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Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela

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ABSTRACT

The worldwide decline in carnivore populations has been attributed to various human impacts. However, our understanding of the mechanisms behind these declines is insufficient to predict the timing and location of local extinctions. We collected data on presence/absence and time since extirpation of jaguars across Venezuela. To test if human impacts or ecosystem productivity better explain the observed spatial variation in probability of jaguar occurrence we compared logistic regression models fit with different combinations of anthropogenic and environmental variables. Similarly, we modelled the time since extirpation, using a multiple regression approach. Our study supported the hypothesis that jaguar extirpations and distribution are determined by a joint effect of anthropogenic factors and environmental variables, mainly those related with ecosystem productivity. Human population density and habitat alterations exerted strong negative effects on jaguar populations, while annual precipitation, mean temperature, forest cover, primary productivity, and other vegetation indices had positive effects. The strength of human impact is shaped by ecosystem productivity: jaguars disappear faster in dry, unproductive areas, and survive better in humid, productive areas even when human densities are higher. We estimated that jaguars in Venezuela have been extirpated from approximately 26% of the territory of Venezuela; present jaguar range covers approximately 66% of the country. We demonstrate that human population density alone cannot adequately explain past extirpations nor predict future jaguar declines. We conclude that the predicted future growth of the human population will not necessarily determine jaguar declines, and proper management and conservation programs could potentially prevent jaguar extirpations.

1. Introduction

The natural distribution of species is shaped by their evolutionary adaptation to certain habitats and the spatial distribution of these habitats, by their dispersal and extirpation rates, and through interactions

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with other species (Krebs, 2001, Holt, 2003). Various natural biotic and abiotic factors can limit species distributions, but today the majority of species are confronting anthropogenic impacts that can alter, and generally limit, their natural ranges. Large carnivores are among the most vulnerable species to human activities, as their high energetic demands require abundant prey and extensive tracts of land, and in consequence their populations are declining worldwide (Ceballos and Ehrlich, 2002, Treves and Karanth, 2003, Carbone et al., 2011, Ripple et al., 2014).

The range of the jaguar (*Panthera onca*) has declined by approximately 50% during the 20th century (Swank and Teer, 1989, Sanderson et al., 2002a). Widespread hunting for jaguars, in response to the demand for their skins, took place throughout South and Central America from 1950 through the 1970s, and was an important factor in the decline of the species (Fitzgerald, 1989, Hoogesteijn and Mondolfi, 1992, Payán and Trujillo, 2006). Despite international measures to stop the skin trade and the introduction of legal protection of the jaguar in many countries, the extirpation process has not been halted. The continuing persistent decline and extirpations of jaguar populations have been attributed to three main anthropogenic impacts: human-caused habitat transformation, direct hunting, and persecution owing to conflicts with cattle breeding (Quigley and Crawshaw, 1992, Nowell and Jackson, 1996, Zeller, 2007, de Oliveira et al., 2012).

The current distribution of the jaguar may, however, result from human caused extirpations during the last century as well as from natural environmental limits. Understanding the extirpation process could help in conservation planning and potentially in preventing further reduction of jaguar range. Altrichter et al. (2006) showed that the time since jaguar extirpation in various localities in Argentina was related to the age of human settlements, suggesting that the growth of human populations is the decisive factor in jaguar declines. Similarly, it has been proposed that extinction rates of large carnivores can be predicted based on human densities alone (Purvis et al., 2000, Cardillo et al., 2004). Woodroffe (2000) estimated critical human densities at which large carnivore populations became extinct; for jaguars the estimated threshold was 17 people/km^2. This estimation provokes two important questions: first, is that threshold the same under all environmental conditions; and second, how will the predicted growth of human population in South American countries impact jaguar range over the coming decades?

Species distribution models developed for jaguars indicate that human-related factors, (i.e. human population density, road density, and agriculture) limit jaguar occurrence. Further, they demonstrate that environmental factors are also important. Jaguar occurrence is related to forest cover, specific habitat types, and to the proximity of water. Mean annual temperature and annual precipitation may also affect jaguar distribution (Tôrres et al., 2008, Rabinowitz and Zeller, 2010, Rodríguez-Soto et al., 2011, Ferraz et al., 2012). Models combining anthropogenic and environmental factors have shown the highest predictive power for jaguar populations in the Atlantic Forest in Brazil, Paraguay, and Argentina (De Angelo et al., 2013).

The mechanism by which environmental factors such as precipitation, temperature, or habitat type influence jaguar distribution is unclear. A possible explanation would be that these factors are related to ecosystem productivity and prey availability, which in turn may influence jaguar populations. In more productive habitats, prey populations are more abundant, which presumably leads to higher densities of carnivore populations (Gasaway et al., 1992, Jędrzejewski and Jędrzejewska, 1996, Jędrzejewska and Jędrzejewski, 1998, Karanth et al., 2004). Thus, the capacity of carnivore populations to compensate for mortality factors, including hunting by humans, should be higher in more productive ecosystems, which in turn should affect a carnivore's extirpation rate and finally its distribution. Based on this reasoning, we hypothesize that not all jaguar populations are equally susceptible to human impacts, and that the negative effect of human populations will vary depending on environmental conditions, mainly on ecosystem productivity.

In this paper we analysed presence/absence records and estimated time since extirpation of jaguars from throughout Venezuela. We aimed at explaining factors and mechanisms that determine the process of local extinctions and lead to changes in spatial distribution of the jaguar. We addressed the following specific questions: (1) What are the relative roles of human impacts and environmental variables, especially ecosystem productivity, in determining jaguar distribution, persistence, and extirpation risk? (2) Does the strength of anthropogenic impacts on jaguar populations depend on environmental variables?

We modelled the probability of jaguar occurrence and time since jaguar extirpation with various sets of predictive variables to test whether anthropogenic, environmental, or a combination of both factors best explain the observed spatial variation in both dependent variables. We presented spatial predictions of these models for Venezuela. To test if human densities alone can be used for predicting jaguar extirpations we estimated an average threshold of human density at which jaguar populations decline and we used this threshold to predict how the expected growth of human population in Venezuela would impact jaguar range by 2050. Finally, we compared the results of this approach with predictions based on our models, which included joint effects of anthropogenic and environmental variables, to test if the growth of human population would inevitably lead to jaguar extinction.

2. Methods

2.1. Study area

Continental Venezuela occupies an area of 916,175 km^2, ranging from 0°39′ to 12°12′ N, and from 59°48′ to 73°23′ W. The topography is complex, and includes vast plains and various mountain systems: Andes (Cordillera de Mérida and Sierra de Perijá) on the west, Cordillera de la Costa in the north, and Guiana Highlands with diverse hills, mountain chains, and tepuis in the south. In 2011, Venezuela had a population of 28.9 million people (INE, 2011), most living in cities in the north where most of the industry is located. Large-scale habitat transformations have occurred mainly north of the Orinoco River, while the south has retained more pristine habitats (Rodríguez, 2000, Rodríguez et al., 2010).

Globally, the jaguar is classified as ‘Near Threatened’ and in Venezuela as ‘Vulnerable’ (Caso et al., 2008; Ojasti and Lacabana, 2008). Jaguars have been officially protected in Venezuela since 1996 (Venezuela, 1996a, 1996b), but habitat alterations, poaching and retaliatory killing due to conflicts with cattle breeding continue to affect the species (Hoogesteijn and Mondolfi, 1992, Hoogesteijn et al., 1993, Jędrzejewski et al., 2011).

2.2. Dependent variables and data acquisition

We created two dependent variables: (1) probability of jaguar occurrence and (2) time since jaguar extirpation. We compiled data to estimate these variables from four different sources: (a) public interviews, (b) direct observation (i.e. camera-trapping and track detection), (c) museum records, and (d) published literature and reports. Between 2009 and 2015 we conducted qualitative and semi-structured field interviews in rural localities across Venezuela, avoiding highly populated areas. To conduct interviews we followed the general procedure applied by Zeller et al. (2011). Interviews targeted hunters, ranchers, and other local residents likely to have had direct contact with jaguars. We attempted to document reliable records of jaguar occurrence, including hunting/poaching, direct observations, attacks on livestock, and other information concerning recent and historical presence of jaguars. The location, date, and detailed description of each observation were noted. We also asked about the current status of the jaguar (present or absent) and an opinion on jaguar presence or absence during the last eight decades (since 1940). The time span of the latter information depended on the age of the interviewed person and on the length of time that he/she had lived in the area. Interviews with any uncertainties or missing exact locations were discarded. Interview data have been used in other studies modelling jaguar distribution, location of ecological corridors, and jaguar extirpation rates (e.g. Altrichter et al., 2006, Zeller, 2007, Zeller et al., 2011, Tôrres et al., 2012, Zeilhofer et al., 2014). Further details on the process of collecting and validating our interview data are provided in the Appendix A.

We supplemented the interview data with camera-trapping and track surveys in 17 localities distributed across Venezuela, representing various habitat types that included all geographic regions of the country. In each locality we set approximately 30 camera-traps (Reconyx and Bushnell) for 3–5 weeks. We set cameras along transects, at an average distance of 1 km from one another, in areas with the highest probability of jaguar presence as indicated by local guides. While tending the cameras and during other field work, we also recorded observations of jaguar tracks. We also collected information on jaguars from the databases of two zoological museums, the Museo de la Estación Biológica de Rancho Grande (Maracay), and the Museo de Historia Natural La Salle (Caracas). This information included the coordinates, date, and circumstances of collection of each of the museum specimens. Finally, we reviewed recently published papers documenting jaguar records and reports on faunal inventories conducted across the country by the Venezuelan Ministry of the Environment - Ministerio del Poder Popular para Ecosocialismo y Aguas (Appendix B).

As 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 all four sources have equal reliability (Hoogesteijn and Mondolfi, 1992, Zeller et al., 2011). We assigned each data point the status of either “presence” (1) or “absence” (0). “Presence” was assigned when in a given locality there were recent records, i.e. between 2006 and 2015, and the interviewed local residents indicated current presence of jaguars in the area. “Absence” was assigned when there were no recent records of jaguars and the individuals interviewed indicated the absence of jaguars. In order to reduce spatial autocorrelation, we reduced densely distributed points, leaving only one if the distance between neighbouring points was less than 5 km (Rodríguez-Soto et al., 2011). This reduces the chances of using records of the same individual, as it approximates the diameter of a core jaguar home range (i.e. 50% kernel estimate; Cavalcanti and Gese, 2009). Based on the last record of a jaguar in the localities with confirmed absence of the species, we estimated the time since jaguar extirpation.

2.3. Predictive variables

We used a set of predictive spatial candidate variables that included 3 anthropogenic and 13 environmental factors (Table C1). As anthropogenic variables we used: (a) human population density - we assume it is related to the density of hunters and intensity of jaguar hunting, (b) livestock density - related to the intensity of jaguar-human conflicts; and (c) human footprint index - which reflects the degree of anthropogenic habitat changes (Sanderson et al., 2002b, De Angelo et al., 2013). We assumed that each of these three variables has a different, albeit negative, effect on jaguars. As environmental variables we used a set of vegetation indices derived from satellite images related to ecosystem productivity, which in turn may affect prey biomass (Field et al., 1995, Sims et al., 2006, Melis et al., 2009, Pettorelli et al., 2011): (a) mean net primary productivity (NPP), (b) mean gross primary productivity (GPP), (c) mean normalized difference vegetation index (NDVI), and (d) mean enhanced vegetation index (EVI). As each of these indices reflects partially different components of vegetation productivity with potentially different effects on jaguar prey, we could not give initial priority to any of them and therefore included all in our candidate variable set. In addition to the mean values, we also used the standard deviations of these variables reflecting environmental variability or seasonality strength, as they may also affect jaguar prey availability. We also included mean annual temperature and annual precipitation, which have been shown to have an impact on jaguar distribution and are related to ecosystem productivity (Lieth, 1975, Ferraz et al., 2012, Gutiérrez-González et al., 2012). Because forests and water are considered important components of the jaguar habitat (Hoogesteijn and Mondolfi, 1992, De Angelo et al., 2013), we also included mean forest canopy cover and mean and standard deviation of the normalized difference water index (NDWI). See Table C1 for the list, sources, further references, and more detailed description of the variables used.

We standardized all raster data to a 1 km × 1 km pixel size. We applied a log-transformation to human population density and livestock density, which had considerable skew (Quinn and Keough, 2002). We evaluated possible correlations between pairs of variables by calculating Pearson correlation coefficients. In the case of correlations above 0.7, the least predictive of the correlated variables was removed from the analysis to avoid multicollinearity in the models (Tables C2 and C3).

2.4. Data analysis

2.4.1. Testing hypotheses on factors determining probability of jaguar occurrence

To model jaguar distribution, we fitted a set of logistic regression models to the presence/absence data with the explanatory variables described above. We organized these models into three main groups of competing hypotheses regarding the factors that determine jaguar occurrence: (1) anthropogenic factors, (2) environmental factors, (3) a combination of anthropogenic and environmental factors. We considered adding interaction terms between human density and annual precipitation, mean annual temperature, net primary productivity, and enhanced vegetation index, but we discarded such models. Models with interaction terms were indeed well suited for prediction, but resulted in changes in the coefficient signs that were not interpretable in a biological sense, and that could be harder to generalize to different geographical contexts due to the difference in human population patterns in the other countries of Latin America.

We calculated Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values, and AIC and BIC weights for each model and selected the best models from within each group (Akaike, 1973, Schwarz, 1978, Burnham and Anderson, 2002, Wagenmakers and Farrell, 2004). We considered both criterions because they showed slightly different patterns in indicating best models. The best supported model by both criterions across all models was selected for further analysis and hereafter we refer to it as the “occurrence model”.

We converted the obtained logit values $g(x)$ to probabilities with the function $p(x) = \exp[g(x)]/\{1 + \exp[g(x)]\}$ (Hosmer and Lemeshow, 2004). Using a GIS, we then spatially projected the occurrence model to the whole territory of Venezuela. We validated our occurrence model using Naglekerke's R^2, an area under ROC curve (AUC), and a classification table. To check if the regression coefficients were robust, we used bootstrap resampling with 5000 replications and calculated bias values of the estimates. To test the predictive performance of the occurrence model, we performed cross validation. We randomly split our data into 75% and 25% subsamples, and then, with the predictive variables selected for the main model, we estimated model parameters based on the first subsample. With this new model, we predicted probability values for the second (25%) subsample and we calculated the area under ROC curve (AUC). We repeated this procedure ten times and calculated the mean AUC (Boyce et al., 2002).

2.4.2. Modelling time since extirpation

We modelled the "time since extirpation" data similarly, using multiple regression but still grouping plausible models into three main groups. Again we used AIC/BIC criterions to select the "best" models within each group and to select a single top "extirpation model". We tested standard regression assumptions by examining residual plots (plots of the standardized residuals as a function of standardized predicted values), histograms, and normal probability plots (Tabachnick and Fidell, 1983). As with the occurrence model we validated the extirpation model using a combination of bootstrapping and cross validation. In the cross validation we calculated mean R^2 between actual and predicted values of the smaller subsample. We projected our model in a raster map indicating predicted time since extirpation. We also calculated a raster with the inverse value to indicate an index of resistance of jaguar populations to extirpation that can be interpreted as an index of the probability of jaguar persistence within the next 75 years (JPers) with the formula $\mathrm{JPers} = 1 - \mathrm{TiExt}/75$, where TiExt is the predicted time since extirpation and 75 is the maximum recorded value. Accuracy of such a prediction assumes the rate and distribution of environmental change and human population increase will be similar in future as they were in the past 75 years. All model fitting was conducted using SYSTAT 13.0 (Systat Software, Inc., San Jose, CA, USA) and SPSS ver. 20 (IBM SPSS Statistics). Spatial analysis was conducted using ArcGIS 10.1 (ESRI, Redlands CA, USA).

2.4.3. Estimating current distribution and extirpation area of jaguars

In order to estimate current jaguar range in Venezuela and an area of extirpation we compared the spatial prediction of our logistic regression occurrence model with the results of spatial prediction obtained by kriging interpolation of the presence/absence data (0 or 1). Kriging is a geostatistical method that has been widely used to predict animal distribution and abundance with spatially autocorrelated data (e.g. Monestiez et al., 2006, Hengl et al., 2009, Nazeri et al., 2015). In this technique, the probability of an animal occurrence calculated for a particular raster cell depends upon: (1) distance of the cell from the data points entered into calculation, (2) the number and values of data points used for this calculation, and (3) the values predicted by a semivariogram model reflecting general spatial autocorrelation of the data. We used the kriging function within ArcGis 10.1 to calculate the spatial prediction of probabilities of jaguar presence (hereafter referred to as the "interpolation model"). Within ArcGIS we specified: ordinary kriging, the spherical semivariogram model, and six nearest data points for the calculation of each raster cell value. We also calculated the spatial variance of the predicted values for each cell and made a spatial projection of this variance in order to control which parts of the spatial prediction of presence/absence were less reliable. We overlayed the resulting spatial prediction of presence/absence areas (interpolation model) with the projection of the occurrence model obtained using logistic regression. In both models, we applied a 0.5 cut-off value to distinguish between predicted presence and absence areas. We accepted as current jaguar range those areas where both the interpolation and occurrence models predicted jaguar presence. In areas with scarce presence/absence data and high variance of the spatial prediction we gave priority to the occurrence model that incorporated environmental predictors. We calculated the extirpation area as the area outside the estimated current jaguar range, excluding also those areas that were originally hostile for jaguars and were probably never inhabited by them or inhabited only sporadically. Based on the results of our interviews and past literature, we expected those areas to include high mountains (over 2000 m), open dry savannahs, and dry unproductive savannah with sparse scrublands (Swank and Teer, 1989, Sanderson et al., 2002a, Zeller, 2007, Rabinowitz and Zeller, 2010). We used a vegetation map of Venezuela (Huber and Oliveira-Miranda, 2010) and a Global Digital Elevation Model http://gdex.cr.usgs.gov/gdex/ to estimate these areas.

2.4.4. Testing the hypothesis that jaguar declines can be predicted based on human population densities alone

To test if human density alone could be used to predict jaguar extirpations, in addition to evaluating models constructed only with the anthropogenic variables, we also estimated two threshold human densities at which jaguars decline and become extirpated. We considered the approach of Woodroffe (2000), who proposed calculating such critical human population density for large carnivores using logistic regression applied to presence/absence data; the threshold would be that human density for which logistic regression predicts a 50% probability of jaguar occurrence. However, a result obtained with this method would depend upon human densities at both jaguar presence and absence points and will tend to increase if absence points are collected at higher human densities. To avoid this potential bias, we estimated the threshold values based on the distribution of jaguar presence points for differing levels of human density. We set two threshold values: (1) a decline threshold as the human population density below which 75% of jaguar presence points were found and, (2) an extirpation threshold as the human population density below which 95% of jaguar presence points were found. We predicted possible future changes in jaguar distribution related to the increase of human populations, using actual data from the 2011 census (Table C1), and the predicted 2050 human population estimate. To calculate this second layer, we used the rate of human population increase for each municipality in Venezuela, based on data of the Instituto Nacional de Estadística (INE, 2011). For all of Venezuela, we calculated the change in area with human population density lower than both threshold values between 2011 and 2050. We verified this result with the prediction based on spatial projections of our occurrence model calculated with the same human density data for 2011 and 2050. For both years we calculated the areas with predicted probabilities of jaguar presence higher than 0.5.

3. Results

3.1. Jaguar occurrence - factors and prediction

We interviewed 485 hunters, ranchers, and other local people of various ages across Venezuela. These interviews yielded a total of 1401 data records that included 895 cases of jaguar presence and 506 cases of jaguar absence. We obtained 94 jaguar photos with camera traps and encountered 196 track sets. Literature data, ministerial reports, and museum databases provided 90 additional records (56 presence and 34 absence). In total, we gathered 1241 confirmations of jaguar presence and 540 of jaguar absence. After reducing the data points that were within 5 km of each other we were left with 641 presence and 402 absence points (Fig. 1).

Jaguar occurrence models with a combination of anthropogenic and environmental factors had the lowest AIC and BIC values. Models fit only with anthropogenic or only with environmental factors had no support (Table 1). The top model of jaguar occurrence included seven variables (Table 2). It has predicted that the highest probabilities of jaguar occurrence are found in areas with high values of precipitation, temperature, forest cover, and productivity (mean NPP and standard deviation of EVI), and with low values of human density and human footprint index. The model was highly significant (overall $p < 0.00000$) and had good predictive performance (Naglekerke's R-Squared $= 0.59$, AUC $= 0.902$, $N = 1036$). All coefficient estimates of the bootstrapped model were significant and biases were small (Table 2). In a cross validation, the mean AUC value for the estimated probabilities of the smaller subsamples was 0.901 (range 0.864–0.926).

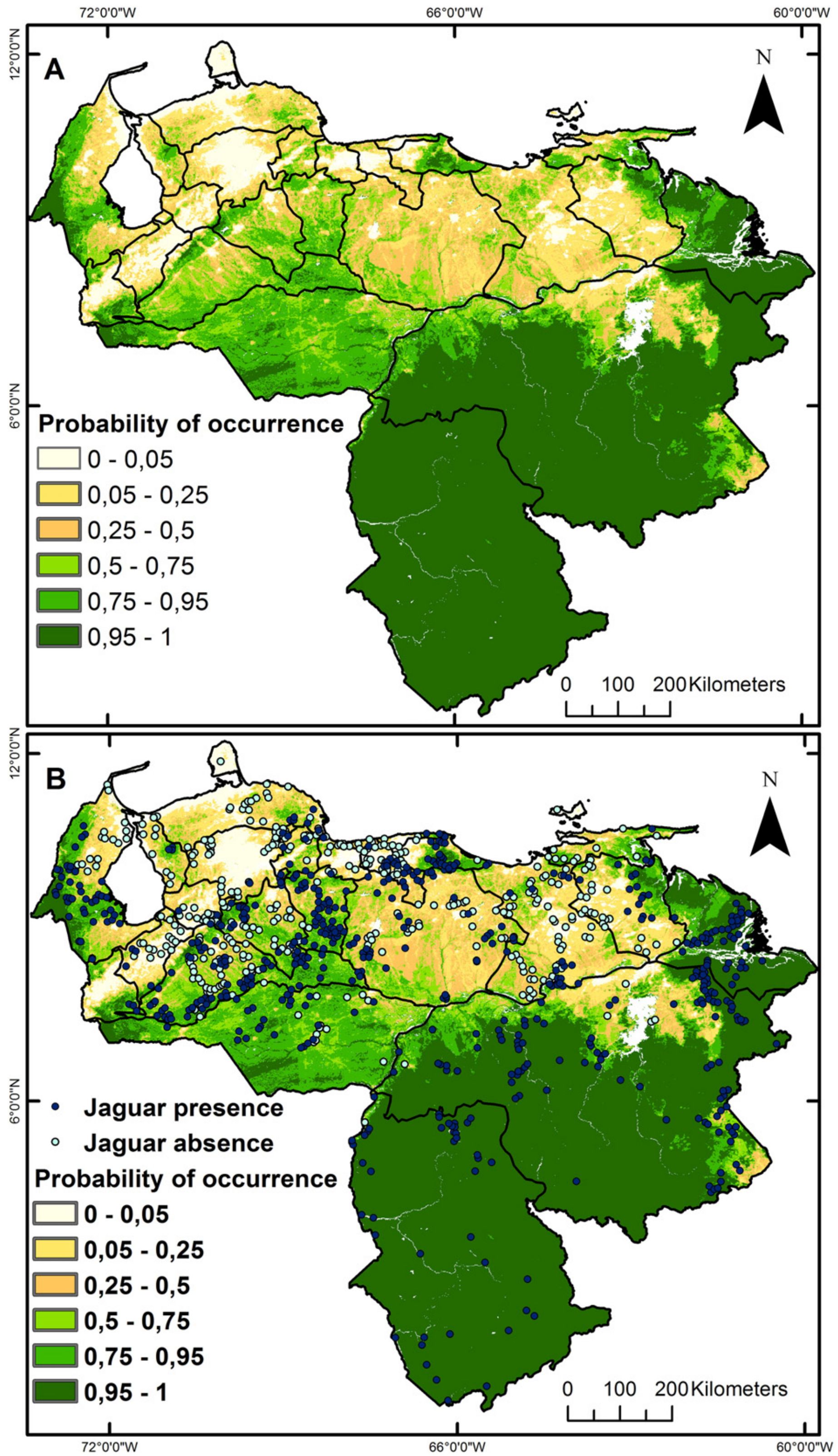

Fig. 1. Spatial projection of the habitat suitability model fit with environmental and anthropogenic variables (as in Table 2). A. Distribution of the estimated probabilities of current jaguar occurrence in Venezuela. B. Comparison of the estimated probabilities with distribution of the actual jaguar presence (dark blue points) and absence (light blue points) records. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our top model indicates that the areas with the highest probability of jaguar occurrence, hence with the most suitable habitat for jaguars, are located south of the Orinoco River, in the Orinoco Delta, in the western Llanos, in the south-eastern foothills of Andes, in the area south-west of Maracaibo Lake, and in the Perijá Mountains (Fig. 1A). By contrast, the probability of jaguar presence is low in most of northern and central Venezuela. The spatial distribution of our predicted probabilities agrees well with the distribution of

Table 1
Comparison of different jaguar occurrence models and their selection parameters. Models are organized in 3 groups representing three main competing hypotheses on which factors determine probability of jaguar occurrence: (1) only anthropogenic factors, (2) only environmental factors, (3) combination of anthropogenic and environmental factors. Variable acronyms as in Table C1.

Group	Model no	Variables	AIC	ΔAIC	wAIC	BIC	ΔBIC	wBIC
Anthropogenic	1	HFOOTP	1123.03	321.54	0.00	1132.93	291.89	0.00
	2	HPDENLG	1234.52	433.03	0.00	1244.42	403.38	0.00
	3	HPDENLG, HFOOTP	1110.33	308.84	0.00	1125.18	284.14	0.00
Environmental	4	PREC_{B12}	1074.89	273.40	0.00	1084.79	243.75	0.00
	5	CANOPY	1181.34	379.85	0.00	1191.24	350.20	0.00
	6	PREC_{B12}, TEMP_{B1}, CANOPY	946.88	145.39	0.00	966.68	125.64	0.00
	7	PREC_{B12}, TEMP_{B1}, CANOPY, NPP_{MEAN}	938.89	137.40	0.00	963.61	122.57	0.00
	8	PREC_{B12}, CANOPY, NPP_{MEAN}	986.38	184.89	0.00	1006.15	165.11	0.00
	9	PREC_{B12}, TEMP_{B1}, CANOPY, NPP_{MEAN}, EVI_{SD}	937.61	136.12	0.00	967.27	126.23	0.00
	10	PREC_{B12}, TEMP_{B1}, CANOPY, NPP_{MEAN}, EVI_{MEAN}, EVI_{SD}	931.39	129.90	0.00	965.99	124.95	0.00
Anthropogenic - environmental	11	PREC_{B12}, TEMP_{B1}, NPP_{MEAN}, EVI_{MEAN}, HPDENLG, HFOOTP	839.66	38.17	0.00	874.26	33.22	0.00
	12	PREC_{B12}, TEMP_{B1}, CANOPY, HPDENLG, HFOOTP	812.39	10.90	0.00	842.09	1.05	0.25
	13	PREC_{B12}, TEMP_{B1}, CANOPY, NPP_{MEAN}, HPDENLG, HFOOTP	806.80	5.31	0.07	841.41	0.37	0.34
	14	**$\mathbf{PREC}_{\mathbf{B12}}$, $\mathbf{TEMP}_{\mathbf{B1}}$, CANOPY, $\mathbf{NPP}_{\mathbf{MEAN}}$, $\mathbf{EVI}_{\mathbf{SD}}$, HPDENLG, HFOOTP**	801.49	0.00	0.93	841.04	0.00	0.41

Bold indicates the selected model.

jaguar presence/absence data points (Fig. 1B). The best cut-off value of predicted probabilities was about 0.5. At that point 88% of presence points and 72% of absence points were correctly classified; total correct classification rate was 0.83.

3.2. Current range of jaguars in Venezuela

The combination of our occurrence model, based on environmental and anthropogenic covariates, together with our kriging interpolation model based on the distribution of presence/absence points, results in 4 possible outcomes: both maps predict presence, both maps predict absence, or one map predicts presence while the second predicts absence (Fig. 2A). Where both maps predicted presence (64% of the national territory) - we considered this as a confirmed and reliable estimation of jaguar distribution areas. Both models predicted absence of jaguar in 19% of the country. Areas where jaguar occurrence cannot be completely accounted for by environmental and anthropogenic variables (i.e. the kriging interpolation predicted presence while the occurrence model predicted absence) accounted for 10% of the study area. Finally, a small fraction of the country (7%) apparently has suitable conditions (occurrence model > 0.5) but contains no evidence of jaguar presence. Overall, after taking into account the spatial variance of values predicted with the kriging interpolation, we estimated the current jaguar range in Venezuela at approximately 601,000 km^2, or 66% of the country's total area (Fig. 2B).

3.3. Jaguar extirpations and persistence prospects

We could estimate the time since jaguar extirpation for 295 of the 540 jaguar absence points. This time ranged from 5 to 75 years. Twenty percent of documented extirpation cases occurred between years 1940 and 1965, 21% between 1966 and 1980, 39% between 1981 and 2000, and 20% after year 2000. Although the majority of extirpations in Venezuela appear to have occurred within the last 75 years, for the open dry savannahs and dry unproductive savannah-scrubland formations in the Anzoátegui state, as well as for the higher parts of the Andes, we were unable to collect reliable information on the past presence or date of jaguar extirpation. This perhaps indicates that the jaguars in these areas became extinct long ago or that jaguars never inhabited these regions. Based on the current habitat map and digital elevation model we estimated that these areas cover about 8% of the country's territory. Thus, taking into account the estimated current jaguar range, we estimate that human caused extirpations of jaguars occurred on about 26% of the territory of Venezuela or about 29% of the original jaguar range in Venezuela.

Table 2
Parameters of the top model of jaguar occurrence in Venezuela. Included biases, standard errors (Standard Error_{BOO}) and p-values (p_{BOO}) for regression coefficients of the bootstrapped model.

Parameter	Estimate	Std. Error	Z	p-Value	Bias	Standard Error_{BOO}	p_{BOO}
CONSTANT	−8.2767	1.25	−6.64	0.0000	−0.12	1.16	0.00
Precipitation	0.0023	0.00	7.49	0.0000	0.00	0.00	0.00
Temperature	0.1851	0.04	4.42	0.0000	0.00	0.04	0.00
NPP_{MEAN}	0.0012	0.00	2.64	0.0083	0.00	0.00	0.01
EVI_{SD}	7.7322	2.88	2.68	0.0074	0.09	2.97	0.01
Canopy	0.0521	0.01	7.40	0.0000	0.00	0.01	0.00
Log(Human Density)	−0.2668	0.08	−3.31	0.0009	0.00	0.09	0.00
Human footprint	−0.0813	0.01	−7.69	0.0000	0.00	0.01	0.00

Jaguar extirpation models fit with the combination of anthropogenic and environmental factors were supported with the lowest AIC/BIC values. Models using only environmental factors were only slightly worse, while models fit only with anthropogenic factors were not significant (Table 3). The best model for the time since extirpation included four variables: precipitation, mean and standard deviation of the enhanced vegetation index, and human density ($R^2 = 0.27$, Standard Error of Estimate = 14.67, $p < 0.000000$, N = 295, Table 4). This model suggests that jaguars were extirpated first in the dry and low productive areas with high human density, and that the extirpation rate is slowest in humid and high productive areas with low human density. However, the coefficient of human density in this model was not significantly different from zero (Table 4). A second model, without human density, had almost equal support (i.e. ΔAIC < 2 and the lowest BIC value) and included only the three environmental variables: annual precipitation and mean and standard deviation of the enhanced vegetation index (Tables 3, 4). This model was highly significant, but with lower predictive precision than the occurrence model ($R^2 = 0.26$, Standard Error of Estimate = 14.73, $p < 0.00000$, N = 295). We found no evidence of heteroscedasticity or non-linearity that would imply violation of model assumptions.

We projected the extirpation model onto the whole territory of Venezuela and overlaid it with the jaguar range derived from Fig. 2B. Outside of current jaguar range, this map presents the estimated times since jaguar extirpation (Fig. 3A). It indicates dry areas and high altitude sectors of the Andes as regions where jaguars disappeared long ago and other areas where jaguars became extirpated more recently. Reverse values indicate resistance to extirpation or probability of persistence of jaguar populations over next 75 years if environmental conditions and rate of anthropogenic alterations do not change (Fig. 3B).

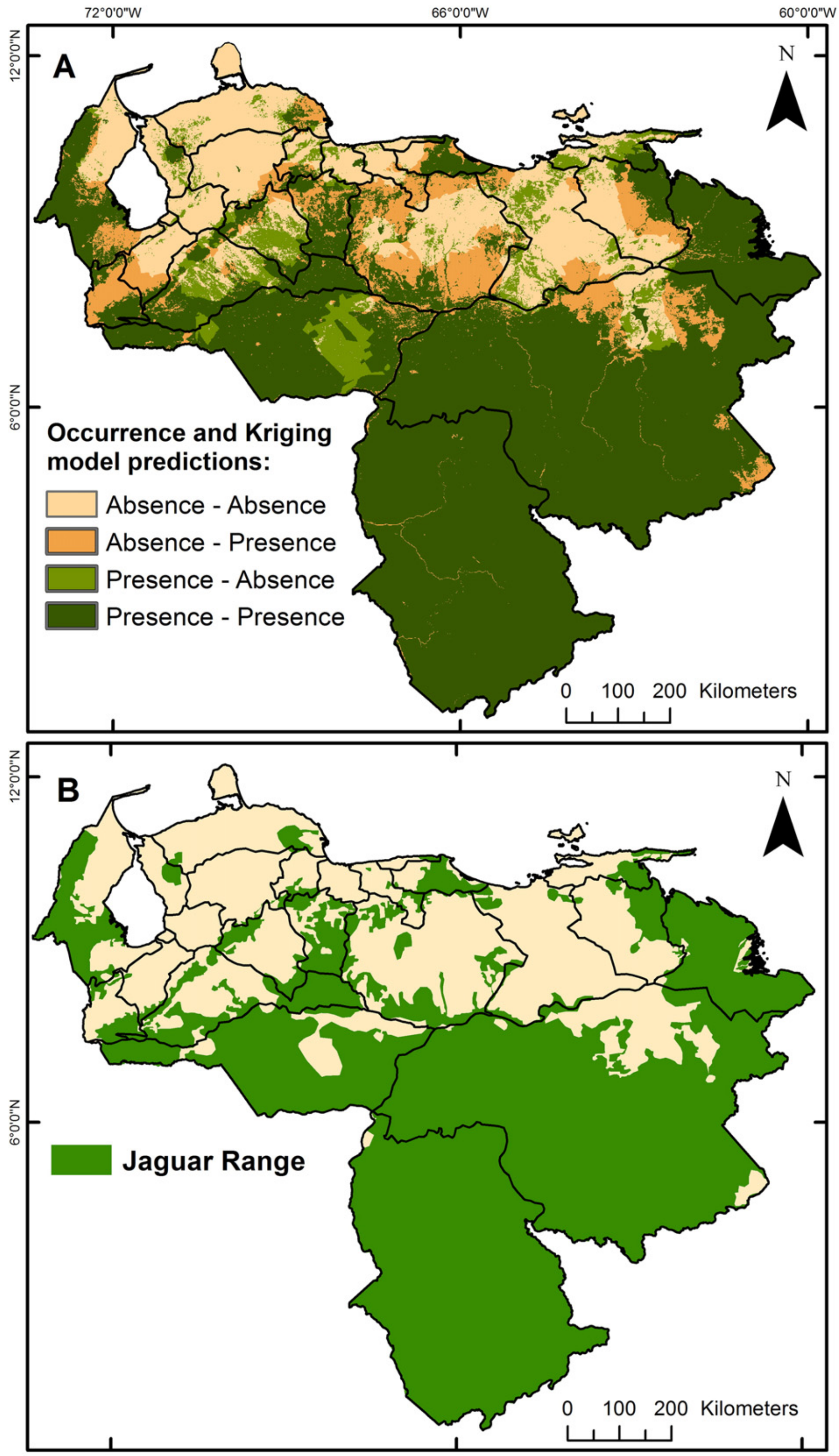

Fig. 2. Prediction of the current jaguar distribution in Venezuela. A. An overlay of the occurrence model and the kriging interpolation model. B. Predicted current jaguar range.

3.4. Predicting jaguar extirpations based on human density thresholds

Approximately 95% of the recorded cases of jaguar presence occurred in areas with human densities lower than 40 people/km^2. However, the percentage of jaguar presence points declined markedly above 6–8 people/km^2; 75% of presence points were at human densities lower than this (Fig. 4). Following this distribution, for further calculations we designated 8 people/km^2 as the "decline threshold" and 40 people/km^2 as the "extirpation threshold". Today, only 5% of the area of Venezuela has a human population density higher than 8 people/km^2, and only

Table 3
Comparison of models of time since jaguar extirpation across Venezuela (1940–2015). Models are organized in 2 groups representing competing hypotheses on which factors determine extirpation rate: (1) only environmental factors, (2) combination of anthropogenic and environmental factors. Models fit with only anthropogenic factors were not significant.

Model group	Model no	Variables	AIC	ΔAIC	wAIC	BIC	ΔBIC	wBIC
Environmental	1	$PREC_{B12}$	2478.98	50.18	0.00	2490.04	41.59	0.00
	2	EVI_{MEAN}	2467.50	38.70	0.00	2478.56	30.12	0.00
	3	$PREC_{B12}$, EVI_{MEAN},	2438.11	9.31	0.01	2452.86	4.41	0.08
	4	**$PREC_{B12}$, EVI_{MEAN}, EVI_{SD}**	2430.01	1.21	0.35	**2448.45**	**0.00**	**0.71**
Anthropogenic - environmental	5	**$PREC_{B12}$, EVI_{MEAN}, EVI_{SD}, HPDENLG**	**2428.80**	**0.00**	**0.64**	2450.92	2.48	0.21

Bold indicates models selected with AIC and BIC criterions.

1% higher than 40 people/km^2 (Table 5). However, by 2050 the amount of favourable areas for jaguars (with human density lower than 8 people/km^2) will decline to 71% of the national territory (Table 5). A different, more optimistic prediction resulted from the projection of our occurrence model, which takes into account the joint effect of anthropogenic and environmental factors. This model run with the human densities predicted for 2050, indicated that by 2050 the areas with a probability of jaguar occurrence higher than 0.5 will decrease only by just 1% of the territory of Venezuela (Table 5).

4. Discussion

Our results support the hypothesis that jaguar spatial distribution is shaped by the joint effect of anthropogenic and environmental variables. Similarly, De Angelo et al. (2013) showed that a combination of anthropogenic and environmental factors best explained the current distribution of jaguars in the Atlantic Forest. However, our study for the first time relates the observed distribution of a large carnivore with the dynamic extirpation process and adds a temporal dimension to spatial predictions. Moreover, our analysis reveals the mechanisms that shape the spatial variation in large carnivore local extinctions and determine the observed patterns of their distribution. It demonstrates the importance of ecosystem productivity in these mechanisms. Jaguar populations in dry and unproductive areas with high seasonality appear to be much more vulnerable to extirpations than in humid and highly productive zones. In dry habitats jaguars disappear more quickly than in humid areas, even when human densities are lower. This pattern is likely associated with differences in prey biomass and prey productivity. Higher ecosystem productivity has been shown to lead to higher densities of both herbivores and carnivores (Fritz and Duncan, 1994, Jędrzejewski and Jędrzejewska, 1996, Karanth et al., 2004, Melis et al., 2009, Ripple and Beschta, 2012). Jaguars in dry areas have lower densities than in humid zones (Gutiérrez-González et al., 2012, Quiroga et al., 2014) and possibly a lower reproductive capacity to compensate for human-caused mortality. Higher extirpation rates in arid zones have been observed not only in Venezuela, but also in dry regions of the USA, Mexico, and Argentina, where jaguar extirpations occurred long before jaguars disappeared from other, more humid areas (Swank and Teer, 1989, Nowell and Jackson, 1996). The finding that ecosystem productivity affects extirpation rate may be broadly applicable for obtaining a better understanding of the spatial patterns of declines of other large carnivores which are subjected to anthropogenic impacts.

Table 4
Parameters of the top models of time since jaguar extirpation in Venezuela. A. Best model of the group fit with both anthropogenic and environmental factors. B. Best model of the group fit with environmental factors only. Included biases and standard errors (Standard $Error_{BOO}$) for regression coefficients of the bootstrapped model.

Effect	Coefficient	Standard Error	t	p-Value	Bias	Standard $Error_{BOO}$
A. Anthropogenic – environmental, top model						
CONSTANT	77.4842	6.678	11.60	0.00000	1.729	3.784
Precipitation	−0.0149	0.003	−4.65	0.00001	−0.002	0.003
EVI_{MEAN}	−75.0142	10.414	−7.20	0.00000	0.645	10.033
EVI_{SD}	99.4365	27.878	3.57	0.00042	−3.572	27.651
Log(Human Density)	1.0029	0.563	1.78	0.07587	0.074	0.490
B. Environmental variables only, best model						
CONSTANT	80.4026	6.498	12.37	0.00000	1.465	4.579
Precipitation	−0.0158	0.003	−5.02	0.00000	−0.001	0.004
EVI_{MEAN}	−69.9037	10.048	−6.96	0.00000	3.511	13.350
EVI_{SD}	85.4959	26.857	3.18	0.00161	−14.756	31.770

In contrast to the environmental variables related with productivity, the anthropogenic factors, i.e. human density and human footprint index showed persistent negative effects on the probability of jaguar occurrence. Human density is likely correlated with density of hunters and thus with the impact of hunting on jaguars. The human footprint index reflects habitat deterioration. The high significance of the effects of human footprint and forest canopy cover in our models also indicates the importance of deforestations in limiting jaguar occurrence. Thus our study suggests that jaguar hunting and habitat alterations, postulated as the main human pressures on jaguar populations in several studies, exert a real impact which has a general character and is reflected by changes in jaguar distribution on a large scale (Quigley and Crawshaw, 1992, Cavalcanti et al., 2010, de Oliveira et al., 2012).

Our extirpation model explained only part of the observed variation in the time since jaguar extirpations (i.e. $R^2 = 0.29$), suggesting that additional factors, not related to vegetation productivity or human density, must have also influenced jaguar extirpations. The factor most often mentioned during our interviews was the time of large scale deforestations that took place in Venezuela between 1960 and 1995 (Pacheco, et al., 2011). Another possibly important factor, not included in our models, could be habitat fragmentation, known to play an important role in local extinctions of birds and other animal groups (Newmark, 1995).

We estimated that jaguar range today covers approximately 66% of Venezuela and that jaguars have been extirpated from approximately 29% of their natural range. This is less than the estimated 50% total reduction across the species range (Swank and Teer, 1989). Giacopini-Zárraga (1992) stated that jaguars were widespread across most of Venezuela at least until 1950. The intensive jaguar hunting that occurred all over South America from the 1950s to the 1970s likely contributed to the decline of jaguars in various parts of Venezuela (Fitzgerald, 1989, Hoogesteijn and Mondolfi, 1992, Linares, 1998, Payán and Trujillo, 2006, Ojasti and Lacabana, 2008). Our results appear to confirm that the current jaguar distribution in Venezuela is largely the result of recent extirpations within the last 75 years, and that it is a continuous, quick, and on-going process. Official protection of the jaguar has not stopped its local extinctions and we can expect further jaguar declines. Our extirpation model and the persistence probability map indicate that populations most susceptible to human impacts are located in the drier parts, where, in the case of Venezuela, also the rates of human population increase and deforestation are high. Conservation actions may be best targeted at these low productivity areas across jaguar range to prevent further extirpations.

Species distribution modelling can be an important tool for understanding environmental limits, anthropogenic impacts, and spatial and temporal dynamics of geographic ranges of species (Guisan and

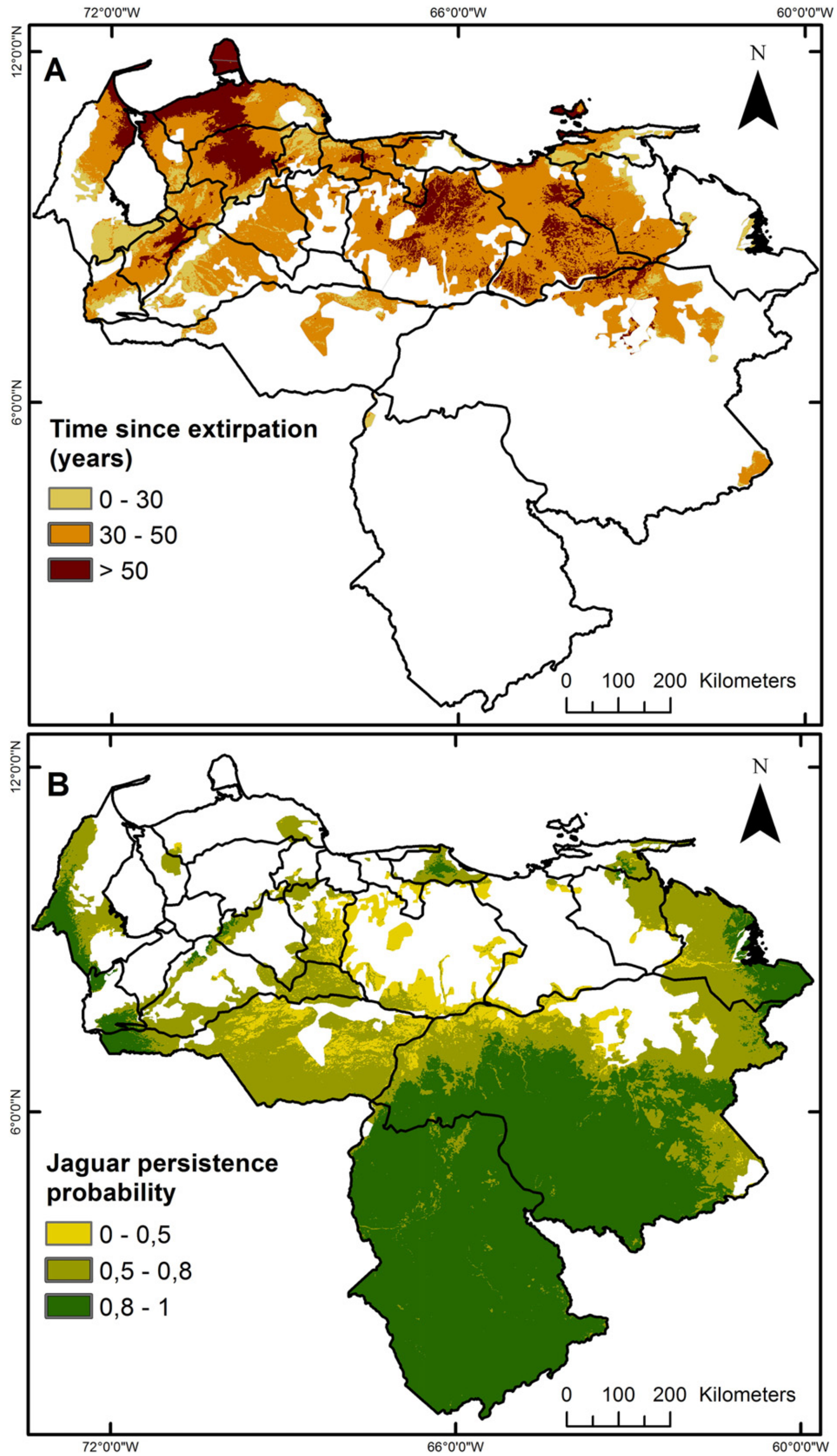

Fig. 3. Spatial projection of the extirpation model (as in Table 4B) and the estimated persistence probability. A. Estimated time since jaguar extirpation in areas outside of the present jaguar range in Venezuela (after Fig. 2B). B. Estimated index of resistance of jaguar populations to extirpation that can be interpreted also as an index of the probability of jaguar persistence within the next 75 years; inside the present jaguar range.

Thuiller, 2005, Elith and Leathwick, 2009). We believe that our models, fit with general, globally available environmental and anthropogenic variables, can be applicable outside of Venezuela to predict distribution, evaluate habitat suitability or to indicate areas with higher extirpation risk for jaguar populations. Therefore, they can help in designing carnivore conservation units, conservation plans, or even planning

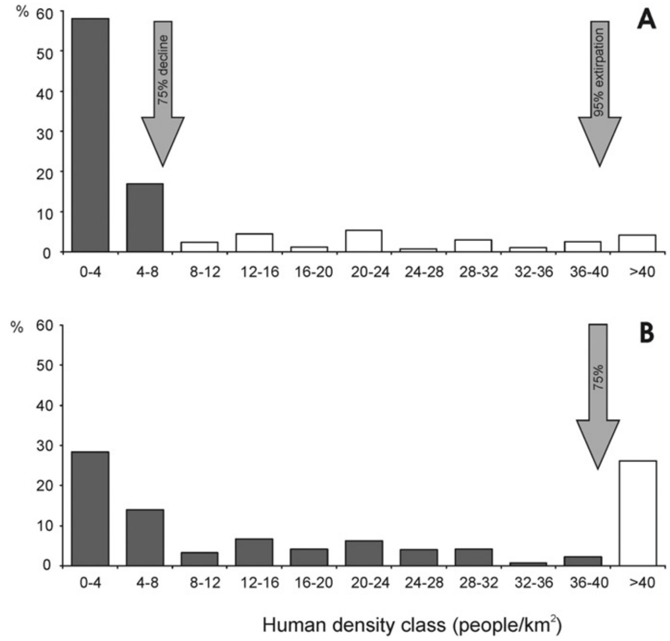

Fig. 4. Frequency distribution (percent of cases) of jaguar presence (A) and absence (B) points at different levels of human density. For the jaguar presence points (N = 641) two threshold levels of human densities are indicated: (1) "decline threshold" = 8 people/km^2, with 75% of jaguar presence points (shaded area) occurring where human densities are lower than this value; (2) "extirpation threshold" = 40 people/km^2, with 95% of presence points occurring where human population densities are below this value. In the case of absence points (N = 402), 25% of cases occur where human densities are higher than 40 people/km^2.

ecological corridors. It is interesting that our occurrence and extirpation/persistence models, although based on largely independent data sets (presence/absence vs. estimated time since extirpation for absence points only), come to very similar spatial predictions.

In our analyses, models constructed only with anthropogenic variables had poor predictive power. However, other authors have proposed that extinctions of large carnivores can be predicted based on human densities alone (Purvis et al., 2000, Cardillo et al., 2004). Woodroffe (2000) predicted a critical human density of 17.3 people/km^2, at which jaguars become extirpated. Applying a similar approach, we found that on average, jaguar populations in Venezuela decline at densities of 6 to 8 people/km^2 and are rarely found at densities higher than 40 people/km^2. However, we have also shown that these threshold human densities alone neither adequately explain past extirpations nor can be reliably used to predict future declines. Environmental and other anthropogenic factors, most likely deforestation and livestock breeding, probably also contributed to the past extirpations, as indicated by our models and other research (Hoogesteijn et al., 1993, González Fernández, 1995). An optimistic conclusion from our analysis is that proper management and effective conservation programs can halt extirpations of large carnivores, even where human populations are increasing.

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Table 5

Projection of the changes in the area of Venezuela occupied by jaguars between years 2011 and 2050, applying three different methods of prediction: (a) considering only areas with human population density lower than 8 people/km^2 (decline threshold) as suitable for jaguars, (b) considering areas with human population density lower than 40 people/km^2 (extirpation threshold) as suitable for jaguars, (c) considering areas with the probability of jaguar occurrence estimated with our logistic regression model higher than 0.5.

	% area with Human Density < 8 people/km^2		% area with Human Density < 40 people/km^2		% area with the probability predicted by the occurrence model > 0.5	
Total area (thousand km^2)	2011	2050	2011	2050	2011	2050
916	95	71	99	90	71	70

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