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RESEARCH ARTICLE

Jaguar distribution, biological corridors and protected areas in Mexico: from science to public policies

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Abstract
Context Land use change, habitat loss and fragmentation are the major threats to jaguar conservation in Latin America. Here, we integrate the information of jaguar's distribution to identify priority areas for its conservation.
Objective We evaluated the effect of topographic, anthropogenic and landscape variables on habitat suitability to evaluate potential core areas and biological corridors for jaguar conservation across Mexico.
Methods We compiled a database of jaguar occurrence records, geospatial data-set of all Natural Protected Areas and using the expert criterion of the Mexican jaguar specialists to define Jaguar Geographic Regions; i.e. well-defined large units with similar ecological characteristics across the geographic range of jaguars in Mexico. We then conducted analyses of ecological niche models to identify Jaguar Conservation Units; i.e. core units with jaguar populations of 15 or more individuals. We used Least

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Cost Path and Circuit Theory analyses to define the Biological Corridors; i.e. regions with enough habitat to allow for jaguar dispersal along their geographic range, but putting emphasis in connecting Jaguar Conservation Units.

Results We identified 5 Jaguar Geographic Regions (JGRs), 10 Jaguar Conservation Units (JCUs), and 13 Biological Corridors to maintain the connectivity of jaguar's populations across their whole geographic range in Mexico. Our results showed that JGRs cover 25% of the country but only 21% of those regions are currently protected in nature reserves. So, our study illustrates the importance of the creation of new protected areas or the implementation of other schemes of conservation to protect larger extensions of the jaguars' habitat in Mexico. It also indicates that despite the reduction of jaguar range in Mexico, there are still relatively large and well conserved areas capable of maintaining jaguar populations.

Conclusions Our results are a fundamental tool to guide the conservation and management of jaguars in Mexico. Our findings indicate that public jaguar conservation policy to protect the remaining jaguar habitat in Mexico should include the following actions: i) Strengthen established protected areas, ii) Create new protected areas, iii) Implement sustainable development programs to stimulate land owners to protect their lands, and iv) Develop mitigation measures for infrastructure. Although the window of opportunity is closing, our results indicate that there is still time to save jaguars and the plethora of species that share their habitat in Mexico.

Keywords Corridor · Circuit theory · Protected areas · Jaguar conservation · Landscape connectivity · Least-cost path

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Introduction

Habitat loss and fragmentation are particularly relevant for the conservation of large carnivores, especially in developing countries where natural habitats are under unprecedented threats due to excessive population growth, demands by human populations for new lands, and unplanned economic development (Ceballos and Ehrlich 2002; Ripple et al. 2014; de la Torre et al. 2017c; Ceballos et al. 2020; Torres-Romero et al. 2020). Consequences of this effect include reduction of population size, fragmentation of populations, and disruption of the original patterns of gene flow, and many other problems (Cardillo et al. 2005). Small, isolated populations are more susceptible to extinction because of both stochastic and deterministic natural or human induced causes (Cardillo et al. 2005; Hill et al. 2019). Limited population size, diseases and habitat fragmentation, among other factors, impedes the genetic and demographic viability of populations (Uphyrkina et al. 2002; Janečka et al. 2007; Haag et al. 2010). Populations that are too small and isolated can collapse to extinction due to excessive interbreeding after long periods (Haag et al. 2010; Yumnam et al. 2014). One of the main solutions for mending the negative effects of habitat fragmentation on large carnivore populations is to maintain or restore connectivity through wildlife corridors (Rabinowitz and Zeller 2010; Rodríguez-Soto et al. 2011; Dickson et al. 2013). Connectivity is the degree to which the landscape is suitable for movement among habitat patches. It depends on the landscape characteristics and on the ability of species to move through habitats and corridors (Crooks and Sanjayan 2006; Rudnick et al. 2012).

The jaguar is the largest felid in the Neotropics, and formerly occurred from southwestern United States to central Argentina (Seymour 1989; Sanderson et al.

2002). However, it has been extirpated from almost 55% of its original range over the last 100 years. Recent conservation assessments have all concluded that jaguars are declining in much of its geographic range size (Medellín et al. 2016; de la Torre et al. 2017a; Quigley et al. 2017). Most of its populations are considered as Endangered or Critically Endangered (de la Torre et al. 2017a). Main threats for jaguars are habitat destruction and fragmentation, retaliatory killing, prey depletion, and diseases transmitted by domestic animals (Sanderson et al. 2002; Quigley et al. 2017). The loss of livestock by jaguar depredation represents economic losses for local communities that inhabit in nearby sites of jaguar habitat and at the same time has great repercussions in jaguar conservation because cattle owners affected often kill the jaguars in retaliation of predation (Treves and Bruskotter 2014; Peña-Mondragón et al. 2016; Tortato et al. 2017). Indeed, jaguar habitats are being converted to agricultural lands, pastures, and human settlements, while roads and other human infrastructure are destroying jaguar habitat as well (Conde et al. 2010; Haag et al. 2010; Colchero et al. 2011; Cullen et al. 2013, 2016; Ceballos et al. 2016; de la Torre et al. 2017c). Jaguar main prey are exploited by local communities for subsistence and commercial purposes throughout the species geographic range, reducing the habitat capacity to maintain jaguar populations (Sanderson et al. 2002; Quigley et al. 2017). These threats exert synergic effects on jaguar populations (Romero-Muñoz et al. 2018).

Historically, jaguars roamed in Mexico in a great variety of environments, including the semi-arid zones of Sonora and Tamaulipas in Northen Mexico through the coast plain areas of the Pacific and Mexican Gulf states as far as the tropical rainforests of Chiapas and Yucatan Peninsula (Leopold 1959; Ceballos et al. 2016; Chávez et al. 2016). Currently, jaguars are found in areas with well-preserved natural vegetation cover and remote areas across the Pacific and Gulf of Mexico lowlands and the foothills of the Sierra Madre Occidental and Oriental mountain ranges, as well as the Yucatan Peninsula (Rodríguez-Soto et al. 2011; Chávez et al. 2016). There are recent records in 21 states, including Sonora, Sinaloa, Nayarit, Jalisco Colima, Michoacán, Mexico, Morelos, Guerrero and Chiapas, along the Pacific slope; Tamaulipas, Nuevo Leon, San Luis Potosi, Hidalgo, Queretaro, Puebla, Veracruz, and Tabasco along the Gulf of Mexico Slope; and Yucatan, Quintana Roo, Campeche, in the Yucatan Peninsula (Rodríguez-Soto et al. 2011; Chávez et al. 2016; Ceballos et al. 2016; de la Torre et al. 2017a; Ceballos et al. in review). Due to the reduction of its population, jaguars are included in the list of threatened species by the Mexican Federal Government (SEMARNAT 2019). Between 2008 and 2010 (2010 hereafter), and 2016 and 2018 (2018 hereafter), the first and second Jaguar National Census were carried on with the collaboration of more than fifty experts from academic institutions, Non-Governmental Organizations, the Federal Government and the private sector. National Jaguar Census was implemented in fifteen sites and this represents the largest endeavor in the American Continent to assess the conservation status of the species at nationwide scale. The results indicate that the jaguar population increased from 4000 in 2010 to 4800 in 2018, indicating a very positive population trend (Ceballos et al. in review).

To consolidate the conservation status of jaguars in Mexico, it's critical to design a strategy which ensures the long-term maintenance and connectivity of its populations in the country. It's estimated that the conversion of natural landscapes has caused the loss of 40% of their historic range size in Mexico since 1900 (Chávez et al. 2016). Presently, roughly 30% of Mexican territory is suitable for jaguar presence and 13% is found in Natural Protected Areas (Rodríguez-Soto et al. 2011; Ceballos et al. 2016). For this reason, it is fundamental to identify core areas with large extensions of suitable habitat, that could acts as either protected areas or biological corridors to maintain the critical habitat and connectivity among jaguar populations. So, the main objective of this study was to carry out an analysis to identify critical corridors to maintain both the functional connectivity between priority conservation areas and the long-term viability of jaguar populations in the country.

Other studies have addressed the connectivity of jaguar populations at continental, regional and local scales. In Mexico there are several proposals constructed through diverse methodologies and approaches to define biological corridors to maintain the connectivity of jaguar populations in the country (Rabinowitz and Zeller 2010; Rodríguez-Soto et al. 2011, 2013; de la Torre et al. 2017b). In this study, we integrate spatial and temporal information of species occurrence, published or not published, over the last

Table 1 Sources of the jaguar records in Mexico used to implement the analyses of this study

Region	Number of records	Contribution of Mexican jaguar experts with unpublished records	Published sources
1. North Pacific	340	(a) Yamel Rubio, University of Sinaloa (b) Horacio Bárcenas, Facultad de Ciencias-UNAM (c) Ivonne Cassaigne, Primero Conservation, A.C. (d) Oscar Moctezuma, Naturalia A.C (e) Gerardo Carreón, Naturalia A.C	Navarro-Serment et al. (2005), Ceballos et al. (2007), Valera-Aguilar (2010), Rodríguez-Soto et al. (2011)
2. Central Pacific	64	(a) Andrés García, Instituto de Biología UNAM (b) Gerardo Ceballos, Instituto de Ecología-UNAM (c) Rodrigo Nuñez, COVIDEC A.C	Ceballos et al. (2007), Monroy-Vilchis et al. (2008), Rodríguez-Soto et al. (2011), Charre-Medellín et al. (2014), Figel et al. (2016)
3. South Pacific	703	(a) Fernando Ruiz-Gutiérrez, Proyecto Guerrero Jaguar (b) Alfonso Aquino, Preconjaguar A.C (c) Víctor Rosas, Yaguar Xoo (d) Epigmenio Cruz, Secretaria del Medio Ambiente del Estado de Chiapas (e) Gabriela Palacios, Secretaria del Medio Ambiente del Estado de Chiapas (f) Valeria Towns, CONANP-Mexico (g) Antonio de la Torre, Instituto de Ecología-UNAM	Ceballos et al. (2007), Rodríguez-Soto et al. (2011), Briones-salas et al. (2012), Almazán-Catalán et al. (2013), Aquino et al. (2013), CONANP (2014), Dueñas-López et al. (2015), Hidalgo-Mihart et al. (2015), Valenzuela-Galván et al. (2015), Briones-Salas et al. (2016), UAEM (2016), de la Torre et al. (2017b)
Yucatan Peninsula	675	(a) Marco Lazcano, Reserva Ecológica el Edén A.C. (b) Cuauhtémoc Chávez, UAM-Lerma (c) Heliot Zarza, UAM-Lerma (d) Gerardo Ceballos, Instituto de Ecología-UNAM (e) Carlos Alcérreca, Biocenosis A.C (f) Luis Pereira, Biocenosis A.C	Colchero et al. (2005), Pereira (2006), Ceballos et al. (2007), Conde et al. (2010), Colchero et al. (2011), Rodríguez-Soto et al. (2011), CONANP (2013), Hidalgo-Mihart et al. (2015), Chávez et al. (2016)
North East	148	(a) Arturo Caso, Predator Conservation A. C (b) Sasha Carvajal, Predator Conservation A. C (c) Jonathan Morales, Biofutura A.C (d) Daen Morales, Biofutura A.C (e) Roberto Pedraza, Grupo Ecológico Sierra Gorda A.C. (f) Horacio Bárcenas, Facultad de Ciencias-UNAM	Ceballos et al. (2007), Villordo-Galván et al. (2010), Rodríguez-Soto et al. (2011, 2013), CONANP (2013), Cuevas-Fernandez (2013), Dueñas-López et al. (2015), Carvajal-Villareal (2016)

Fig. 1 Jaguar records (black dots) in Mexico in the last 25 years and three different jaguar published range maps identifying biological corridors. The green area represent the Jaguar Subpopulations defined by de la Torre et al. (2018), the yellow are the corridors defined by Rodriguez-Soto et al. (2013), and the orange range represent the jaguar corridors defined by Rabinowitz and Zeller (2010). Our Jaguar Geographic Regions (Fig. 2) matched between 72 and 82% of those published biological corridors. The main differences are based in the more extensive data base that we used; for example. Rabinowitz and Zeller (2010) included a corridor across the arid regions in northern Mexico where there no jaguars.

two decades, and local expert knowledge to identify what we call Jaguar Geographic Regions (JGRs) in Mexico. Those are well-defined large units with similar ecological characteristics across the jaguar distribution range. We then identify Jaguar Conservation Units (JCUs) in the JGRs using habitat suitability models. Finally, we identified the areas more likely to maintain the connectivity between the JCUs integrating our habitat suitability model with Least Cost Path and Circuit Theory analyses. With this approach, we modeled jaguar habitat and corridors and to develop a regional conservation planning tool for the species at country scale. An additional goal is that this information can be used by stakeholders such as the Mexican Federal Government, State's Governments, local and international Non-Governmental Organizations, international agencies, scientists, and local people to implement sustainable development policies to reduce habitat loss and fragmentation, and maintain the connectivity among JCUs.

In our study, we specifically addressed the following issues: (i) Define Jaguar Geographic Regions throughout the jaguar distribution range in Mexico; (ii) Determine the core areas for conservation (i.e. Jaguar Conservation Units); (iii) Identify biological corridors to connect Jaguar Conservation Units and other regions in the jaguar geographic range; (iv) identify the most important protected areas and additional areas that need to be protected.

Methods

Jaguar occurrence compilation

We compiled a data set of all available records of jaguar occurrence in Mexico from diverse sources which included indexed journal articles, technical reports, thesis, books, book chapters, and the grey literature. We also incorporate unpublished jaguar records provided by Mexican jaguar specialists. We compiled and georeferenced all the unpublished jaguar records from recent years obtained from jaguar specialists in annual workshops. Our data set has 1913 jaguar records (Table 1, Fig. 1). This data-set only included records obtained in the last 25 years.

Table 2 Landscape information layers used to delimit Jaguar Geographic Regions

Type	Name	Description	Source
Environmental layers	Vegetation and land use (Serie I and V)	Vegetation types and their degradation degree by human activities for Mexico. This dataset also describes other land cover types such as crops, induced pastures, urbanized area and water. We included areas that maintain natural vegetation and we excluded transformed territories by human activities such as agriculture or urbanized areas	INEGI (1997,2015)
	Elevation	Digital Elevation Model (90 m) of all the country. We included areas such as mountain ranges or canyons because most of the jaguar range in Mexico is associated to the Sierra Madre Occidental and Oriental Mountain ranges	INEGI (2010)
	Hydrological basins	This layer describes the hydrological drainages at the scale of the whole country	INEGI (2010)
	Key Biodiversity areas	Sites that contribute significantly to the global persistence of the biodiversity in the terrestrial ecosystem of Mexico with the approach of use the jaguar as umbrella species	CONABIO (1998)
	Ramsar sites	Wetlands areas in Mexico which are complementary to the natural protected areas in Mexico	CONANP (2016)
	Priority Land Regions	Regions in Mexico that maintain the richest areas in biodiversity and ecosystem integrity	CONABIO (1998)
	Omitted areas for conservation	Important areas for conservation which are not included currently within the conservation schemes in Mexico	CONABIO et al. (2007)
Social layers	Paved roads, towns and cities	Paved road network, and the location of towns and cities. Areas with urbanized areas or crossed by several paved roads were avoided	SCT (2016), INEGI (2010)
	Human population per locality	Population size of towns and cities. Areas with high human density were avoided in the delimitation of the BJC	INEGI (2010)
	Land tenure	Most of the BJC included lands of rural communities. The land tenure in the delimitation of the corridors was crucial to involve key communities where in the future should be implemented conservation and management actions to allow the connectivity between jaguar populations	RAN (2015)
	Land use zoning	A legal mechanism of the Mexico Government to regulate the land use and the productive activities for protect the natural ecosystems and promote the sustainable use of the natural resources in the rural communities. We incorporate within the Biological Jaguar Corridors the areas designed to conservation by the rural communities	SEMARNAT (2016)
	Protected areas and political division	Presence of Natural Protected Areas, Conservation Management Units, states and municipal limits	INEGI (2010)

Protection level of jaguar range in Mexico

We compiled a geospatial data-set of all Natural Protected Areas in Mexico which overlap with jaguar distribution and potentially could protect jaguar populations or habitat (Bezauri-Creel et al. 2009; CONANP 2018). In this database we integrated all potential reserves designated for biodiversity protection according to the Mexican laws: (1) Federal Natural Protected Areas, which are reserves administered by the Mexican Federal Government through the National Commission of Protected Areas of Mexico (CONANP-Mexico); (2) State Natural Protected Areas, which are natural reserves administrated by the state governments; and (3) Private Areas Voluntarily Destined for Conservation (AVDC), which is a conservation scheme that includes all private or rural communities lands that were voluntarily destined for conservation and which were certified by the Mexican federal government. We identified all protected areas that have occurrence of jaguars overlaying our jaguar dataset with the polygons of these protected areas.

Jaguar geographic regions in Mexico

We delineated the Jaguar Geographic Regions (JGRs) as units to facilitate the jaguar conservation and management across their current geographic range in Mexico. JGRs were defined mostly with a geographic perspective, using information available of jaguar occurrence, areas of activity (Torre et al. 2017b; Cruz et al. 2021), and corridors previously compiled (Table 1). Our basic assumption is that it is fundamental to maintain of the connectivity of the JGRs to maintain the viability of jaguar populations by linking protected areas and conserved regions, and facilitating the movement of the jaguars between suitable habitat patches. Such connectivity is essential to increase the probability of maintaining the genetic flux between the core populations of the species in Mexico. Under this framework, JGRs should offer: (1) Structural connectivity allowed by the spatial distribution of the suitable habitat or by the habitat configuration, (2) Functional connectivity which is related with the behavioral response of individuals to the landscape configuration, and (3) Opportunities to promote the sustainable development for ensuring the wellbeing of the local communities.

We adjusted the JGRs using two different groups of landscape information. The first group included environmental information and was composed of seven layers, and the second group included social information and included five layers (Table 2) as follows:

(1) We included all the areas that maintain natural vegetation and tried to exclude large-scale territories transformed by human activities, since jaguars are restricted mostly to areas of conserved habitat where they find their natural prey and refuge. Jaguars commonly avoid areas with high human density or high human land use (Rabinowitz and Nottingham 1986; Conde et al. 2010; Cullen et al. 2013).

(2) We included areas with rugged terrain since jaguars can persist or disperse through mountain ranges or canyons, and because a relatively large part of the jaguar range in Mexico is associated with the Sierra Madre Occidental and Oriental Mountain ranges.

(3) We delimited JGRs based on the hydrological basins. We considered the potential areas where jaguars could move across riparian forest since jaguars are known to use riparian habitats to move through landscapes and use sites with permanent water more frequently (Schaller and Vasconcelos 1978; Rabinowitz and Nottingham 1986; Nuñez 2006).

(4) We included different kinds of conservation areas such as Key Biodiversity Areas, Raamsar sites, Priority Land Regions and Jaguar Conservation Units where jaguar occurrence has been recorded in the last 25 years and where JGRs could act as umbrella for the conservation of all biodiversity in general.

(5) We evaluate land tenure, political division, protected areas, and land use zoning. Land use zoning is a legal mechanism of the Mexican Government to regulate the land use and the productive activities with the aim of protecting the natural ecosystems and the sustainable use of the natural resources.

Jaguar conservation units

To identify the JCUs we modeled habitat suitability for jaguars in the country through the maximum entropy model, using Maxent version 3.4.1 (Phillips et al. 2017). Maxent allows estimating the probability of distribution of the species following the principle of maximum entropy and assuming that all environmental constraints that regulate the species presence are included in the modeling process (Phillips et al. 2006). We used a similar approach proposed by Rodríguez-Soto et al. (2011) and Morato et al. (2014) to generate our habitat suitability model. We considered the logistic output, with habitat suitability values ranging from 0 (unsuitable) to 1 (optimal habitat). To avoid model over-fitting, we only used quadratic and hinge features and a regularization multiplier of 1. We ran tenfold cross-validation and assessed variable importance through jackknife estimation (Phillips et al. 2006).

Since Maxent requires occurrence and background data, we used the 1913 jaguar records from Mexico. To reduce sampling bias, we applied spatial filtering

Table 3 Predictor variables used for modeling habitat suitability of jaguars in Mexico

Type	Variable name	Source	Description	Expected effect	Justification
Land cover	Tropical forest	National Forest Inventory	Areas covered by primary tropical forests	+	Jaguars are restricted mostly to areas of primary forest where they find their natural prey and refuge (Rabinowitz and Nottingham 1986; Conde et al. 2010; Colchero et al. 2011; Cullen et al. 2013, 2016; de la Torre et al. 2017b). Jaguars in Mexico occur in tropical forest, dry forests, oaks and pine forests, and flooded habitats such as mangroves (Leopold 1959; Sanderson et al. 2002; Rodríguez-Soto et al. 2011; Ceballos et al. 2016). The dataset contains information about natural vegetation (e.g.dry forests), cover and its degree of human degradation (INEGI 2015). It also include information on the land that has been transformed in crops, pastures, and urbanized areas (INEGI 2015).
	Dry forest	National Forest Inventory	Areas covered by primary dry forests	+	
	Other forest	National Forest Inventory	Areas covered by primary oak, pine, cloud forests	+	
	Flooded vegetation	National Forest Inventory	Areas covered by mangroves, tular and petenes habitat types	+	
	Arid vegetation	National Forest Inventory	Areas covered by arid vegetation such as xeric shrubland vegetation types	–	
	Secondary vegetation	National Forest Inventory	Secondary vegetation of all the vegetation types	+	
	Crops	National Forest Inventory	Areas of agriculture across the country	–	
	Grasslands	INEGI, 2015	Areas associated to pastures for cattle	–	
Topography	Elevation	Digital Elevation Model	Elevation ranges across Mexico generated from a Digital Elevation Model (1 km) of all the country	–	Jaguar habitat use is affected by different terrain conditions. Jaguars are frequently associated with lowland areas. Jaguar occupancy and movements would be hampered by the mountain ranges at higher altitudes (Rabinowitz and Zeller 2010; Rodríguez-Soto et al. 2011; Zeller et al. 2011; Morato et al. 2014; de la Torre et al. 2017c)
	Slope	Digital Elevation Model	Slope values generated from a Digital Elevation Model (1 km) of all the country	–	
Human perturbation	Distance to urban areas	INEGI, 2010	The minimum distance to the nearest urban area	–	Human activity affects habitat use by jaguars negatively due to disturbance and persecution (Conde et al. 2010; Colchero et al. 2011; Espinosa et al. 2014, 2018; Cullen et al. 2016; de la Torre et al. 2017c). Information of urban areas, towns and roads was obtained from INEGI (2010)
	Density of towns	INEGI, 2010	Density of towns around 7.5 km which is the radius of the female home range jaguars in southern Mexico	–	
	Distance to paved roads	INEGI, 2010	The minimum distance to the nearest paved roads	–	

by randomly selecting occurrence record within a radius of 7.5 km, which represent the radius of the average female home range size (180 km^2) in southern Mexico (de la Torre et al. 2017b), obtaining a total of 695 records for the analysis. We sampled 50,000 random locations across all the country territory as background points. We evaluated the predictive performance of our model by dividing the jaguar records locations randomly into two groups before model development: 80% of the data comprised a

Table 4 Models compiled in order to evaluate the jaguar range and the potential corridors in Mexico

ID	Range map and/or corridors	Scale	Approach use to define jaguar range or corridors	Proximately area covered in the Mexican country	References for published sources
1	Panthera Jaguar Corridor	Continental	Expert opinion and least cost path analysis	274,325 km^2	Rabinowitz and Zeller (2010)
2	Jaguar sub-populations in Mexico	Continental	Compilation of information of several sources	335,313 km^2	de la Torre et al. (2017a)
3	Jaguar distribución map in Mexico	Country/ Mexico	Ecological Niche Modeling	310,557 km^2	Rodríguez-Soto et al. (2011)
4	Jaguar corridors Mexico	Country/ Mexico	Least Cost Path Analysis	415,197 km^2	Rodríguez-Soto et al. (2013)
5	Map of jaguar records and corridors in Sonora	Regional/ North Pacific	Expert opinion	24,693 km^2	
6	Biological corridors for jaguars in Central Pacific (Nayarit to Michoacán states)	Regional/ Central Pacific	Expert opinion	18,289 km^2	
7	Biological corridors for jaguars in Central Pacific (Sinaloa to Michoacán states)	Regional/ Central Pacific	Expert opinion and Least Cost Path Analysis	18,329 km^2	
8	Map of jaguar records and corridors in Guerrero	Regional/ South Pacific	Expert opinion	22,752 km^2	
9	Map of jaguar corridors in Oaxaca	Regional/ South Pacific	Expert opinion	44,704 km^2	Huerta (2016)
10	Habitats and corridors for jaguars in the Southern Mayan Forest	Regional/ South Pacific	Step Functions Models and Circuit Theory	5,412 km^2	de la Torre et al. (2017b)
11	Map of jaguar conservation units and corridors for the Yucatan Peninsula	Regional/ Yucatan Peninsula	Expert opinion	7,830 km^2	
12	Ecological Corridors in the Sierra Madre Oriental	Regional/ North East	Expert opinion and Least Cost Path analysis	41,480 km^2	Cuevas -Fernandez (2013), Dueñas-López et al. (2015)

"model training" group and the remaining 20% comprised a "model testing" group for validation. We evaluated the performance of our model by calculating the area under the receiver operating characteristic (ROC) curve using the 139 points of presence (20% of the filtered records) for model validation.

We used three groups of predictor landscape variables in our habitat suitability model assuming that these would be important to determine jaguar habitat across the country (Table 3). For all these variables we generated raster layers of 1 km^2 cell size. Given that our model was generated to evaluate the JCUs for jaguars across the country, we identified the optimal threshold at which to discriminate our habitat suitability model by calculating the Receiver Operating Characteristic (ROC) (Pearce and Ferrier 2000). We implemented the ROC analysis using the package "pROC" (Robin et al. 2013) from R 3.1.1 (R Core Team 2016). We converted the raster data set of our habitat suitability model into polygons using the ArcGIS10.2 (ESRI, Redlands, California, USA), to calculated the surface and the center of each polygon. We classified the polygons identified by our model as JCUs within the JGRs to those areas large enough to support a potential population of jaguars of at least 15 individuals using a similar criterion than Rodríguez-Soto et al. (2011):

$$[(MMHR * n\,Males) + MFHR * n\,Females/2]$$

where MMHR is the mean male home range and MFHR is the mean female home range. Under the assumptions that sex ratio is of at least one male every two females home ranges, considering 5 males and 10 females and an average home range of 180 km^2 for females and of 430 km^2 for males (de la Torre et al. 2017b), and a complete overlap of home range of one male with the two females and no overlapping home ranges between the females. Using these criteria, we assume that the smallest continuous area with suitable habitat to maintain a population of at least 15 jaguars in Mexico would be around 1,975 km^2. This criterion is very conservative and was used only with the aim of identifying the largest patches with suitable habitat for jaguars within the Jaguar Geographic Regions.

Then, we overlaid all the layers with primary and secondary vegetation with the JCUs to estimate the area covered with forest within these areas. For this, we used vegetation and land cover layer 1:250,000 from National Institute of Statistic and Geography (INEGI 2015). Finally, with the aim of evaluating the importance of the natural protected areas for the long-term conservation of the JCUs, we estimated the percentage of the JCUs which are protected by Federal, State Protected, and AVDC protected areas.

Compilation of jaguar range and corridors models

In order to evaluate jaguar range and potential corridors in Mexico, we compiled in a Geographic Information System seven different jaguar range maps and/or proposals to maintain the connectivity across jaguar populations in this country (Fig. 1). These maps included analyses constructed by other jaguar scientists and specialists using diverse methodologies and approaches (Table 4). The compiled information included models of connectivity across jaguar populations both at country and regional scales. Jaguar range and corridors compilation included maps constructed by expert criterion opinion only (Sanderson et al. 2002). This criterion combined with resistance surfaces was implemented with least-cost path analysis for evaluating the connectivity (Rabinowitz and Zeller 2010), presence points and resistance surfaces to implement a least-cost path analysis (Rodríguez-Soto et al. 2013), and probabilistic models based in the movement patterns of jaguar tracked using GPS telemetry (see de la Torre et al. 2017c; Morato et al. 2018) (Table 4).

Biological corridors to maintain the connectivity among Jaguar Conservation Units

We integrated our habitat suitability model with Least Cost Path and Circuit Theory to identify the critical areas to maintain the functional connectivity across JCUs. We used the inverse of our habitat suitability model to generate a resistance surface to model the connectivity using Least Cost Path and Circuit Theory methods (Zeller et al. 2018). With the Least Cost Path method we estimate the cost-effective distances between JCUs and estimate the shortest distance between two JCUs while considering the resistance to movement (Adriaensen et al. 2003). With Circuit theory, we estimate the current density which is a proxy for the probability of a random walker (i.e. a stochastic process describing a path conformed by a succession of random steps on some mathematical space) moving between patches found within any pixel (MacRae 2008). We calculated and mosaicked the cost-weighted distance surfaces to build a single network of links across the focal habitat patches. Then we estimated effective resistances and current flow centrality for focal habitat patches and corridors. Current flow centrality analysis evaluates the importance of patches and links using a graph theoretic approach by ranking their contribution to facilitating connectivity across a network of JCUs (Carrol et al. 2012). All connectivity analyses were conducted in Linkage Mapper and Circuitscape 4.0.

Results

Jaguar geographic regions

The current jaguar distribution in Mexico is about 556,000 km^2, which represents a little more than a quarter of the total extension of Mexican territory. In

Table 5 Variable contribution to the habitat suitability model performed in Maxent for jaguar in Mexico

Variable	Percent of contribution	Permutation importance	Effect
Elevation	26	42.2	–
Arid vegetation	23.5	15.6	–
Crops	9.6	1.4	–
Tropical forests	8.1	2.3	+
Grasslands	6.7	5.2	–
Slope	6.2	13	+
Flooded vegetation	6	1.5	+
Distance to urban areas	5	8.5	+
Density of towns	3.8	4.7	–
Secondary vegetation	2	1.8	+
Distance to roads	1.2	1.5	+
Other forest	0.9	1.6	+
Dry forests	0.9	0.7	+

that geographic range, we identified the following five JGRs as described in detail below: (1) *North Pacific region,* which includes Sinaloa, Sonora, Chihuahua and Durango states; (2) *Central Pacific region*, which includes Nayarit, Jalisco, Colima, Michoacán, and Estado de México states; (3) *South Pacific region*, that includes Chiapas, Oaxaca, Guerrero, Tabasco, southern Veracruz, Puebla and Morelos states; (4) *Yucatan Peninsula region*, formed by Campeche, Quintana Roo and Yucatan states; and (5) *Northeast region*, which includes Nuevo León, Coahuila, Tamaulipas, San Luis Potosí, Guanajuato, Querétaro, Hidalgo, Puebla and northernVeracruz states (Fig. 2). The JGRs include a great variety of tropical and subtropical ecosystems (i.e., tropical forests, dry forests), temperate forest (i.e., pine, oak), cloud forests, arid vegetation, mangroves and other flooded vegetation as well as, areas covered for agricultural purposes.

According to our estimates, the area that is protected within the JGRs is around 21% (~ 121,722 km^2). Those protected areas are the strongholds of the species conservation in Mexico (Fig. 2). There were 88 Federal Natural Protected Areas which are located within the JGRs, and these cover an approximate area of ~ 99,200 km^2 (Fig. 2). There were an additional 81 State Natural Protected Areas and 257 private protected areas included in the Jaguar Geographic Regions which cover around ~ 19,491 km^2 and ~ 3,031 km^2, respectively. The rest of the jaguar range in Mexico is not protected under any conservation category.

Jaguar conservation units

Our habitat suitability model showed that the presence of the jaguar in Mexico is mainly associated with areas covered by tropical, dry and other forests and flooded vegetation, with strong avoidance for arid vegetation, high elevation ranges, grasslands, and areas impacted by human activities (Table 5). The areas identified by our model as high suitability habitat includes the coastal areas from Tamaulipas and Sonora in the north of the country, to the Yucatan Peninsula and Chiapas in the south. Our model also identified the foothilss of both the Sierra Madre Oriental and Occidental, and the Balsas basin river as important areas for jaguars in Mexico.

The AUC value, as a measure of model performance, gave a reasonably value of 0.82 (± 0.72, 0.85) for true positives and 0.24 (± 0.18, 0.34) for false positives, which indicated a good discrimination at a probability threshold of occurrence of 0.40 (± 0.29, 0.42) for our habitat suitability model. Suitable habitat for jaguars encompassed approximately ~ 302,000 km^2 within the network of the JGRs (the upper 0.40 probability of occurrence), which represents ~ 15% of the country. We identified 10 JCUs larger than 1,975 km^2, which are essential habitat patches for jaguar's populations in Mexico (Fig. 3). These JCUs

Table 6 Jaguar Conservation Units and their extension protected ranked according their values of core centrality

Jaguar conservation units	Extension (km^2)	Protected by federal natural protected areas (km^2)	Protected by state natural protected areas (km^2)	Areas voluntarily destined for conservation (km^2)	Core centrality	Rank
South Pacific	59,643	4,383	15	1,245	37.9	1
Selva Lacandona	10,777	4,806	–	40	18.9	2
Coast of Colima	2,379	–	–		18.0	3
Central Pacific	41,289	8,871	690	8	17.3	4
Sierra Madre Oriental	7,504	683	1,093	–	17.0	5
Sierra Madre de Chiapas	4,162	2,974	104	5	15.2	6
Pantanos de Centla-Laguna de Términos	10,056	6,108	8	–	14.2	7
Yucatan Peninsula	71,209	17,570	7,597	73	12.0	8
North Pacific	31,910	919	559	–	9.0	9
Sierra de Tamaulipas	2,747	1,851	115	8	9.0	10
Total	241,676	48,165	10,182	1,378	–	–

encompassed an area of 241,676 km^2 and were distributed across the five JGRs (Table 6).

According with our analysis, not all the extension that covers the protected areas within the JGRs was considered as JCUs. The total extension of JCUs which is formally protected is 59,725 km^2, which represents 24.2% of the total area covered by the JCUs. Federal Natural Protected Areas cover approximately 48,165 km^2 (19.6%) of the Jaguar Conservation Units, and the State Natural Protected Areas and AVDC cover $\sim$ 10,182 km^2 (4.1%) and 1,378 km^2 (0.5%), respectively (Table 6). Agreeing to current-flow centrality scores, the most important Jaguar Conservation Units to maintain the network connectivity are the South Pacific, Selva Lacandona, Coast of Colima and Central Pacific Priority Areas (Table 6). These Jaguar Conservation Units are important because of their role maintaining the whole connectivity network for jaguars in Mexico (Table 6).

Biological corridors

We identified 13 critical biological corridors to maintain the connectivity between Jaguar Conservation Units in Mexico using Least Cost Path and circuit theory analyses (Fig. 4). The five most important cost-weighted corridors identified were Coast of Colima-South Pacific, Sierra Madre Oriental-South Pacific, South Pacific-Sierra Madre de Chiapas, Central Pacific-Coast of Colima, and North Pacific-Central Pacific (Table 7). The corridors that link the Coast of Colima with the Central and South Pacific regions are crucial to maintain the connectivity of jaguar populations in the Sierra Madre Occidental. The corridor that connect the Sierra Madre Oriental with the South Pacific region is the largest area within the Jaguar Geographic Regions where occurs a great distance between two Jaguar Conservation Units without any other patch of habitat larger than 1,975 km^2, which could act as stepping stone. This corridor is priority to maintain the connectivity of the populations of jaguars in the Sierra Madre Oriental. The link between the North Pacific and Central Pacific is critical to maintain the connectivity of the northern most jaguar population with the southern populations in Mexico. The South Pacific-Sierra Madre de Chiapas link allows the connectivity between the Sierra Madre Occidental with the southern for jaguars across Mexico.

Our results also suggest that connectivity is compromised in several of the theoretical corridors identified. Circuit theory analysis, through visual inspection of the current density map, suggests that

Fig. 2 Federal, state, and private protected areas with recent jaguar records in the Jaguar Geographic Regions in Mexico. Many of the state and private protected areas are too small to be visible at the scale of the map. The Jaguar Geographic Regions are: 1) North Pacific; 2) Central Pacific; 3) South Pacific; 4) Yucatan Peninsula; 5) North East.

connectivity for jaguars would be more restricted for links in the Sierra Madre Occidental-South Pacific, Central Pacific-South Pacific, Coast of Colima-Central Pacific, South Pacific-Selva Lacandona, and Selva Lacandona-Sierra Madre de Chiapas, Yucatan Peninsula-Selva Lacandona (Fig. 4).

Discussion

In this study, we defined the Jaguar Geographic Regions to establish a spatial explicit framework to conserve the species at the country level. We also identified the Jaguar Conservation Units which are those areas that maintain large extensions of adequate habitat for prey and biodiversity. And we identified the critical areas or biological corridors to maintain the habitat connectivity in JGRs and JCUs. This information should be used by the decision makers at Mexican Federal Government level as guidelines to reduce habitat loss and fragmentation of the sensitive areas to maintain jaguars in Mexico. Such public jaguar conservation policies should include consolidating established protected areas, creation of new protected areas, and the implementation of strategies and actions such as the payment of environmental services and sustainable development projects to stimulate the conservation of jaguar habitat in private lands to maintain connectivity between jaguar populations at regional scale.

Although, previous exercises have been carried on evaluating jaguar range distribution and connectivity across Mexico (Rabinowitz and Zeller 2010; Rodríguez-Soto et al. 2013), our approach is innovative because we are defining the JGRs across Mexico to promote the conservation of the remaining populations of jaguar under several conservation and integrated landscape management schemes. The JGRs would be critical to propose and design new protected areas, implement sustainable development programs, and putting into practice pilot programs to mitigate both jaguar-cattle conflict and infrastructure development. The advantages of our approach were the integration of the information of spatial corridors and maps of jaguar range. Our effort was carried out with the collaborative work of several national experts from academic institutions and local and international Non-Governmental Organizations. Additionally, we incorporated in this analysis all information of jaguar records collected by the authors and compiled in other sources. This approach allowed us to model a more precise and current estimation of the jaguar range-size in Mexico, and to define the most critical areas to protect the species' habitat and to maintain the connectivity between suitable habitat patches at a country scale.

Our results can be used to guide the policy actions that should be implemented in each JGRs. For example, most of the land of the natural protected areas and the JGRs belong to peasants (i.e., ejidos),

Fig. 3 Jaguar Conservation Units (JCUs) in Mexico. These polygons encompassed 241,676 km^2 and are distributed across the five JGRs. The 10 JCUs for conservation are the following ones: (1) Sierra Madre- North Pacific (31,910 km^2); (2) Sinaloa-Central Pacific (41,289 km^2); (3) Coast of Colima (2,379 km^2); (4) Sierra Madre-South Pacific (Guerrero Oaxaca; 59,643 km^2); (5) Sierra Madre de Chiapas (4,162 km^2); (6) Selva Lacandona (10,777 km^2); (7) Yucatan Peninsula (71,209 km^2); (8) Pantanos de Centla-Laguna de Términos (10,056 km^2); (9) Sierra Madre Oriental (7,504 km^2); (10) Sierra de Tamaulipas (2,747 km^2).

indigenous communities, and private properties. Such land tenure makes the conservation and management of the natural protected areas and corridors very complex. Paradoxically, many of those well- conserved lands are in remote regions with high poverty levels. For example, 82% of the South Pacific region is owned by the local communities (i.e., ejidos and indigenous communities) in poverty levels (52%). This makes imperative that the public policies to conserve jaguars and their habitat in such regions, should take into consideration both the needs for jaguar conservation and the promotion of sustainable local economic activities. Changes in husbandry practices to reduce the risk of predation by jaguars and to increase livestock productivity, sustainable logging practices to maintain jaguar habitat and corridors (Tobler et al. 2018; de la Torre et al. 2021), and payment of environmental services to maintain jaguar habitat should be implemented (Ceballos et al. 2018). But, the North Pacific region is completely different in this context, because around half of the territory is private property and the extreme poverty indicator is around 25%.

The JGRs cover approximately 25% of the country but only ~ 21% of this extension is protected by some scheme of protected areas. The extension of ~ 556,000 km^2 that cover the JGRs has the potential to hold more individuals than the estimated jaguar population of roughly 4,800 individuals for Mexico (Ceballos et al. in review). However, considering the extension that is formally protected within the JGRs and the total population estimated for the country, we speculate that around ~ 1,500 jaguars are found within the protected areas. Furthermore, only 24.2% of the JCUs is formally included in protected areas, evidencing the need of increasing the protected areas across the jaguar´s range and core habitat in Mexico. Natural Protected Areas are one of the most robust strategies of conservation in Mexico to ENSURE FOR maintain the biological diversity and endangered species, though most of the extension of the jaguar range is not protected in long term. Within the network of identified JGRs there are 426 natural protected areas of different levels of protection; i.e. Federal, State, Voluntary Protected Areas (private protected areas hereafter), which cover ~ 3.6% of the Mexican territory. All these areas have a relevant role in protecting jaguar habitat, but only a few of them cover enough land to maintain large populations of this species. For example, within five JGRs where the

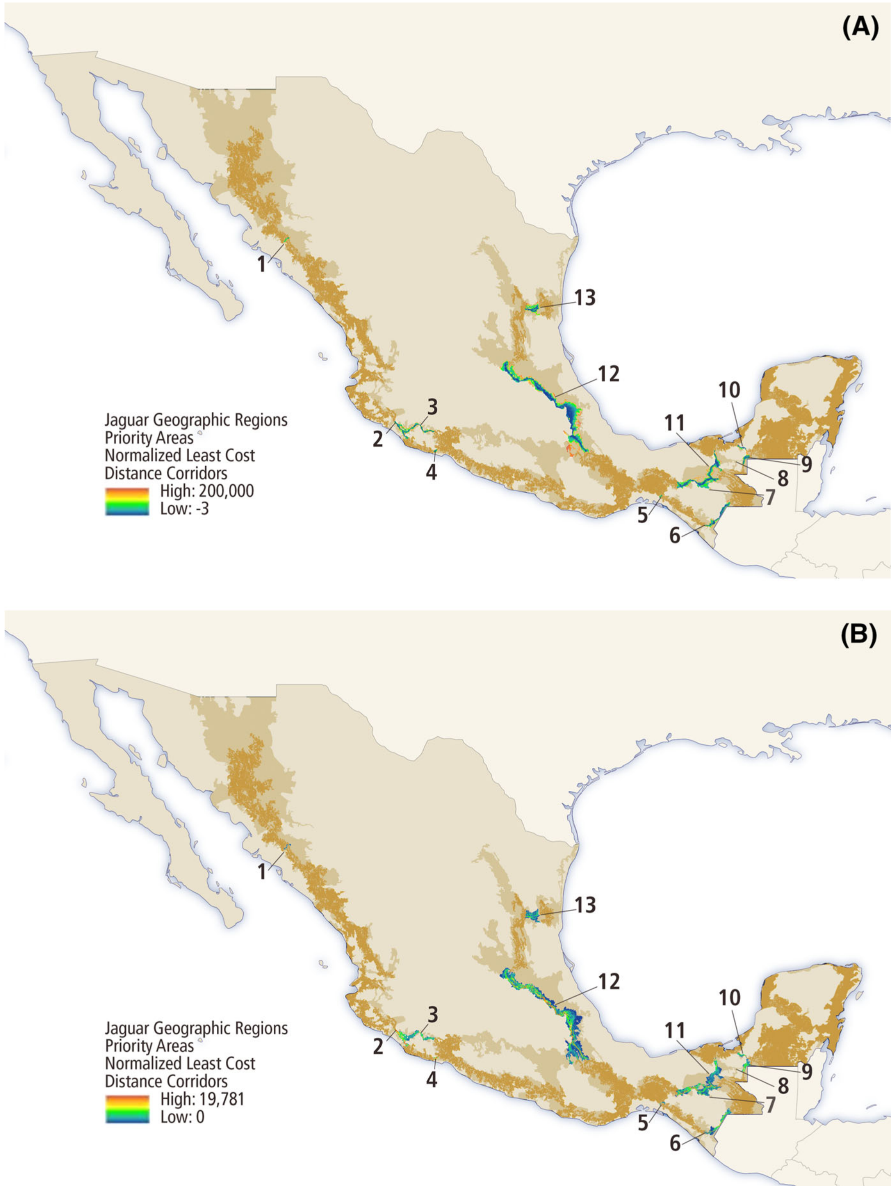

Fig. 4 Habitat patches and connectivity areas to maintain linked all jaguar populations in Mexico identified according our (A) Least Cost Path analysis (low resistance in blue higher resistance in red) and (B) Circuit theory analysis (low current in blue, higher current in red). Critical biological corridors are: (1) North Pacific-Central Pacific; (2) Central Pacific-Coast of Colima; (3) Central Pacific-South Pacific; (4) Coast of Colima-South Pacific; (5) South Pacific-Sierra Madre de Chiapas; (6) Selva Lacandona-Sierra de Chiapas; (7) Selva Lacandona-South Pacific; (8) Pantanos de Centla-Laguna de Términos-Selva Lacandona; (9) Yucatan Peninsula-Selva Lacandona; (10) Pantanos de Centla-Laguna de Términos-Yucatan Peninsula; (11) Pantanos de Centla-Laguna de Términos-South Pacific; (12) Sierra Madre Oriental-South Pacific; (13) Sierra de Tamaulipas-Sierra Madre Oriental.

jaguar is distributed there are 42 important natural protected areas (Table 8) with potential to conserve larger populations, such as: (a) *Calakmul region:* comprises the Calakmul, Bala'an K'aax, Balam Kin and Balam-Kú natural protected areas; (b) *Selva Lacandona region*, which includes Montes Azules, Lacantún, Chankin, Bonampak, Yaxchilan, Naha and Metzabok; (c) *Sian ka'an region*, that comprises the Sian ka´an, Uaymil, and the Manatee Sanctuary Bahia de Chetumal natural protected areas; (d) *Laguna de Términos region*, which includes the Pantanos de Centla and Laguna de Términos natural protected areas. It is essential to actively promote the creation of new networks of protected areas across the jaguar geographic range large enough to ensure the protection of jaguars in regions such as Guerrero and Oaxaca (South Pacific region) where most of the jaguar habitat across the Sierra Madre Occidental is completely unprotected.

The JGRs network and the results of our suitability habitat model indicate that current jaguar range in Mexico still includes a vast area from Sonora to

Table 7 Potential critical connectivity zones between Jaguar Conservation Units (JCUs) according to their centrality value. Corridors were identified using Least Cost Path and Circuit Theory analysis, which connect the 10 JCUs to conserve the jaguars in Mexico

From JCUs	To JCUs	Euclidean distance (mts)	Least Cost Distance	Cost Weighted Distance to Path	Effective resistance	Centrality	Rank
Coast of Colima	South Pacific	9,911	498,991.0	31.5	1,444,745.4	16.3	1
Sierra Madre Oriental	South Pacific	324,461	2,382,672.8	3.9	1,581,689.0	16.0	2
South Pacific	Sierra Madre de Chiapas	1,176	74,009.5	44.5	110,952.9	14.0	3
Central Pacific	Coast of Colima	72,175	314,3594.0	33.4	12,750,284.8	10.7	4
North Pacific	Central Pacific	1,176	71,514.8	43.0	85,574.8	9.0	5
Sierra de Tamaulipas	Sierra Madre Oriental	43,083	762,536.1	12.2	568,306.9	9.0	6
Selva Lacandona	South Pacific	157,717	1,811,045.5	7.9	2,276,766.9	8.5	7
Pantanos de Centla-Laguna de Términos	Yucatan Peninsula	28,981	656,635.9	15.8	2,110,352.9	7.8	8
Selva Lacandona	Sierra Madre de Chiapas	132,142	2,047,086.3	12.0	51,25,637.5	7.4	9
Yucatan Peninsula	Selva Lacandona	40,673	1,403,565.8	26.0	2,732,166.1	7.3	10
Pantanos de Centla-Laguna de Términos	South Pacific	140,312	3,691,420.3	11.1	65,71,666.2	6.0	11
Central Pacific	South Pacific	154,882	6,552,456.0	30.0	23,752,799.2	6.0	12
Pantanos de Centla-Laguna de Términos	Selva Lacandona	69,975	1,682,736.3	16.8	4,961,346.0	5.7	13

Chiapas along the Pacific lowlands and the foothills of Sierra Madre Occidental and Sierra Madre del Sur; and from Tamaulipas to Tabasco along the Gulf of Mexico lowlands and the foothills of the Sierra Madre Oriental; and the Yucatan Peninsula. In the south important areas for jaguar conservation include the Selva Lacandona, region and all the Yucatan Peninsula. Our results of habitat suitability model are consistent with previous efforts to evaluate jaguar range in Mexico (Rodríguez-Soto et al. 2011; Chávez et al. 2016; de la Torre et al. 2017a), and indicate that jaguar avoids arid vegetation, grasslands, crops and high elevation ranges (Rodríguez-Soto et al. 2011; de la Torre et al. 2017c). However, jaguar habitat in Mexico includes a high diversity of habitat types such as tropical rainforests, dry forests, oak and pine forests, cloud forests, flooded vegetation known as "petenes" and "tulares", mangroves and arid shrubs (Leopold 1959; Rodríguez-Soto et al. 2011; Chávez et al. 2016), therefore illustrating the ecological flexibility of the species for adapting to several environments (Sanderson et al. 2002).

Our habitat suitability model revealed 10 JCUs which should be the core of the species conservation in Mexico. The Yucatan Peninsula represents the largest area with habitat availability for jaguars with the higher densities estimated for the species in Mexico (Ceballos et al. 2016; Chávez et al. 2016). Overall, other regions that present large extents of jaguar habitat are the South Pacific region, which includes the Sierra Madre in Guerrero and the Chimalapas in Oaxaca, the Central Pacific region which includes Nayarit and Sinaloa states across the Sierra Madre, and the North Pacific region which covers the north section of Sinaloa and Sonora. The Selva Lacandona, Pantanos de Centla-Laguna de Términos region and Sierra de Tamaulipas region maintain large extensions for jaguars in Mexico, as well. Conservation efforts should be allocated to these areas to improve the

Table 8 Larger natural protected areas within Jaguar Geographic Regions

Jaguar geographic regions	Natural protected areas (km^2)
North Pacific	Reserva Especial de la Biosfera Cajón del Diablo, Sonora (1,470 km^2)
	Área de Protección de Flora y Fauna Bavispe, Sonora (2,000 km^2)
	Área de Protección de Flora y Fauna Sierra de Álamos—Río Cuchujaqui, Sonora (928,89 km^2)
	Área de Protección de Flora y Fauna Meseta de Cacaxtla, Sinaloa (508,62 km^2)
Central Pacific	Reserva de la Biosfera Manantlán, Jalisco y Colima (1,395.77 km^2)
	Reserva de la Biosfera Chamela-Cuixmala, Jalisco (131.41 km^2)
	Reserva de la Biosfera Zicuirán-Infiernillo, Michoacán (2,651.17 km^2)
	Reserva de la Biosfera Marismas Nacionales, Nayarit (1,338.54 km^2)
South Pacific	Reserva de la Biosfera Selva El Ocote, Chiapas (1,012.88 km^2)
	Reserva de la Biosfera La Sepultura, Chiapas (1,673.09 km^2)
	Reserva de la Biosfera La Encrucijada, Chiapas (1,448.68 km^2)
	Reserva de la Biosfera Montes Azules, Chiapas (3,312.00 km^2)
	Reserva de la Biosfera El Triunfo, Chiapas (1,191.77 km^2)
	Monumento Natural Bonampak, Chiapas (43.57 km^2)
	Monumento Natural Yaxchilán, Chiapas (26.21 km^2)
	Área de Protección de Flora y Fauna Chan-kin, Chiapas (121.84 km^2)
	Reserva de la Biosfera Lacantún, Chiapas (618.73 km^2)
	Área de Protección de Flora y Fauna Cañón del Usumacinta, Tabasco (461.28 km^2)
	Reserva de la Biosfera Huautla, Morelos (590.30 km^2)
Yucatan Peninsula	Área de Protección de Flora y Fauna Uaymil, Quintana Roo (891.18 km^2)
	Reserva Ecológica El Edén, Quintana Roo (30.74 km^2)
	Área de Protección de Flora y Fauna Laguna de Términos, Tabasco y Campeche (7,061.47 km^2)
	Reserva de la Biosfera Los Petenes, Campeche (2,828.57 km^2)
	Reserva de la Biosfera Ría Celestún, Campeche y Yucatán (814.82 km^2)
	Reserva de la Biosfera Calakmul, Campeche (7,231.85 km^2)
	Zona Sujeta a Conservación Ecológica Balam-Kú, Campeche (4,092.00 km^2)
	Zona Sujeta a Conservación Ecológica Balam-Kin, Campeche (1,109.90 km^2)
	Reserva de la Biosfera Sian Ka'an, Quintana Roo (5,281.47 km^2)
	Reserva de la Biosfera Bala'an k'aax, Quintana Roo, Yucatán y Campeche (1,283.90 km^2)
	Área de Protección de Flora y Fauna Yum Balam, Yucatán (1,540.52 km^2)
	Reserva de la Biosfera Ría Lagartos, Yucatán (603.47 km^2)
	Reserva Estatal Dzilam, Yucatán (690.39 km^2)
	Reserva El Zapotal, Yucatán (23.00 km^2)
	Reserva Estatal Biocultural del Puuc, Yucatán (1,358.49 km^2)
	Reserva Estatal Ciénegas y Manglares de la Costa Norte de Yucatán (547.77 km^2)
North East	Reserva de la Biosfera Sierra de Tamaulipas, Tamaulipas (3,088.88 km^2)
	Reserva de la Biosfera Sierra del Abra Tanchipa, San Luis Potosí (214.64 km^2)
	Reserva de la Biosfera El Cielo, Tamaulipas (1,445.30 km^2)
	Reserva de la Biosfera Sierra Gorda, Querétaro (3,835.67 km^2)
	Reserva de la Biosfera Sierra Gorda, Guanajuato (2,368.82 km^2)
	Reserva de la Biosfera Tehuacán-Cuicatlán, Puebla y Oaxaca (4,901.86 km^2)
	Parque Nacional Los Mármoles, Hidalgo (231.53 km^2)

conservation of jaguar under the Natural Protected Areas and other conservation schemes.

We proposed 13 critical areas or biological corridors to maintain the connectivity between the JCUs of the JGRs. The most critical area is the one that maintains the connectivity between the South Pacific with the Sierra of Tamaulipas. Jaguar habitat in this critical area is limited because is mostly desforested and fragmented, with many rural communities (Dueñas-López et al. 2015). One initiative that would help to maintain the connectivity across this critical area is the Ecological Corridor of the Sierra Madre Oriental CESMO, which is an initiative of the Mexican Federal Government and the German Development Cooperation Agency that will invest in sustainable and economic development to contribute to conserving the natural ecosystems of this area (Cuevas-Fernandez 2013). This Ecological corridor comprises $\sim$ 40,000 km^2 in 273 municipalities of the Sierra Madre Oriental between San Luis Potosí, Hidalgo, Querétaro, Puebla, and Veracruz states. Another critical core area for connectivity is between the Selva Lacandona and the South Pacific region through the north section of the state of Chiapas. This region includes several mountain ranges and maintains large amounts of secondary vegetation, but it's extremely populated by indigenous communities. The functionality of this critical area as corridor should be questioned because jaguar presence in the region has not been recorded at least in the last 25 years. The critical area that links Yucatan Peninsula with the Pantanos de Centla-Laguna de Términos region is also essential to maintain the integrity of jaguar population in the south of Mexico, and previous studies have shown that the connectivity through this area is reliable (Hidalgo-Mihart et al. 2018). One priority in the future should be evaluate the functionality of all 13 critical areas to maintain the connectivity (theorical corridors) between the Jaguar Conservation Units through ground verification of jaguar presence in these areas or probabilistic models based in the movement patterns of jaguar tracked using GPS telemetry (de la Torre et al. 2017c). On the other hand, future studies should be aim to better understanding the distribution pattern of the species across this corridor and evaluates the feasibility that allows the functional connectivity between Jaguar Conservation Units. Previously, a study by the NGO Panthera proposed a corridor through the Mexican Central Altiplano to connect the jaguar populations of the Sierra Madre Occidental with those with Sierra Madre Oriental (Fig. 1, Rabinowitz and Zeller 2010). However, this corridor for jaguars is not reliable because the species has not been recorded within that region in at least historic times and because the feasibility to implement conservation actions to maintain the connectivity between the jaguar populations through corridor is unrealizable.

Conservation and management implications

In this study, we introduced a spatial explicit proposal for both planning the conservation of the jaguar habitat and maintain connectivity among jaguar populations across Mexico. This information should be incorporated in the conservation and development planning by agencies such as the National Commission of Protected Areas (CONANP), the National Commission for Knowledge and Use of Biodiversity (CONABIO-Mexico), the National Forestry Commission (CONAFOR), the Secretariat of Agriculture and Rural Development (SEDAR), the National Water Commission (CONAGUA), the Secretariat of Economy (SE), the Secretary of Tourism (ST), and the Secretariat of Communication and Transportation (SCT). This will promote cross-cutting public policies that includes mechanisms for community participation for ensuring the conservation of jaguar habitat and populations in Mexico. It is fundamental to continue updating the national jaguar conservation program of the National Alliance for Jaguar Conservation and to permeate that information in all sectors involved in the jaguar conservation. The efforts to promote sustainable development programs aimed at local communities that share their territory with jaguars need to be increased. Since most area covered by the Jaguar Geographic Regions is not covered by Natural Protected Areas ($\sim$ 79%), it's critical to establish new protected areas and promote other schemes such as payment of ecosystem services to incentive the conservation of jaguars, biological diversity, land, and ecosystem services with the landowners of the crucial areas for jaguars in Mexico.

Federal Natural Protected Areas are administered by the National Commission of Protected Areas (CONANP-Mexico) and proposals for new protected areas within the Jaguar Geographic Regions are in course by that agency. First, it is necessary to consolidate the management and protection with appropriate funds, personnel, and infrastructure of the protected areas with populations of jaguars such as the biosphere reserves of Calakmul in the state of Campeche and the Montes Azules in the state of Chiapas. Second, several protected areas have been proposed and efforst to establish them must continue. For example, the Jaguar del Norte flora and fauna protection area ($\sim$ 199 km^2) in Sonora, and Monte Mojino flora and fauna protection area (2,012 km^2) in Sinaloa have been proposed in the North Pacific Jaguar Geographic Region. The Uxpanapa Biosphere Reserve in Veracruz ($\sim$ 3,333 km^2) has been proposed in the South Pacific region; and the Geohidrological Corridor reserve in Quintana Roo (4,490 km^2), and the enlargement of the Calakmul biosphere reserve have been proposed in the Yucatan Peninsula Jaguar Geographic Region. Finally, The Sierra la Silleta Biosphere Reserve in San Luis Potosí ($\sim$ 131 km^2) has been proposed in the North East Jaguar Geographic Region.

The payment for ecosystem services is another conservation scheme used by the Mexican Federal Government that provides economic compensation to local communities for conserving their land with natural forests, and this program is administered by the National Commission of Forestry (CONAFOR-Mexico). Since jaguar habitat is decreasing by habitat transformation and fragmentation across Mexico, Payment for Ecosystem Services can be used to help maintain existing habitat and to support local conservation efforts. We suggest allocating Payment for Ecosystem Services or other similar conservation tools specifically to communities that maintain jaguar habitat or critical areas of connectivity, with a specific spatial focus between core areas and biological corridors. The payment for ecosystem services has been successfully used to protect critical habitat and corridors for jaguars in southern Mexico (de la Torre et al. 2017c). Through this economic incentive, local communities can also be encouraged to implement productive activities compatible with forest conservation. This can be the surveillance of poaching of jaguars and their potential prey species as well as, the implementation of sustainable practices to halt the deforestation and/or mitigation methods to reduce human-carnivore conflict associated with depredation on livestock and domestic pets. Moreover, in areas with high deforestation and poor connectivity, the payment for ecosystem services can be oriented for aiding reforestation and maintain natural vegetation for corridors.

Other critical priorities include the following ones: i) the promotion of a "zero" unplanned deforestation policy within the Jaguar Geographic Regions; ii) establish in the Mexican environmental legislation the concept of "biological corridor" as a type of Natural Protected Area; iii) establish conservation schemes on riparian zones; iv) ecological restoration programs where jaguar populations occur; and v) create a program within the Secretariat of Communication and Transport to diminish the impact of the roads and construct wilflife crossings in core areas and critical zones to maintain biological connectivity. Additionally, we stronlgy suggest that the impact on jaguar habitat connectivity of existing and newpaved roads or other infrastructure within the Jaguar Conservation Units has to be carefully evaluated. Mitigation measures should include the identification and construction of wildlife underpasses and overpasses, the designation of specific habitat corridors, and the establishment or consolidation of protected areas. Despite the massive reduction in the jaguar habitat in Mexico, there is still have time to implement pertinent conservation actions to ensure a viable population of this species in the country. This will be only possible to achive thourgh implementin a Natonal Jaguar Conservation Strategy, such as the one proposed by the National Alliance for Jaguar Conservatoon. The strategy should be implemented by the federal and states governments, academic institutions, NGO's, priivate sector, civil society, and most importantly, by the land owners. The jaguar censuses indicating the increase of the population from 4,000 to 4,800 in 8 years (Ceballos et al. in review) is an actual proof that conservation can be successful. Time is running out but it still possible to save jaguars and most species. Their long-term survival of jaguars and most of biodiversity depends on our conservation actions in the next 15 to 20 years. By saving them we are saving, paradoxically, ourselves.

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