neg. change (-0.2 – -0.05)	No change (-0.05 – 0.05)	Slight pos. change (0.05 – 0.2)	Signif. pos. change (0.2 – 0.8)
Argentina	187	1.1	9.8	87.7	1.2	0.1
Bolivia	766	1.7	8.8	85.1	3.9	0.5
Brazil	6,215	2.0	6.9	88.0	2.9	0.2
Colombia	897	1.5	10.5	83.7	3.9	0.4
Ecuador	117	5.2	20.6	67.6	5.7	0.9
French Guiana	84	0.2	1.8	98.1	0.0	0.0
Guyana	211	0.0	0.3	99.6	0.1	0.0
Paraguay	270	3.4	9.8	86.1	0.6	0.0
Peru	758	1.2	9.2	86.1	2.9	0.6
Suriname	145	0.1	0.8	99.1	0.0	0.0
Venezuela	809	0.5	6.7	90.5	2.1	0.2
Total	**10,459**	**1.7**	**7.6**	**87.6**	**2.9**	**0.2**

Fig. 5. Left: Current (2020) jaguar status in South America within its historic range based on probabilities of occurrence obtained with two methods combined: kriging interpolation of jaguar presence-absence points and logistic regression models (see Methods). The category Extinct corresponds to the averaged probability values from 0 to to 0.25, Possibly Extinct >0.25–0.49, Possibly Extant >0.49–0.75, and Extant >0.75–1. Right: A comparison of the estimated jaguar status with the distribution of data points.

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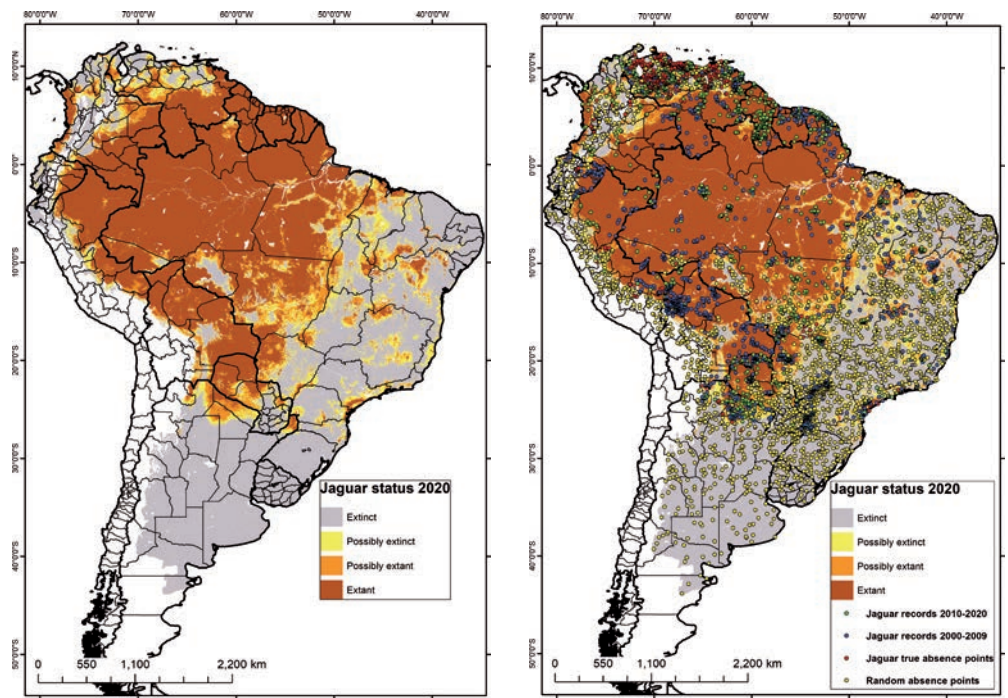
are Extant or Possibly Extant in 53% of the historic range (Table 3, Fig. 5). We assume that these two latter categories combined represent the current jaguar range, with a total area of about 7.9 million km² (Table 3, Fig. 5). The largest areas still occupied by jaguars are in Brazil (4.5 million km², which constitutes about 57% of all jaguar range), followed by Bolivia, Colombia, Peru, and Venezuela, respectively. Countries with the largest overall areas of extinction are Brazil and Argentina, but those with the highest proportion of the extinction area are Uruguay, Argentina, Ecuador, Brazil, Paraguay, Colombia, and Venezuela. The lowest proportion of the

extinction area occurred in the Guiana Shield: in Suriname, French Guiana, and Guyana (Table 3).

A comparison of the results obtained by the combined method (Fig. 5) with the results obtained by only one model, i.e. the kriging-interpolation (records' mapping/ IUCN ap proach; Fig. 2) or the logistic regression (species distribution modelling; Fig. 3), proved that the combined approach gives better results (Table 1). When compared to the national censuses (SOM Fig. F1), the kriging interpolation cut-off some parts and over-estimated other parts of the jaguar range in Peru, Bolivia, and Brazil, while logistic regres-

sion overestimated the jaguar distribution in parts of Peru and Brazil (compare Figs 2, 3, 5, and SOM Fig. F1).

Our estimate of the current (2020) jaguar range (combined categories "Extant" and "Possibly Extant") is substantially different from IUCN estimates of jaguar ranges for 2000 and 2015 (Table 4, Fig. 6). Our results show that several very large areas classified previously as being inhabited by jaguars are now classified as extinct or possibly extinct (Fig. 6). However, some areas were not included in the earlier estimates, which our models show are occupied by jaguars (Fig. 6). In total, our prediction of the area of current jaguar distribution

Table. 3. Total historic area of jaguar occurrence (after Sanderson et al. 2002) and percentage of area where jaguars are Extinct, Possibly Extinct, Possibly Extant, and Extant for each country of South America, based on the combined methods of kriging interpolation and logistic regression models of jaguar presence– absence (see Methods and Fig. 5).

Country	Total historic range (1000s km²)	% Extinct area	% Possibly Extinct area	% Possibly Extant area	% Extant area	Extinct and Possibly Extinct total area (1000s km²)	%	Extant and Possibly Extant total area (1000s km²)	%
Argentina	1,870	88.7	4.3	4.7	2.3	1,740	93.0	130	7.0
Bolivia	784	8.3	5.5	12.0	74.2	108	13.8	676	86.2
Brazil	8,337	33.6	12.7	8.8	44.9	3,867	46.3	4,470	53.7
Colombia	1,026	24.5	12.1	11.5	51.9	376	36.6	650	63.4
Ecuador	187	37.5	16.9	12.2	33.4	102	54.5	85	45.5
French Guiana	83	0.0	0.0	0.4	99.6	0	0.0	83	100.0
Guyana	211	0.1	0.3	2.3	97.3	1	0.5	209	99.5
Paraguay	396	26.1	15.5	14.6	43.8	165	41.7	231	58.3
Peru	784	13.6	7.7	8.9	69.8	167	21.3	617	78.7
Suriname	143	0.0	0.0	0.6	99.4	0	0.0	143	100.0
Uruguay	174	100.0	0.0	0.0	0.0	174	100.0	0	0.0
Venezuela	893	17.0	16.6	14.5	51.9	299	33.5	594	66.5
Total	**14,888**	**36.2**	**10.8**	**8.9**	**44.1**	**7,000**	**47.0**	**7,888**	**53.0**

is 14% (1.2 million square kilometres) smaller than the IUCN's 2015 estimate and 25% (2.6 million square kilometres) smaller than the IUCN's 2000 estimate. Compared with the estimates for 2000, the most significant difference in the jaguar range occurred in Brazil, Colombia, Venezuela, and Peru. A remarkable difference between the 2015 and 2020 estimates was documented for Colombia (26%) and somewhat smaller for Peru and Brazil (17% and 14%, respectively, Table 4).

Discussion

Our study shows that combining kriging interpolation and logistic regression models can improve estimates of species distribution at broad scales. The combination of these methodologies and a large dataset of jaguar records have produced the most detailed map of jaguar distribution across South America. This approach to species distribution modelling shows a high degree of compatibility with the assessments conducted at the national level in some South American countries. Compared to the IUCN's 2015 and 2000 assessments (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018), our estimate of the jaguar range in South America

differs by 14% and 25%, respectively. These differences partly result from methodological dissimilarities and different approaches of the previous studies; however, they also indicate that the jaguar range is decreasing consistently and relatively rapidly. This conclusion was also confirmed by our analysis of changes in jaguar habitat suitability during the same period.

We demonstrated that major and minor negative changes in habitat suitability occurred over several parts of the jaguar's range, including in the Amazon basin. Our models show that the deterioration of jaguar habitats is driven mainly by deforestation combined with the development of agriculture and cattle ranching, an increase in road density, and factors related to increasing human population densities (e.g. hunting, Woodroffe 2000). Similar results, especially the high importance of forest cover for jaguar distribution, have also been indicated by earlier studies (De Angelo et al. 2011, 2013, Olsoy et al. 2016, Paviolo et al. 2016, Jędrzejewski et al. 2017a, 2018, Thompson & Velilla 2017). The negative impact of croplands and pastures in our models confirms that expansion of agriculture and cattle ranching are among the main drivers of jaguar de-

clines. Furthermore, the development of cattle ranching is often related to deforestation and retaliatory killing of jaguars, with the combined effects resulting in rapid extirpation of jaguar populations (Jędrzejewski et al. 2017b, Romero-Muñoz et al. 2019, 2020). In our models, the development of road infrastructure had a particularly strong negative impact on jaguar distribution and areas with high road density in parts of Colombia, Brazil, and Argentina showed the highest rates of fragmentation and jaguar population decline, as also indicated by others (Payán et al. 2016, Rich et al. 2017, Espinosa et al. 2018, Thompson et al. 2020). Conversely, habitat productivity, approximated by vegetation and water abundance indices derived from satellite images, showed a positive effect on jaguar distribution in the models. Higher primary productivity is linked to increases in prey availability and translates to higher jaguar population density, higher reproductive rate, and resiliency to the impact of human activities (Jędrzejewski et al. 2017a, 2018, Santos et al. 2019). Our models also stress the importance of protected areas and indigenous territories for jaguar conservation, agreeing with earlier studies that showed that these protective measures are

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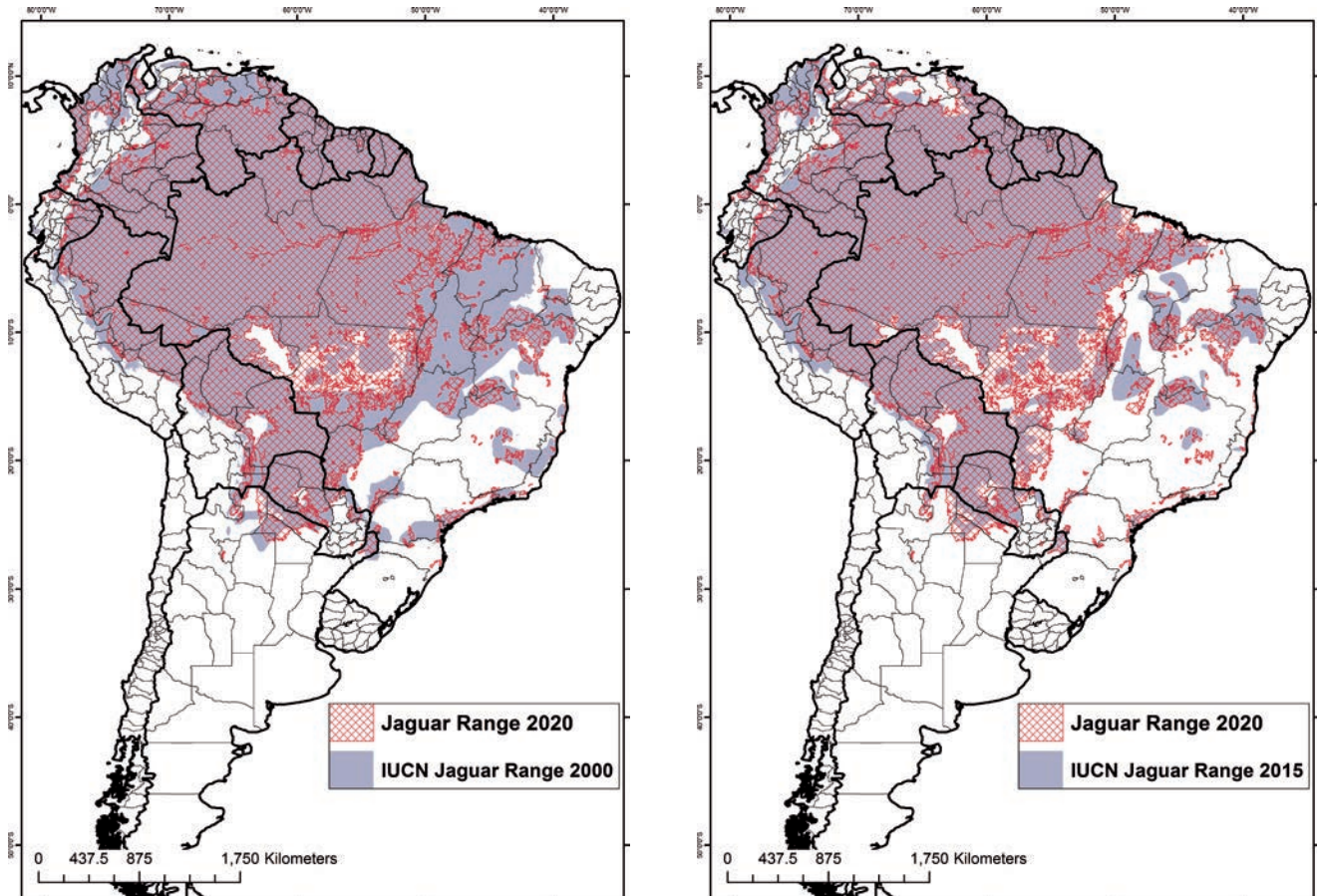
Fig. 6. Comparison of the current jaguar range estimated for 2020 with estimates of jaguar distribution for 2000 (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, left panel) and 2015 (Quigley et al. 2018, right panel).

Table. 4. Comparison of the area of the current (2020) jaguar range estimate (combined classes "Extant" and "Possibly Extant"; Figs 5, 6) with the jaguar ranges from 2000 and 2015. Jaguar ranges for 2000 and 2015 are based on IUCN Red List assessments (Caso et al. 2008, Quigley et al. 2018) extended by additional areas found to be inhabited by jaguars in 2020.

Country	Jaguar range 2000 (1000s km²)	Jaguar range 2015 (1000s km²)	Jaguar range 2020 (1000s km²)	2020–2000 area difference (1000s km²)	% area change 2020–2000	2015–2020 area difference (1000s km²)	% area change 2020–2015
Argentina	187	134	130	-57	-30	-4	-3
Bolivia	766	755	676	-90	-12	-79	-10
Brazil	6,215	5,192	4,470	-1,745	-28	-722	-14
Colombia	897	882	650	-247	-28	-232	-26
Ecuador	117	93	85	-32	-27	-8	-9
French Guiana	84	83	83	-1	-1	0	0
Guyana	211	210	209	-2	-1	-1	-1
Paraguay	270	260	231	-39	-14	-29	-11
Peru	758	739	617	-141	-19	-122	-17
Suriname	145	145	143	-2	-1	-2	-1
Uruguay	0	0	0	0	0	0	0
Venezuela	809	642	594	-215	-27	-48	-7
Total	**10,459**	**9,135**	**7,888**	**-2,571**	**-25**	**-1,247**	**-14**

critical for jaguar and carnivore conservation in general (Weber & Rabinowitz 1996, Rodrigues et al. 2004). Protected areas have been shown to maintain more stable prey populations (Beaudrot et al. 2016) and host lower rates of deforestation and retaliatory killing of jaguars (Jędrzejewski et al. 2017b) when compared to areas under other land tenures. Our study also shows that a different set of ecological factors drives the distribution of jaguar populations in each eco-region. This may result from genetically based adaptations to the environmental conditions of each eco-region, as well as from the variation in the effect of ecological forces at broad scales. For example, jaguar populations inhabiting distinct eco-regions of South America are genetically and morphologically different (Hoogesteijn & Mondolfi 1996, Roques et al. 2016, Lorenzana et al. 2020). These genetic differences likely indicate distinct adaptations for hunting different prey species inhabiting unique habitats, and this may lead to variation in responses to vegetation and water indices in the models. Similar genetic divisions corresponding to the distribution of different biomes and prey communities were identified across populations of European wolves, which also showed different responses to ecological factors (by selecting different prey species) in each biome (Pilot et al. 2006, 2012, Jędrzejewski et al. 2012). However, ecological factors may also affect species differently at continental, regional, or local scales, as was the case of temperature in our models. At the continental scale, temperature had a strong positive effect on jaguar occurrence. In contrast, it has a negative effect in the continent's

hottest and driest habitats, such as Caatinga and Cerrado (as earlier shown by Morato et al. 2014, Portugal et al. 2019), possibly indicating some optimum temperature range for the jaguar. Similarly, a moderate proportion of pastures in the Caatinga and Andes eco-regions positively affected jaguar occurrence (e.g. by increasing a limited prey base), while pastures in other eco-regions had a strong negative effect.

Through this study, we propose a new approach to estimating species distribution across broad scales, combining the interpolation of presence and absence points with species distribution modelling. This combined method capitalizes on the advantages of both records' mapping and SDM methodologies, and the resulting distribution better fits the actual data points and national estimates than any single model alone. Despite the generally high number of data points we collected, the kriging interpolation technique (records' mapping/IUCN approach) produced a prediction of low certainty for large areas, while logistic regression (SDM approach) overestimated jaguar distribution, indicating jaguar presence outside the actual jaguar range. Comparing our predictions for 2000 and 2020 with the IUCN estimates of jaguar distribution in 2000 and 2015 showed several important differences, which the shrinking of the jaguar range cannot entirely explain. Our analysis suggests that IUCN assessments overestimated the jaguar range in parts of Venezuela, Colombia, and Brazil, as was also suggested by other studies. For example, large areas of Venezuela north of the Orinoco where jaguar extirpations are known to have occurred between 1970 and 2000 (Jędrzejewski et al.

2017a) were still included in the IUCN's 2000 jaguar range estimate. Likely, those short-comings were related to insufficient data coverage, which is understandable considering that all these assessments are being made across broad scales for a naturally rare, elusive, and wide-ranging species. However, another likely source of incompatibilities between ours and the IUCN's estimates stems from the methodological differences, especially from the wide use of expert opinions in the earlier estimates (Sanderson et al. 2002, Zeller 2007). In our method, we tried to reduce significantly the role of expert opinions, which in our opinion, carries a high risk of incorrect estimates if not supported by field collected data.

Using such a combined approach and not only the IUCN records' mapping (IUCN Red List Technical Working Group 2019) is especially important when data do not cover the entire potential range of a species or when the actual distribution is a mosaic composed of intermixed presence and absence patches, but the availability of absence data is more limited. Apart from the problems of insufficient data coverage, there are also some important logical differences to consider when compared to the IUCN methodology, given that spatial patterns of species presence/absence do not always result from a gradual extinction process. For example, individuals may recolonise some areas or disperse into unsuitable areas, where the species generally does not occur. None of the IUCN categories meets these conditions. For these reasons, we propose that the interpretation and definition of these categories should be broadened from the original IUCN mapping standards to in-

clude: (1) Extinct = low-quality habitat/adverse conditions and no jaguar records; (2) Possibly/functionally Extinct = low or medium quality habitat and no or few jaguar records; (3) Possibly Extant (possibly present) = good habitat and few records, or numerous records in a poor/adverse habitat; (4) Extant = good habitat and numerous jaguar records.

The final precision of any estimate of species distribution will depend on the amount and quality of data available. In this work, we combined data (in total 2,257 sparsely distributed records) from 2000–2020 to produce an extensive jaguar database which also covered areas where data was previously unavailable. Although we believe that in most cases, older (early 2000) data still represent the current jaguar distribution, this remains a source of uncertainty in our data because jaguar presence at a local scale can change quickly in the face of intense pressure from human activities driven by policy changes, infrastructure development, and economic downturns (Romero-Muñoz et al. 2020). Therefore, it is critical to ensure that data are collected more regularly across a greater proportion of the jaguar's range, ideally using a standardised methodology to increase the precision of future estimates. Collecting data on the species presence and absence is also equally important. Absence data improve the precision of SDM model predictions and, when combined with information on the timing of extirpations and land use changes, it can be used to estimate local extinction rates and model the extinction process (Jędrzejewski et al. 2017a).

We conclude that conservation policies should consider the main positive and negative drivers of jaguar distribution changes identified by this study. These policies should focus on the increase in the area and number of protected areas, supporting indigenous territories and sustainable alternative livelihoods, stopping deforestation, mitigating man-jaguar conflicts, and mitigating negative effects of roads and other infrastructure development, as well as identifying and protecting ecological corridors. We also propose that an international collaboration focused on continuous and coordinated jaguar monitoring covering extensive areas and using standardised techniques and methodology is crucial for the accuracy of future assessments of jaguar distribution and its trends and should remain a cornerstone of the conservation of jaguar populations.

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Supporting Online Material SOM Text T1, Figures F1–F2, Tables T1–T3 and Datasets D1–D5 are available at www.catsg.org.

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