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Land-use change and habitat fragmentation of *Leopardus pardalis* in Highlands of Puebla, Mexico

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Ocelots are relatively tolerant to habitat modification. However, it has been observed that they may be sensitive to habitat loss and fragmentation as a result of human development. The Sierra Norte de Puebla is considered a potential habitat for ocelots and other tropical felines. However, it has suffered heavy loss and fragmentation of its natural ecosystems, which considerably affects habitat availability and quality. This study analyzed the land-use changes and habitat fragmentation in the distribution range of the ocelot in the Sierra Norte de Puebla, Mexico, from 1993 to 2020. Habitat suitability was determined using potential distribution models and vegetation and land-use maps from 1993, 2003, and 2020, obtained using supervised classification of Landsat images. The resulting maps were reclassified in terms of the habitat suitability for *Leopardus pardalis* according to their quality. Land-use changes and habitat loss were quantified with a transition matrix, and fragmentation was assessed using the Morphological Spatial Pattern Analysis tool of the program GUIDOS. These habitat fragments were quantified using the integral index of connectivity with the CONEFOR Sensinode program. We estimated that 22.2 % of the study area has suitable conditions for ocelots. From 1993 to 2020, the area covered by natural vegetation decreased 16 % at an annual rate of -2.4 %. During this period, the mean fragment size and shape index decreased; on the other hand, the number of fragments and the Euclidean distance between fragments increased. The percentages of edge, branch, and islet vegetation dropped from 1993 to 2003 but increased in 2020. The connectivity analysis indicated that two habitat fragments showed high values of the integral index of connectivity. The increase in anthropogenic cover and the habitat loss for *L. pardalis* between 1993 and 2020 affected mainly vegetation fragments considered optimal for the persistence of this species. In these ecosystems, agricultural and livestock practices are expanding vigorously, increasing edge habitats and decreasing the core area of habitat fragments. The areas that recorded the presence of ocelots have optimum conditions to serve as biological corridors in the Sierra Madre Oriental, particularly in the portion of the Sierra Norte de Puebla. The fragmentation of the ocelot habitat is of particular concern and should be addressed strategically for the long-term conservation of the ocelot and regional biodiversity.

Los ocelotes presentan cierta tolerancia a la modificación de su hábitat, sin embargo, se ha observado que pueden ser sensibles a la pérdida y fragmentación como resultado del desarrollo humano. La Sierra Norte de Puebla se considera con potencial para la distribución del ocelote y otros felinos tropicales; no obstante, la pérdida y fragmentación de sus ecosistemas es alta y genera un efecto significativo en la disponibilidad y calidad del hábitat. En este estudio se analizó el cambio de uso de suelo y la fragmentación del hábitat del ocelote en la Sierra Norte de Puebla, México de 1993 a 2020. Se determinó la idoneidad de hábitat del ocelote mediante modelos de distribución potencial y mapas de vegetación y uso de suelo de 1993, 2003 y 2020, obtenidos mediante una clasificación supervisada de imágenes Landsat. Los mapas derivados fueron reclasificados según la aptitud de hábitat de *Leopardus pardalis* de acuerdo con su calidad. Se cuantificó el cambio y pérdida de hábitat mediante una matriz de transición y se evalúo la fragmentación con la herramienta Morphological Spatial Pattern Analysis del programa GUIDOS. A estos fragmentos de hábitat se les cuantificó el Índice Integral de Conectividad con el programa CONEFOR Sensinode. 22.2 % de la superficie total de la zona de estudio tiene condiciones para la presencia del ocelote. De 1993 a 2020 la superficie de vegetación disminuyó 16% a una tasa de cambio de -2.4 %. Durante este periodo el tamaño medio del fragmento e índice de forma disminuyeron; en cambio, el número de fragmentos y la distancia euclidiana entre fragmentos se incrementaron. El porcentaje de borde, rama y relicto disminuyeron de 1993 a 2003, aunque aumentaron en 2020. El análisis de conectividad indicó que dos fragmentos de hábitat presentaron valores altos del índice de conectividad integral. El incremento en la superficie de las coberturas antrópicas y pérdida de hábitat de *L. pardalis* entre 1993 y 2020, se concentró en fragmentos de vegetación considerados óptimos para la persistencia de esta especie. En estos ecosistemas el avance de las prácticas agrícolas y ganaderas es alto, lo cual contribuye a un incremento en el hábitat de borde y una disminución en el área interior de los fragmentos de hábitat. Las áreas en las que se registró la presencia de ocelotes tienen las condiciones ideales para que éstas funcionen como corredores biológicos en la Sierra Madre Oriental, particularmente en la porción de la Sierra Norte de Puebla. La fragmentación del hábitat del ocelote es especialmente preocupante y necesita abordarse estratégicamente para la conservación a largo plazo, no solo del ocelote, sino de la biodiversidad de la región.

Keywords: Carnivores; connectivity; conservation; deforestation; optimal habitat; landscape; habitat loss.

Introduction

Deforestation and fragmentation are among the main threats to natural ecosystems worldwide, with adverse effects on biotic communities (Armenteras *et al.* 2003; Lindenmayer and Fischer 2006; Haddad *et al.* 2015). Long-term fragmentation increases population isolation and decreases connectivity, with consequences for species survival, abundance, and dispersal, as well as for functional connections between habitat fragments (Ewers and Didham 2006; Scolozzi and Geneletti 2012; Gao *et al.* 2013). The functional diversity of wild mammals has been observed to decrease as land-use has become more intensive, and 70 % of species respond negatively to fragmentation (Flynn *et al.* 2009; Thornton *et al.* 2011), to the extent that one-quarter of all mammal species are at risk of extinction (Ceballos and Ehrlich 2002; Baillie *et al.* 2010).

Among mammals, carnivores are one of the groups most vulnerable to habitat loss, fragmentation, and alteration (Fahrig 2003; Michalski and Peres 2005; Crooks *et al.* 2011; Dotta and Verdade 2011) due to their low population density, high habitat requirements, and low reproductive potential. Consequently, populations of terrestrial carnivores have experienced major declines, and their ranges have shrunk (Ripple *et al.* 2014). Particularly, felines face a high risk of extinction as a result of habitat fragmentation and loss (Treves and Karanth 2003; Zanin *et al.* 2015). According to the IUCN Red List (2012), habitat loss and fragmentation affect all 36 species of wild felines and are the main threats to 21 species.

The ocelot is a forest species (Harveson *et al.* 2004; Jackson *et al.* 2005; Haines *et al.* 2006) that can use multiple habitats depending on availability (De Oliveira *et al.* 2010; Fusco-Costa *et al.* 2010), including disturbed and undisturbed habitats (Kolowski and Alonso 2010), although it prefers areas with closed canopy and dense vegetation (López-González *et al.* 2003; Harveson *et al.* 2004; Jackson *et al.* 2005; Haines *et al.* 2006; Martínez-Calderas *et al.* 2011; Torres-Romero *et al.* 2017; Galindo-Aguilar *et al.* 2019). Several studies indicate that the presence of the ocelot is adversely affected by local disturbances, such as land-use changes and forest fragmentation (Garmendia *et al.* 2013; Cruz *et al.* 2018; Wang *et al.* 2019; Lombardi *et al.* 2022). Habitat fragmentation can influence the home range of the ocelot (Cruz *et al.* 2019) by reducing the area of habitat fragments (Garmendia *et al.* 2013; Lombardi *et al.* 2020). It alters the connectivity between populations by increasing the isolation of habitat fragments and reducing the availability of corridors (Tewes and Everett 1986; Jackson *et al.* 2005; Haines *et al.* 2005; Galindo-Aguilar *et al.* 2019), which contribute to the demographic instability of the species (Reed 2004; Janecka *et al.* 2014).

In Mexico, the ocelot is distributed in the coastal areas of the Pacific and the Gulf of Mexico, in semi-arid regions with xeric and semitropical scrubland, tropical and subtropical forests, and temperate forests (Aranda 2005; Martínez-Calderas *et al.* 2011). In Puebla, its presence has been documented in Sierra Negra (Galindo-Aguilar *et al.* 2016; Cacelin-Castillo *et al.* 2020); Ramírez-Bravo *et al.* (2010a) confirmed the presence of ocelots in the Sierra Norte, in tropical evergreen and sub-evergreen forests, which may indicate the mobility of the species across the Sierra Madre Oriental. This region has been identified as critical for the dispersal of the ocelot and other tropical felines and is considered a priority biological corridor from north to south (Ramírez-Bravo *et al.* 2010b; Hernández-Flores *et al.* 2013; Dueñas-López *et al.* 2015; Cacelin-Castillo *et al.* 2020). However, the Sierra Norte de Puebla (SNP) experienced a 30 % habitat loss and fragmentation between 1980 and 2000 due to the growing human population and agricultural expansion (Guevara-Romero 2011), affecting the presence of several species of felines, including the ocelot (Ortega-Huerta and Peterson 2008; Ramírez-Bravo *et al.* 2010b; Villordo-Galván *et al.* 2010; Galindo Aguilar *et al.* 2019). However, there is insufficient information on the effects of land-use change and fragmentation of the ocelot habitat on the SNP. Therefore, analyzing the fragmentation and loss of connectivity between the habitats of *Leopardus pardalis* will allow the preservation of potential displacement routes for ocelots in this region of Mexico. This study aimed to analyze in land-use changes and morphological fragmentation patterns of the *L. pardalis* habitat in the Sierra Norte de Puebla. This approach was used to identify and classify morphological fragmentation types based on habitat availability for the species and to recognize their variation in 1993 to 2003 and 2003 to 2022. We hypothesized that due to the land-use changes in the SNP, the anthropic use matrix will determine the structure and availability of the remaining habitat fragments suitable for *L. pardalis*; therefore, isolated fragments will contribute marginally to maintaining the overall landscape connectivity.

Materials and methods

Study area. The SNP is located at 20° 1′ 48" N, 97° 52′ 18" W (Figure 1) and comprises 64 municipalities. It is part of three morphotectonic provinces: Sierra Madre Oriental, Trans-Mexican Volcanic Belt, and Gulf Coastal Plain (INEGI 2005a). Climates in the region are varied, including warm sub-humid Aw2 and humid Am(f) in the north, humid semi-warm (A)C(fm) and humid temperate C(m) in the central area, and temperate sub-humid C(w2), semi-cold sub-humid C(E)(w2), and temperate semi-dry climates BS1k(w) in the south (INEGI 2005b). The mean annual temperature is 14 °C in the high-altitude regions and 20 °C in the lowlands. The total annual rainfall ranges between 1,000 mm and 3,500 mm, with March being the driest month and September experiencing the highest precipitation (INEGI 2005b). The region is undergoing a heavy deforestation process and has large areas of rainfed agriculture and cultivated pastures, as well as urban areas. However, it still has areas covered by mountain cloud forest, oyamel forest, oak forest, juniper forest, high and medium evergreen forest, and pine and pine-oak forests (INEGI 1997Rzedowski 1990; INEGI 199).

Image processing. Vegetation and land use data were integrated and analyzed using Landsat 4 (TM, October 1993), Landsat 7 (ETM, January 2003), and Landsat 8 (Oli Tirs, January 2020) imagery obtained from the Global Land Cover Facility. Supervised classification of satellite images for each year was carried out to obtain spectral information by estimating maximum likelihood (Lillesand *et al.* 2015). The classification of the 1993 image used 250 reference points from vegetation and land use maps Series I, scale 1:250 000 (INEGI 1997). The 2003 image was classified using 250 reference points based on vegetation and land use maps Series III, scale 1:250 000 (INEGI 2005c). The classification of the 2020 image used 300 randomly defined checkpoints recorded during fieldwork from February to May 2020, supported by Google Earth imagery®.

Selection of habitat fragments. Habitat suitability for *Leopardus pardalis* was determined through a potential distribution model, as this allows for the identification of areas or fragments with a high probability of ocelot presence, which can be considered suitable habitat fragments (Pascual-Hortal and Saura 2008; Decout *et al.* 2012). The model was based on 70 records of *L. pardalis* from 2005 to 2011 in Hidalgo, San Luis Potosí, Veracruz, and Sierra Norte de Puebla in the Sierra Madre Oriental region. These records were obtained from the National Biodiversity Information System (CONABIO 2020), the Global Biodiversity Information Facility (GBIF 2021), and the database of Neotropical Carnivores (Nagy-Reis *et al.* 2020). To reduce spatial bias, ocelot records were processed with the Spatial Thin module (spatial filtering; Aiello-Lammens *et al.* 2015), which consists of a thinning function of data points to filter those that are at a short distance from an adjacent record; this distance was used to define the home range of the ocelot (mean 12 km^2; Dillon and Kelly 2007; González-Borrajo *et al.* 2016).

Records of ocelot presence and environmental variables were processed in the program Wallace 1.0.6.1 in R (Kass *et al.* 2018). Environmental variables were selected based on knowledge of the distribution of the ocelot in the Sierra Madre Oriental (Martínez-Calderas *et al.* 2015; Cacelin-Castillo *et al.* 2020). We used 14 climatic variables (BIO 1, BIO 2, BIO 3, BIO 4, BIO 5, BIO 6, BIO, BIO 7, BIO 8, BIO 13, BIO 14, BIO 15, BIO 16, and BIO 17), with a 1 km^2 resolution, obtained from the WorldClim version 1.4 database (Hijmans *et al.* 2005). The following default settings were selected: maximum number of background points = 10,000; regularization multiplier = 1; replicates = 20; replication run type = boot; convergence threshold = 0.00001; and

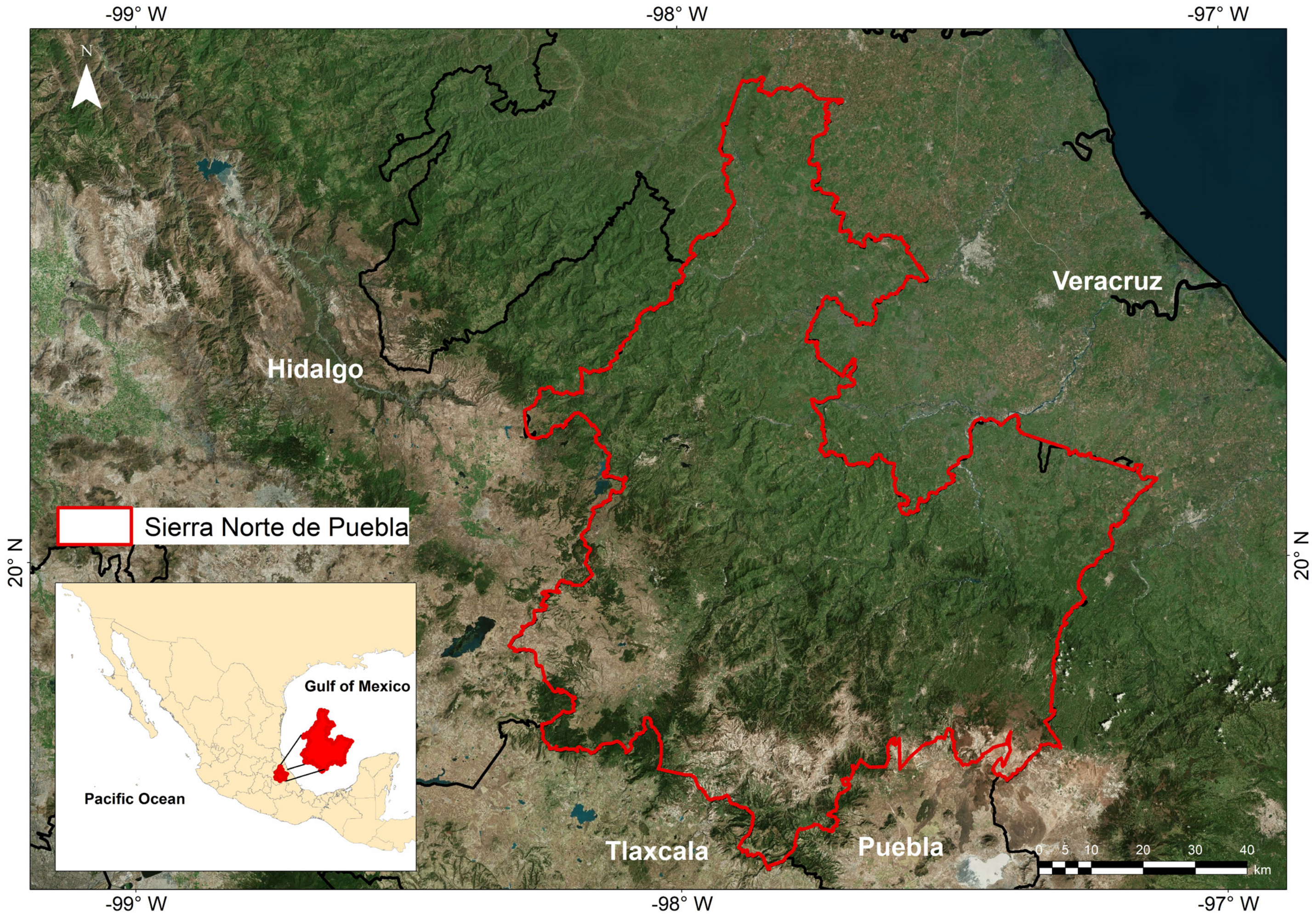

Figure 1. Borders of the study area in the Sierra Norte de Puebla, Mexico.

maximum number of iterations = 10,000. Seventy percent of the occurrence data were used as a training dataset and 30 % as a test dataset. The variables were evaluated using a Jackknife test, which compares the models with all possible combinations of environmental variables by measuring the importance of the variable. The model validation considered the weight of the omission and commission errors for the area under the curve (AUC; Hernández *et al.* 2006).

The vegetation and land use layers of each year were reclassified considering the habitat suitability for *Leopardus pardalis* into three categories (inhospitable, hospitable, and habitat), according to the habitat quality following the method by Tischendorf *et al.* (2003), Rayfield *et al.* (2010) and Correa-Ayram *et al.* (2014). Human settlements, pine forests, and coniferous forests were classified as inhospitable (values from 0 to 30) as these areas are unsuitable or marginally suitable for the ocelot. Plant covers of anthropic origin, such as induced pastures, crops, and agroforestry plantations, were classified as hospitable (values of 31–60), *i. e.*, areas where ocelots may be present or in transit but inadequate to maintain a stable population. The highest interval (60–100) indicated areas with the greatest habitat suitability, corresponding to medium evergreen forests, mountain cloud forests, and oak-pine forests (Tischendorf *et al.* 2003; Di Bitteti *et al.* 2008; Dde Oliveira et al. 2010; Rayfield *et al.* 2010; Martínez-Calderas *et al.* 2015; Cacelín-Castillo et al. 2020; Lambardi et al. 2022).

Layers of slope, elevation, distance from roads, distance from human settlements, and road density were integrated. Each variable was assigned a value from 0 to 100 based on the available information on the habitat requirements of *Leopardus pardalis* (De Oliveira *et al.* 2010; Ramírez-Bravo *et al.* 2010b; Cruz-Rodríguez *et al.* 2015; Gil-Fernández *et al.* 2017; Cruz *et al.* 2018; Wang *et al.* 2019). Values close to 100 were considered to indicate highly suitable areas in terms of habitat quality for ocelots, and vice versa (Tischendorf *et al.* 2003; Rayfield *et al.* 2010). Regarding altitude, values from 0 to 1,500 m were rated as most suitable since ocelots have been observed between 300 m and 1,300 m in this region. Altitudes above 2,100 m were classified as less suitable (Nowell and Jackson 1996; Cacelin-Castillo *et al.* 2020; Lambardi et al. 2022). Regarding slope, the difficulty of movement was considered. Likewise, high values of distance to roads correspond to the potential impact on the species; high values of distance to human settlements estimate the capacity of ocelots to adapt to and use urban and suburban areas, and low values of road density were interpreted as indicating areas of greater habitat suitability. All layers were standardized to homogenize the pixel resolution at 30 meters and processed with QGIS version 3.4.

Raster layers of potential distribution, reclassified plant covers, and land use, slope, altitude, and disturbance were added up using map algebra with the program QGIS version 3.4., to approximate the final potential distribution model to the area corresponding to the actual niche of the species (Sánchez-Cordero *et al.* 2005; Peterson *et al.* 2006). The resulting map values were split into quartiles, with the lower interval classified as poor habitat (absence of habitat), the next interval as suboptimal, and the upper interval as optimal habitat (Tischendorf *et al.* 2003; Correa-Ayram *et al.* 2014). Fragments classified as optimal with a size of less than 100 ha were reclassified as suboptimal. This area has been observed to correspond to the highest recorded home range for the ocelot in Central America, South America, and Mexico (Ludlow and Sunquist 1987; Murray and Gardner 1997). In the definition of the final habitat fragments, only those of the optimal category were considered, and a new binary map (Optimal–Non-optimal) was generated using the QGIS version 3.4 program.

Land-use change. Changes in the ocelot habitat cover in 1993, 2003, and 2020 were analyzed using ArcView version 3.2 (ESRI 1999). Land-use change was estimated using a transition matrix to quantify the gain, loss, and persistence of change trajectories between the covers analyzed (Pontius *et al.* 2004). The annual rate of change (r) proposed by Puyravaud (2003) was calculated using the formula: $r = (100/t_2-t_1) \times \ln (A_2/A_1)$… Where A_1 is the coverage area at the beginning of the period, and A_2 is the coverage area at the end of the period; t_1 is the start year of the analyzed interval and t_2 is the end year.

Morphological Classification of Spatial Patterns of Habitat Patches (MSPA). The morphological types of habitat fragmentation for *Leopardus pardalis* were identified and classified using the program GUIDOS (Vogt *et al.* 2006). MSPA is a sequence of mathematical morphological operators that describe the geometry and connectivity of the components of an image; it uses a binary method of image classification based on the geometry and shapes of the elements to classify the fragmentation patterns into seven morphological categories: core area, edge, loop, perforation, bridge, branch, and islet (Vogt *et al.* 2007; Soille and Vogt 2009; Saura *et al.* 2011; Table 1).

Analysis of landscape connectivity. The connectivity of the habitats of *Leopardus pardalis* at the landscape level was analyzed in 1993, 2003, and 2020, using the integral index of connectivity (IIC) (Saura and Torné 2009), with the program CONEFOR Sensinode version 2.5.8 (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007). The IIC integrates habitat attributes and landscape connectivity into a single connectivity value (Decout *et al.* 2012). In this way, habitat fragments are represented as nodes and the connections between them as links. IIC values range from 0 to 1, which increase as connectivity improves. A value of 1 is reached in the hypothetical case that the landscape is completely occupied by the habitat. The importance of each landscape element or change was determined by the delta values of this index (dIIC) (Pascual-Hortal and Saura 2006). The data were ranked from lowest to highest and then divided into five categories: very high, high, medium, low, and very low. Only those fragments of very high importance for connectivity were considered fragments of interest (Saura and Rubio 2010).

Table 1. Categories and Ecological Implications of Morphological Spatial Patterns of Fragmentation (MSPA).

Morphological Type	Ecological Meaning
Core area	Core areas habitat fragment that are relatively far from the edges between covers classified as habitat and those classified as non-habitat, also considering areas that have not been degraded by the edge effect and fragmentation.
Edge	Habitat zones spanning the width of the boundary between forest and non-forest cover with relatively large spaces corresponding to the outer boundary of a core area.
Perforation	Zones defined by the boundaries between core areas and relatively small gaps within the habitat. Perforation occurs within the edge zone along the boundary between the gap and the non-fragmented area.
Bridge	Narrow fragments contiguous without core area that connect at least two different core areas at their ends. They correspond to structural connectors or corridors that link different forest core habitat areas. Therefore bridges make reachable a higher amount of habitat for those organisms that dwell in any of the two linked cores and that can effectively disperse through these corridors.
Loop	Similar to bridges but with the ends of the element connecting to different parts of the same core area. Therefore, their presence does not increase the amount of core habitat that can be reached by a particular organism.
Branch	Connects bridges, loops, perforations, or islets, but not core areas. They correspond to contiguous elongated forest clusters that emanate from one forest area and do not reach any other forest area at another end.
Islet	Small, isolated fragments degraded due to the edge effect, which do not contain core areas because of their small size.

Results

The area under the curve (AUC) for the potential distribution model of *Leopardus pardalis* was 0.87. The variables with the highest percent contribution were precipitation (driest month, driest quarter, and warmest quarter), temperature seasonality, annual temperature range, and mean temperature of the driest quarter. The potential distribution model indicated that 22.2 % of the study area (189,337

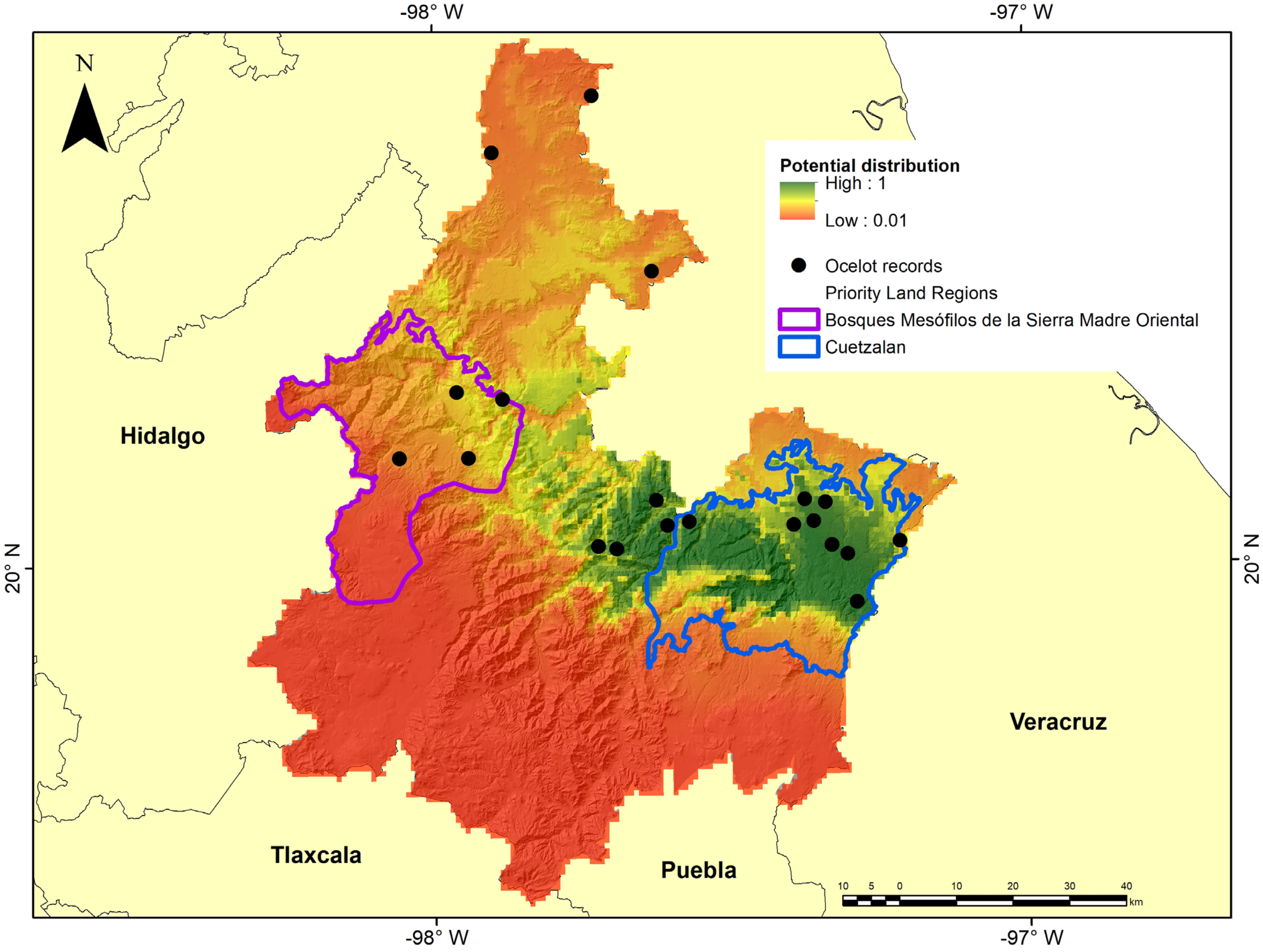

Figure 2. Potential distribution areas and records of *Leopardus pardalis* in the Sierra Norte de Puebla. The blue and purple polygons indicate the borders set for Priority Land Regions.

ha) has conditions compatible with the presence of the ocelot. It also shows areas with potential distribution with no records for the species, such as the Lakes and Volcanoes of Anahuac subprovince. In addition, it showed potential areas within the Bosques Mesófilos de la Sierra Madre Oriental and Cuetzalan Priority Land Regions (Figure 2).

Process of habitat change of *Leopardus pardalis*. From 1993 to 2020, the annual rate of change was -0.18 %. During this period, the area covered by natural vegetation decreased from 63 % to 47 %, while anthropic coverage increased from 36 % to 52 % (Table 2). The mountain cloud forest lost area at an annual rate of -2.4 %, while the medium evergreen forest and the oak forest decreased in area at annual rates of -1.4 % and -2.3 %, respectively. On the other hand, agroforestry crops, rainfed agriculture, and human settlements recorded an expansion in area during this period, of 1.79 %, 1.0 %, and 2.06 %, respectively (Table 2).

Table 2. Area (ha) and percentage of natural and anthropogenic cover in the *Leopardus pardalis* habitat in the Sierra Norte de Puebla, Mexico, for the years 1993, 2003, and 2020.

		1993		**2003**		**2020**		**Overall change 1993–2020**
	Cover Classes	**Area (ha)**	**%**	**Area (ha)**	**%**	**Area (ha)**	**%**	
Natural covers	Mountain cloud forest	14,591	7.47	10,855	5.28	7,623	4.52	-2.40
	Mediumn evergreen forest	71,660	36.68	105,187	51.11	48,697	28.89	-1.43
	Oak forest	26,709	13.67	17,288	8.40	14,033	14.26	-2.38
	Pine-oak forest	1,113	0.01	1,735	0.84	1,775	2.83	1.73
	Coniferous forest	1,236	0.12	918	0.45	1,301	0.77	0.19
	Oak-pine forest	9,964	5.10	10,765	5.23	15,374	15.05	1.61
	Total percent		63.06		71.31		66.33	
Anthrogenic covers	Rainfed agriculture	3,226	1.65	3,950	1.92	4,280	0.59	1.05
	Induced pastures	20,197	10.34	1,339	0.65	15,780	0.94	-0.91
	Agroforestry crops	47,521	24.33	52,149	25.34	77,041	32.06	1.79
	Human settlements	1,222	0.63	1,594	0.78	2,130	0.08	2.06
	Total percent		36.94		28.69		33.67	-0.18

Among the processes of plant cover change in the habitat of *Leopardus pardalis*, the greatest transformation was recorded in the medium evergreen forest from 1993 to 2003, which was converted to agroforestry crops, rainfed agriculture, and induced pastures (representing a 27 % loss). Five-point two percent of the mountain cloud forest area was converted mainly to agroforestry crops and induced pastures. Oak forests were replaced by induced pastures and agroforestry crops (3.3 % loss of total area; Table 3). From 2003 to 2020, 24 % of the area of medium evergreen forest was replaced by agroforestry crops and induced pastures, 4.3 % of the mountain cloud forest area was replaced by rainfed agriculture and agroforestry crops, 6.5 % of the area of oak forests was converted to agroforestry crops, and 1.9 % of oak-pine forests was replaced mainly by rainfed agriculture and agroforestry crops (Table 3).

The greatest natural vegetation recovery from 1993 to 2003 was recorded in medium evergreen forest, mountain cloud forest, and oak forest. From 2003 to 2020, the greatest recovery was observed in medium evergreen forest, mountain cloud forest, oak forest, and oak-pine forest (Table 3).

Structure of *Leopardus pardalis* habitat fragments. From 1993 to 2003, the number of optimal habitat fragments dropped from 639 to 533; however, the habitat area (200,174 ha to 208,459 ha) and the mean fragment size increased (Table 4). Between 2003 and 2020, the number of fragments increased, although the habitat area and mean fragment size decreased (Table 4). As for fragments with areas greater than 100 ha, 12 fragments were quantified in 1993; this number increased in 2003 (18 fragments) and then decreased in 2020 (16 fragments). An average Euclidean distance between fragments of 7.3 km (± 10.5 km) was calculated for 1993; subsequently, it increased to 9.4 km (± 9.1 km) in 2003 and then decreased to 6.6 km (± 9.8 km) in 2020 (Table 4).

Spatial fragmentation patterns of the optimal habitat of *Leopardus pardalis*. The results of the MSPA analysis of habitat fragments between 1993 and 2020 indicate a decrease in the percentage of habitat covered by the loop (yellow), bridge (red), and perforation (blue) categories. In contrast, the percentage of edge, branch, and islet decreased from 1993 to 2003 (Figure 3a, b), although they increased in 2020 (Figure 3c). The same change trend was observed regarding the number of elements in the morphological categories. The number of core area, loop, branch, and islet elements decreased from 1993 to 2003 and subsequently increased in 2020. From 1993 to 2020, the number of loop, perforation, and bridge elements decreased (Table 5).

Table 3. Transitions of *Leopardus pardalis* habitat covers, expressed as a percentage, in the Sierra Norte de Puebla during 1993 to 2003 and 2003 to 2020. Mountain cloud forest (Mcf), medium evergreen forest (Mef), pine-oak forest (Pof), coniferous forest (Cf), oak forest (Of), oak-pine forest (Opf), agroforestry crops (Agro), rainfed agriculture (Ra), induced pastures (Ip), human settlements (Hs). The percentage of area that remains unchanged from one year to the next is indicated in bold. Values above the diagonal indicate area losses, and values below the diagonal indicate gains.

	1993-2003	**Mcf**	**Mef**	**Of**	**Pof**	**Cf**	**Opf**	**Ra**	**Ip**	**Agro**	**Hs**	**Total loss**
Natural covers	Mcf	**0.355**	0.607	0.169	0.004	0.018	0.328	0.045	0.687	3.364	0.060	5.28
	Mef	0.508	**12.659**	0.602	0.001	0.026	0.073	1.811	6.101	18.359	0.239	27.21
	Of	0.387	0.215	**3.036**	—	0.006	0.672	0.376	1.244	0.891	0.118	3.31
	Pof	0.023	0.103	0.096	**0.001**	—	0.047	0.004	0.033	0.110	0.008	0.20
	Cf	0.029	0.064	0.093	—	**0.005**	0.080	0.002	0.020	0.209	0.005	0.32
	Opf	0.511	0.951	0.284	—	0.010	**0.842**	0.252	0.605	1.322	0.075	2.25
Anthropogenic covers	Ra	4.123	2.685	0.336	—	—	0.338	**0.232**	0.431	0.075	0.042	0.55
	Ip	0.038	1.167	0.179	0.001	0.002	0.068	0.016	**0.170**	0.052	0.027	0.08
	Agro	2.483	7.416	3.432	0.001	0.072	1.327	0.082	1.583	**13.94**	0.068	0.07
	Hs	0.042	0.211	0.243	—	0.002	0.055	0.034	0.187	0.037	**0.050**	
	Total recovery	8.146	12.812	4.663	0.002	0.086	1.787	0.133	1.770	0.037		
	2003-2020											
Natural covers	Mcf	**0.290**	0.584	0.453	—	0.013	0.242	0.121	0.050	2.791	0.050	4.30
	Mef	0.199	**19.480**	0.726	0.041	0.020	0.642	0.340	5.206	17.816	0.027	24.82
	Of	0.632	0.979	**1.060**	—	0.064	0.314	0.062	0.060	6.037	0.048	6.59
	Pof	0.157	0.427	0.443	**0.014**	0.011	0.250	0.189	0.043	0.217	0.048	0.76
	Cf	0.080	0.297	0.063	0.007	**0.009**	0.068	0.015	0.015	0.201	0.010	0.31
	Opf	0.467	0.854	1.973	0.030	0.020	**0.906**	0.692	0.112	0.964	0.153	1.92
Anthropogenic covers	Ra	1.016	1.342	0.087	0.001	—	0.051	**0.047**	0.007	0.057	0.014	0.08
	Ip	0.052	2.499	0.106	0.009	0.001	0.039	0.035	**0.019**	0.127	0.034	0.16
	Agro	1.573	6.891	1.307	0.131	0.280	2.526	0.194	0.082	**14.262**	0.047	0.05
	Hs	0.006	0.023	0.012	—	—	0.004	0.007	0.003	0.003	**0.019**	
	Total recovery	4.182	13.312	3.990	0.178	0.300	2.619	0.235	0.085	0.003		

Contribution of *Leopardus pardalis* habitat connectivity to the SNP landscape. From 1993 to 2020, the most important habitat fragment for connectivity had a dIIC value of 99.7, decreasing in 2003 (dIIC = 97.7), and then increasing in 2020 (dIIC = 99.9) (Figure 4). The same trend was observed with the area of this fragment, increasing from 1993 to 2003 (from 230,152 ha to 240,439 ha) and decreasing in 2020 (197,595 ha). From 1993 to 2003, seven fragments were recorded in the very low and low categories, respectively, with dIIC values of less than 1 % (Figure 5a, b). In 2020, 15 fragments were recorded in the very low category. Two fragments were also quantified in the high category for connectivity during 1993 (2 %); from 2003 to 2020, no fragments were observed in this category (Figure 5b, c).

Discussion

The distribution patterns of *Leopardus pardalis* in the study area indicate that it is located along one of the most important mountain ranges in the state of Puebla, the Sierra Madre Oriental, and one of the most extensive plains that covers part of Veracruz, the Gulf of Mexico Plain, which includes the portion of the Carso Huasteco and Chiconquiaco physiographic subprovinces. Ocelots have been reported in some areas of Hidalgo and Puebla (Ramírez-Bravo *et al.* 2010b; Hernández-Flores *et al.* 2013), which may indicate their mobility through the Sierra Madre Oriental. Ceballos-González *et al.* (2006) point out that the sites where favorable conditions for the presence of ocelots most probably exist are found in the Pacific Coastal Plains and the Gulf of Mexico, as well as throughout the south of México in the humid tropics (Di Bitetti *et al.* 2006; Dillon and Kelly 2007); however, ocelots can also be found in sub-humid climates (Trolle and Kerry 20036; Maffei *et al.* 2005). These results are consistent with our findings, where the potential distribution model indicates that precipitation (driest month, driest quarter, and warmest quarter) contributes to explaining the potential distribution of the ocelot in the study area. However, no records were obtained in the Lakes and Volcanoes of Anahuac subprovince, so the potential distribution of the ocelot was low in this region (probability less than 0.1). This finding is probably consistent with the fact that this region has arid climates with extreme temperatures and sparse vegetation, characteristics that are unfavorable for the presence of the species (Martínez-Calderas *et al.* 2011).

Change of *Leopardus pardalis* habitat cover. The optimal habitat still maintains 25 % of medium evergreen forest, 7 % of oak forest, and 4 % of mountain cloud forest, although

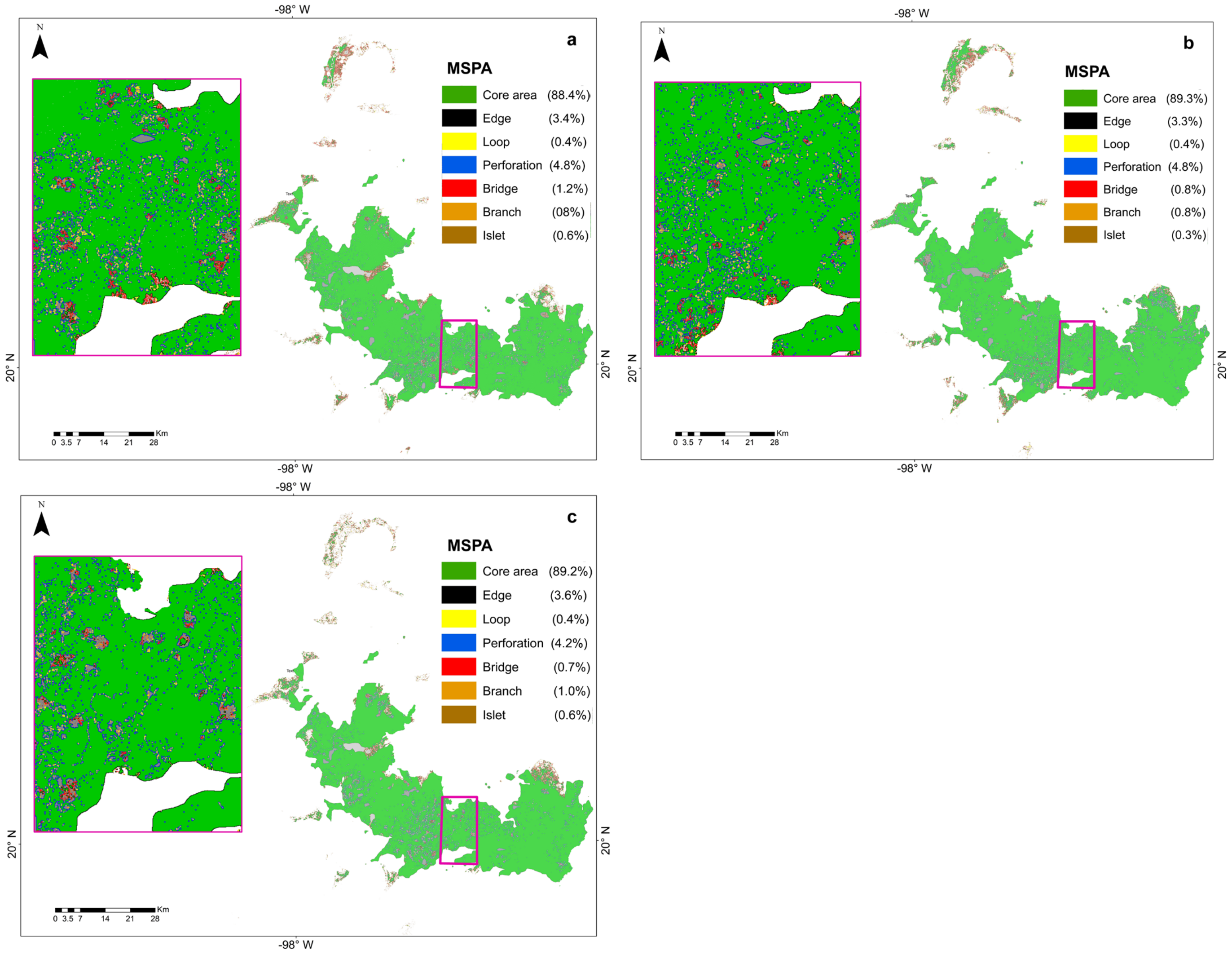

Figure 3. Morphological classification of spatial fragmentation patterns (MSPA) of the optimal habitat of *Leopardus pardalis* in 1993 (a), 2003 (b), and 2020 (c) in the Sierra Norte de Puebla.

the latter vegetation may be mostly secondary because about 90 % of the vegetation in the Sierra Norte de Puebla has been altered (Galván *et al.* 1999). Evangelista-Oliva *et al.* (2010) state that there were still 15.1 % of areas with tropical forest and mountain cloud forest in this region in 2003, although they included advanced-stage secondary vegetation, coinciding with the increase in vegetation loss in recent decades (Mass *et al.* 2004; Rosete-Vergés *et al.* 2014). It is estimated that more than 50 % of mountain cloud forest area in México was lost between 1968 and 2011 (Ochoa-Ochoa *et al.* 2017). The data obtained in the present study is consistent with this estimate, since, from 1993 to 2020 in the distribution range of *L. pardalis*, the area of mountain cloud forest underwent a 54 % decrease at an annual rate of change of -2.4 %, a figure similar to that observed for Latin America (-2.9 %; Armenteras and Rodríguez-Eraso 2014). It has been pointed out that the main cause of deforestation of tropical forests in Mexico is their conversion to pastures (Williams-Linera *et al.* 2002; Cayuela *et al.* 2006); however, in the study area, these forests were mainly replaced by shade coffee plantations.

In the study area, shaded coffee plantations are the main source of income for the agricultural sector (Evangelista-Oliva *et al.* 2010). The coffee register indicates an area of 61,460 hectares cultivated with coffee, distributed in 548 localities in 46 municipalities of the state of Puebla (SIAP 2005). In addition, in 2017, this productive activity covered 18.86 % of the region, making this system crucial for the conservation of biodiversity (Moguel and Toledo 1999; Williams-Linera *et al.* 2002; Pineda-López *et al.* 2005; Redo *et al.* 2009; Perfecto and Vandeermer 2010). Shade coffee plantations have been considered biodiversity refuges with slightly modified land use, since they are generally established in such a way that only the understory is replaced by coffee trees, maintaining elements of the native vegetation; sometimes, some fruit and timber trees are also included (Moguel and Toledo 1999). Although some studies question the biodiversity conservation aspect of these production systems (Rappole *et al.* 2003), others point out that diversified shade coffee plantations are a habitat that may have less impact on biodiversity compared to other activities such as cattle ranching and seasonal or permanent crops, although they may not have the same species richness as native forests (Greenberg *et al.* 1997; Cruz-Lara *et al.* 2004).

The greatest recovery in vegetation cover from 1993 to 2020 was recorded in medium evergreen forest, mountain cloud forest, and oak forest. This recovery may be related to the abandonment of agricultural areas, the shift in productive activities, proper forest management, and the implementation of reforestation programs (TuiránTuiran 2002; García-Barrios *et al.* 2009). The abandonment of farmland in the study area is likely due to the decrease in subsidies for agriculture and livestock raising implemented by the Mexican government since 1994 (De Janvry *et al.* 2001; Pascual and Barbier 2007). It was also observed that part of this recovery of vegetation cover occurred along with the decrease in coffee plantations. Espinoza-Guzmán *et al.* (2020) points out that from 1993 to 2017, shaded coffee plantations in Veracruz were abandoned and mostly evolved into secondary vegetation, which is related to low coffee productivity due to pests and diseases, among other factors. Some research indicates that the abandonment of agricultural land, the growth of secondary forests, and the recovery of forest cover could influence the decrease in the rate of change (Muñoz-Villers and López-Blanco 2008; García-Barrios *et al.* 2009; López-Barrera *et al.* 2014).

Table 4. Values of changes (1993, 2003, and 2020) in the structure and configuration of *Leopardus pardalis* habitat fragments in the Sierra Norte de Puebla.

	1993	2003	2020
Number of optimal habitat fragments ≤ 100 ha	639	533	904
Number of optimal habitat fragments ≥ 100 ha	12	18	16
Euclidean distance between fragments (m)	6,682	7365	9,423
Fragment Shape Index	11	9.4	7.3
Mean Fragment Edge (m)	169	260	301
Mean Fragment Size (ha)	310	391	214
Total habitat area (ha)	197,445	217,838	188,038

Structure and configuration of *Leopardus pardalis* habitat fragments. In recent decades, the ocelot habitat has been affected by a progressive fragmentation of vegetation patches due to their shrinking area associated with land-use change. It has been suggested that the conversion of carnivore habitats is related to population declines (Ripple *et al.* 2014). Likewise, local disturbances, such as land-use changes, can influence the home range of the ocelot, becoming a potentially more sensitive indicator of the impact of disturbances (Cruz *et al.* 2019). For example, some studies indicate that ocelots prefer closed-canopy areas and avoid open areas (López-González *et al.* 2003; Harveson *et al.* 2004; Martínez-Calderas *et al.* 2011; Torres-Romero *et al.* 2017; Galindo-Aguilar *et al.* 2019). Cruz *et al.*

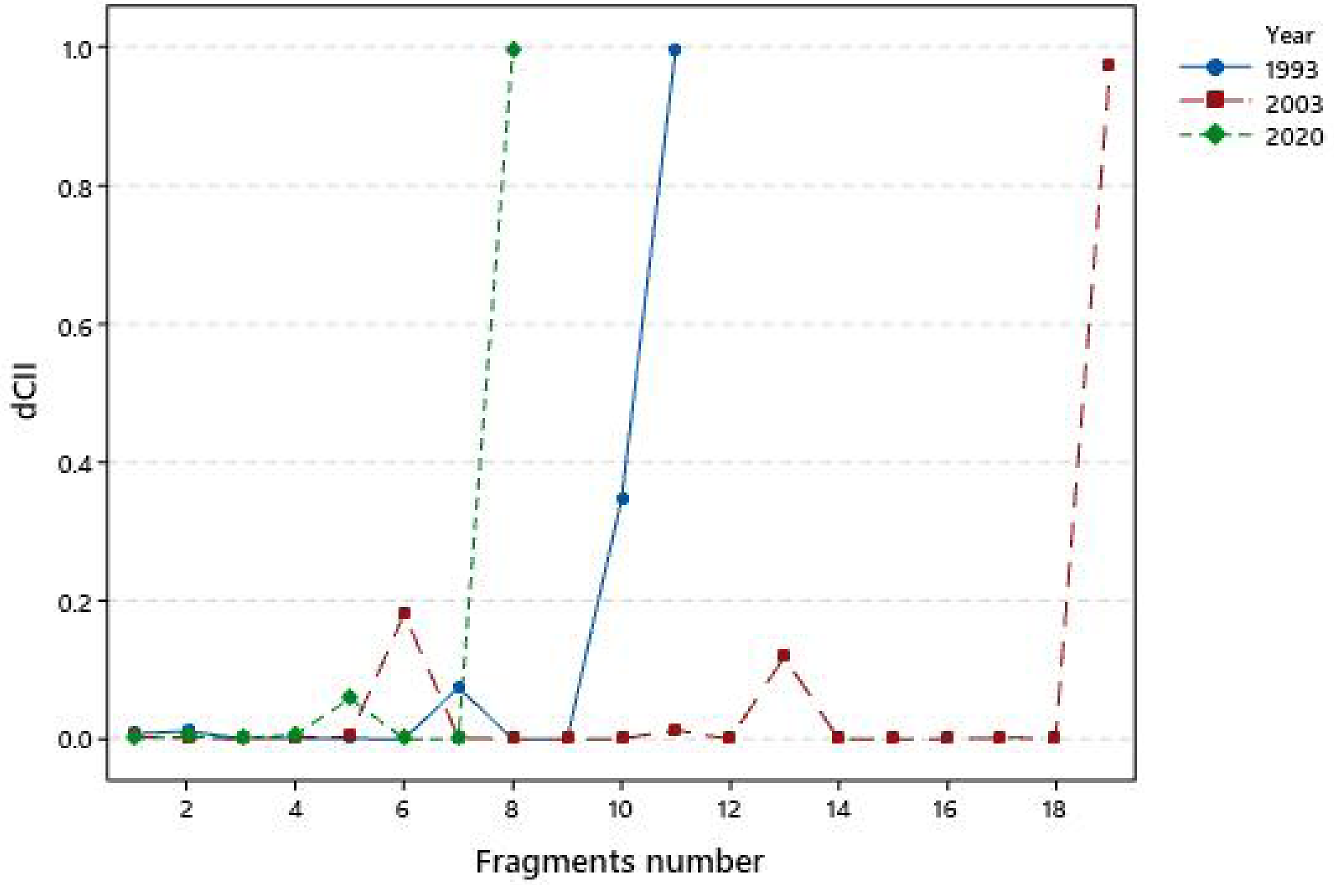

Figure 4. Integral Index of Connectivity (dIIC) of *Leopardus pardalis* optimal habitat fragments larger than 100 hectares during 1993, 2003, and 2020 in the Sierra Norte de Puebla.

(2018) point out that ocelots prefer better-preserved areas, whereas smaller felines are more prevalent in suboptimal habitats (Nowell and Jackson 1996; De Oliveira *et al.* 2010; Di Bitetti *et al.* 2010). In addition, in areas with less tree cover, medium and large prey, which are important for the ocelot, are less abundant (Cruz et al. 2018). In addition, these areas pose greater threats (presence of dogs, higher road density, and others), which may also negatively affect the presence of this species in open areas (Tewes and Everett 1986; López González et al. 2003; Haines *et al.* 2005; Cruz *et al.* 2019).

In the present study, the largest number of ocelot records were obtained in areas with agricultural activity. Some studies describe that ocelots tolerate fragmentation (Gil-Fernández *et al.* 2017) and move across disturbed vegetation (crops, pasture, scrub, and secondary vegetation) (Cruz-Rodríguez *et al.* 2015). According to Bisbal (1991), ocelots are relatively tolerant to habitat modification compared to other large felines, such as jaguars and pumas, because their home range is smaller and their prey are abundant, including rodents, reptiles, and birds. However, other studies indicate that ocelots can use different habitats, both disturbed and conserved (Kolowski and Alonso 2010), according to their availability (Fusco-Costa *et al.* 2010), which are frequently used to move towards more structurally complex and closed fragments (López González et al. 2003; Cruz *et al.* 2018).

The percentage of large habitat fragments with core area decreased from 2003 to 2020, while the number of smaller fragments increased. Galindo-Aguilar *et al.* (2019) also observed a decrease in the size of *Leopardus pardalis* habitat fragments in the Sierra Negra de Puebla and considered that the remaining fragments are insufficient to sustain an ocelot population in this region. In this sense, it has been observed that medium and small felines are adversely affected by habitat loss and that ocelots are most affected by this decrease in vegetation cover, compared to smaller species with which it coexists, such as *Leopardus weidii* and *Herpailurus yagouaroundi* (Cruz *et al.* 2019). Nowell and Jackson (1996) point out that some feline species depend on large, preserved fragments, and others are more tolerant of degraded habitats because they are more flexible regard-

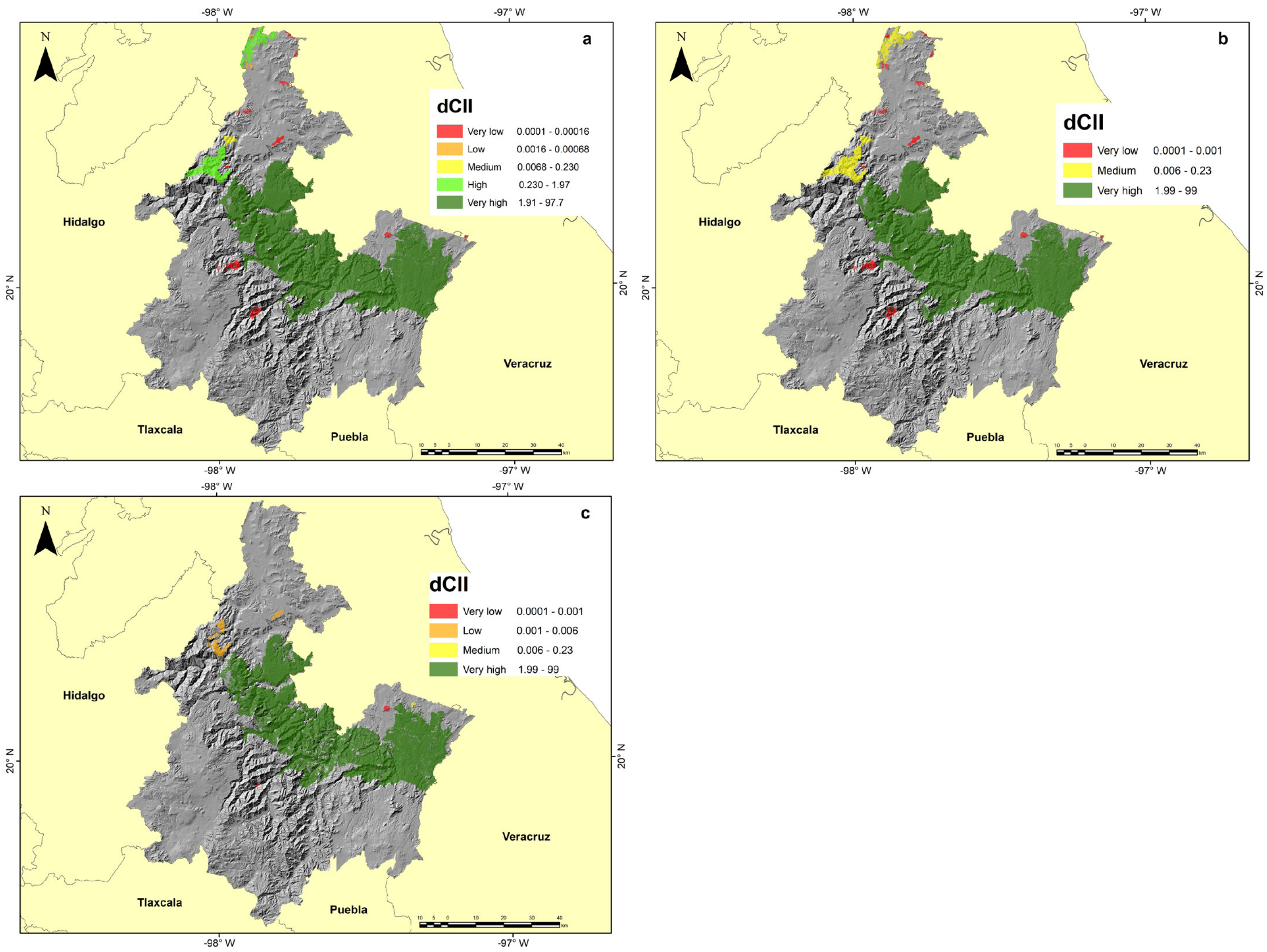

Figure 5. Changes in integral index of connectivity (dIIC) values and importance of *Leopardus pardalis* habitat fragments in the functional connectivity of the landscape of the Sierra Norte de Puebla during 1993 (a), 2003 (b), and 2020 (c).

ing habitat requirements. Land-use change, in addition to modifying natural vegetation, also alters the spatial configuration and quality of the remaining fragments, resulting in smaller fragments being more exposed to human interference (Fischer and Lindenmayer 2004; Bennett and Saunders 2010), which could have major implications for the conservation of the *L. pardalis* habitat (Ludlow and Sunquist 1987; Dillon and Kelly 2007; Lambardi et al. 2022).

The percentage of islet categories decreased in 2003 and then increased in 2020, which could indicate that the habitat of *Leopardus pardalis* includes a high number of small habitat fragments, isolated by the fragmentation process, with a gradual loss of core area. The increase in islet elements coincides with the increase in habitat fragments smaller than 100 ha, which may be insufficient to maintain ocelot populations in the study area (Moreno *et al.* 2012; Torres-Romero *et al.* 2017). On the other hand, it could be a gain in transit habitat fragments, which reduces the resistance of the anthropic matrix. These could function as intermediate elements, temporary shelters, and transit sites between larger habitat fragments (Correa-Ayram and Mendoza-Cantú 2013). Smaller fragments could play a key role in promoting connectivity for the ocelot and other species in the study area (Saura *et al.* 2014; Diniz *et al.* 2021).

The classes categorized as connectors, bridge, and loop elements decreased between 1993 and 2020. This decrease is consistent with the increase in Euclidean distance from habitat fragments, which could be related to the fragmentation and loss of the *Leopardus pardalis* habitat in the study area. Correa-Ayram and Mendoza-Cantú (2013) state that the decrease in bridge and loop connectors may negatively affect habitat connectivity and force ocelots to take a longer and more expensive route to cover the same habitat fragment. By facilitating dispersal and sustaining long-distance movements, loop and bridge elements allow species to colonize suitable new fragments and expand their range (Saura *et al.* 2014), which is particularly important when considering land-use changes in the region. Maintaining landscape connectors and transit paths could be critical for *L. pardalis* and other widely distributed carnivores in fragmented landscapes (Beier and Noss 1998; Crooks *et al.* 2011; Cruz-Rodríguez *et al.* 2015; Khosravi *et al.* 2018; Ashrafzadeh *et al.* 2020). For example, Cruz *et al.* (2018) observed that ocelots are adversely affected by the distance between fragments. These authors also mention that the presence of felines in small fragments could depend on the presence of other nearby populations; therefore, connectivity between fragments is essential for small and medium-sized felines in anthropic landscapes.

Table 5. Number of elements of the morphological categories of the *Leopardus pardalis* optimal habitat in the Sierra Norte de Puebla in 1993, 2003, and 2020.

Categories	**Number of elements**		
	1993	**2003**	**2020**
Core area	2,254	1,893	2,231
Edge	1,282	1,110	1,436
Loop	3,158	3,034	2,482
Perforation	5,435	5,416	3,950
Bridge	2,686	2,333	2,272
Branch	7,688	7,626	8,244
Islet	4,826	2,878	4,291

Elements considered branches are areas derived from fragmentation processes due to the rupture of bridges connecting two habitat fragments, particularly islets, but not core areas (Soille and Vogt 2009; Correa-Ayram and Mendoza-Cantú 2013). In the present study, an increase of this element was observed in the habitat of *Leopardus pardalis* during the period analyzed, which could indicate an increasing rupture of bridges between smaller fragments, thus decreasing the connectivity between them. Fragmentation can cause loss of connectivity with adverse effects on the persistence of other carnivores, increasing the risk of extinction (Saura and Pascual-Hortal 2007; Cavalcanti and Gese 2009; Reding *et al.* 2013). In addition, the loss of structural connectivity can also alter the movement patterns of felines; by increasing the isolation between fragments, species consumed as prey become less abundant (Zemanova *et al.* 2017).

Regarding the habitat fragmentation processes of *Leopardus pardalis*, an increase in the percentage and number of edge elements was observed between 1993 and 2020. The increase in edge fragments of the ocelot's habitat may be related to the constant extraction of wood for fuel and the conversion of small areas for agriculture (Ochoa-Gaona 2001; López-Barrera *et al.* 2014). The increase of edges leads to a higher risk of mortality for those species specialized in the habitat inside the fragment (Murcia 1995), increasing the probability of local extinction. For example, large-sized felines are more abundant in fragments with large core areas, making them susceptible to edge effects, where they conflict with livestock and humans (Luskin *et al.* 2017; Cruz *et al.* 2018). Lombardi *et al.* (2022) observed that ocelots avoid areas with edge habitats and are more prevalent in core areas of the fragment (Wang *et al.* 2019). Other felines with more flexible diets are more tolerant of edge habitats or even become more abundant in degraded habitats because they adapt to the changing prey availability near the edges (Prugh *et al.* 2009; Delibes-Mateos *et al.* 2014; Gil-Fernández et al. 20157; Cruz *et al.* 2018).

The number of perforation elements in the habitat increased from 1993 to 2020. It should be considered that the perforation is one of the initial stages in the habitat fragmentation process and begins when anthropogenic activities such as deforestation, produce small clearings that act as gaps within habitat fragments, which increase in area until they split the fragment, with the consequent reduction in its area (Forman 1995). In Mexico, some vegetation fragments are deforested from the interior to the edge, resulting in fragments without defined edges and a smaller core area; this could affect the conservation value of the remaining vegetation (López-Barrera *et al.* 2014). Although different studies point to the plasticity of ocelots to use different habitats according to their availability (Fusco-Costa *et al.* 2010; Kolowski and Alonso 2010; Cruz-Rodríguez *et al.* 2015; Gil-Fernández *et al.* 2017), their preference for more conserved habitats has also been recorded (López-González *et al.* 2003; Cruz *et al.* 2018). Habitat loss and fragmentation favor certain feline species and adversely affect others, depending on the predominant matrix type, as species differ in their environmental plasticity and ability to use suboptimal habitats (Ripple *et al.* 2014; Zanin *et al.* 2015).

Contribution of *Leopardus pardalis* habitat fragments to connectivity. The integral index of connectivity (dIIC) of the *L. pardalis* habitat was high compared to values obtained in other feline studies. For instance, Correa-Ayram *et al.* (2014) recorded dIIC values of 0.15 to 85 for the *Linx rufus* habitat between 1975 and 2008. Other studies of functional connectivity in terrestrial mammals in the mountain cloud forests of Veracruz indicate that low dIIC values indicate a serious threat to their persistence in fragmented landscapes. Pascual-Hortal and Saura (2008) consider that dIIC is a good indicator of habitat availability because it integrates the connectivity network and the area of fragments as an attribute. The fragment with the highest dIIC during the period analyzed is located in the central part of the study area (Figure 5), being the fragment with the largest surface area that could function as a bridge between ocelot populations of Puebla and those living in the north of Oaxaca. Cacelin-Castillo (2020) points out that ocelots are likely to use the lowest-quality habitat (northern Puebla, western Veracruz) only to disperse; therefore, the survival of the ocelot in the Sierra Madre Oriental and most of the eastern region of Mexico would depend on its ability to move in inhospitable fragments and get resources (Gil-Fernández *et al.* 2017). In addition, some studies have stressed the need to establish the Sierra Madre Oriental as a priority area as a biological corridor connecting ocelot populations between northern and southern Mexico (Grigione *et al.* 2009; Ramírez-Bravo *et al.* 2010b).

It was also observed that the best performance in the connectivity of the habitat of *Leopardus pardalis* occurred in fragments ≥ 2,000 ha. A minimal fragment size was previously identified as important for landscape connectivity (Pascual-Hortal and Saura 2007). In addition, it has been recorded that fragments of potential use as habitats that are most important for the overall connectivity of medium and large feline habitats are generally those fragments with the largest surface area (Ramírez-Reyes *et al.* 2016). Other studies report that large fragments are more important in the landscape since they can function as transit fragments and habitat simultaneously (Saura and Pascual-Hortal 2007; Pascual-Hortal and Saura 2008; Saura and Rubio 2010).

The increase in anthropogenic cover and the loss of natural vegetation in the habitat of *Leopardus pardalis* between 1993 and 2020 is associated with economic activities in the region. One of the ecosystems most affected by these activities is the mountain cloud forest. In these ecosystems, the advance of agricultural and livestock practices is high and jeopardizes the persistence of this type of vegetation. In addition, these alterations contribute to the increase in edge habitats and a decrease in core areas of the remaining habitat fragments of *L. pardalis*. However, the recovery of the medium evergreen forest from 1993 to 2003 stands out, attributable to factors that allowed the growth of secondary vegetation and the recovery of forest cover, such as land abandonment, changes in productive activities, and the implementation of reforestation programs.

The areas that recorded the presence of ocelots have optimum conditions to function as biological corridors in the Sierra Madre Oriental, in the portion that comprises the Sierra Norte de Puebla. In addition, *Leopardus pardalis* tends to prefer areas covered with primary vegetation, or at least with a similar structure and good connectivity, although they are able to move through the anthropic matrix. However, the study area shows continued growth of human settlements, which may exacerbate habitat loss. Areas with human settlements could affect the movements of *L. pardalis* because they generate greater resistance, unlike transit areas such as agroforestry crops. In this regard, components with buffer capacity, such as shade coffee plantations, include corridors and fragments with significant core areas habitat, which should be prioritized in conservation strategies, as they serve as core reserves and maintain the functional connectivity of the study area. However, a few habitat fragments located in the central part of the Sierra Norte de Puebla, corresponding to the Sierra Madre Oriental, were categorized as important and very important. Therefore, preserving these fragments would allow the functional connectivity within the region to be largely preserved.

We recommend systematically monitoring the areas adjacent to the study area to determine how anthropogenic activities affect the distribution of ocelots in the Sierra Madre Oriental. In addition, recording ocelots in contiguous areas provides relevant information that will support the development of a more robust habitat connectivity model to better understand the south-to-north dispersal of ocelot populations. The fragmentation of the Sierra Norte de Puebla is an issue that should be addressed strategically for the long-term conservation of the regional biodiversity in general and the ocelot in particular.

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