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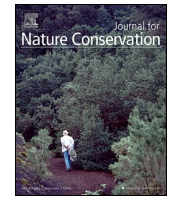

A continental approach to jaguar extirpation: A tradeoff between anthropic and intrinsic causes

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ABSTRACT

Human impacts are blamed for range contraction in several animal species worldwide. Remarkably, carnivores and particularly top predators are threatened by humans despite their key role in maintaining ecosystem balance and functions. Conservation strategies to allow human-carnivore coexistence are urgently needed. These strategies must be built on evidence and driven by knowledge of population risk at a broad scale. However, knowledge on wide distributed species is often based on regional expert opinions in which uncertainty is not quantifiable, making data incomparable across regions. Here we develop a method to assess the endangerment status of a species based on its range contractions and the main threats using the jaguar *Panthera onca* as model. The use of GLM with the main intrinsic and extrinsic drivers of jaguar extinction allowed us to assess the endangerment status at continental and population scale. We found this method to be a valuable tool to obtain a broad picture of human-induced endangerment in animal species. Intrinsic traits (summarized in the demographic contraction theory) and anthropic traits (based on agriculture, cattle and human densities) explained jaguar extinction highlighting the particular importance of livestock activity. Our results suggest that livestock ranching has a pervasive effect on the species likely due to habitat loss combined with retaliatory hunting. We highlight the need to rethink policies, practice and law enforcement in relation to livestock and suggest the development of action plans based in local evidence in those countries where endangered populations have been detected. We also recommend involving and encouraging land owners and private companies in the conservation of private lands that comprise much of the endangered jaguar range.

1. Introduction

Understanding the general dynamics of species range contraction is key for effective conservation, and predicting population extinction risk is an important step toward achieve this goal (Safi & Pettorelli, 2010). Species extinctions generally start with the vanishing of particular populations that continues until no populations remain (Yackulic et al. 2011). There are two main factors determining carnivores' extinction risk (Purvis et al., 2000): 1) intrinsic traits, such as body mass (Inskip & Zimmermann, 2009), life history (Pearson et al., 2014) or population genetics (Frankham, 2005), and 2) extrinsic causes based on modern exposure to external anthropogenic threats (Bruskotter et al., 2017), including human-driven disease expansion (Pedersen et al., 2007). Extrinsic causes have been repeatedly suggested as important traits that affect direct or indirectly carnivore populations. In fact, human density (Woodroffe, 2000), prey depletion (Craigie et al., 2010), habitat loss (Cardinale et al., 2012) or retaliation (Jędrzejewski et al., 2017) have been highlighted as the most important drivers of many carnivore species. Intrinsic traits may be summarized by the demographic contraction theory (Lawton, 1993, Brown et al., 1995), which is derived from basic population dynamics. It assumes that environmental conditions and resources for species at the center of their distribution are more suitable than at the border, resulting in higher population growth rates and thus, higher abundance in central areas. This theory predicts that populations would be first extirpated along the range border (where density is lower) and would continue toward the center. On the other hand, more humanized landscapes are associated with higher risk of extirpation (Laliberte & Ripple, 2004, Schipper et al., 2008, Hoffmann et al., 2010, Fisher & Blomberg, 2011, Pomara et al., 2014), predicting that populations would be first extirpated in areas where human activities such as agriculture, cattle raising and urbanization dominate.

Risk models have been widely used to provide valuable information for conservation purposes. Most risk model assessments, particularly for larger mammalian carnivores, are based on habitat suitability often omitting anthropic traits that are usually indicated as responsible for the non-explicated variation (Cardillo et al., 2004; Brashares et al., 2001;

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Harcourt et al., 2001; MacKinney, 2001; Ceballos & Ehrlich, 2002; Parks & Harcourt, 2002). Studies taking into account anthropic variables (Rodríguez-Soto et al., 2011, 2013, 2017; Zarco-González et al., 2013) become more realistic models but use to be local scaled (but see Jędrzejewski et al., 2018). However, knowledge of both drivers of population declines and ultimately species extinction should be one of the main focusses to facilitate the allocation of the limited resources to specific conservation interventions (Davies et al., 2008; Travers et al., 2016).

During the past decade, knowledge about the ecology and conservation of top predators has increased widely. In particular, jaguars (*Panthera onca*) received great attention since they have suffered a reduction of at least 46% (Sanderson et al., 2002) of their historic range. Since Sanderson et al. (2002) defined Jaguar Conservation Units (henceforth JCU), many updates and revisions of jaguar status have been made and this percentage has been currently set to 51% in the last IUCN expert assessment (Quigley et al., 2017). Global experts made contributions and reviewed the state of the art completing the actual conservation snapshot for many regions (i.e., Quigley et al. 2017; Medellín et al. 2016). This effort generated a large amount of information that not only promotes jaguar conservation but also enables the use of the species as a model to test for specific hypotheses about species range contraction. Again, most of the continental scale research has been focused on niche prediction and the relation that it has with ecological patterns, demonstrating the efficiency of climatic variables as predictors of felid niche suitability (Torres et al., 2012; Martínez-Meyer et al., 2013; Caruso et al., 2015; Zanin et al., 2019). However most continental scale approaches ignore anthropic disturbances, vital to understand species decline, and have been only assessed at a regional scale (Cavalcanti et al., 2010; Zimmermann et al., 2005; Rodriguez-Soto et al., 2011, 2013; Marchini & Macdonald, 2012; Villalva & Palomares, 2019). Moreover, ecological research on jaguars has largely focused on populations inhabiting protected areas (Foster et al., 2020). Consequently, few data are available on jaguars occupying the mosaic of human settlements and agriculture. These areas comprise typical unprotected landscapes, including jaguar movement corridors and private properties that have been identified as vital to maintain jaguars genetic connectivity (Zeller et al., 2013). Furthermore, global estimates are based on "expert opinion" which is burdened with a high and unquantifiable level of uncertainty (Akçakaya et al., 2000; Rodrigues et al., 2006) that may result in a possible over or underreporting of threats to jaguars in certain areas (Zeller, 2007). The role of spatially explicit models appears to be a valuable tool as they can be a compliment to expert-based information (Bernal-Escobar et al., 2015).

The aim of this study is to identify the endangerment of jaguars across their current range. As mentioned, jaguars are mainly threatened by intrinsic and external factors. The intrinsic threats are related to their large size, high trophic level, slow population dynamics and fragmentation of its populations that increases their extinction risk (Purvis et al., 2000). Thus, we expect them to exhibit a periphery-to-center extinction pattern. The extrinsic threats are related to human activities such as habitat loss on behalf of agriculture, cattle ranching (including persecution by predation on livestock) and urbanization (Boron et al., 2016, Quigley et al., 2017). We expect the probability of jaguar extirpation to increase in areas with higher human pressures compared to more natural areas. More concisely, we expect to find jaguars especially affected by livestock due to the combined effect of habitat loss and the deeply rooted retaliatory killing used to minimize economic losses, while agriculture and urbanization may moderately affect the species due to the lower conflict level with the main economic interests. Accordingly, we build an extinction threat model based on aforementioned intrinsic and extrinsic traits that will contribute to generate a comprehensive snapshot of current jaguar endangerment that may help in the elaboration of conservation strategies.

2. Methods

We examine the extinction probability of jaguars in the entire distribution range using General Linear Models (GLM). We used current and historic distribution to construct a binomial response variable, assigning value zero to areas where jaguars still persist and value one to areas where jaguars have been extirpated (Fig. 1. Supp. 1). Current range (Quigley et al., 2017) was subtracted from historic range (Seymour, 1989) to obtain the area where jaguars have been locally extinct. To generate the dataset, we randomly displayed a set of 1000 points on current and extirpated areas extracting the same amount of data in each to avoid overdispersion.

We used a set of predictor variables based on intrinsic and extrinsic traits. The intrinsic variable was defined as the distance to the border from the historic distribution grounded on the demographic range contraction hypothesis. The extrinsic predictors contained a selection of the main reported human drivers of jaguar extinction such as fragmentation, habitat loss and felid persecution by humans (Quigley et al., 2017). Thus, we selected urban, agriculture and cattle ranching as the main human disturbances related to the aforementioned drivers. Human density was used as a proxy for urban disturbance based on the SEDAC-NASA model GRUMP 2000 (CIESIN, 2017). This is a population estimate at the municipal level, corrected for night-light. Agriculture disturbance was based on Global Land Cover (Bartholome et al., 2002; Eva et al., 2004) from The European Council. We clustered all types of agriculture (Cultivated and managed areas, Mosaic cropland with tree and Mosaic cropland with shrub) and resampled from 1 to 10 Km^2 pixel size obtaining the percentage of agriculture cover. Livestock pressure was acquired from Global Livestock of the World (Robinson et al., 2014) based on livestock data at a municipal level representing cattle density (number of heads/km^2). All layers were unified at a pixel value of 100 Km^2 based on a conservative home range size for a jaguar male (Gonzalez-Borrajo et al., 2017). When redefining pixel size, human and livestock pressure data took the mean value of the underlying pixels, while agriculture pressure, as explained above, was obtained as a percentage of cover regarding the 100 underlying pixels of 1 Km^2 contained in each sample grid of 100 km^2.

We tested the effect of intrinsic and external traits on jaguar extinction using a logit link with species extinction as the response variable. We first constructed univariate models to graphically evince the relationship of extinction to each independent variable. Then, using an information-theoretic approach, we analyzed the effect of intrinsic and extrinsic variables on the probability of jaguar extinction by comparing the generated presence-absence data, guided by three general hypotheses: (i) extrinsic traits (human disturbance) caused jaguar extinction; (ii) intrinsic traits (inherent species contraction) caused extinction; and (iii) the combination of the two influenced extinction. We also constructed a null model that included no explanatory variables. Prior to modelling we searched for confounding effects among predictor variables using Pearsońs rank correlation to avoid multicollinearity (Zar, 1999).

We made the best model spatially explicit within the jaguar current range using the logit function. Note that the intrinsic variable used here was the distance to the border from the current distribution range rather than the distance to the historic distribution. All other variables remained unchanged.

Finally, we focused on Jaguar Conservation Units (Sanderson et al., 2002) to compare the endangerment status among the most important and stable jaguar populations. Values for each Jaguar Conservation Unit were calculated as the mean value of pixels contained in the polygon.

We transformed and processed the data with Q-Gis (2.8.9-Wien), and raster (Hijmans, 2020), spatial (Venables, 2002), terra (Hijmans, 2021) and sf (Pebesma, 2018) packages in R, and carried out the statistical analyses using the MuMIn (Barton, 2020) package in R version 4.0.3 (R Core Team, 2021).

3. Results

Univariant models showed the relationship of all predictors with jaguar extirpation (Table1). Distance to the border relate negatively with extinction whereas anthropic variables showed a positive relationship. Cattle density showed the lowest AIC among univariant predictors. Each variable affected extinction differently (Fig. 1). Probability of extinction reached saturation with cattle and human densities, but not with agriculture or distance to the border. Saturation was reached over values of 150 and 350 (individuals/Km^2), respectively. Extinction likelihood reached a maximum value of 0.86 when agriculture cover was maximized.

Correlation tests showed cattle and agriculture as the most correlated variables with a marginal correlation of r pearson = 0.57 (Table 1. Supp. 1). Therefore, we retained all variables for multivariate models. Model selection showed that, in terms of AIC, extinction was better explained by anthropic variables rather than intrinsic traits, however both natural and human induced variables composed the best model characterized by the lowest AIC value among the tested hypotheses (Table 2) with a goodness of fit $D^2 = 0.20$.

When the saturated model was made spatially explicit, we found 4.15 million Km^2 (corresponding to 46.9% of current distribution) to have a probability of extinction over 0.5 while 4.7 million Km^2 (53.1%) took values under this figure (Fig. 2). Four Jaguar Conservation Units are already out of the current distribution range therefore appear to be currently extinct and 68% of JCUs (n = 51) showed a mean probability of extinction over 0.5. Regarding to the aggregated JCUs area more than 55% took values over 0.5, corresponding to 886.834 Km^2 (Fig. 1, Table 1. Supp.2).

4. Discussion

In our study, anthropic drivers contributed the most to jaguar extirpations, suggesting that jaguar extinction is mostly human-driven. However, we also found that the edge effect is important for jaguar extinction as it makes part of the best model. This result likely indicates a combined effect among the limited jaguar recolonization from sources and the greater human pressure intensity at the distribution edge. Anthropic variables showed scarce correlation with distance to the border (Table 1. Supp. 1) however, human pressure may locally be more intense at the border than at the core of the distribution where ecosystems are more pristine and human industries have less impact. The lethal combination among edge effect and human induced mortality has been previously detected in protected areas for many large carnivore species, including jaguars (Woodroffe & Ginsberg, 1998) but, to our knowledge, it has not been detected in the entire range of any carnivore species. In summary, we found that both intrinsic and anthropic variables affect jaguar extirpations. We highlight the need to consider both human activities and natural intrinsic traits to understand the range contraction of a species, a conclusion recently shown for different mammalian species (Pacifici et al., 2020), in line with prior findings where combining distance to range border and human impacts are needed to define terrestrial vertebrate range contraction (Lucas et al., 2016).

Table 1
Univariate models for jaguar extinction. Comparison of models based on AIC and Beta, Standard error (S.E.) and significance level (*p-value*) are also shown.

	Variables	AIC	ß	S.E.	*p value*
Natural contraction					
	Intercept		0.820	0.108	<0.001
	Distance to border	1255	−0.211	0.022	<0.001
Anthropic variables					
	Intercept		−0.621	0.085	<0.001
	Cattle density	1212	0.033	0.003	<0.001
	Intercept		−0.532	0.082	<0.001
	Agriculture	1258	0.023	0.002	<0.001
	Intercept		−0.166	0.071	0.01
	Human density	1339	0.020	0.004	<0.001

From the set of extinction drivers we test here, cattle density showed the best performance in both univariant and multivariant models, suggesting the major role of cattle industry for jaguar extirpations. On the other hand, the rest of anthropic drivers didn't perform well to explain jaguar extinction compared to cattle ranching, even though agriculture (Petracca et al., 2014) and human density (De Angelo et al., 2013) are main factors limiting jaguar use of space at regional scales. We highlight the limited effect of agriculture, which only reached a moderate extinction risk in the univariant model even when agriculture cover was maximized. Still, agriculture and urbanization are important drivers of habitat loss but these human activities lack the deeply rooted motivation of retaliatory hunting that characterizes livestock ranching, which appears to be the main reason for human-induced jaguar extinction. The implications of these results are relevant at the continental scale, since livestock and agriculture are the essential drivers of habitat loss and fragmentation in Latin America (FAO & UNEP, 2020). Predictions of world population growth (U.N., 2019) and the resulting increase on food demand (FAO, 2017) portends an increase in the area occupied by these industries in the neotropical region. Therefore, identifying livestock growth policies in particular may help to get ahead of jaguar extirpations in the near future.

The spatially explicit model revealed that more than 46% of the current jaguar distribution may be endangered ($p > 0.5$). However, observing the frequency histogram of extinction probabilities in Fig. 2, there is a sharp decrease in extinction probability of 0.7. Thus, to avoid overestimation of endangered areas we may consider areas with a high endangerment level to be those with extinction probability values over 0.7, and those with values over 0.9 to be at a very high endangerment level. Thus, 14.5% of the predicted jaguar distribution area would be highly endangered, and 3.5% extremely endangered, suggesting that in these areas local extinction may have already occurred or will soon be complete. This area covers 1.5 million km^2, which implies that jaguar distribution may be currently occupying 40.1% of its historic range, or will soon reach that level. Our results show higher range contraction than estimations from last decades (Zeller, 2007; Sanderson et al., 2002), but are aligned with the later estimations (Quigley et al., 2017), suggesting that jaguar extinction is still occuring at a broad scale. On the other hand, we find that 53.1% of the current distribution (4.7 million Km^2) is under low endangerment levels ($p < 0.5$). Most of these areas correspond to the main jaguar sources located in the Amazon basin and surroundings where human business is still not magnified, seeming to be vital to maintain jaguar core populations and therefore to maintain their integral role in trophic cascades and prey regulation of neotropical ecosystems (Cavalcanti & Gese, 2009; Terborgh et al., 2001).

We noted that four Jaguar Conservation Units have currently been extirpated according to the last distribution range updates. These populations corresponded to the northern Sierra Madre Occidental in Mexico, Honduras South, Mache-Chindul and Manglares Cayapas in Ecuador. Moreover, our model identified 15 highly endangered ($p > 0.7$) populations distributed throughout the current range, results supported by local assessments. Populations in Central America stand out due to their lack of connectivity and high extinction risk (Rabinowitz & Zeller, 2010), showing high endangerment in our model with the exception of Yucatan ($p = 0.55$), where anthropic pressure is more controlled (Chavez et al., 2016), and Belize ($p = 0.57$), where conservation has been historically promoted through ecotourism (Kroshus, 2010). Additional Central American populations such as Guatemala and Honduras show high-risk values, which reveal their critical situation (Sanderson et al., 2002) due to conflicts with ranchers and inefficiency of protected areas (Mora et al., 2016). Most endangered populations in northern South America are located in Colombia and Venezuela, and have been identified as highly threatened key populations for maintaining connectivity between Central and South American populations (Zeller et al., 2013). Finally, our model shows endangered populations

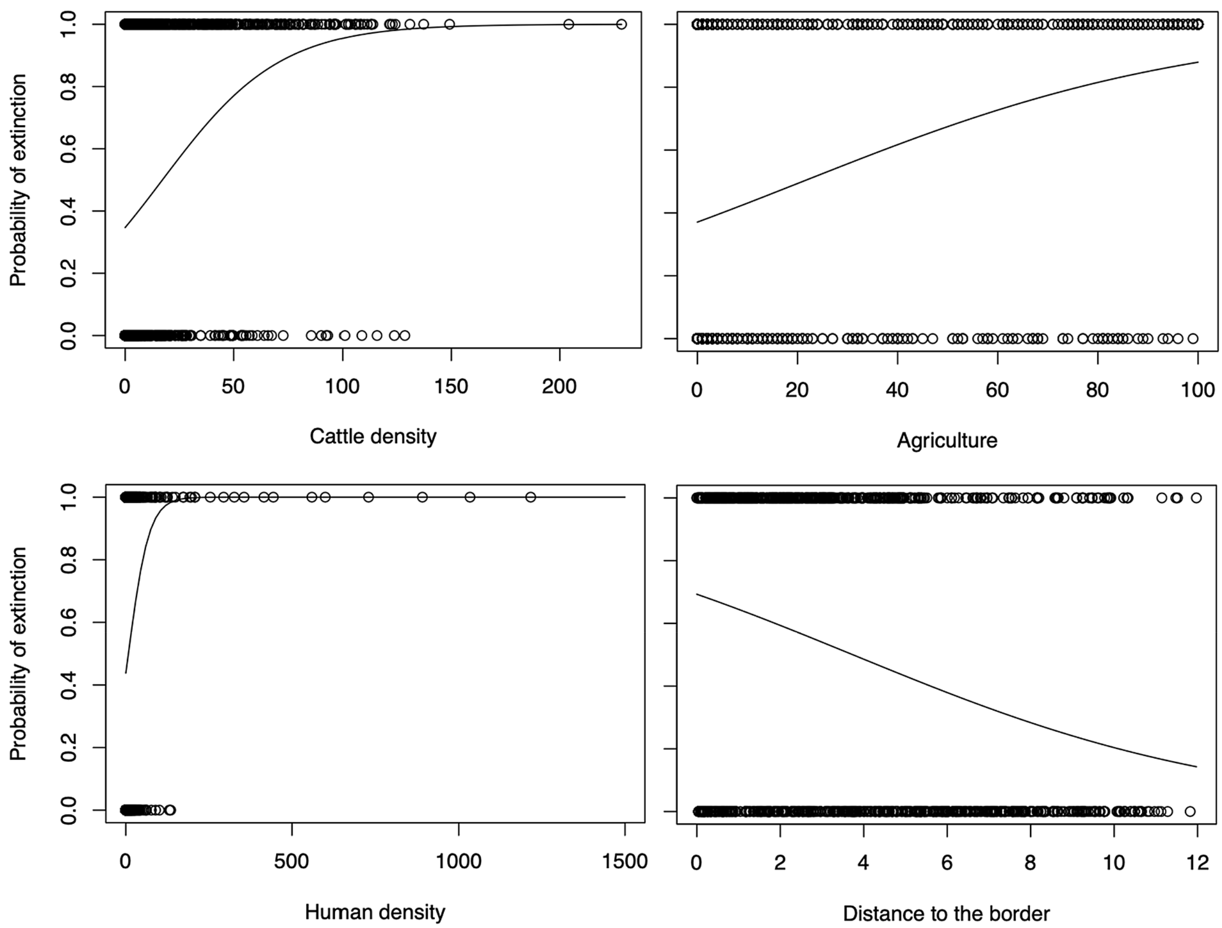

Fig. 1. Univariate models for cattle density (heads/Km^2), agriculture coverage (%), human density (people/Km^2) and distance to the border (DD) related to probability of extinction.

Table 2
Model selection (information theory approach) based on three hypotheses: H1. Natural contraction explains extinction; H2. Anthropic disturbance explains extinction; H3. The combination of intrinsic (H1) and extrinsic (H2) variables explain extinction.

Hypothesis	Intercept	Agriculture	Cattle density	Human density	Distance to border	AIC	delta
H1	−0.008				−0.651	1287	174
H2	0.150	0.409	0.659	1.043		1199	86
H3	0.094	0.291	0.876	0.396	−0.728	1113	0

in Southern Brazil and Argentina corresponding to populations that have shown alarming conservation problems due to their reduced size (Paviolo et al., 2008; Paviolo et al., 2016). Overall, extremely endangered populations ($p > 0.9$) occupy 2.1% (34,280 Km^2) of the aggregated Jaguar Conservation Units area, while 44.7% (718,101 Km^2) of the area is under moderate or low ($p < 0.5$) extinction risk. These results show that high endangerment is less frequent in JCUs compared to the surrounding matrix, hinting at a hopeful scenario for the species in these areas.

Limitations of our model are mainly related to the spatial data used, which were obtained in 2010 and 2000 for cattle and human densities, and agriculture, respectively. Some of these variables have increased over the last one or two decades (e.g., Hansen et al., 2013); therefore, we will expect that our model may overestimate potentially occupied areas, unveiling our results as conservative. Despite these limitations, we believe that this approach is useful for assessing the conservation status of jaguars as well as understanding carnivores range contraction at a broad scale.

Our conclusions demonstrate that livestock ranching, most likely via persecution and retaliatory hunting, has a pervasive effect on jaguars, becoming the main cause of the species extinction. Persecution and retaliatory hunting have been detected in most regions where jaguars coexist with livestock (review in Medellín et al., 2016). However, there are numerous examples to evince successful coexistence between livestock and big cats (Hoogesteijn et al., 2016; Tortato et al., 2017; Tortato and Izzo, 2017; Nassar et al., 2013), generally linked to ecotourism. Coexistence strategies such as the mentioned above need to be promoted for Neotropical big cat conservation. Moreover, our results show that most current jaguar range is unprotected and is highly affected by human industries, thus conservation requires measures that ensure wide connected areas (Rabinowitz & Zeller, 2010; Sanderson et al., 2002). Besides the protected-area strategy fail to effectively protect top carnivores, including jaguars (Woodroffe & Ginsberg, 1998), reason why management of humanized landscapes should be a more realistic scenario for carnivores' long-term survival (Athreya et al., 2013; Chapron et al., 2014; but see Gilroy et al., 2015). In this context, we believe that it is essential to use livestock ranching as a tool for jaguar conservation and highlight the need to rethink law enforcement and livestock policies and practice. We suggest the development of action plans based on local evidence in those countries where endangered populations have been

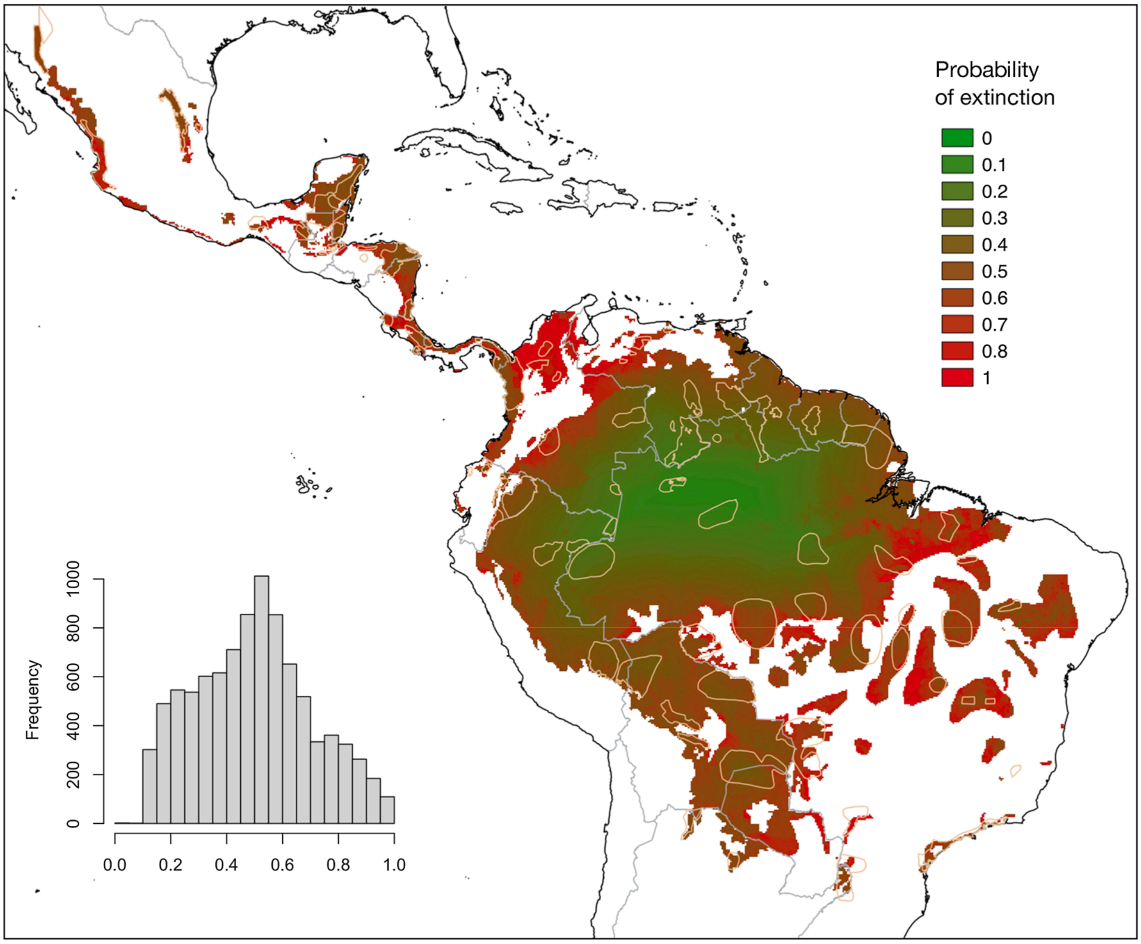

Fig. 2. Probability of extinction in jaguar current range based on the saturated model. Red pixels correspond to high endangerment levels while green pixels are related to low endangerment. Polygons demarcated in orange correspond to Jaguar Conservation Units (Sanderson et al., 2002). Probability frequency distribution is also shown (bottom-left). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detected as well as to involve and encourage land owners and private companies to integrate conservation practices.

CRediT authorship contribution statement

Pablo Villalva: Conceptualization, Data curation, Formal analysis, Writing. **Francisco Palomares:** Supervision, Validation, Review and editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126145.

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