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Connectivity of priority areas for the conservation of large carnivores in northern Mexico

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A R T I C L E I N F O

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A B S T R A C T

The loss and fragmentation of habitat has negative effects on populations of large carnivores, but ecological corridors that allow dispersal of individuals among habitat remnants mitigate these effects. Our objectives were to identify 1) priority areas for the conservation of three species of large carnivores in northern Mexico, 2) the corridors that can maintain connectivity between them, and 3) pinch points signifying habitat loss that threatens connectivity. We generated species distribution models using MaxEnt and GLM to obtain a consensus model for each species. We applied an inverse function to the probability gradient of the consensus models to calculate the resistance and identify the corridors between priority areas. With Linkage Mapper software, we generated the corridors, calculated their centrality and that of the priority areas, and identified the areas where the corridors are narrower (i.e., pinch points). Finally, we identified the main anthropic fragmentation elements in the most important corridors. We identified 6 priority areas for jaguar, 20 for puma and 21 for black bear, with 5 corridors for jaguar, 22 for puma and 29 for black bear. The pinch points were produced by agricultural fields, human settlements, roads, or combinations of these factors. Depending on the element of fragmentation in each corridor, we propose specific strategies at the pinch points, e.g., applying restoration programs, including wildlife crossings to mitigate road killed cases, promoting payment programs for environmental services or compensation in cases of conflict, to increase the support of local inhabitants for conservation.

1. Introduction

Habitat loss and fragmentation are two main threats to biodiversity (Crooks et al., 2017; Wilson et al., 2016). Isolation of habitat patches reduces their ecological functionality, limits interchange of individuals, reduces gene flow and increases the risk of species extinction (Goossens et al., 2016; Kutschera et al., 2016). To mitigate the effects of fragmentation, it is important to preserve connectivity between populations that have been isolated (Correa-Ayram et al., 2016; Zanin et al., 2016). For this, it is necessary to identify core habitat areas, ecological corridors connecting these core areas, and other landscape elements such as "stepping stones" (Di Minin et al., 2016; Monroy-Vilchis et al., 2019; Rodríguez-Soto et al., 2013).

There are different challenges to assessing the connectivity between patches of habitat, since the distribution of species, the resistance exerted by the landscape and the dispersal capacity of organisms is unknown in some cases (Cushman et al., 2013). The implementation of new methods in landscape ecology has provided solutions to these challenges (Correa-Ayram et al., 2016; McRae et al., 2008). Connectivity analysis has used different theories and algorithms such as circuit theory and graph theory, however, the least-cost route has been applied more frequently (Correa-Ayram et al., 2016; McRae et al., 2008, 2012).

There are several connectivity studies focused on the order Carnivora (Correa-Ayram et al., 2016; Dickson et al., 2019). Being top predators, large mammalian carnivores are considered key species and play an important role in the regulation of ecological interactions (Atkins et al., 2019; Di Minin et al., 2016; Ripple et al., 2014). In Mexico, carnivores are the fourth most diverse order of mammals, however, approximately

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63% are in some category of risk (SEMARNAT, 2010). Three large carnivores inhabit northern Mexico: *Panthera onca* (endangered), *Puma concolor* (no risk), and *Ursus americanus* (endangered, SEMARNAT, 2010). At an international level, only the jaguar is listed as "near threatened" (Quigley et al., 2017). Northern Mexico is an important region since it is the only one where these three species coexist. However, this area is threatened by habitat loss and fragmentation, as well as hunting, urbanization, and conflicts over agricultural activities (Zarco-González et al., 2013).

There are studies focused on identifying priority areas for jaguar conservation in Mexico (2011) as well as the ecological corridors that can keep them connected (Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2013). However, the corridors identified in these two studies have important differences, mainly in northern Mexico. Also, the study by Rabinowitz and Zeller (2010) may be biased since it was based on expert opinion. Connectivity studies of black bear habitat have been developed mainly in the United States (Gantchoff & Belan, 2017). In Mexico there are corridors that can maintain connectivity through different regions of the north of the country, even between two subpopulations that are isolated (González-Saucedo et al., 2021; Lara-Díaz et al., 2021). In the case of the puma, we only know of one study of habitat connectivity (González-Saucedo et al., 2021). They found that anthropic activities such as urbanization, road networks and the border wall with the United States can all limit the movements of this species.

Because of the attention that has recently been focused on the relevance of habitat connectivity for the conservation of wild species, and the increasing accessibility to tools for connectivity analysis, the number of studies of connectivity rapidly increased. We identified corridors while also characterized them, by analyzing factors threatening functionality. These data allow to identify specific threats or pressures, whether agricultural activities, roads, railways, or human settlements, and thus to plan actions to specifically mitigate the impacts of these elements on each corridor, increasing the probability that these actions will be effective.

Our objectives were: 1) to identify priority areas for the conservation of three species of large carnivores in northern Mexico; 2) identify the corridors that can maintain connectivity between them; and 3) identify pinch points where there could be habitat loss that threatens connectivity.

2. Methods

2.1. Study area

Eleven biogeographic provinces in northern Mexico were included (Del Cabo, Baja California, California, Sonorense, Costa del Pacífico, Sierra Madre Occidental, Altiplano Norte, Altiplano Sur, Sierra Madre Oriental, Tamaulipeca and Golfo de México). The study area was approximately 1,346,786.8 km^2, its southern limit was delimited by the Eje Neovolcánico Transversal province (1997). The predominant vegetation types are scrubland, temperate forest, and tropical deciduous forest. Altitudes vary from 0 to 3,700 m above sea level. It is a fragmented region with cities of up to 8,000 inhabitants per km^2 and a highway network of 95,674 km, with an approximate road density of 0.078 km/km^2 (Appendix A.1).

2.2. Obtaining records

Presence records of the three carnivores were obtained from three sources: 1) digital databases: National Commission for the Knowledge and Use of Biodiversity (CONABIO), Global Biodiversity Information Facility (GBIF) and INaturalist. We considered only records in these databases with the following characteristics: a) individuals reported in the wild (i.e., we excluded records of carnivores in captivity), b) records from museums and scientific collections, and b) citizen science data. For these, we considered only records with a "research grade", i.e., that were validated by at least three observers, 2) records from scientific literature if the publication mentioned the record's coordinates, and 3) records derived by camera-trapping. Camera traps were placed and georeferenced in five protected areas (Ajos-Bavispe, Sierra de Zapalinamé, Parque Nacional Cumbres de Monterrey, Maderas del Carmen and Reserva de la Biosfera "El Cielo"), during different time intervals in each zone (2009, 2012–2013 and 2014–2016).

A database was generated with date, species, type of record and coordinates, including only those from the year 2000 to 2018. To avoid spatial autocorrelation between records, we applied spatial filtering (Boria et al., 2014). Large carnivores move great distances and have large home ranges, so it is likely that two spatially close records belong to the same individual. This could result in overrepresentation in local sampling areas. Under this assumption, we considered filtering criteria using only one record within an area equal to the home range reported for each species. We eliminated the records separated by a distance less than the radius of the largest home range reported for each species in the study area: 6 km for jaguar, 5.4 km for puma (Núñez-Pérez & Miller, 2019) and 3.2 km for black bear (Espinosa-Flores et al., 2012). We used the Morans I test to determine the autocorrelation between the records, specifically to verify if the dispersion pattern changed after filtering. Records retained for each species were randomly divided into two subsets: 70% to calibrate and 30% to evaluate the models.

2.3. Variables' processing

To create the models, we included 16 important variables for distribution of carnivores (González-Saucedo et al., 2021). We selected vegetation types for their relationship with the jaguar presence (2011); topographic variables, since altitude and slope influence the presence of black bear and puma (Dickson et al., 2013; Monroy-Vilchis et al., 2016); and anthropic variables due to their effect on habitat fragmentation and human-carnivore conflicts (Lara-Díaz et al., 2021; Zarco-González et al., 2013, Appendix B.1). Distance maps were generated for categorical variables with the Euclidean distance function in ArcGis 10.4.1 (Appendix B.1). Altitude, slope, and human population density were downscaled to 500 m. Cattle density was processed to increase its resolution, as all variables were processed in raster format at a resolution of 500 m (0.25 km^2). To avoid autocorrelation, bias, and overrepresentation, we conducted Pearson correlation analysis with all variables on BioMapper V4.0.6 (Hirzel & Le Lay, 2008). When a pair of variables presented statistically significant correlation (correlation coefficient $|r| > 0.70$), the least important was eliminated and the most important variable retained.

2.4. Calibration and evaluation of the models

Two algorithms were used to create the species distribution models: Maximum Entropy (MaxEnt 3.3.4v) and Generalized Linear Models (GLMs). Using a set of environmental variables and georeferenced occurrence localities, the model expresses in each grid cell a predicted probability of presence for the target species (Phillips et al., 2006). We used MaxEnt to generate the models modifying some parameters, such as two levels of regularization: 2 and 4, (Radosavljevic & Anderson, 2014). For the feature classes we used "Hinge features" (Phillips & Dudík, 2008). However, the models generated with the default parameters produced higher Area Under Curve (AUC) values, so we maintained the parameters established by default (Phillips et al., 2006).

GLMs were created with the "sdm" package (Naimi & Araújo, 2016) in R software. GLMs represent a generalization of the classical linear regression method. We employed parametric functions to link the response variable to a combination of explanatory variables. To do this we specified an output with binomial distribution (Link = logit, Shabani et al., 2016). To calibrate GLMs and MaxEnt we generated 10,000 random background points throughout the study area.

An individual model was generated for each algorithm, by species.

Models were evaluated with the area under the curve (AUC-ROC), the difference between calibration and evaluation AUC (=AUCdiff), and omission rates (Boria et al., 2014). Two AUC values were calculated from the two subsets of records: external (AUC_{ext}, 30%) and internal (AUC_{int}, 70%, Hanley & McNeil, 1982). The models with $AUC_{ext} > 0.7$ were used to generate a consensus model using the weighted average (Marmion et al., 2009). The output of the consensus model provides values from 0 to 100, which represent the probability of species presence. Consensus models also were evaluated through AUC using the module Receiver Operating Characteristic (ROC) on the software IDRISI Selva.

2.5. Identification of priority areas

Consensus models for each species (Appendix A.2 (step 1)) were reclassified using the maximum test sum sensitivity plus specificity (maxSSS). This metric has been shown to be statistically robust to select cut-off thresholds in SDM (De Barros et al., 2012; Smith et al., 2019). The result was a binary map of areas with low or high probability presence (step 2).

We eliminated all polygons that were smaller than the home range size reported for each species. Although these polygons had suitable habitat conditions, they were too small to maintain individuals. Those polygons with larger areas were identified as suitable habitat (step 3). After suitable habitat patches were identified, we applied two more criteria to consider them as priority areas for conservation (step 4): a) areas with records of the species' presence, b) areas with records to a distance lesser than the radius of home range. These criteria were based on the argument that individuals can move outside the patches, but no greater distance than their normal home range (Paviolo et al., 2016). The priority areas identified were used as nodes for the creation of the connectivity models.

2.6. Connectivity models

To generate the connectivity models, a permeability map was developed for each carnivore species. We applied an inverse function to the probability of presence. Thus, pixels with values close to 100 represent less permeable areas. This approach assumes that the quality of the habitat has a direct positive relationship with the ease of movement. That is, the landscape in the areas with a high probability of presence offers less resistance to the movement of individuals (Paviolo et al., 2016; Rodríguez-Soto et al., 2013).

To identify connectivity between priority areas, we used the Linkage Mapper program in ArcGis 10.4.1. Different Linkage Mapper modules were used to perform the connectivity analyses (McRae & Kavanagh, 2011). These tools integrate least-cost path (LCP) approaches with circuit theory. Linkage Pathways use maps of priority areas and resistance surfaces to identify linkages between core areas, calculate cost-weighted distances and lowest-cost routes to create least-cost corridors. To delimit the size of the corridors we used a width limit equal to the average distance travelled by each species multiplied by 100 days. This value was established to standardize this measure and can be applied to other animal movement data. The calculated distances were 267.3 km for jaguar, and 213.7 km for puma (Núñez-Pérez & Miller, 2019) in tropical deciduous forest. For black bear, this distance was calculated from telemetry data collected in the northeast of the country (unpublished data) and corridor width limit was 195 km.

We calculated the cost weighted distance between two areas (CWD) and the dispersion difficulty between priority areas. This parameter considers the relationship between the Euclidean distance and the length of the least cost route (EuD:LCP). Subsequently, we also calculated the average resistance per unit along the corridors (CWD:LCP), is the relationship between the accumulated cost and the length of the corridor (Dutta et al., 2016).

After identifying corridors (Linkage Pathways), we used the Centrality Mapper module to quantify the relative importance of priority areas and corridors. Using current flow centrality, this measures the importance of a link in keeping the overall network connected. Centrality Mapper treats each priority area as a "node", each link has a unique resistance, and a resistance equal to the cost-weighted distance of the corresponding lowest cost corridor is assigned (Dutta et al., 2016; McRae, 2012a).

We used Pinch-point Mapper (McRae, 2012b) to produce current maps that identify pinch-points, (i.e., constrictions or bottlenecks) within corridors. Pinch points disproportionately compromise connectivity (Castilho et al., 2015). We defined a threshold from the mean value in the resistance range in each corridor, so the higher resistance values were considered as pinch points (González-Saucedo et al., 2021). Corridors with highest centrality values (the highest third) were characterized considering anthropic fragmentation elements, such as the density of roads, presence of cities, percentage of crops, density of human population and percentage of pinch points per corridor.

3. Results

We obtained 195 records for jaguar, 270 for puma and 903 for black bear. Before filtering the records, the dispersion patterns for the 3 species were clustered according to Morans I test. After filtering patterns were random and spatial autocorrelation decreased for puma (0.050) and black bear (0.105). However, for jaguar (0.109), the dispersion pattern continued to be clustered, although the autocorrelation value decreased. After data filtering, 95 records for jaguar, 120 for puma and 420 for black bear were retained. No variables were correlated (p less than 0.05), so 16 proposed variables were included in the calibration of the models.

3.1. Species distribution models and priority areas

The species distribution models performed well, with AUC_{ext} values > 0.70 (Appendix B.2). The significance values and distributions of the errors are in the Appendix C. The cut-off thresholds were 0.131 for jaguar, 0.374 for puma, and 0.240 for black bear.

Vegetation type and topographic were the two variables most related to the distribution of puma and jaguar. For black bear, the influence of distance to urban areas (an anthropic variable) was considered important (Table 1). Jaguar showed affinity to tropical deciduous forest, in the provinces of Costa Del Pacífico and Golfo de México, in areas of lower altitude. For black bear and puma, the variable with the greatest contribution was the distance to temperate forest. The distribution models of both species highlight important areas in the Sierra Madre Occidental, Sierra Madre Oriental, and the northern region of the Altiplano Sur (Fig. 1). Six priority areas were identified for jaguar, 20 for puma and 21 for black bear, with a total of 108,325 km^2, 107,578 km^2 and 171,578 km^2, respectively (Fig. 1).

3.2. Connectivity analysis

We identified 56 corridors among the priority areas: 5 for jaguar, 22 for puma and 29 for black bear (Fig. 2). The longest corridor (237 km in Costa del Pacífico) and shortest (1 km in Golfo de México) were for jaguar (Table 2). Area 1 for jaguar had only one link, thus it was the most isolated. For puma, the areas of the province of California (1 and 4) and Altiplano Norte (5) were not connected with any other; areas 6 and 10 only had one corridor. For black bear, only area 18 was considered vulnerable, although had an area >25,000 km^2, it only had one connection, so it is an important area, but it is isolated.

For jaguar, the areas in Golfo de México (2, 3 and 6) had greater centrality than those of Costa del Pacífico (areas 1 and 5). For puma, high centrality was observed in areas of the central region of Costa del Pacífico and Sierra Madre Occidental (areas 7, 8, 9, 12, 14, 15 and 18). The black bear model identified areas with greater centrality in the

Table 1
Three variables with the highest percentage of contribution to the species distribution models.

Species	Variable	Influence	Highest probability interval	Interval in the study area	Contribution percentage
Panthera onca	Shrubland	Negative	>100 km	0–250 km	46.5
	Tropical deciduous forests	Positive	0–50 km	0–800 km	35.7
	Altitude	Negative	0–850 masl	0–3,600 masl	7.0
Puma concolor	Temperate forest	Positive	0–10 km	0–70 km	37.2
	Slope	Positive	10–70 degrees	0–90 degrees	12.4
	Shrubland	Negative	>200 km	0–250 km	11.6
Ursus americanus	Temperate forest	Positive	0–50 km	0–70 km	25.6
	Tropical deciduous forests	Negative	0–500 km	0–800 km	18.9
	Urban zones	Negative	60–120 km	0–150 km	14.8

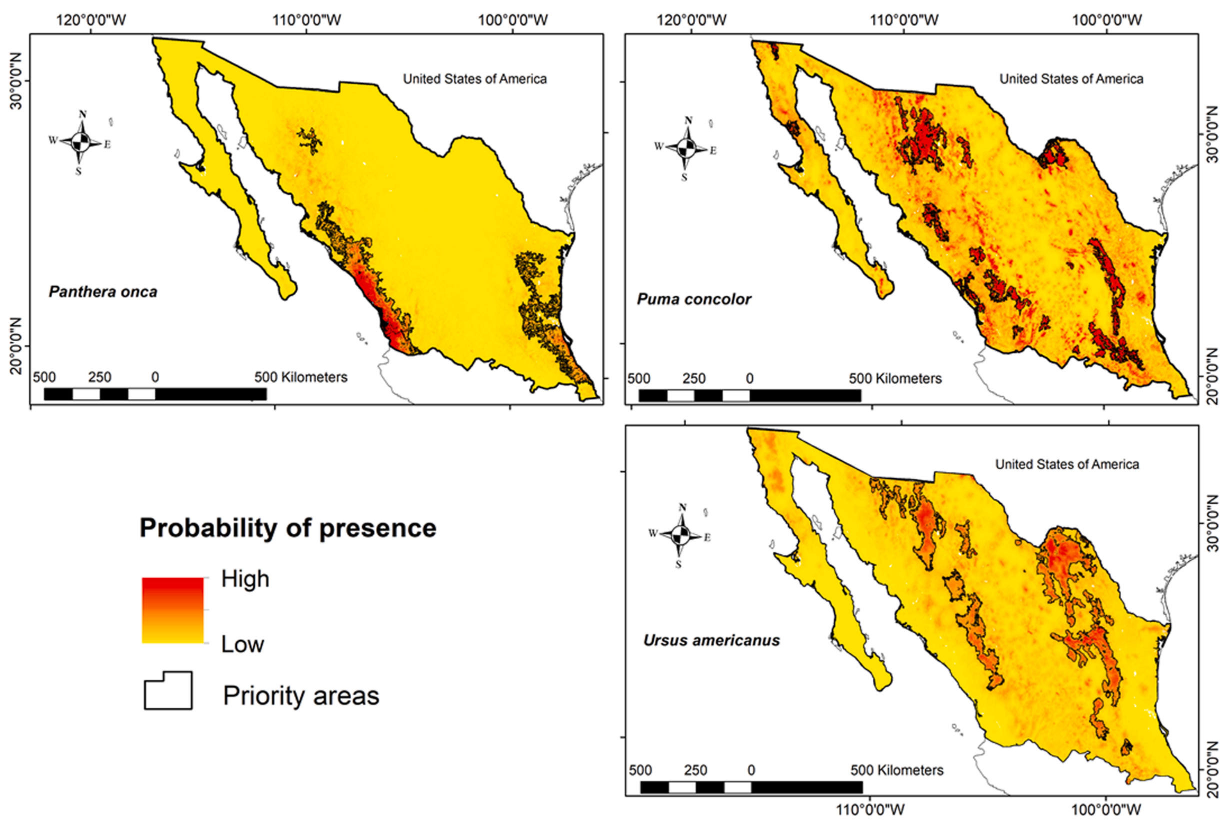

Fig. 1. Species distribution models and priority areas for the conservation of jaguar, puma, and black bear in northern Mexico.

northern region of Sierra Madre Occidental and Sierra Madre Oriental (6, 8, 9, 11, 12, 16, and 19) (Fig. 3). Areas with low centrality had few connections, therefore should be considered as vulnerable as being at more risk of becoming isolated.

Pinch points were found in corridor C connecting areas 1 and 5 for jaguar in Costa del Pacífico. For puma, 11 corridors had pinch points. We found 12 pinch points for black bear, the largest number being in the northeast region (Fig. 4). According to the characterization of the corridors, corridor B for jaguar and D for black bear presented the highest percentage of pinch points; however, they did not exceed 20% of the area of each one (Table 3).

4. Discussion

Maintaining habitat connectivity is one of the main strategies to reduce the effects of fragmentation on populations with broad ecological needs such as carnivores (Di Minin et al., 2016). Priority areas for puma conservation in northern Mexico were identified, in addition updating the information of the distribution for black bear and jaguar (2011; Lara-Díaz et al., 2021; Monroy-Vilchis et al., 2016). We identified vulnerable priority areas due both to the presence of pinch points in the corridors, and also isolation. The corridors with pinch points are of great importance to maintain the movement of species (González-Saucedo et al., 2021). Loss of corridors risks connectivity between priority areas. However, it is possible to propose conservation strategies focused on specific areas to increase connectivity (Angelieri et al., 2016; Castilho et al., 2015).

4.1. Priority areas for conservation and most important variables

The priority areas that we identified for jaguar coincide with previous research. They are found in the Costa del Pacífico and the Golfo de México, as well as the Sierra Madre Oriental (2011; Rabinowitz & Zeller, 2010). It is important to note that the model identified the northern area of the Sierra Madre Occidental as a priority, however, the probability of presence tends to decrease as it approaches the border with the United States. Only one patch of suitable habitat large enough to be considered a priority area for jaguar was identified in the northernmost portion of the range in Mexico. Probably the lack of jaguar records in this area causes its relevance to be underestimated (Chen & Lei, 2012). Since stable jaguar populations have been reported there (Gutiérrez-González et al., 2012).

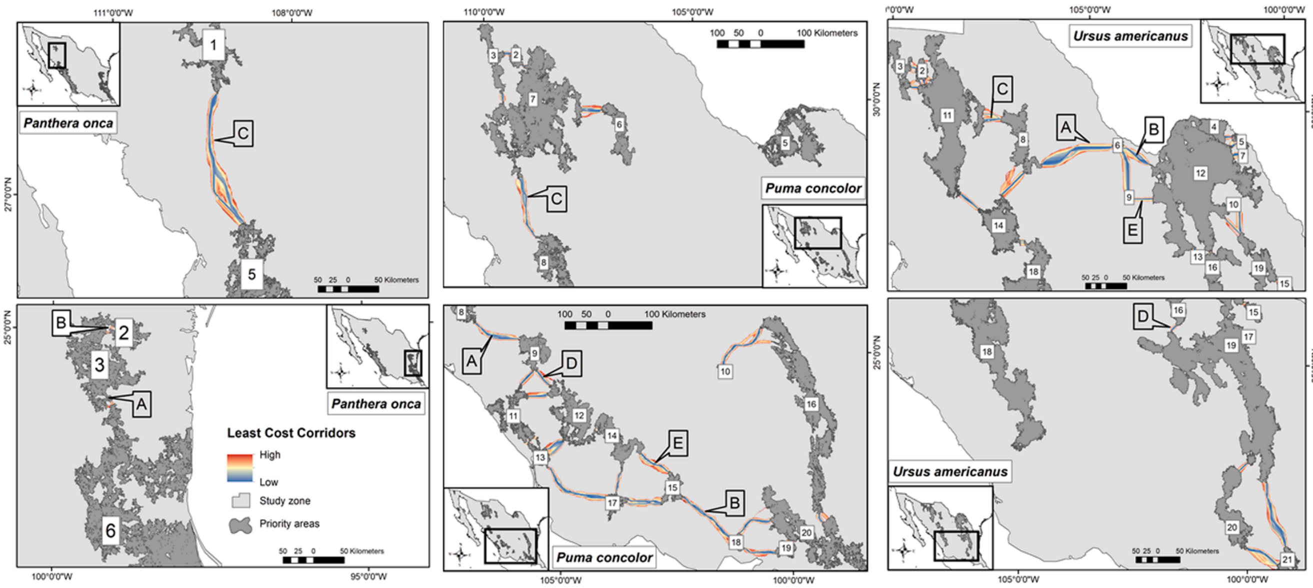

Fig. 2. Least-cost corridors (letters) between priority areas (numbers) to conserve large carnivores in northern Mexico. Routes with least resistance are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Parameters of the most important corridors for jaguar, puma, and black bear in northern Mexico. The corridors are in descending order according to their centrality value.

Species	Connected areas	Corridor	Euclidean distance (EucD, km)	Cost-weighted distance (CWD)	Least-cost path (LCP, km)	EucD: LCP	CWD: LCP	Current flow centrality (Amps)
Panthera onca	3–6	A	0.92	120.02	1.33	0.69	90.24	2.00
	2–3	B	0.42	76.71	0.89	0.47	86.58	1.86
	1–5	C	211.28	18727.72	237.83	0.88	78.75	1.00
Puma concolor	8–9	A	100.86	8283.91	111.34	0.90	74.40	60.00
	15–18	B	141.34	10972.14	150.05	0.94	73.13	59.00
	7–8	C	138.59	10369.78	151.13	0.91	68.62	52.00
	9–12	D	40.65	3118.58	44.62	0.91	69.90	40.43
	14–15	E	73.31	5453.97	79.24	0.92	68.83	39.32
Ursus americanus	6–8	A	177.16	17008.25	190.25	0.93	89.40	98.00
	6–12	B	74.34	6069.86	79.76	0.93	76.10	75.27
	8–11	C	38.40	3069.23	40.42	0.95	75.94	61.85
	16–19	D	15.86	1366.59	16.75	0.94	81.59	50.39
	9–12	E	51.02	4646.94	52.07	0.97	89.25	40.69

CWD:EuD: Cost of dispersion between priority areas; CWD:LCP: Resistance per unit cost of length along the corridors.

Areas identified for puma and black bear had a similar distribution pattern, most of them are in the mountains of the Sierra Madre Oriental and Occidental (Lara-Díaz et al., 2021). Suitable habitat for puma was less than that reported by Ceballos et al. (2006). However, Ceballos et al. (2006) used only bioclimatic variables, which excludes the effect of vegetation cover and land use change on the habitat suitability, thus overestimating species distribution. Using the entire set of variables available from WorldClim affects the performance of the models, due to the high correlation between them (Bedia et al., 2013).

The black bear model is different from that reported by Monroy-Vilchis et al. (2016), with the largest number of patches identified in the Sierra Madre Occidental. In the north of the Sierra Madre Oriental and the Altiplano Norte the distribution was underestimated. This is one region with confirmed presence of black bear in the protected areas of Sierra del Burro, Maderas del Carmen, Cumbres de Monterrey, and others (Juárez-Casillas & Varas, 2013). The model published by Monroy-Vilchis et al. (2016) did not include the tropical region of the Golfo de México. This region is important since the bear presence has been reported in tropical environments such as El Cielo Biosphere Reserve (tropical rainforest, Carrera-Treviño et al., 2015). On the other hand, this model did not include the southern recent records in the state of Hidalgo (Rojas-Martínez & Juárez-Casillas, 2013) and the Sierra Gorda in Querétaro (López-González et al., 2019).

For jaguar, the most important variables were distance to scrubland, distance to tropical deciduous forest and altitude. Jaguar are distributed in areas with less human impact since it is more sensitive to disturbances and habitat loss (Castilho et al., 2015). These results agree with (2011), since jaguar have not been recorded in areas with arid vegetation in the Altiplano. Studies carried out at local level show that jaguar use different vegetation types, including oak forest and tropical deciduous forest, at altitudes of 40 to 2400 masl, in the state of San Luis Potosí (Villordo-Galván et al., 2010), this coincides with our model.

The variable with the highest percentage of contribution to the puma model was the distance to temperate forest, followed by the slope and the distance to scrubland. Although there are records of puma in scrubland areas, they are few compared to records from temperate forest. Accordingly, our model identified these areas with a higher probability of presence. Also, several studies report that puma presence is associated with areas with steep slopes (Dickson et al., 2013; Zarco-González et al., 2013), apparently because these areas represent refuges by limiting accessibility to human.

The distance to temperate forest had the highest percentage of contribution to the black bear model, followed by distance to tropical deciduous forest and urban areas. These variables differ from those

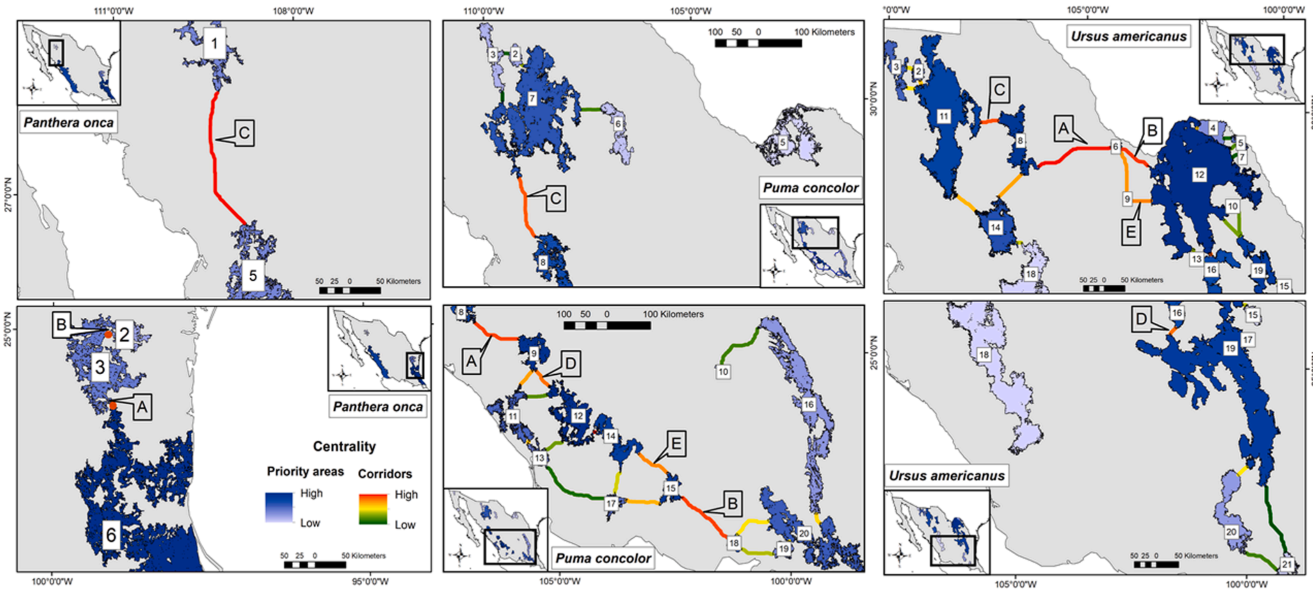

Fig. 3. Centrality of the priority areas and corridors identified for jaguar, puma, and black bear in northern Mexico. The letters indicate the corridors with the highest centrality.

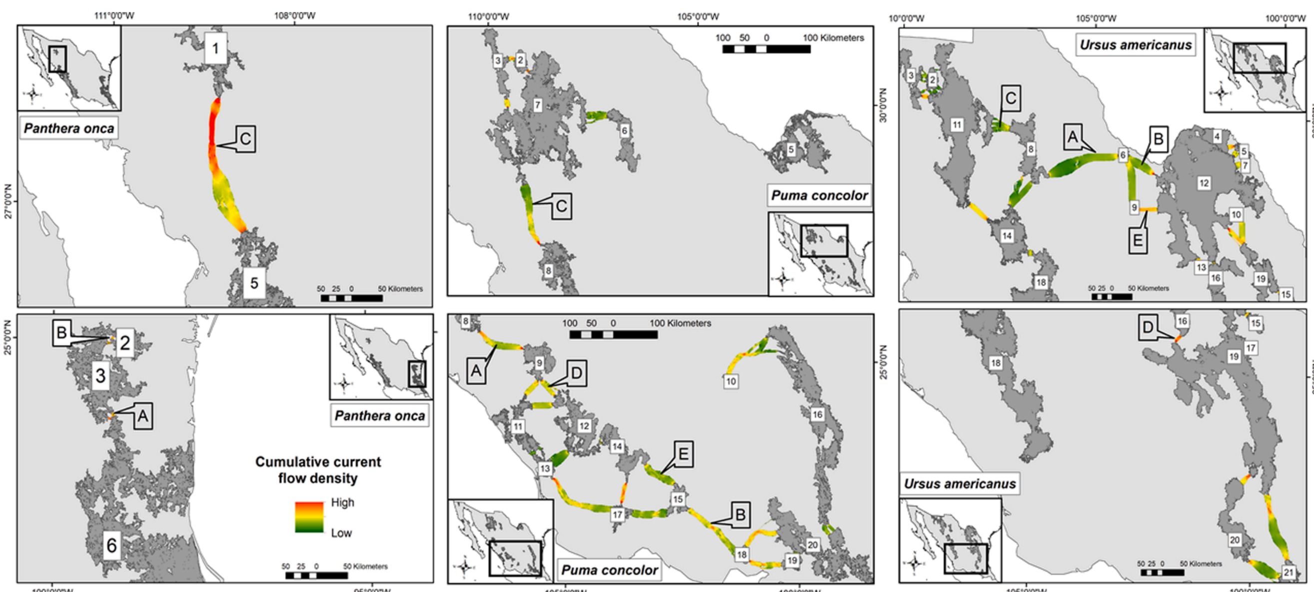

Fig. 4. Pinch points in the corridors that connect the priority areas for jaguar, puma, and black bear conservation in northern Mexico.

proposed by Delfín-Alfonso et al. (2012). They identified slope, altitude, precipitation, and temperature as the most important variables. Monroy-Vilchis et al. (2016) identified temperate forests, altitude and tropical deciduous forest as the variables that best explain the black bear distribution. Temperate forest is important as refuge and feeding area for this species (Juárez-Casillas & Varas, 2013). Although black bears are a generalist species, with high ecological plasticity, capable of living even in areas modified by human presence (Merkle et al., 2013), our model identified these areas with a low probability of presence. This is because the records in conflict situations were not included for generate the model, since the objective was to identify areas of suitable habitat. The sites where there is conflict are usually marginal habitat for bears, where conditions for its presence are not ideal, but rather is due to attraction of some element, such as sources of anthropic food. Another reason for excluding records of conflict situations is that at these sites bears are more vulnerable to retaliatory hunting, roadkill, and other human-caused mortality (González-Saucedo et al., 2021). Therefore, it is not appropriate to include information about these sites in a connectivity model.

4.2. Connectivity analysis

Habitat fragmentation derived from human development threaten carnivores' conservation in northern Mexico and prioritizing and protecting corridors is essential to keep populations stable. Although jaguars move great distances, no corridors were found between the populations of Costa del Pacífico and Golfo de México. Our distribution models did not identify potential habitat in the Altiplano, so the distance between the closest patches of habitat in these provinces is approximately 500 km. The corridors that we identified differ from those proposed by Rabinowitz and Zeller (2010) but resemble those identified by Rodríguez-Soto et al. (2013), all being along the coasts of the country.

Table 3
Characterization of the corridors with the highest centrality that connect the priority areas for the conservation of puma, jaguar, and black bear in northern Mexico. The table shows the main fragmentation elements in each corridor in bold.

Species	Connected areas	Corridor	Centrality (Amps)	Corridor area (km^2)	Road's density (km/km^2)	Human settlements percentage	Percentage of area with crops	Percentage with pinch points
Pantheraonca	3–6	A	2.00	19.86	**0.19**	0.00	0.00	8.86
	2–3	B	1.86	26.54	**0.43**	0.00	**92.43**	**14.81**
	1–5	C	1.00	3817.60	**0.04**	**0.04**	**8.09**	1.37
Puma concolor	8–9	A	60.00	1322.29	**0.07**	0.04	**4.62**	0.52
	15–18	B	59.00	1810.77	**0.18**	**5.49**	**30.76**	0.01
	7–8	C	52.00	2067.99	0.00	0.00	**1.57**	1.22
	9–12	D	40.43	541.38	**0.10**	0.00	**2.60**	0.25
	14–15	E	39.32	1242.44	**0.16**	**1.43**	**31.00**	0.00
Ursus americanus	6–8	A	98.00	4266.56	**0.05**	**4.82**	**25.23**	0.00
	6–12	B	75.27	1350.8	**0.01**	**0.11**	**1.64**	0.79
	8–11	C	61.85	997.61	**0.04**	0.00	**3.84**	0.00
	16–19	D	50.39	162.43	0.00	0.00	**2.52**	**12.83**
	9–12	E	40.69	516.40	0.00	0.00	0.00	2.51

The connection between the two large populations of black bear (Eastern and Western) occurs through the Altiplano Norte, where the corridors with the highest centrality values were found (González-Saucedo et al., 2021; Lara-Díaz et al., 2021). For puma, the most important corridors were in Altiplano Sur and Costa del Pacífico (González-Saucedo et al., 2021).

Many of the identified corridors are compromised by agricultural fields, human settlements, roads, or combinations of these factors, which make it difficult for animals to move. We emphasize roads since they are considered one of the main causes of carnivore mortality in Mexico (González-Gallina & Hidalgo-Mihart, 2018). Maintaining movement paths for wildlife in a human-dominated landscape is a difficult task, but connectivity maps can be an effective tool to inform conservation and management decisions (Dutta et al., 2016), these include habitat restoration in or around the corridors (Shepherd & Whittington, 2006), and construction of wildlife crossings around large highways (Manteca-Rodríguez et al., 2021).

4.3. Conservation implications

Fragmentation has generated numerous patches of habitat. Identifying corridors between them is a key tool to conserve carnivore populations in northern Mexico. Resources for conservation are generally limited, therefore, it is necessary to prioritize conservation actions in areas with low connectivity or those areas that are isolated. Conservation strategies should focus on corridors with pinch points to maintain functionality (Carroll et al., 2012; McRae et al., 2012).

When pinch points were relatively few (i.e., less than 20% in each corridor), connectivity may not be as compromised. Identifying these sites can be the basis for establishing restoration areas. However, these opportunities are likely to be lost due to creation of transport routes and urban development, leading to permanent fragmentation, unless appropriate mitigation measures are incorporated (Yumnam et al., 2014).

It is urgent to decree conservation policies for priority areas and corridors, since without continuous political support important areas could be eliminated, ignored, or authorized for occupied by agriculture and industry (Brodie et al., 2016). As an example of the applicability of our results, we identified a jaguar corridor in Golfo de México (Table 3), with an area of approximately 26 km^2. The main cause of fragmentation are crops, since 92.4% of the corridor presents this type of land use. However, 14.5% of the area has pinch points, so we can infer that the models identified potential habitat, indicate a corridor, and focus on a site to apply agroecological practices and conflict mitigation measures to maintain or improve permeability and functionality (Angelieri et al., 2016). Paviolo et al. (2018) demonstrated that maintaining areas with forest cover near monocrops can allow occupation by puma and jaguar, although vigilance should be increased to avoid hunting, and other conflicts with humans (Zarco-González et al., 2013).

In corridors where the main fragmentation is caused by urban development, it is essential to identify the type of human settlement that is limiting corridor continuity. Maintaining connectivity depends on infrastructure that has been built. In rural areas with lower human population density barriers may be more permeable. There it is possible to implement development schemes that reduce fragmentation (Brodie et al., 2015). For example, in those areas the promotion of ecotourism activities (Broadbent et al., 2012), and land use focused on community conservation (Lavariega et al., 2020) should be implemented. These should also include economic incentives for ecosystem services and compensation in conflict cases (Goswami & Vasudev, 2017). In addition, awareness and citizen participation programs should prove beneficial (Bonnet-Lebrun et al., 2019). These strategies can be implemented in corridors C and D for puma and C, D and E for black bear.

Some fragmentation elements like roads and railways may be permanent (Yumnam et al., 2014). Road development plans have not considered fragmentation of wild animals' dispersal areas (Colchero et al., 2011), nor the layout of corridors. We identified the presence of road networks in most of the corridors analyzed. In these cases, it will be essential to include wildlife crossings to mitigate the risks that the roads imply for animals. The results of this study also represent a tool for planning future roadway projects, integrating mitigation measures, such as wildlife underpasses and overpasses to maintain habitat connectivity (Ceia-Hasse et al., 2017).

The precision of the species distribution models, as any predictive model, depends on the quality of the input information, in this case of the environmental layers and the presence records, for this reason it was important to carry out the filtering of both based on the criteria described in the methods. Even so, some of the environmental layers are based on extrapolations or interpolations of the original information. This imposes some degree of error. The ideal for a connectivity model would be to include records of animals in transit, but those are difficult to obtain in sufficient quantity to generate models. In Mexico there are few studies that apply satellite telemetry in wild carnivores. Some of the black bear records were obtained by this way, but there is not enough information to analyze connectivity based on these records.

Unfortunately, the rate of land use change, loss of habitat and patch isolation that this generates occur at greater speed than the generation of spatial and ecological information. Therefore, we decided to generating models with the most accurate data now available, to present an overview of the connectivity of the puma, jaguar, and black bear habitat in Mexico. Doing so highlights existing priority areas and corridors, as well as elements that may represent a threat. These data can be used to implement short-term protection and restoration measures. In the medium term, we suggest validating the effectiveness of the corridors we identified by assessing their use by carnivores through field monitoring. Corridor characterization and the pressure factors that we identified should also be used to implement actions that increase their effectiveness.

5. Conclusions

We identified 47 priority areas for the conservation of three large carnivores in northern Mexico, in addition to corridors that could potentially keep them connected. Pinch points were identified where habitat could be lost, threatening connectivity between priority areas. This study can be taken as a frame of reference for the implementation of conservation actions in the identified areas and corridors.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2021.126116.

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