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Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation

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ABSTRACT

Aim The jaguar, *Panthera onca*, is a species of global conservation concern. In Mexico, the northernmost part of its distribution range, its conservation status, is particularly critical, while its potential and actual distribution is poorly known. We propose an ensemble model (EM) of the potential distribution for the jaguar in Mexico and identify the priority areas for conservation.

Location Mexico.

Methods We generated our EM based on three presence-only methods (Ecological Niche Factor Analysis, Mahalanobis distance, Maxent) and considering environmental, biological and anthropogenic factors. We used this model to evaluate the efficacy of the existing Mexican protected areas (PAs), to evaluate the adequacy of the jaguar conservation units (JCUs) and to propose new areas that should be considered for conservation and management of the species in Mexico.

Results Our results outline that 16% of Mexico (*c.* 312,000 km^2) can be considered as suitable for the presence of the jaguar. Furthermore, 13% of the suitable areas are included in existing PAs and 14% are included in JCUs (Sanderson *et al.*, 2002).

Main conclusions Clearly much more should be carried out to establish a proactive conservation strategy. Based on our results, we propose here new jaguar conservation and management areas that are important for a nationwide conservation blueprint.

Keywords
Consensus methods, ENFA, ensemble model, jaguar conservation, Mahalanobis Distance, Maxent.

INTRODUCTION

The jaguar (*Panthera onca*) is the largest felid in the Americas with a distribution ranging from Mexico to Argentina (Rabinowitz, 1999). It lives in various habitats, where their abundance is likely related to the abundance of prey, water and vegetation coverage, from sea level to 1200 m (Sunquist & Sunquist, 2002). Jaguar populations face severe problems such as poaching, competition for prey with humans' subsistence hunting, and habitat fragmentation, deterioration and loss (Swank & Teer, 1989; Sanderson *et al.*, 2002; Ceballos *et al.*, 2007). As a consequence, the species is listed as Near Threatened on the IUCN Red List (Caso *et al.*, 2010). It is estimated that jaguar has lost almost 54% of its geographic range since the 1900s, even disappearing in some countries such as El Salvador and Uruguay, so 51 priority areas at continental level as a base for the conservation of the species (Sanderson *et al.*, 2002).

In Mexico, the jaguar is classified as endangered (SEMARNAT 2001), and in the last decade, there have been many studies that have called for a spatially explicit revision of the current conservation strategies (e.g. Monroy-Vilchis *et al.*, 2008). A preliminary assessment of the identification of priority areas

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in Mexico using a Genetic Algorithm for Rule-set Prediction (GARP) distribution model (Chávez & Ceballos, 2007). However, the accuracy of the model is unknown (no independent validation was provided), limiting its value as a conservation framework (Loiselle *et al.*, 2003). Moreover, GARP has been shown to perform poorly in comparison with other new available modelling techniques (Stockman *et al.*, 2006; Roura-Pascual *et al.*, 2008). The number of currently available methods, which can be used to model species distribution patterns is increasing (Guisan & Thuiller, 2005), and the relative performance has been evaluated more than once (Elith *et al.*, 2006; Tsoar *et al.*, 2007). However, no general result could be obtained from these studies, with the same methods having different performances with different data sets and in different regions (Elith *et al.*, 2006). Based on these studies, it is clearly more appropriate to use multiple modelling methods to identify consensual areas of consistent prediction (Araújo *et al.*, 2006; Marmion *et al.*, 2008), which incorporate modelling uncertainties and producing more reliable estimates of species potential distributions (Hartley *et al.*, 2006).

So, the purpose of this study is to evaluate the potential jaguar distribution in Mexico using ensemble (consensus) model (sensu Araújo & New, 2007), considering three modelling approaches that rely on presence data only: Ecological Niche Factor Analysis (ENFA; Hirzel *et al.*, 2002), Maximum entropy (Maxent; Phillips *et al.*, 2006) and Mahalanobis Distance (MD; Corsi *et al.*, 1999). The three methods have been widely applied to model the distribution in large carnivores (e.g. Lovallo, 2000; Podruzni *et al.*, 2002; Falcucci *et al.*, 2009). In building our model, we had three main objectives: (1) to produce a model for the potential distribution of the jaguar in Mexico; (2) to evaluate the efficacy of the existing protected areas (PAs) and of the jaguar conservation units (JCUs) proposed by Sanderson *et al.* (2002); and (3) to propose new areas that should be considered for management and conservation of the jaguar in Mexico.

METHODS

Study area

Mexico is a large and heterogeneous country, covering almost 2 million km^2 and ranging from 32°43′ to 14°32′. The topography is very complex, with more than 65% of the country's area above 1000 m and with a large variety of habitat types, from tropical forests to deserts and a mixture of South and North American fauna and flora (De Alba & Reyes, 1998). These characteristics have contributed to making Mexico one of the mega-diverse countries (Ramamoorthy *et al.*, 1993) and one of the most important biodiversity hotspots (CBD, 2009).

Species data

We obtained two presence-only data sets on jaguar occurrence in Mexico. The first data set, which was used to calibrate the models, included direct or indirect signs of presence obtained from the scientific literature (Brown & López-González, 2001; Medellín *et al.*, 2002; Jiménez & López-González, 2003; Ortega, 2005; Chávez & Ceballos, 2007; Núñez, 2007; Cruz *et al.*, 2008; De la Torre de Lara & Medellín, 2008; Gómez *et al.*, 2008; González *et al.*, 2008; Luna-Krauletz *et al.*, 2008; Méndez *et al.*, 2008; Monroy-Vilchis *et al.*, 2008; Rodríguez & Iñiguez, 2008; Valera, 2008; Villordo-Galván *et al.*, 2010) and from four freely available data sets: CONABIO (http://www.conabio.gob.mx), GBIF (http://www.gbif.org), MaNIS (http://www.manisnet.org) and Jaguar GIS (http://www.savethejaguar.org). Deforestation and more generally habitat destruction has been increasing at alarming rates between 1964 and 1990 (FAO, 2001) being particularly important for tropical regions (Laurance, 1999) and Mexico has not been spared (Velázquez *et al.*, 2002). For this reason, to avoid including old and potentially inaccurate data, all points collected before 1990 were discarded. Also, we used only one data point per locality and considered just one record of presence for each 5 km^2 (minimum home range of jaguar females, Núñez *et al.*, 2002), decreasing strongly the level of autocorrelation and leaving 197 points of presence collected between 1990 and 2008 (Fig. 1, Table S1).

To evaluate the model, we used a second data set, including VHF-locations of five collared jaguars (all adult females living in five different regions) and camera-trapping locations from eight additional regions in the southeast, northeast, west and central Mexico. In total 104 points of presence, all collected between 2000 and 2008, were used for model evaluation (Fig. 1).

Environmental data

We considered six environmental and anthropogenic factors assumed to be important to determine the distribution of the jaguar (Schaller & Crawshaw, 1980; Tewes & Schmidly, 1987; Seymour, 1989; Swank & Teer, 1989; Quigley & Crawshaw, 1992; Rabinowitz, 1999; Brown & López-González, 2001; Sunquist & Sunquist, 2002; Monroy-Vilchis *et al.*, 2009), all resample using a common origin and a 1-km^2 cell size. In particular, we considered vegetation, human population density and distance to roads, elevation, slope and presence of prey species.

We obtained a digital map of vegetation from the Mexican National Forest Inventory (SEMARNAT *et al.*, 2001). The map was derived from Landsat ETM+ satellite images integrated with local-scale land use and vegetation maps (series II INEGI; Velázquez *et al.*, 2002; Mas *et al.*, 2002). We reclassified the vegetation map into seven mutually exclusive classes (tropical rain forests, dry forests, other forests, arid vegetation, grasslands, regularly flooded vegetation, agriculture) considered as important for the jaguar (Table 1, Sanderson *et al.*, 2002).

We obtained antropogenic perturbation from human population density from Salvatore *et al.* (2005) and distance to roads from http://conabioweb.conabio.gob.mx/metacarto/metadatos.pl. Elevation was available through the USGS/NASA Shuttle Radar Topography Mission (USGS, 2007), and it was used to calculate slope (Table 1).

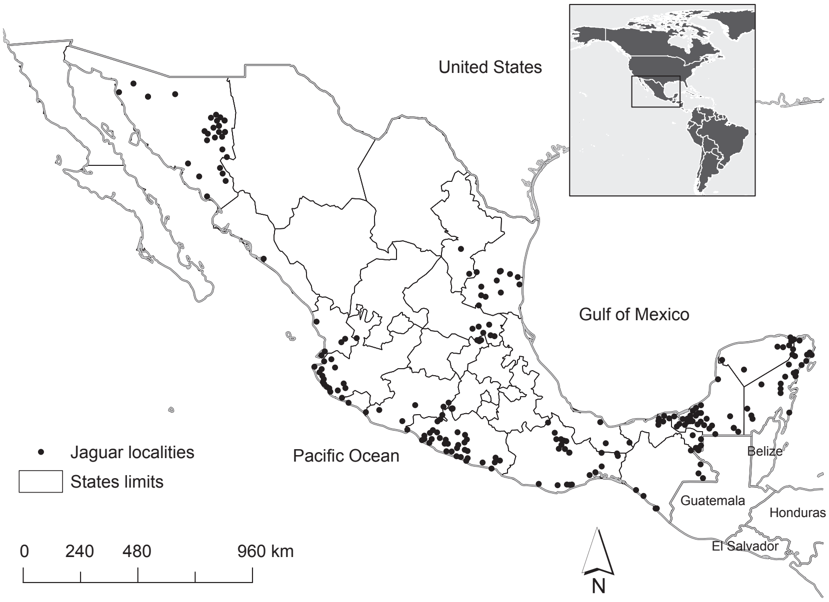

Figure 1 Locations of the 301 records used in the jaguar models.

Table 1 Habitat variables considered for the distribution models.

	Variable	Source	Author(s)
1	Dry forest	National Forest Inventory	SEMARNAT *et al.* (2001)
2	Tropical rain forest	National Forest Inventory	SEMARNAT *et al.* (2001)
3	Other forest	National Forest Inventory	SEMARNAT *et al.* (2001)
4	Arid vegetation	National Forest Inventory	SEMARNAT *et al.* (2001)
5	Grassland	National Forest Inventory	SEMARNAT *et al.* (2001)
6	Regularly flooded vegetation	National Forest Inventory	SEMARNAT *et al.* (2001)
7	Agriculture	National Forest Inventory	SEMARNAT *et al.* (2001)
8	Anthropogenic perturbation	Roads (distance)	CONABIO (2008)
		Human population density	FAO (2005)
9	Elevation	Digital elevation model	USGS (2007)
10	Slope	Digital elevation model	USGS (2007)
11	Prey-species richness	Literature (prey distribution)	Núñez *et al.* (2002), Ceballos *et al.* (2002), Scognamillo *et al.* (2003), Ortega (2005), Rosas-Rosas *et al.* (2008)
		National Forest Inventory	SEMARNAT *et al.* (2001)
		Digital elevation model	USGS (2007)
		Global Mammal Assessment	Patterson *et al.* (2007)

To account for the presence/absence of the main prey species used by the jaguar in Mexico (*Odocoileus virginianus, Tayassu pecari, T. tajacu, Dasypus novemcinctus, Nasua narica, Mazama americana, Didelphis virginiana, Dasyprocta mexicana*; Ceballos *et al.*, 2002; Rosas-Rosas *et al.*, 2008), we used the data available in the Global Mammal Assessment (Patterson *et al.*, 2007). In particular, we considered all data available on ecology and distribution for each prey species, and we built a deductive distribution model following the approach outlined in Maiorano *et al.* (2006). We used all models to build a map of prey-species richness for the jaguar in Mexico (Fig. S1).

Finally, we generate a background raster to homogenize all the variables. This background was generated excluding the water areas and absence pixels (pixels without data in one or more variables) from Mexico polygon.

Ecological niche and ensemble models

We considered three modelling techniques (ENFA, MD and Maxent) to produce a final ensemble model (EM) (Araújo & New, 2007) for the potential distribution of jaguar in Mexico. We implemented the ENFA algorithm using BioMapper4 (Hirzel *et al.*, 2004). ENFA identifies the main environmental gradients to which a species respond within a study area from a series of environmental variables while minimizing collinearity and redundancy. ENFA calculates a set of new independent predictor factors combining the original environmental variables. The first factor accounts for marginality (the difference between the species habitat use and the average environmental conditions in the study area; marginality values range from 0 to 1, with higher values indicating higher differences), while the others consider specialization (tolerance with respect to each environmental variable; tolerance values range from 0 to 1, with higher values indicating higher tolerance). Further details can be found in Hirzel *et al.* (2002).

Maxent is a machine-learning method that estimates the probability distribution of a species following the principle of maximum entropy and thus assuming that all environmental constraints that regulate the presence of a species are included in the estimation procedure (Phillips *et al.*, 2006). To avoid model over-fitting, we developed our model using the settings outlined in Phillips & Dudik (2008) and we considered a logistic output, with suitability values ranging from 0 (unsuitable) to 1 (optimal habitat).

Mahalanobis distance, a generalized squared distance statistic, has been used as a multivariate index of environmental quality in species distribution modelling (Corsi *et al.*, 1999). We calculated for each pixel of Mexico the multivariate distance between the environmental condition in the pixel and the jaguar ecological profile; the smaller the distance, the more similar the environmental conditions and the higher the habitat suitability (Corsi *et al.*, 1999). We calculated the MD using the algorithm available in Idrisi Andes (ClarkLabs 2007).

For each model, we used the Idrisi Andes area under the curve (AUC) module (for more details on the AUC see model validation) in a bootstrap procedure similar to the one implemented in Maxent (Phillips *et al.*, 2006) to calculate an internal AUC value (AUC_i) based on the same 197 points used to calibrate the three models. To obtain the final EM, we used the AUC_i as weights for each model in a weighted average as suggested by Marmion *et al.* (2008).

To allow for an easier interpretation of the final EM, we reclassified the original continuous model (ranging from 0 to 100) into two suitability classes: low suitability (below the median suitability value of 54) and high suitability (above the median) (Liu *et al.*, 2005). Given that our model was developed for conservation purposes, we only considered high suitability areas in all subsequent analyses as jaguar potential habitat.

Model evaluation

We evaluated the performance of the EM by calculating the area under the receiver operating characteristic (ROC) curve (Hanley & McNeil, 1982) using the 104 independent points of presence. We followed the approach outlined by Niels & ter Steege (2007) to test the statistical significance of AUC considering a total of 1000 null models. Moreover, we measured the overall concordance among the three models on a cell-by-cell basis calculating Pearson correlations, and we identified the areas with the highest discrepancies calculating the variance for each cell.

Conservation status and future strategies

To obtain a proxy for the efficacy of national and international conservation policies for the jaguar, we measured the extent of high suitability areas inside both PAs and the JCUs (Sanderson *et al.*, 2002). In particular, Sanderson *et al.* (2002) calculated that a jaguar population of 50 individuals living in suitable habitat could be genetically stable for 100 years. To calculate the smallest continuous area that should be protected if we want to focus our conservation efforts on viable populations (under the limiting assumption that genetic stability is enough), we used the '50 individuals' threshold as follows:

$$[(\mathrm{MMHR} * n\ \mathrm{Males}) + (\mathrm{MFHR} * n\ \mathrm{Females})]/2$$

where MMHR is the mean male home range and MFHR is the mean female home range. Assuming (1) a sex ratio of at least one male every two females (Schaller & Crawshaw, 1980; Sunquist & Sunquist, 2002) and thus counting on 15 males and 35 females, (2) an average home range of 25 km^2 for females (Núñez *et al.*, 2002) and of 65 km^2 for males (Maffei *et al.*, 2005) and (3) a complete overlap of the home range of one male with two females (Scognamillo *et al.*, 2003), we calculated that the smallest continuous area necessary to preserve a viable jaguar population corresponds roughly to 900km^2 of high suitability habitats. We applied this definition to our distribution model to propose new jaguar conservation and management areas (JCMAs) in Mexico.

RESULTS

Our results show that although the jaguar in Mexico actively selects particular habitat types, it retains a relatively high ecological flexibility (ENFA global marginality = 0.803; global tolerance = 0.7). In particular, the presence of the species is mainly associated with tropical rain forests, high prey-species richness and regularly flooded vegetation, with a clear avoidance for arid vegetation, higher elevations and grasslands (Table 2).

Overall, ENFA, MD and Maxent produced similar models, with fairly high correlation values (Fig. 2, Table 3), even though the Maxent model was more conservative compared to the other two. ENFA predicts 434,790 km^2 of high suitability habitat (22.3% of Mexico), and it is comparable to MD, which predicts 422,219 km^2 (21.6%); Maxent, however, predicts only 152,469 km^2 of high suitability habitat (7.85%, Fig. 2a–d). There is a general agreement between the models on the spatial distribution of high suitability habitat, with only four main areas of discrepancy: Tehuantepec isthmus, Tabasco, Campeche and Tamaulipas (Fig. 3).

The three models gave reasonably good values for AUC (ENFA-AUC = 0.786; MD-AUC = 0.756; Maxent-AUC = 0.826), while the AUC for the EM was 0.829 ($P < 0.0001$).

Table 2 Marginalization and specialization according to Ecological Niche Factor Analysis (ENFA) and percent contribution according to Maxent. Only the six most important variables are shown.

	ENFA	Maxent	
Variables	Marginalization	Specialization	Contribution percent
Tropical rain forest	0.505	4.203	3.3
Preys	0.461	3.436	27.5
Regularly flooded vegetation	0.404	2.505	6
Elevation	−0.391	7.807	25.5
Arid vegetation	−0.374	10.144	14.9
Grassland	−0.185	6.007	2.5

Considering the final EM, more than 312,318 km^2 of Mexico (16%) was classified as high suitability habitat for the jaguar, with coastal areas (from Tamaulipas and Sonora to Yucatan and Chiapas), the Balsas basin river, Soconusco and the Sierra Madre Oriental being the most important areas (Fig. 4).

Only 12.93% (27,139 km^2) of these areas are included in the existing PAs: mainly Sierra Gorda, Municipios La Concordia, Ángel Albino, Villa Flores and Jiquipil in Chiapas, Zicuiran-Infiernillo and Cuenca Alimentadora in Nayarit (Fig. 4). Along the same line, the JCUs proposed by Sanderson *et al.* (2002) only cover 14% of the jaguar potential habitat (117,000 km^2) and, in particular, they do not include the areas with the largest extent of jaguar potential habitat in the Pacific coast, the Balsas River basin, the Eastern part of the Sierra Madre del Sur, Yucatan, the central part of the Sierra Madre Oriental and Tamaulipas (Fig. 4).

To integrate the existing conservation networks, we identified eight new JCMAs (complementary to the existing conservation efforts) based on our criteria for a viable jaguar population (Fig. 5):

JCMA-1. North Pacific coast: from the centre of Sonora to the north of Nayarit (86,326 km^2). It represents the northernmost distribution of the jaguar in Mexico; it is limited by Sierra Madre Occidental towards the east and by the agricultural area along the Pacific coast.

JCMA-2. Central Pacific coast: from the Centre of Nayarit to Colima, including the northeastern part of the

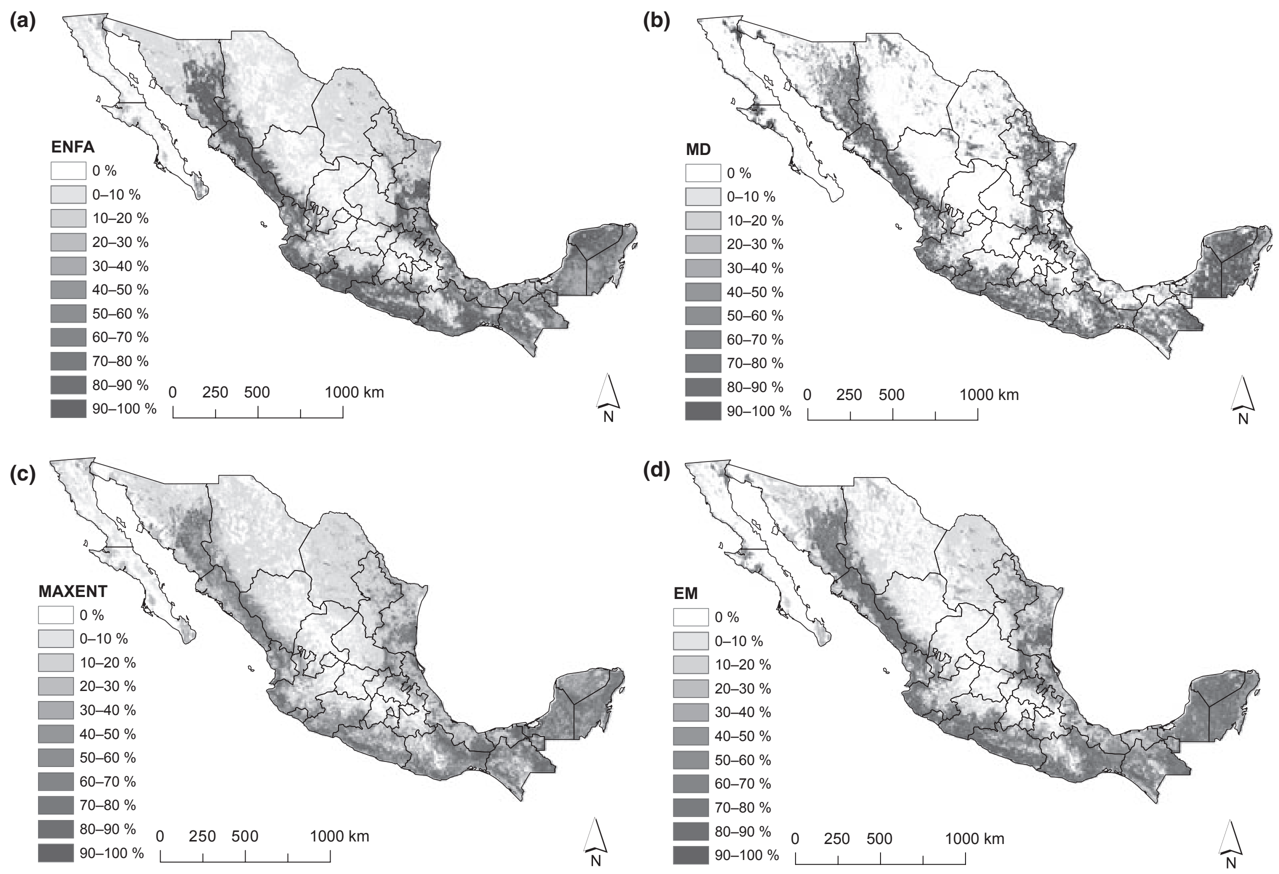

Figure 2 Potential distribution of the jaguar in Mexico according to: (a) ecological niche factor analysis (ENFA), (b) Mahalanobis distance (MD), (c) MAXENT and (d) ensemble model (EM).

Table 3 Spatial correlation matrix between the habitat models.

	ENFA	MD	Maxent	EM
ENFA	1			
MD	0.713	1		
Maxent	0.715	0.649	1	
EM	0.914	0.904	0.85	1

ENFA, environmental niche factor analysis; MD, Mahalanobis distance; Maxent, Maximum entropy; EM, ensemble model.

Trans-Mexican Volcanic Belt (18,157 km^2). It is limited by the high mountain ranges to the east and by the high human population densities to the west.

JCMA-3. South Pacific coast and Balsas River basin: from Michoacán to south-central Oaxaca, including the northern and central parts of the Balsas River (58,039 km^2).

JCMA-4. Eastern Sierra Madre del Sur and Soconusco: from the northeastern part of Oaxaca, Sierra Madre del Sur and Soconusco to the borders with Guatemala (41,314 km^2).

JCMA-5. Southern Gulf of Mexico: the Montes Azules Reservation, eastern Chiapas (23,451 km^2).

JCMA-6. Peninsula of Yucatan: Yucatan, Campeche and Quintana Roo (44,708 km^2).

JCMA-7. Sierra Madre Oriental: San Luis Potosi, southeast Tamaulipas, Queretaro and Hidalgo (15,835 km^2).

JCMA-8. Northern Gulf of Mexico: from the centre of Tamaulipas to the north of Veracruz (19,224 km^2).

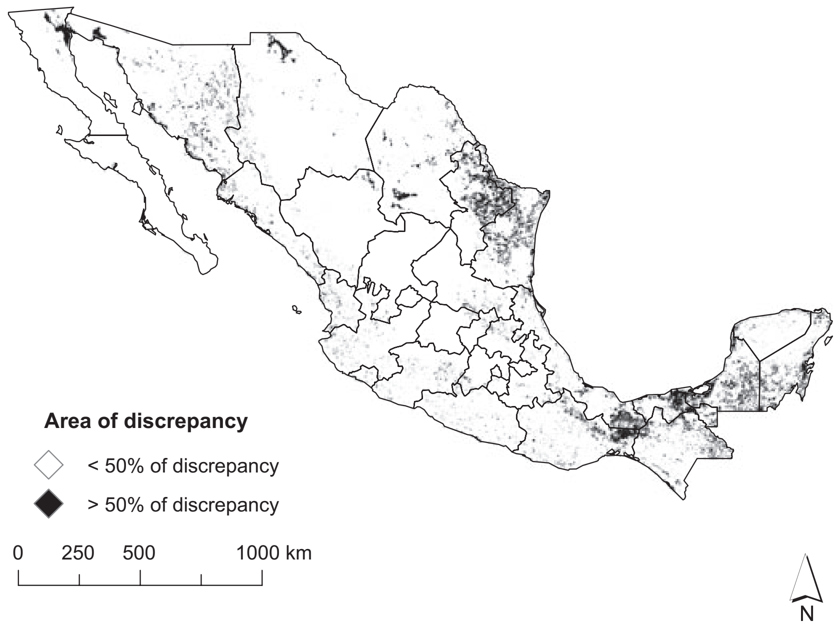

Figure 3 Discrepancy areas between of the three models.

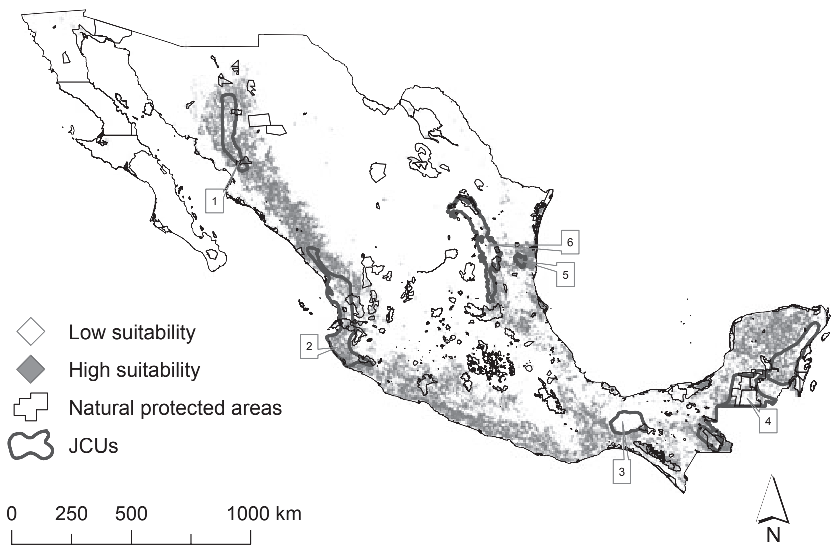

Figure 4 Potential habitat for jaguars in Mexico as defined by the ensemble model (EM). Protected areas and Jaguar Conservation Units (JCUs), (1) Sonora, (2) Jalisco, (3) Istmo de Tehuantepec, (4) Selva Maya, (5) Sierra Tamaulipas, (6) Sierra Madre Oriental (Sanderson *et al.*, 2002).

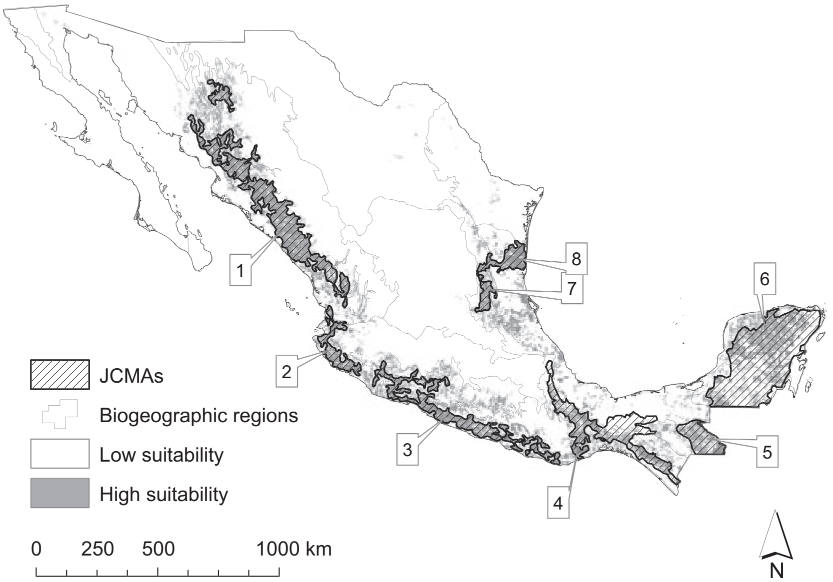

Figure 5 Proposed Jaguar Conservation and Management Areas (JCMA's).

DISCUSSION

Many international conservation efforts have considered Mexico as a priority for conservation (CBD, 2009), with a number of national and international projects explicitly focusing on the jaguar as a flagship/umbrella species (e.g. http://www.savethejaguar.org; Sanderson *et al.*, 2002; Rabinowitz & Zeller, 2010).

Large carnivore conservation, and the jaguar is no exception, can potentially attract many economic and political resources, being at the same time beneficial for overall biodiversity (Sergio *et al.*, 2006). However, any conservation effort should be based on reliable and detailed spatially explicit knowledge of the available conservation options, especially when dealing with a species at the fringes of its geographical range and at the top of the food web, as is the case for the jaguar in Mexico.

We built a model of potential distribution for the jaguar in Mexico using the most updated and reliable data set available on species presence, and we also evaluated the model using independent field data. We developed our model in the framework of ensemble forecasting (Araújo & New, 2007), incorporating model uncertainties and producing a more reliable estimate of the species potential distribution (Hartley *et al.*, 2006). We based our EM on three consistent models (ENFA, Maxent and the MD), which gave similar indications on the species ecology (with tropical rain forests, high prey-species richness and regularly flooded vegetation being the most important variables to explain species presence).

The results of our modelling effort are consistent with the available literature on species ecology (Swank & Teer, 1989; Quigley & Crawshaw, 1992). In fact, it is well known that the jaguar can tolerate many different types of vegetation (e.g. even dry forests), with much lower population densities compared to tropical rain forests (Rabinowitz, 1999; Sanderson *et al.*, 2002). In our model, arid vegetation, higher elevations and grasslands were mainly characterized by low suitability values, even though the high ecological flexibility of the species allows for some individuals to occur at elevations above 1200 m (Brown & López-González, 2001; Hatten *et al.*, 2005; Monroy-Vilchis *et al.*, 2008) and in semi-deserts (McCain & Childs, 2008), where the jaguar may be easily out-competed by *Puma concolor* (Monroy-Vilchis *et al.*, 2009).

Maxent, according to the AUC value that we measured, showed the best performance in this study, a result that has already been obtained before (Elith *et al.*, 2006; but see Peterson *et al.*, 2008 and Roura-Pascual *et al.*, 2008). Overall, ENFA, MD and Maxent gave comparable potential distributions, but with important differences. These differences, although preventing the use of a single method and calling for an EM (Marmion *et al.*, 2008; Roura-Pascual *et al.*, 2008), may indicate regions where the species ecology and distribution are not well understood (Hartley *et al.*, 2006; Roura-Pascual *et al.*, 2008) and where further studies should be carried out (Fig. 1). The Tehuantepec Isthmus, Tabasco, Campeche and the north of Tamaulipas represent important candidates for further detailed surveys aimed at investigating species presence. Also, the lack of jaguar studies in these regions contributes to discrepancies between the models. In particular, Tamaulipas and Yucatán have highly transformed by agricultural activities, and it is urgent to obtain a better understanding of the local jaguar population status. Apparently, the Isthmus of Tehuantepec still hosts an important jaguar population (Lira & Ramos-Fernández, 2007) even if a number of threats (e.g. commerce of skins and live animals, extraction of prey species, growing jaguar-cattle conflicts) are present. Tabasco, on the other hand is probably hosts a viable population of jaguars, but only in wetland areas (Valera, 2008), and further field studies are urgently needed.

Overall, the Pacific coast presents the largest extent of jaguar potential habitat, with the Yucatan and the Sierra Madre Oriental also being able to host large continuous populations, even though Yucatan is highly fragmented by agricultural activities, with potential negative consequences for the jaguar. The Gulf of Mexico is particularly important as an area of connection between Tamaulipas and the Pacific coast, but it is by far the least studied and, probably, one of the areas that has been most disturbed by human activities. Other areas, such as Nayarit, Sinaloa, Guerrero, Michoacán, Morelos and Oaxaca, should also be considered for studies on the status of the local jaguar populations, as they all contain areas of high suitability jaguar habitat and have yet to be studied in detail.

It is important to emphasize that the entire jaguar distribution in Mexico almost entirely overlaps with important areas for livestock raising in communal lands, and consequently conflicts with livestock activities have already been document in some regions (Rosas-Rosas *et al.*, 2008) calling for the inclusion of special livestock-jaguar management program both in national law and in practical conservation and management actions.

Overall, the existing PAs, although important, cannot be considered as sufficient to save the species in Mexico. In fact, PAs are not always effective in preserving biodiversity and/or preventing land-use change (Maiorano *et al.*, 2008), and this is also true for Mexico where 35% of the existing biosphere reserves have not been successful in preventing changes in land use and natural vegetation (Sánchez-Cordero & Figueroa, 2007). The most important areas for the conservation of the jaguar, the areas hosting the largest continuous high suitability habitats, are the biosphere reserves of Montes Azules, Calakmul, Sierra Gorda and Zicuiran-Infiernillo. Sierra Gorda in particular has been considered as highly threatened and with a limited capacity for conservation enforcement (Sánchez-Cordero & Figueroa, 2007), thus requiring particular attention. Overall, national PAs have a higher suitability for the jaguar compared to state PAs, which are also smaller on average. However, state PAs may still play an important role, specifically as stepping-stones in a jaguar-oriented national ecological network (sensu Boitani *et al.*, 2007).

The JCUs proposed by Sanderson *et al.* (2002) cover only 14% of the jaguar potential habitat in Mexico but in any case represent an important contribution, particularly in Jalisco, the Maya jungle, the Sierra de Tamaulipas and Soconusco. According to our model, the JCU in Jalisco is the biggest and probably the most important area of potential jaguar habitat. Jointly, both the existing JCU of Jalisco, and areas that we propose, include almost half of the Sierra Madre Occidental and can potentially facilitate the connection between the southwest and northwest of Mexico. The Maya jungle is also very important: it is already partially protected and Ceballos *et al.* (2002) reported a large and viable jaguar population in the region, confirming what was reported in 1989 (Swank & Teer, 1989). However, according to our analysis, most of the habitat in the Maya jungle is highly fragmented by agricultural activities, highlighting a potential future threat for the local population and strongly calling for an active involvement of local people in all conservation strategies. The Sierra de Tamaulipas and Soconusco have a really limited extent (considering the spatial requirement of jaguars), but they are located in areas with high suitability values, and we strongly recommend increasing their extents and giving them the highest priority for conservation.

Jaguar conservation and management areas

Based on our EM, we suggest, in addition to the PAs and JCUs, eight new JCMAs, which we assume would greatly improve the conservation of jaguars in Mexico and tare intended to complement existing conservation strategies. Knowing that it would be difficult to directly protect all the JCMAs that we propose, we would like to stress the importance of conservation and management actions that should be taken in these areas. Management actions aimed at improving the coexistence of people, and jaguars should receive the highest priority particularly with direct support from the national government to traditional, non-invasive economic activities. It is important to provide in the JCMAs governmental incentives, such as payments for ecosystem services, livestock insurance programs, increased financial support to national and state PAs for their effective operation, building capacity and increasing environmental education for local people and park rangers.

It is important to note that embedded within many JCMAs there are large areas of the existing JCUs, with the exception of two areas: the Istmo de Tehuantepec and the Maya jungle. For both areas, we strongly recommend more detailed studies on the current availability of habitat and on the status of the existing jaguar populations.

The North Pacific coast (JCMA-1) represents the northern limits for the distribution of the jaguar, and it is probably the source of the few individuals reported in Arizona, USA. The Central Pacific coast (JCMA-2) is extremely important because of its potential role in connecting JCMA-1 with JCMA-3. JCMA-2 would include an existing JCU, the Chamela–Cuixmala that is currently considered as high priority. However, high human population densities heavily affect this area, and the protected area of the Sierra de Manantlán alone is too small to support a stable population of jaguars. The 'South Pacific coast and Balsas River' (JCMA-3) is the second most extensive, with high suitability habitat along the Balsas River, it potentially can work as a functional connection between eastern and western jaguar populations in Mexico, contrary to Rabinowitz & Zeller (2010) who propose this connection from the Sierra Madre Oriental to Sierra Madre Occidental through northern Plateau Mexican. Unfortunately high human population densities and many agricultural activities characterize the entire Balsas River basin. Nevertheless, we assume that the JCMA-3 can still be managed to promote the movement of dispersing individuals. The 'Sierra Madre del Sur and Soconusco' (JCMA-4) can act as an important connection between the populations of the jaguar from the Pacific coast, Chiapas, Central America and the Sierra Madre Oriental.

The main variables that might limit the distribution of jaguars in this area are elevation along the Sierra de Oaxaca and agricultural activities along the Gulf of Mexico coast.

The Southern Gulf of Mexico (JCMA-5) corresponds to the main corridor going from Mexico to Guatemala. The mountainous regions with steep slopes, which are inaccessible to humans, represent high suitability habitats. In this same region, Sanderson *et al.* (2002) identified the Maya jungle JCU where, according to our model, the extent of potential habitat has been dramatically reduced. The Yucatan Peninsula (JCMA-6) is the region in Mexico with the largest extent of tropical rain forest, but it is highly fragmented and it is facing severe anthropogenic threats (Faller *et al.*, 2007). The region still hosts patches of potential habitat, large enough to support a stable jaguar population for the next 100 years. In fact, a population of more than 900 individuals has already been reported in the southeastern part of the unit (Chávez *et al.*, 2007), with smaller populations (between 120 and 240 individuals; which are still viable populations according to our criteria) living in the northeastern part (Faller *et al.*, 2007). The Sierra Madre Oriental (JCMA-7) is small and isolated (except for connections with the Gulf of Mexico), and it would be important to obtain a more detailed evaluation of the potential for this area to act as corridor. Grigione *et al.* (2009) suggested this area as a high conservation priority. The Northern Gulf of Mexico (JCMA-8) is mainly characterized by dry forests. Sanderson *et al.* (2002) classified the area as having a low probability of supporting a viable jaguar population in the long term, but our analyses show that JCMA-8 could be extremely important, especially if new PAs are established to complement the four existing PAs.

Conservation options

To conserve species such as the jaguar, it is necessary to consider several factors, such as extent, status, distribution and connectivity of the habitat, as well as the availability of prey species, status of the jaguar populations and human disturbance. It is clear that a comprehensive species assessment would require data that is currently unavailable for the jaguar in Mexico, such as the demographic status of the species, the abundance of prey. However, at least we present a robust analysis on the quality, characteristics and distribution of the habitat for the jaguar, and we have evaluated our model using completely independent data. In this way, we are strengthening and complementing the results by Sanderson *et al.* (2002) with a more detailed analysis for Mexico.

A further important step for future research would be to identify the area of potential conflicts (e.g. areas with livestock ranching and with jaguar-human conflict, or approaches similar to the one developed in Falcucci *et al.*, 2009) and carry out a specific analysis of the possible habitat corridors for the jaguar (a long distance disperser), more than 800 km, according to Sunquist & Sunquist (2002), making it possible to create a management program for the species in a multinational, metapopulation framework.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Deductive distribution models for (a) *Dasyprocta mexicana,* (b) *Dasypus novemcinctus,* (c) *Didelphis virginiana,* (d) *Mazama americana,* (e) *Nasua narica,* (f) *Odocoileus virginianus,* (g) *Tayassu pecari,* (h) *Tayassu tajacu.*

Table S1 Geo-referenced records (geographic projection, decimal degrees, datum: WGS84) of jaguar presence in Mexico. Data collected from 1990 to 2008.

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BIOSKETCH

Focus of the research teams:

First team – ecology and conservation of threatened species, http://www.uaemex.mx/ebsn/ (**C.R.S.** and **O.M.V.**).

Second team – conservation biology, systematic conservation planning and spatial predictive modelling (focus in terrestrial mammals), http://www.gisbau.uniroma1.it (**L.M.**, **A.F.** and **L.B.**).

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