# Living on the edge: regional distribution and retracting range of the jaguar (*Panthera onca*)

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**Abstract**

*Living on the edge: regional distribution and retracting range of the jaguar (*Panthera onca*).—* To preserve biodiversity we need to understand how species are distributed and which aspects of the environment determine these distributions. Human–induced changes in land–cover and loss of habitat threaten many species, particularly large carnivores, in many parts of the world. Differentiating the influence of climate and human land use on the distribution of the jaguar (*Panthera onca*) is important for the species' conservation. Historically distributed from the United States to southern Argentina, the jaguar has seen its distribution range decreased at regional and local scales. Here we predict the species' distribution range using historical records of its presence, climate variables, and MaxEnt predictive algorithms. We focus especially on its southernmost limit in Argentina to indicate the historical limits of this species, and describe its present niche in these edge populations. To estimate the effect of human activity we used a raster of land cover to restrict the jaguar's distribution. We collected a large amount of presence records through the species' historical range, and estimated a historical regional distribution ranging from Patagonia up to latitude –50°S. Our findings show the range of the jaguar is decreasing severely in its southern limit and also in its northern limit, and that changes in land cover/use are threats to the species. After subtracting non–suitable land–cover from the studied niche, we found the environmentally suitable area for the jaguar in the study area has decreased to 5.2% of its original size. We thus warn of the high extinction risk of the jaguar in Argentina.

Key words: Habitat suitability, Land–cover, MaxEnt, Species distribution models (SDM), Ecological Niche Factor Analysis (ENFA)

**Resumen**

*Vivir al límite: distribución regional y superficie ocupada por el jaguar en retroceso (*Panthera onca*).—* Para conservar la biodiversidad, es necesario entender cómo se distribuyen las especies y qué variables ambientales determinan dicha distribución. Los cambios inducidos por el hombre en la ocupación del suelo y la pérdida de hábitat ponen en peligro a numerosas especies de todo el mundo, especialmente grandes carnívoros. Diferenciar la influencia del clima y la de los usos del suelo en la distribución de jaguar (*Panthera onca*) es importante para su conservación. Esta especie, que tradicionalmente se distribuía desde los Estados Unidos hasta el sur de Argentina, ha visto reducida su distribución a escala regional y local. En este trabajo predecimos el rango de distribución de la especie utilizando registros de presencia histórica, variables climáticas y algoritmos predictivos obtenidos con MaxEnt. Nos centramos especialmente en su límite más austral en Argentina para indicar los límites históricos de esta especie y describir el nicho que ocupa actualmente en estas poblaciones marginales. Para estimar el efecto de las acciones antrópicas, utilizamos una capa de ocupación del suelo para limitar la distribución del jaguar. Recopilamos una buena cantidad de registros de presencia en todo el área de distribución histórica de la especie y estimamos una distribución regional histórica desde la Patagonia hasta los –50° de latitud. Nuestros resultados ponen de manifiesto que el área de distribución del jaguar se está contrayendo de forma alarmante en el límite meridional y también en el septentrional, y que los cambios de ocupación y de uso del suelo son una amenaza para la especie. Tras restar del nicho estudiado la ocupación del suelo que no es adecuada, descubrimos que la superficie idónea para el jaguar desde el punto de vista ambiental en la zona del estudio se ha reducido hasta el 5,2% de su tamaño original. Por consiguiente, advertimos del elevado riesgo de extinción que acecha al jaguar en Argentina.

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## Introduction

Habitat loss and degradation are the main threats to mammals and can cause considerable range contractions (Schipper et al., 2008). Large carnivores, in particular, are highly affected by such threats (Rabinowitz & Zeller, 2010) because they need extensive surfaces and have low population densities. Some carnivore species can inhabit the anthropogenic habitats that have replaced natural landscapes, but in such areas they are especially vulnerable to killing associated with livestock depredation (McLellan, 1990) and direct hunting. Edge populations (groups of individuals near the boundaries of their geographic ranges) are particularly vulnerable to extinction due to stochastic factors (Sodhi et al., 2009) because abundances in the periphery of the distribution of species tend to decrease and unusual (and often random and detrimental) events become prominent when population sizes are small. Habitat fragmentation causes gaps in distribution ranges, reducing the area of occupancy (IUCN Standards and Petitions Subcommittee, 2011), depending on the species' ability to use the surrounding matrix of habitats. In the management and conservation of species it is fundamental to determine the species' niche in order to describe habitat requirements and estimate the amount and arrangement of suitable habitats in a landscape (Araújo & Guisan, 2006; Millspaugh & Thompson, 2009).

Predictive modelling of species distributions is a useful tool for answering practical questions in applied ecology and conservation biology (Guisan & Thuiller, 2005). Species distribution modelling (SDM) is the most widely used approach to answer questions about the present and historical distributions of a species. Combined with geographic information systems (GIS) and land cover data, SDM enable geographical analysis of species distribution ranges (Guisan & Thuiller, 2005; Kearney & Porter, 2009). It is important to understand the underlying principles and assumptions of SDM. A convenient and practical postulation is to assume that the modelled species is in pseudo–equilibrium with its environment (Guisan & Theurillat, 2000). In practice, few species are in equilibrium with their environment and the retraction or expansion of species can violate this principle. Furthermore, SDM does not solve the conservation problems related to the Wallacean shortfall (Whittaker et al., 2005); *i.e.* insufficient knowledge of distributions could have consequences on conservation prioritisation, and local or smaller scale conservation assessments are still required. It is also important to bear in mind the reliance of these techniques on the niche concept (Guisan & Zimmermann, 2000).

The niche concept can help understand geographical distributions of species. Nevertheless, this concept is not only one of the most confusing terms in ecology but also one of the most extensively discussed and rethought (Morrison & Hall, 2002; Mitchell, 2005). Its definition is a subject of debate (Milesi & Lopez de Casenave, 2005) and it is difficult to determine which niche theory is applied to species distribution modelling (Shenbrot, 2009). Soberón & Peterson (2005) clarified this confusion by introducing the BAM–diagram which indicates that the occupied distributional area of a species is the intersection of the area where biotic variables are suitable (B), the area where scenopoetic variables are suitable (A) and the area accessible for this species (M); (for more details see Soberón & Peterson, 2005). Jackson & Overpeck (2000), working with scenopoetic environmental spaces and following the main ideas of Hutchinson, defined the 'fundamental niche' as the subset of the environmental space defined by the *n* dimensions that describe the suite of combinations of variables that permit survival and reproduction of individuals. The 'realized niche' of Hutchinson (1957) represents the part of the existing fundamental niche that remains habitable after reductions caused by competitors and other negative interactors (Soberón, 2007). The portion of the fundamental niche that actually exists somewhere in the study region at the time of analysis is 'the existing fundamental niche' (Soberón 2007), also called the potential niche (Jackson & Overpeck, 2000). Species distribution models estimate niche–related objects along a continuum between the existing fundamental niche and the realized niche (Jiménez–Valverde et al., 2008).

The most relevant ecological factors shaping habitat suitability can be identified by ecological–niche factor analysis (ENFA) (Hirzel et al., 2002; Basille et al., 2008; Calenge & Basille, 2008). This analysis identifies the response of a species to the main environmental variations in a study area (Rotenberry et al., 2006), thereby reflecting its realized niche (Braunisch et al., 2008). This niche can be geographically projected (Guisan & Zimmermann, 2000) and the resulting map summarises environmental suitability across the landscape (*i.e*. an estimate of the abiotically suitable area). Additional refinements to and analyses of model outputs can be used to estimate the occupied distributional area (Peterson, 2011). The distributional areas of a species are subsets of geographic space in which the presence of individuals or populations of a species can be detected (Soberón, 2007). Some other areas, lacking observable populations or individuals, but otherwise suitable, can also be defined (Peterson, 2011).

The jaguar (*Panthera onca*) is a large and widely distributed felid, which, according to the IUCN, is considered to be Near–Threatened due to habitat loss and persecution (Caso et al., 2008). Historically, it was distributed from the Southwestern United States to southern Argentina. In its northern limit in the USA, the species underwent range contractions and it has almost disappeared there since the 1990s (Van Pelt & Johnson, 2002). In the southern limit, its range has been decreasing since the 19th century (Arra, 1974) and it is currently extinct in Uruguay (González & Martínez Lanfranco, 2010) and El Salvador (Sanderson et al., 2002b). Changes in land cover have caused local extinctions and led to further fragmentation of its distribution (Swank & Teer, 1989; Koford, 1991; Sanderson et al., 2002b). The jaguar is more sensitive to habitat transformation than other big felids such as the puma (*Puma concolor*) (De Angelo, 2011). The historical southernmost distribution limit is unknown, but the species could have inhabited landscapes as far south as the Negro River at latitude 40ºS (Carman, 1984) or the Colorado River, at 39ºS (Lehmann–Nitsche, 1907) (fig. 1s in Supplementary material). The ancestor of the current species, *P. onca augusta*, was present during the Pleistocene and Rancholabreano in Chilean and Argentine Patagonia (Borrero, 2001), but it is not clear if today's species reached these latitudes even though it was reported in historical documents (see Diaz, 2010).

The lack of information on species' distribution (dubbed the Wallacean Shortfall) can have consequences on conservation prioritisation (Whittaker et al., 2005). It may be particularly important for fringe populations that are extremely vulnerable to extinction and of utmost importance for the focus of conservation actions. For this reason, we assessed the geographical aspects of the conservation status of the jaguar in Argentina, the country with the southernmost occurrence of this species. The jaguar today is only present in the northern portion of the country (as far as latitude 55° south in the Misiones province), with rapid local extinctions reducing its local distribution (Perovic & Herrán, 1998; Altrichter et al., 2006; Quiroga et al., 2014). Argentina is an agricultural–oriented country with a strong soybean production (Gudynas, 2008; Izquierdo & Grau, 2009). This involves transforming land to use that is incompatible with the jaguar's ecological requirements. To protect the most adequate areas for conservation and management of the species and its habitat, several issues must be addressed: the decreasing regional distribution, the doubts regarding the southernmost limit of the species, and the loss of suitable areas for jaguar in Argentina due to changes in land cover/use.

The main aim of this study was to model the historical niche of the jaguar in its entire range using SDM and records from the bibliography. We aimed to model how its distribution has changed over the last centuries. To do so, we modelled the present niche in Argentina using only current presence records and compared this with the historical niche. We estimated the impact of changes in human land use by subtracting non suitable areas from the distribution map. We also attempted to clarify the southern–most historical distribution limit in Argentina.

## Methods

We gathered presence records of the jaguar throughout the species' historical range from published literature, grey literature, publicly–available databases, museum collections, and previous works by some of the authors, and unpublished field data kindly shared by colleagues (see table 1s in supplementary material for a complete list). Distributions recorded across different time periods can be used to test predictions of range shifts over time (Araújo et al., 2005; Martínez–Meyer & Peterson, 2006). To do this we separated the records arbitrarily into historical records (from 1741 to 2011) and present records for Argentina (from 1994 to 2011). In total we obtained 1,447 presence records for the entire range of the jaguar (from 1741 to 2011).

To avoid errors in identifying the species we carefully checked all records (Newbold, 2010) using different methods. For published historical records, we read the description of the original authors; we excluded records that were not clear (for example, if only 'big felid' was mentioned) or when records were based on general place names (for example, 'El Tigre'). Presence indicated by Diaz (2010) in Chilean and Argentine Patagonia based on place names and historical stories were revised carefully, but we used only three as the others possibly implied observer bias or misidentification of species. For databases we carefully checked the metadata and we did not use records flagged as dubious. For museum records we used records previously checked by colleagues for correct species identification, and the museum records of the Argentinean museums were checked by ourselves. Finally, we filtered historical records using a shapefile of the historical species' distribution (kindly provided by the Panthera Foundation, and hereafter called the Historical Known Range); no historical records outside of these limits were used for modelling. We used all the records provided by felid specialists. To georeference records, we used the coordinates provided with each record; when not provided, we digitalized the record based on maps given in the publication (*i.e.* Carman, 1984). Museum records were georeferenced with gazeteers, but we used only those records that could be georeferenced with an error of < 1 km. As our presence records were spatially biased because they were not gathered following a standardised method, we used a bias file in MaxEnt (see below) to upweight records with few neighbors in geographic space (Elith et al., 2010, 2011; Yackulic et al., 2013).

We dealt with contingent, environmental and methodological absences (*sensu* Lobo et al., 2010) by creating background points to use in MaxEnt; these were not real absences although we assumed they corresponded to absences. Lobo et al. (2010) defined contingent absences as 'environmentally favourable places from where a species is absent due to restrictive forces such as dispersal limitations or local extinctions'. To determine contingent absences we used the Historical Known Range, assuming that the area outside of this range implies historical absence and locating records along the spatial gradient under consideration (Lobo et al., 2010). To deal with environmental absences, we first created a minimum convex polygon (i.e. the smallest polygon in which no internal angle exceeds 180 degrees and contains all presence sites) using records from the present day. We used areas outside this polygon to randomly create environmental absences (Yackulic et al., 2013). To interpret methodological absences we calculated the Kernel density to identify places where representation is uncertain and places which are underrepresented.

The Ecological–Niche Factor Analysis (ENFA) provides an exploratory analysis of the distribution of a species (Hirzel et al., 2002; Basille et al., 2008; Calenge & Basille, 2008). It is used to identify the species' response to the main environmental variations in the study area (Rotenberry et al., 2006). Climate and topography are considered the main determinants of the distribution of species at continental and sub–continental scales such as that studied here (Caughley et al., 1987; Wiens et al., 1987; Pearson et al., 2002, 2004; Soberón & Peterson, 2005). Hence, as input for the ecogeographical variables of the ENFA, we used the nineteen bioclimatic variables derived from monthly temperature and rainfall values, provided by the WorldClim ver. 1.4 interpolated map database (Hijmans et al., 2005; www.worldclim.org/). The ENFA was performed using Biomapper (Hirzel et al., 2002). The first factor extracted by the ENFA maximizes the marginality of the species, i.e. the ecological distance between the optimum for the species and the average condition in the study area. The other factors generated by the ENFA maximize specialization, defined as the ratio between the average overall variance for the study area and the variance observed for the species. The first five factors from eigenvalues were selected for mapping habitat suitability (HS). Biomapper provides the Boyce index (B) to indicate the spatial robustness of the model (Boyce et al., 2002).

Species distribution models were generated with MaxEnt (Phillips et al., 2006). Although a number of different modeling approaches are available, MaxEnt performs relatively well compared to alternative approaches for modeling species that are widely distributed (Hernandez et al., 2008; Norris, 2014), such as the jaguar. One study claimed it has a good general performance when only presence records are available (Elith et al., 2006), but this work has been criticized for its design and findings (Lobo, 2008; Hijmans, 2012), especially because the Area Under the Receiving Operator Curve (AUC) was used to evaluate performance. When the potential distribution is the goal of the research, the AUC is not an appropriate performance measure because the weight of commission errors is much lower than that of omission errors (Jiménez–Valverde, 2012) and the AUC value can be artificially inflated because of distances between training and testing points (Hijmans, 2012). We therefore used specificity to evaluate the models as it is suitable for the distribution performed (Tessarolo et al., 2014). Specificity is the probability that the model will correctly classify an absence (Allouche et al., 2006).

MaxEnt uses the principle of maximum entropy and presence–background data to estimate a set of functions that relate environmental variables with habitat suitability to approximate the species' potential geographic distribution (Phillips et al., 2006). We set the program so that it performed both linear and quadratic features, as these generally perform better than the models which consider just linear features (Anderson & Gonzalez, 2011). We used the logistic output of MaxEnt which approximates better to the probability of occurrence; however, due to its effectiveness in describing the geographic distribution of the species' record, Maxent should be interpreted as a measure of the realized distribution of the species, rather than of the potential distribution that is typically characterised by habitat suitability (Jiménez–Valverde et al., 2008). This makes this tool adequate to characterise the changes in the current geographic distribution of the jaguar.

We developed two species distribution models. The first one was for the entire distribution range of the species, from USA to Argentina, using historical presence records (1741 to 2011), hereafter called the Historical Regional Model. As we had a lot of dubious records (see stars in fig. 1) we trained the model using only presence records of the species that fell inside their Known Historical Range and, to the same extent, environmental variables. We then projected the model for the entire extension of America to check whether those records that were not used for model training were predicted as suitable. As we had more presence records (see Kernel density map; fig. 2) from Argentina, due to personal work in this area, and because we wanted to assess distributions of fringe populations in the said area, a smaller–scale analysis was more appropriate to meet our objectives. We thus developed a second model for Argentina alone that included current presence records f (from 1994 to 2011), hereafter called the Present Argentine Model. In this way we modeled the realized niche of the past and present in Argentina.

We used 19 bioclimatic variables (WorldClim) that consist of interpolated data, derived from monthly temperature and rainfall (Hijmans et al., 2005). We used variables at a resolution scale of 2.5 arc–minutes (~21 km$^2$) that captures local to regional climate variability and avoids reflecting internal dynamics of the communities (competition, predation, mutualisms, etc) of more refined resolutions. To define which environmental variables to use, we chose the variables of the ENFA analysis that were not intercorrelated (Pearson $R$ < 0.7). We selected temperature seasonality, minimum temperature of the coldest month, and precipitation of the warmest quarter.

MaxEnt offers a range suitability map as a logistic output. A threshold should be applied to transform this probability map into a binary presence/absence map. Applying a threshold is one of the most controversial issues in MaxEnt (Papeş & Gaubert, 2007; Rebelo & Jones, 2010). Therefore, we used a different threshold in each model because we had different objectives. For the Historical Regional Model we applied the fixed cumulative value 1 logistic threshold, which was 0.0878. When mapping, we divided the areas into white (non suitable) and grey (suitable) areas; the suitable areas were divided into 'low' (probability values of 0.25 or lower), intermediate (0.25–0.50), high (0.5–0.75) and maximum (> 0.75) suitability.

To represent a niche more closely related to the niche for the Present Argentine Model we used a stricter threshold; the 10 percentile training presence logistic threshold commonly used for conservation objectives which was 0.4212. This threshold excludes 10% of presence records (according to a statistically calculated error), ensures that species presence is not exaggerated and enables us to focus better on conservation actions on site. To estimate losses due to human land use, we extracted all pixels with land covers incompatible with jaguar presence, and obtained in this way the occupied distributional area using a raster from the Global Land Cover database (ESA & UCLouvain, 2010). We considered 'croplands' (rain–fed

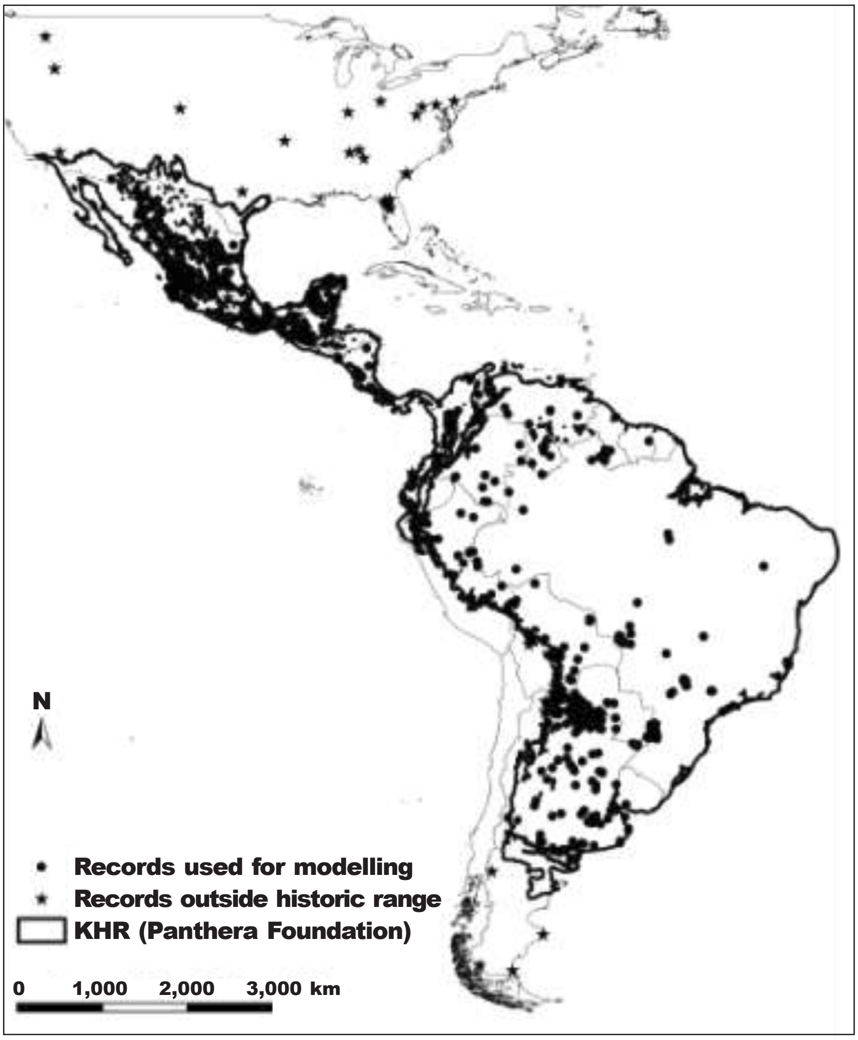


Fig. 1. Presence records (●) of jaguar *Panthera onca* used for modelling and outside the known distribution range (★); the black line indicates known historical range (KHR, based on the Panthera Foundation shapefile).

*Fig. 1. Registros de presencia del jaguar* Panthera onca *empleados para la elaboración del modelo (●) y fuera del rango de distribución conocida (★); la línea negra indica el rango histórico conocido (KHR, basado en el archivo Shape de la Fundación Panthera).*

and mosaic) and 'artificial areas' as not suitable for the maintenance of jaguar populations.

We compared the historical and present distribution of the species in Argentina by superimposing the Regional Model (projected in Argentina) with the Present Argentine Model. We also compared the occupied distributional area with the present fundamental niche to indicate how much of the jaguar's potential area was already lost by changes in human land use. These analyses provide calculations of the overall surface area occupied by each aspect of the distribution of the jaguar. We also indicate historical and current presence of the species in the ecoregions and provinces of Argentina.

## Results

From a total of 1,447 presence records obtained for the species (fig. 1), only 718 records were used for the Historical Regional Model after considering only those that were inside the Known Historical Range and filtering them on a scale of 21 km$^2$. This model had a specificity of 0.996.

Despite the limitations of this model, it shows that the jaguar was historically present in 19,921,440 km$^2$, from the south–eastern United States, including Mexico and Central America, to Argentina and Chile (fig. 2). This range includes part of Argentinean Patagonia,

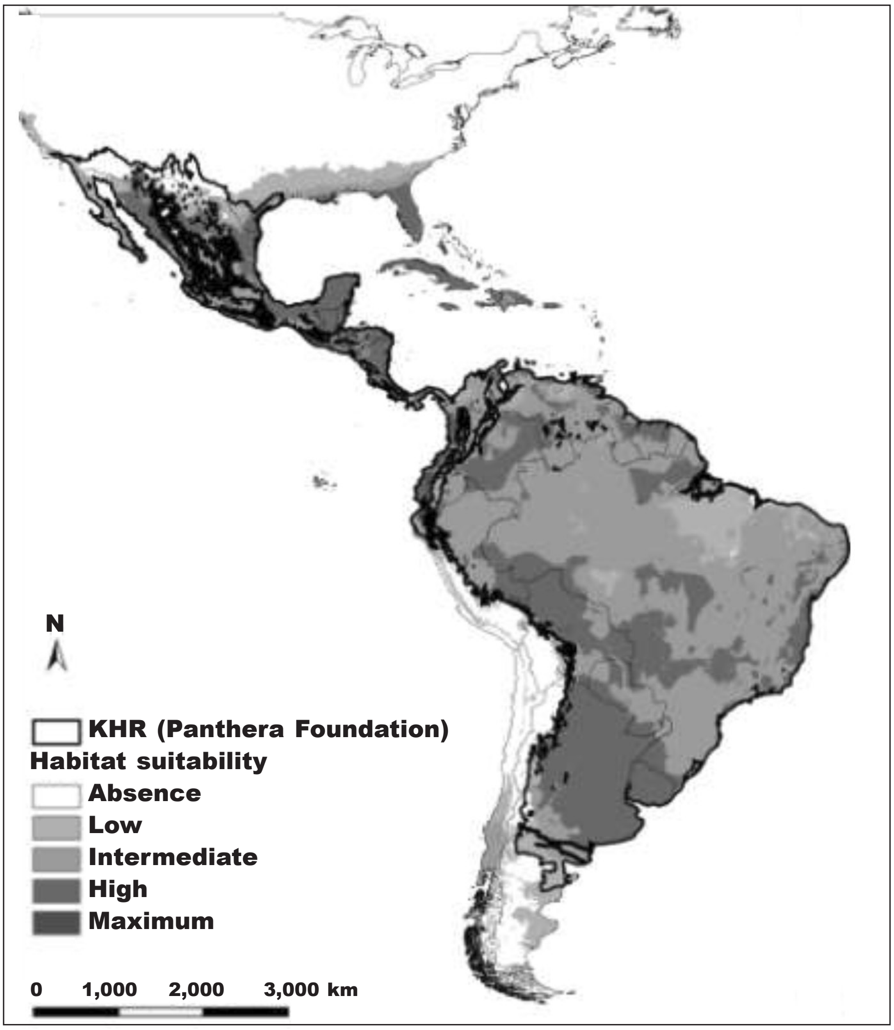


Fig. 2. Geographic projection of the historical (1741 to 2011) regional distribution of *Panthera onca*, based on environmental variables (temperature seasonality, minimum temperature of coldest month, and precipitation of warmest quarter). White areas are not suitable for the species and the scale of grey indicates increasing suitability.

*Fig. 2. Proyección geográfica de la distribución regional histórica (entre 1741 y 2011) de* Panthera onca*, basada en variables ambientales (estacionalidad de la temperaturas, temperatura mínima del mes más frío y precipitación del trimestre más cálido). Las zonas blancas no son adecuadas para la especie y la escala de grises indica el aumento de idoneidad.*

especially the coastal area, the coast of the Chilean Valdivian Forests and part of the Chilean Matorral. The kernel density map (fig. 3) indicates that Brazil was under–sampled and northern Argentina and parts of Mexico were over–sampled.

The map of presence records indicates a historical range contraction from latitudes 39.9º to 26.3º South (fig. 4). According to the Historical Regional Model, 77% of the Argentinean territory was environmentally suitable for the jaguar in the past (see light grey areas in fig. 5). Since 1994 this extent has been reduced to 5.5% of the territory, according to the model for the present day (see dark grey areas in fig. 6), which had a good specificity of 0.904. We found 25% of this environmentally suitable area has already been lost due to changes in human land use, leaving a suitability of 4.2% of the Argentine territory or 5.2% of the area originally (historically) suitable for the jaguar (fig. 6). The species survives in only 6 of the original 23 Argentinean provinces (fig. 5). While it was originally present in almost all 12 Argentine ecoregions, today it survives only in the Dry Chaco (DCH), Humid Chaco (HCH), Yungas (YU) (including High pastures), a small part of Campos and Malezales, and Esteros de Iberá (IB) (fig. 6).

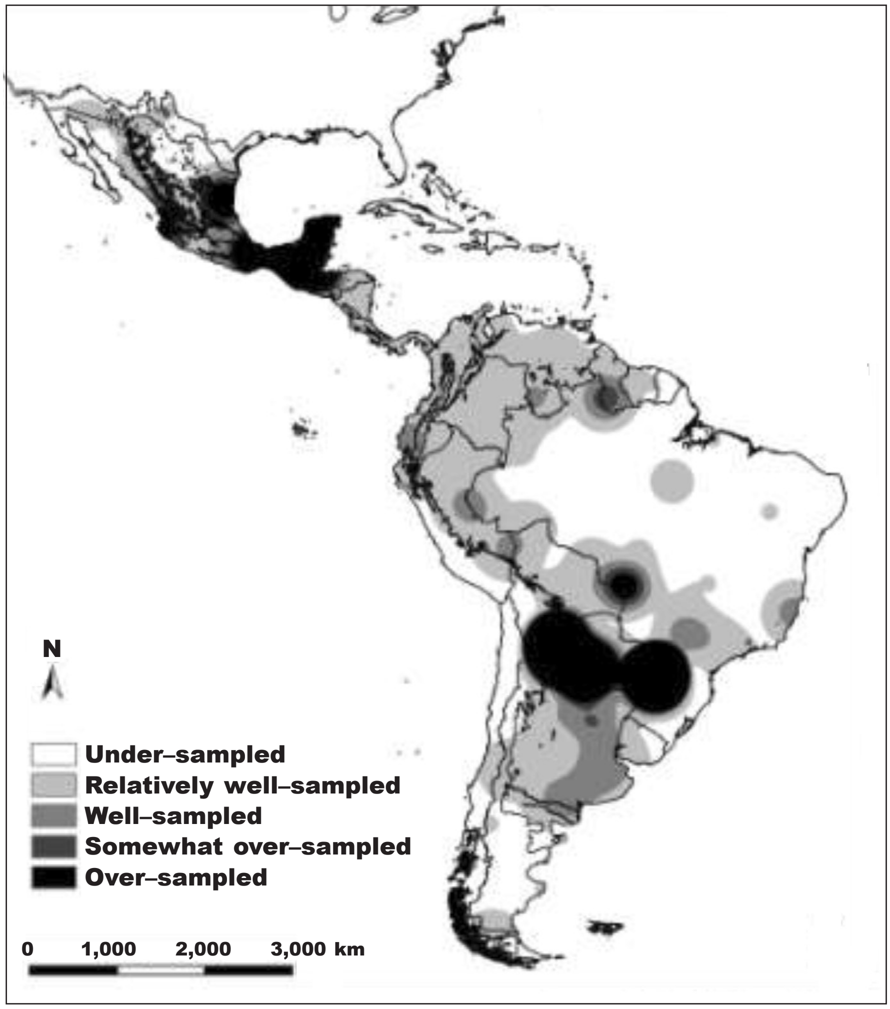


Fig. 3. Kernel density of presence records used for modelling, as proxy for sample density.

*Fig. 3. Densidad del kernel de los registros de presencia utilizados para la elaboración del modelo, como variable sustitutiva de la densidad de la muestra.*

The ENFA identifies that the most important environmental variables in determining jaguar distribution are temperature seasonality and minimum temperature of the coldest month, contributing to 14 and 12% of the variability, respectively. The ENFA indicates a high marginality for the jaguar. The first five factors were selected for mapping habitat suitability, and their accumulative contribution reached 75.1%, accounting for 100% of marginality and 75.1% of the total specialization. The habitat suitability model showed a high predictive power (B = 0.64; s = 0.32). The limit value to differentiate between marginal habitat and suitable habitat was 25.

## Discussion

We collected a large number of presence records for the jaguar through the species' historical range, allowing us to assess changes in the distribution of a species of high conservation value that is undergoing a retracting range process. Thereby, we provided a broad coverage of the environmental and geographical variability shown in current records (Lobo et al., 2007). According to our models, the jaguar occupies intermediate values of temperature seasonality, indicating the optimality of relatively stable climates for the species. The importance of precipitation in the warmest quarter, a variable related to plant growth, may indicate the importance of vegetation cover for the jaguar to hunt (Hopcraft et al., 2005). Minimum temperature of the coldest month was less important but could indicate the coldest limits to jaguar distribution.

The regional distribution map presented here is the first to represent the historical distribution of the jaguar in South America. Our model adequately represents jaguar absence from the high altitudes of the Puna or

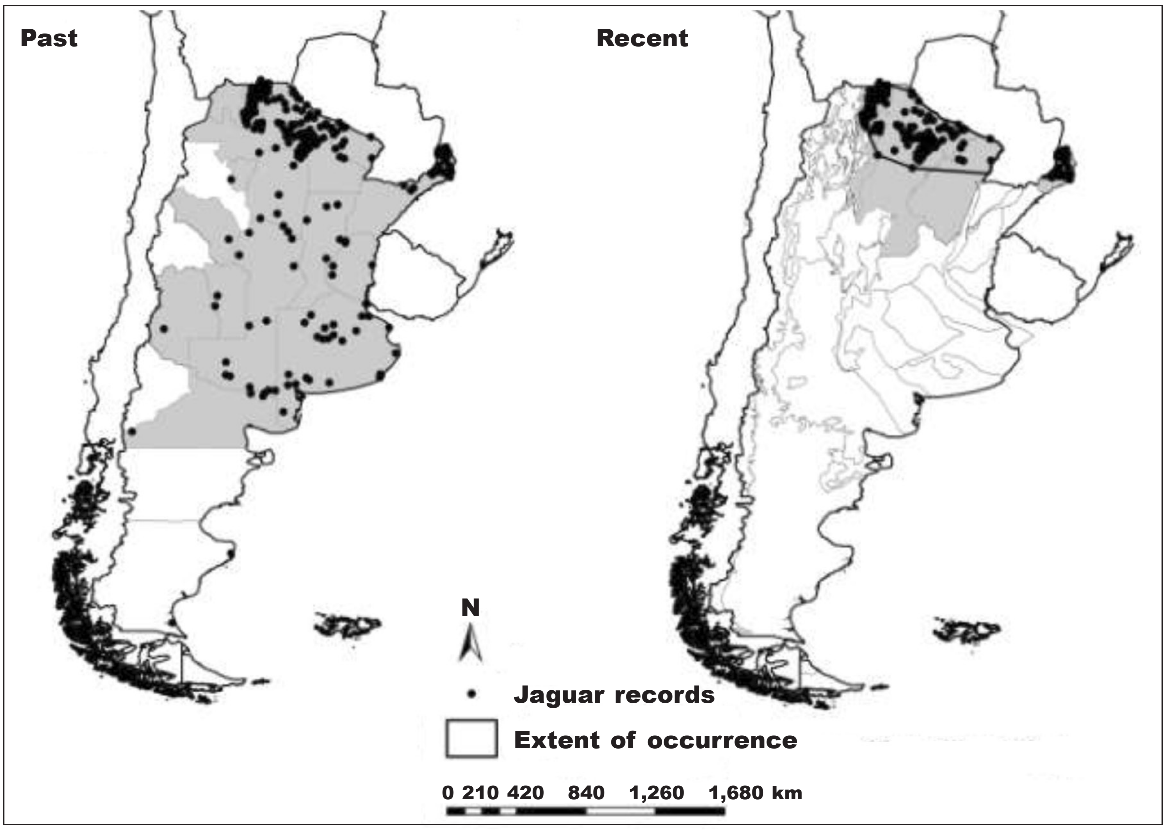


Fig. 4. Historical (1741 to 2011) and present (from 1994 to 2011) presence records and distribution range (Convex hull; black line) of jaguar (*Panthera onca*) in Argentina.

*Fig. 4. Registros de presencia histórica (entre 1741 y 2011) y actual (entre 1994 y 2011) y rango de distribución (envolvente convexa; línea negra) del jaguar (*Panthera onca*) en Argentina.*

High Andes (Perovic & Herrán, 1998; Sanderson et al., 2002a). In this area, the main environmental factor restricting jaguar distribution could be extreme aridity (Clarke, 2006). This result contrasts with the prediction of presence in Chilean Valdivian Forests and Matorral, which never hosted jaguar populations. SDM results are independent of the presence of geographic barriers and therefore may extrapolate the species distribution towards areas that are not truly reachable for the species, such as the many islands deemed suitable by our model, *i.e.* the Caribbean Islands or Tierra del Fuego. It is therefore clear that dispersal limitations have played a role (Svenning & Skov, 2005) in shaping the jaguar's distribution, and can be as important as or even more important than environmental suitability.

The absence from Central Patagonia predicted by our model could be explained by a lack of vegetation cover (Burkart et al., 1999). The jaguar needs a certain level of cover to apply its hunting technique of ambushing (Brown & López–González, 2001; Hopcraft et al., 2005). Besides the lack of records, the model indicates a wide cover in Brazil, although with low suitability in the Brazilian basin, as mentioned by Tôrres et al. (2007). Although the Historical Regional Model shows a wide distribution of areas of high suitability, the ENFA indicates that the jaguar has high marginality, which, in turn, indicates that it inhabits landscapes different from the majority present in the study area.

Out of the dubious presence records (outside the Known Historical Range), only one group in Florida, United States and two records in the Argentine Patagonia were predicted by our model. Therefore, we deduce that a higher proportion of northern records were erroneous and that the model predicts well in Argentine Patagonia and is therefore useful to indicate the historical southern distribution limit. Interestingly, the southern limit of the distribution of the jaguar was neither the Colorado nor the Negro River, but an irregular limit further southwards. This makes sense as rivers do not imply determinative restrictions or limitations to jaguar dispersal, as they are excellent swimmers. Two records observed by historians were neither used nor predicted by the model (stars in fig. 1). The difference between the predicted presence by our Historical Regional Model and the Known

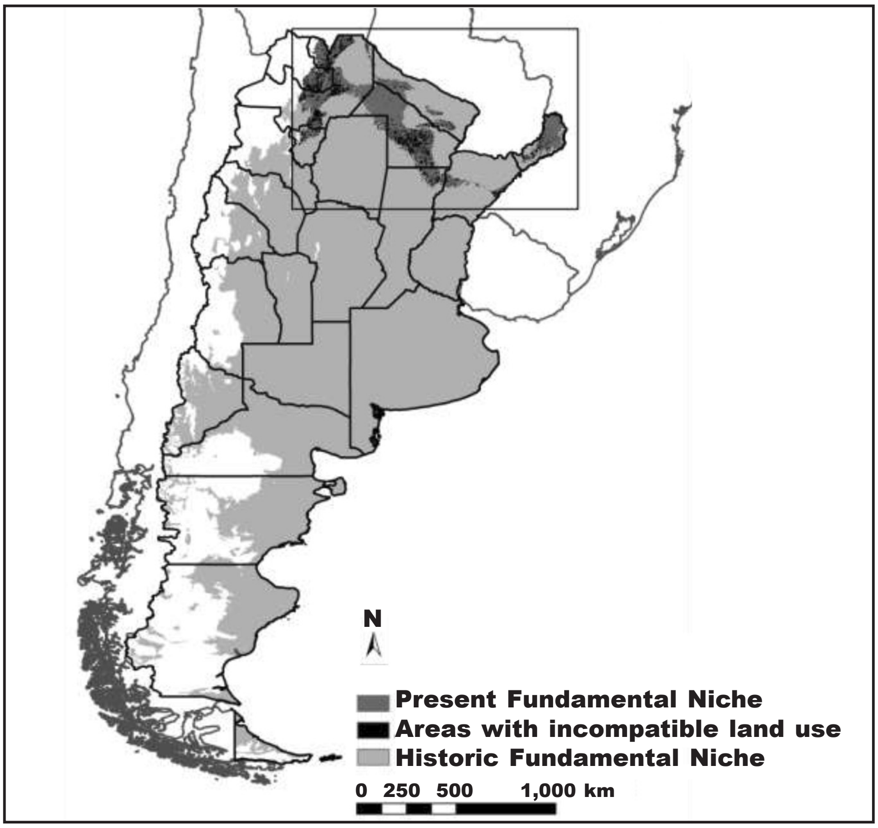


Fig. 5. Superimposition of the geographic projection of the Historical Regional Model (light grey area) and present Argentina (dark grey area) of jaguar (*Panthera onca*). (Present distribution is totally included in the historical distribution). Areas not suitable for jaguar presence due to land–use inside current range (black areas). Rectangle shows zoom in view in figure 6.

*Fig. 5. Superposición de la proyección geográfica del modelo regional histórico (área de color gris claro) y presente en Argentina (área de color gris oscuro) del jaguar (*Panthera onca*). (La distribución presente queda totalmente dentro de la distribución histórica). Zonas que no son idóneas para la presencia del jaguar debido al uso de la tierra dentro del rango actual (zonas negras). El rectángulo ampliado se encuentra en la figura 6.*

Historical Range in the extreme north of its distribution in the southern USA (a small white strip in fig. 2) can be due to recent retraction of the species in those areas, suggesting southwards retractions of the species. The Kernel density map indicates over–sampling in the north of Argentina and Mexico. This is encouraging as these are fringe populations and conservation actions are more urgently needed. It further indicates many areas in Brazil are under–sampled, probably due to their difficult access.

According to our estimates, the Historical Regional Distribution of the jaguar encompassed more than 19 million km$^2$, more than twice the 8.75 million km$^2$ estimated previously by Sanderson et al. (2002a). There are some key differences between the two maps. In the southern portion of the potential distribution, our model predicts presence in the Valdivian forest and Chilean Matorral, and the area of predicted presence in Patagonia is larger than formerly accepted. Also, our model predicts a strip of suitable territory on the southern–eastern coast of the USA (Texas, Louisiana, Mississippi, Alabama and Florida), not indicated on the Sanderson map. Furthermore, our model correctly classifies several historical presence records from Florida that were not used for its calibration, so it is possible that the jaguar once reached this region.

The distribution of the jaguar could be depicted by a current records map and the Argentinean convex hull (fig. 4). However, using only atlas records is limited as it does not provide information on species presence between known records. Furthermore, the convex hull may generalise too much, failing to delineate the distribution of species populations at finer scales (for example, at a local scale) (Hurlbert & Jetz, 2007; Hortal, 2008), thereby overestimating the area of occupancy (Hurlbert & Jetz, 2007). Therefore, we believe that our SDM results are a better approximation of the actual distribution.

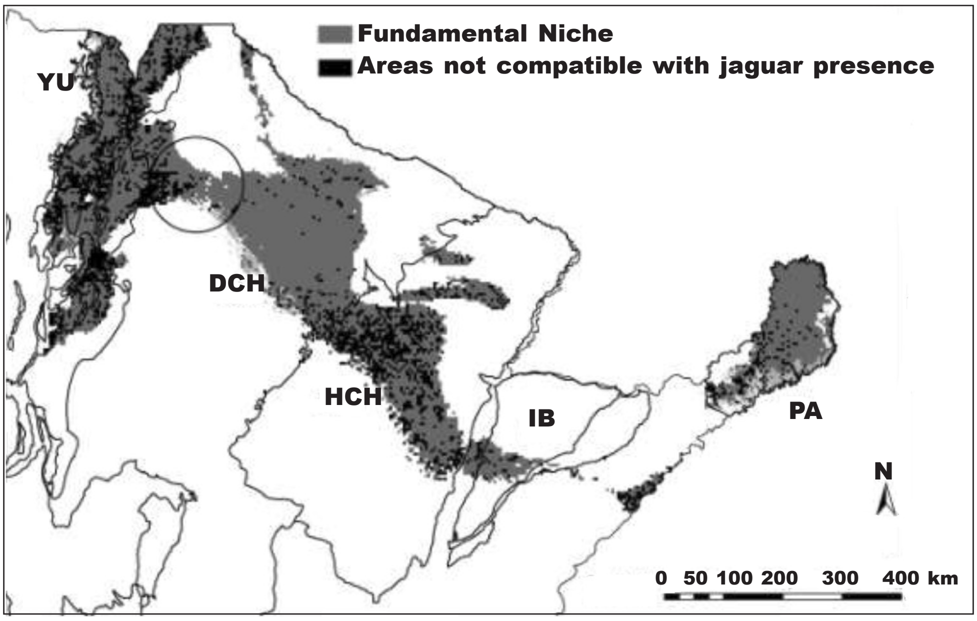


Fig. 6. Fundamental Niche and areas not suitable for jaguar presence due to land–use. Black circle indicates imminent loss of connection between Yungas and Chaco ecoregions: YU. Yungas; DCH. Dry Chaco; HCH. Humid Chaco; IB. Ibera Wetlands; PA. Paranaen Forests.

*Fig. 6. Nicho fundamental y zonas que no son adecuadas para la presencia del jaguar debido al uso del suelo. El círculo negro indica la pérdida inminente de conexión entre las ecorregiones de Yungas y Chaco: YU. Yungas; DCH. Chaco seco; HCH. Chaco húmedo; IB. Humedales Iberá; PA. Bosques paranaenses.*

No records further south than latitude –26.5º of were observed after 1994, suggesting a contraction of the southern range limit towards the north. Both the map with presence records of Argentina and the difference between the Historical Fundamental Niche and the Present Niche (fig. 5) indicate that the jaguar has contracted its range in the past 200 years. This contraction and local habitat loss are indicated by the black areas in its current species range, suggesting that the present known distribution is smaller than its potential distribution in Argentina. Areas suitable for the species, but where the species is not present or was not detected, need special attention and could probably be recovered provided that conservation strategies are implemented.

The Present Argentinean Model (figs. 5, 6) represents the current known distribution of the species well, with presence in only six, and marginally in seven, political provinces of the original 23 provinces of Argentina with environmentally suitable areas (fig. 5). The species is currently present in only five ecoregions: Dry Chaco, Humid Chaco, Yungas, Paranaen forest and Iberá Wetlands (fig. 6). The lowest elevation of the Argentinean Yungas forest, piedmont forest, has been highly transformed to other land uses (Brown & Malizia, 2004). Therefore, the jaguar is locally extinct in most of this ecoregion (black areas in fig. 6B), except for the higher elevations. In the Yungas, jaguars have currently disappeared from sites where they were still present two decades ago (Perovic & Herrán, 1998), indicating the speed at which the distribution of this species is diminishing. The highest probabilities of occurrence in Argentina occur in just a few pixels, in the Upper Bermejo River, on the border with Bolivia. These areas are important to ensure connectivity with the Bolivian jaguar populations (Cuyckens et al., 2014). Also, the Upper Bermejo River Basin has already been signalled as important for Yungas conservation, due to its high biodiversity and presence of continuous forest (Brown et al., 2006).

Although the models indicate a high probability of presence, and there are several presence records from the Dry and Humid Chaco (fig. 4), jaguar populations are rapidly declining in this ecoregion (Altrichter et al., 2006; Quiroga et al., 2014). This indicates that, despite environmental suitability, jaguar populations are threatened, probably by direct hunting and prey losses or land uses changes not detected by the scale and time of our land cover data. Furthermore, the connectivity between Chaco and Yungas ecoregions is disappearing (black circle in fig. 6), jeopardizing the connection. The connection is also lost between Chaco and Paranaen Forests, as no jaguar individuals were recorded in Iberá Wetlands, despite its suitability for the species and historical presence of the species. In the southeast of Argentina, in the Paranaen forest, the highest probabilities occur on the limit with Brazil. This ecoregion is isolated from others in Argentina, but still has connections with Brazil and Paraguay. Therefore, tri–national conservation actions for jaguars would be crucial here (Paviolo et al., 2006). Jaguars have been seriously affected by habitat destruction and are more vulnerable to changes in land–cover than, for example, the puma; their habitat was already reduced by more than 90% in this ecoregion (De Angelo et al., 2011).

Argentina represents the edge of distribution of the species and thus has a key role in jaguar conservation, with possible consequences for the species in neighbouring countries (Brazil, Bolivia, and Paraguay). The species is considered as a 'Natural Monument', the highest conservation category in the country (National Law 25.463), and hunting is totally prohibited. Nevertheless, there seems to be a lack of implementation of protection measures where it would be most important due to the small numbers of individuals present and the threat of direct hunting. On the other hand, Argentina is a country oriented towards crop production, promoting the increase of soy bean crops and other cultivars which directly threaten jaguars through habitat loss. The challenge is to combine production with jaguar conservation, while simultaneously promoting the peaceful coexistence between rural communities and this large carnivore.

Jaguar distribution has been used as an example of the problems of biodiversity data and how it is mapped (McInerny et al., 2014), so we applied several methods to improve the models and the scientific rigor of the MaxEnt analyses. We gathered larger numbers of more widely distributed presence records and used adequate absence records as a bias file in MaxEnt (Elith et al., 2010; Anderson, 2012), worked at a finer scale (21 $km^2$ *vs.* 100 $km^2$), and selected uncorrelated environmental variables (Rocchini et al., 2011). We also had knowledge about the species to interpret the map and we focused on the area we know best. We generated a Kernel density map as a proxy for sample density in accordance with 'ignorance maps' (*sensu* Rocchini et al., 2011). We therefore believe that our results are robust and provide a fair representation of the distribution of the jaguar. However, our model presents several limitations, as the jaguar is not a species in equilibrium with its environment due to its ever–decreasing distribution. Nevertheless, we believe that the method we applied here was adequate to accomplish the proposed aims.

This work contributes significantly to understanding the distribution of the jaguar and its conservation status, including the interpretation of the factors that could be influencing the conservation of this endangered species. We found evidence of range retraction in both the southern and the northern distribution limits. Due to our personal experience, we were able to assess the retraction in its southern limit in more detail. Our results support the idea that there is an imminent, high extinction risk of the jaguar in Argentina, as evidenced by its northward range contraction over time and the velocity of this decline, its range contraction in the Chaco ecoregion (Quiroga et al., 2014), and the lack of areas of growth or recovery of populations. We encourage changes in policies as records of killed animals are still common, and there is a general lack of assessment of which actions may be worth taking.

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## Supplementary material

Tabla 1s. Sources and types of sources of presence records gathered.

*Tabla 1s. Fuentes y el tipo de fuentes de registros de presencia recopilados.*

| Source | Type of source |
|---|---|
| French, 1839 | Published literature |
| Chauvet, 1857 | |
| de Moussy, 1864 | |
| Dobson, 1900 | |
| Río & Achával, 1904 | |
| Cann, 1939 | |
| Sánchez, 1946 | |
| Saenz, 1970 | |
| Carman, 1984 | |
| Zeballos, 1994 | |
| Barquez, 1997 | |
| Perovic & Herrán, 1998 | |
| Sierra Iglesias, 1998 | |
| Anderson, Peterson & Gómez–Laverde, 2002 | |
| Altrichter et al., 2006 | |
| Pautasso, 2008 | |
| Diaz, 2010 | |
| Estrada Hernández & Juárez Sánchez, 2003 | Grey literature |
| De Angelo, 2009 | |
| CONABIO, 2010 | Publicly available databases |
| Centro de Referência em Informação Ambiental | |
| CRIA & Fundação de Amparo à Pesquisa | |
| do Estado de São Paulo, 2014 | |
| Global Biodiversity Information Facility (GBIF) | |
| Administration of National Parks of Argentina (APN) | |
| Jaguar Network (Red Yaguareté) | |
| American Museum of Natural History (AMNH) | Museum collections |
| New York, USA | |
| Argentine Museum of Natural Sciences | |
| 'Bernardino Rivadavia' (MACN), Buenos Aires, Argentine | |
| Perovic, 2002 | Previous works by some of the authors |
| Cuyckens, 2013 | |
| C. de Angelo pers. comm. | Unpublished field data kindly |
| A. Paviolo pers. comm. | shared by colleagues |
| V. Quiroga pers. comm. | |
| M. Castro, pers. comm | |

Supplementary material (Cont.)

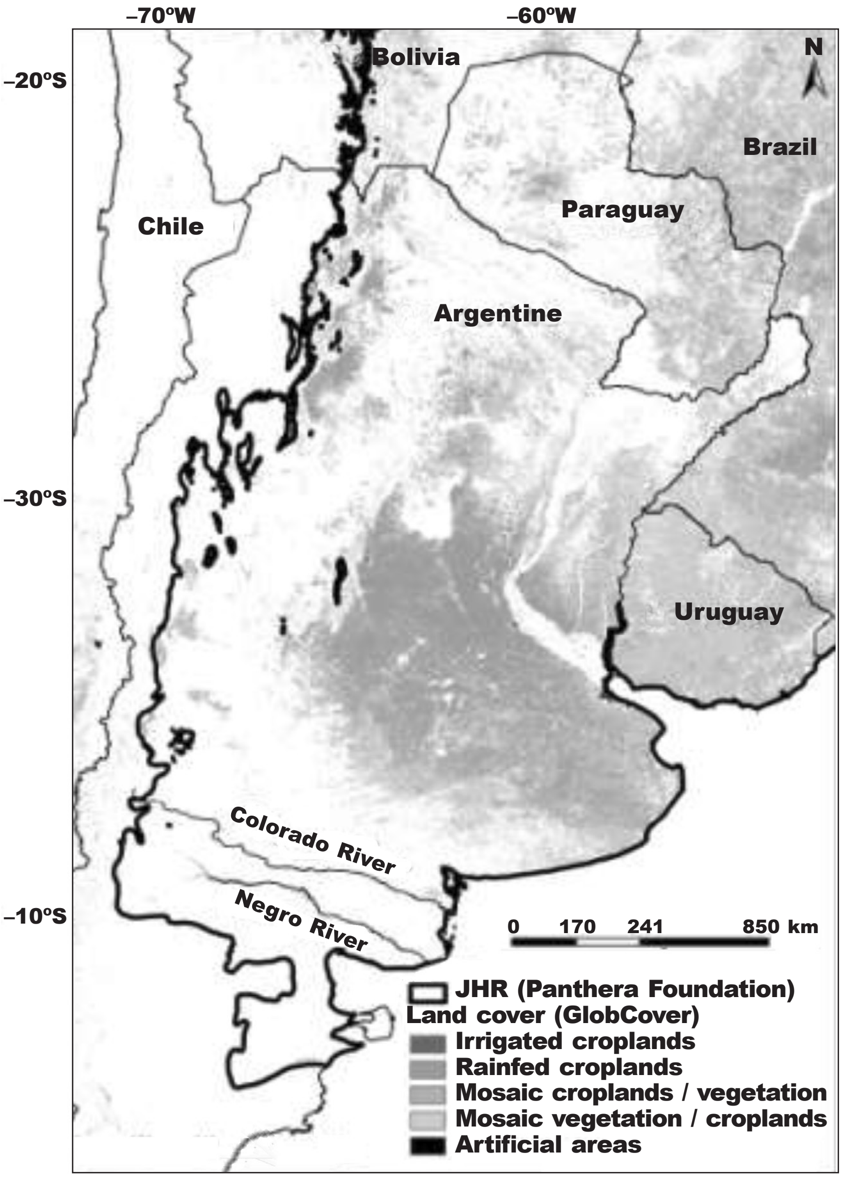


Fig. 1s. Land cover in the southern cone of South America, indicating uses not compatible with jaguar presence (scale of greys). The black line indicates jaguar's historical distribution (JHR according to Panthera Foundation) and we indicated the Negro and Colorado Rivers which were signalized as possible southernmost limits of jaguar's distribution (Carman, 1984; Lehmann–Nitsche, 1907).

*Fig. 1s. Ocupación en el suelo del cono meridional de América del Sur que indica los usos incompatibles con la presencia del jaguar (escala de grises). La línea negra indica la distribución histórica del jaguar (según la Fundación Panthera) y nosotros indicamos los ríos Negro y Colorado que se señalizaron como los posibles límites más meridionales de la distribución del jaguar (Carman, 1984; Lehmann–Nitsche, 1907).*