Mexican wolf habitat suitability analysis in historical range in the Southwestern US and Mexico

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Summary

In the last three decades, important efforts have been made to evaluate the habitat suitability for the reintroduction and long-term persistence of the Mexican wolf (*Canis lupus baileyi*) both in the US and Mexico. However, such efforts have used different methodological approaches and have covered only some portions of the historical distribution range of this subspecies, making it impossible to have a comprehensive understanding of where and how much habitat is left for maintaining long-term, viable free-ranging populations of the Mexican wolf. This project aims to fill this gap by carrying out a habitat suitability analysis across the whole historical range of the Mexican wolf, from southern Arizona and New Mexico and western Texas, in the US, to central Oaxaca, Mexico, using input information for both countries and under a uniform methodological scheme. We implemented an additive model integrating geographic information of critical environmental variables for the Mexican wolf, including climatic-topographic suitability, land cover use based on frequency of occurrences, ungulate biomass, road density, and human density. Data available for the ungulate biomass index was not robust enough to generate reliable rangewide estimates, so we present a series of maps representing different scenarios depending on the thresholds used in the anthropogenic factors (road and human density) and also with and without the inclusion of the ungulate biomass. We found concordant areas of high suitability irrespective of the scenario, suggesting that such areas are the most favorable to explore for future reintroductions. The largest suitable areas were found both in the US and Mexico, particularly the higher elevation areas of east central Arizona and west central New Mexico in the Mexican Wolf Experimental Populations Area Management (MWEPA) in the US, and in northern Chihuahua-Sonora and Durango in the Sierra Madre Occidental in Mexico. Our results suggest that there is still sufficient suitable habitat for the Mexican wolf both in the US and Mexico, but specific sites for reintroductions in Mexico and estimations of the potential number of wolves need to consider reliable field data of prey density, cattle density, land tenure, natural protected areas, safety to the field team, and acceptability of wolves by local people.

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Introduction

The Mexican wolf, *Canis lupus baileyi*, is currently one of the five recognized subspecies of gray wolf (*Canis lupus*) in North America and has been described as the smallest of all gray wolf subspecies in this continent. This subspecies lived in the arid areas and temperate forests of southwestern US and northern and central Mexico, in many different habitats at altitudes higher than 1300 meters above sea level (msl), including areas of chaparral, desert, grasslands, forests and temperate uplands (Gish 1977), but preferring those habitats with high ungulate biomass (McBride 1980).

The history of the extermination of the Mexican gray wolf is inextricably linked to the conquest of the West by the Euroamerican settlers. In the United States, the expansion to the West started in 1804 with the Lewis & Clark expedition (Lavender 1998) and continued throughout the century. Followed by colonization, an ecological catastrophe commenced and reached its climax with the railway construction, between 1863 and 1869. With the railroad, the influx of people and settlements increased all along those routes, and so did the need for goods and supplies. Along with the increase in cattle ranching and settlement (Brown 1983), a depletion of wild animal populations took place, in which the bison (*Bison bison*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and pronghorn (*Antilocapra americana*) experienced an exceptional population decline. These species were hunted for food, leather and fur. Some historians suggest that the amount of carcasses left in this period probably benefited the local predators (coyotes, bears, wolves) due to the increase of food in the form of carrion. As the abundance of wild prey decreased, the increasing human population demanded more food, thus cattle raising expanded and gradually replaced wild herds of bison and other ungulates that comprised the natural prey of wolves, including the elk (*Cervus elaphus*), white-tailed deer and mule deer (Brown 1983). After the short-term availability of meat as carrion for predators in the region, wolf populations may have been elevated and cattle predation increased, triggering the onset of human-predator intense competition.

During the first half of the 20th century, several environmental and political events happened that triggered direct actions against predators, particularly towards the wolf. In the late 19th and early 20th centuries a series of droughts (1880-1902) ended with one of the harshest winters recorded (NOAA 2016). Thousands of cattle were lost and hundreds of villages abandoned; surviving abandoned cattle became feral. Cattle became part of a new source of food for opportunistic predators/scavengers, like the wolf. In 1917, under the pressure from livestock associations in different states incurring the loss of cattle, predator extermination became a central goal and a government branch, the Predator and Rodent Control (PARC), was created to control harmful species; therefore, persecution and extermination of predators took on renewed force and trappers were hired across the United States for a substantial pay, driving the gray wolf to near extinction.

In the southwestern US, history was no different. Settlers in Arizona, New Mexico and Texas used various kinds of methods to eliminate the wolf population, so that by 1950 wolves were scarce. In Cochise Valley, a PARC report from 1926 states that after previous years and less than 50 wolves captured, the county was considered free of wolves. In 1951 another report concluded that the eradication program of wolves took only eight years to achieve the goal of eliminating the Mexican gray wolf, stating that this could be the first "conservation program" completed in Arizona. However, some people in Arizona and New Mexico complained about the constant incursion of gray wolves from Mexico, which did not have a predator control program. In 1949, Mexico and United States signed a binational treaty to control predators –known as the Convention of Nogales–, in which the control scheme was based on the prevention of serious livestock damage and for rabies control (Baker and Villa 1960). By this time sodium fluoroacetate (better known as 1080) was available. Workshops took place in the states of Chihuahua and Sonora to teach Mexican ranchers the adequate and safe use of this chemical. In 1958, a PARC report in Arizona stated that several reliable stockmen in Mexico reported no livestock predation since 1080 was implemented around 1950. The control was absolute, 20 years later, wolves were rarely seen and it was difficult to trap them.

Although it is not clear when the Mexican wolf went extinct in the wild (Hoffmeister 1986; Leopold 1959), by 1976 the USFWS listed the wolf (*C. lupus*) as an endangered species (Parsons 1996). At this time the population of the Mexican wolf in the wild was estimated at less than 50 individuals located in the Sierra Madre Occidental (Brown 1983). This designation encouraged efforts to prevent extinction and favored the creation of a captive breeding program, allocating resources to capture the last wolves in the wild. Between 1977 and 1980, the USFWS hired Roy McBride, an expert in wolf behavior and trapper, in order to capture the last wolves in the wild. McBride caught five wild wolves in the states of Durango and Chihuahua, Mexico. With these individuals (known as the McBride lineage) the US government launched a captive breeding program. Later, with the recognition of another two lineages, Ghost Ranch and Aragón (Hedrick et al. 1997), the captive breeding program became a binational effort. Today, it is considered a successful program having about 240 individuals of the three certified genetic lineages in several institutions both in the US and Mexico (Siminski 2016).

In 1996, the US government started preparations for the release and establishment of a nonessential experimental population of the Mexican wolf in the Blue Range Wolf Recovery Area (BRWRA). The first releases were in Arizona in 1998. The first Mexican Wolf Recovery Plan seeked “to conserve and ensure the survival of *Canis lupus baileyi* by maintaining a captive breeding program and re-establishing a viable, self-sustaining population of at least 100 Mexican wolves in the middle to high elevations of a 5,000-square-mile area within the Mexican wolf's historic range.” (USFWS 1982). Currently, this program has reached this goal by achieving a wild population of at least 113 individuals in the US. Nonetheless, as part of the ecological principles in species’ recovery, ‘redundancy’ (more than one population recovered) is an important element (Wolf et al. 2015), thus the identification of additional release areas was necessary. Therefore, parallel efforts began in Mexico in the early 1980s, with an interdisciplinary group interested in restoring the Mexican wolf in the country, generating different initiatives to determine the best sites in Mexico to establish a Mexican wolf population (CONANP 2009).

In October 2011, after a series of public meetings with ranchers and private owners, the first family group of Mexican wolves was released into the wild in the northern part of the Sierra Madre Occidental (Moctezuma-Orozco 2011). Five wolves (three females and two males) were set free in a private ranch in Sierra San Luis, Sonora. However, within the next two months, four of the wolves were killed, and a lone wolf headed south along the Sierra Madre Occidental in an approximately 400 km dispersing journey to end up in Madera municipality, in the state of Chihuahua. One year after the first release, another pair was released in a private ranch in Chihuahua (López-González et al. 2012), not far from one of the sites that the last single wolf remained for a couple of days during her journey. After another release in the same ranch, the pair produced the first wild litter in Mexico (CONANP 2013). Several other releases have been carried out since 2011, with the support of the private land owner; however, soon after release, the wolves broke apart and wandered away from the release site (CONANP 2014), highlighting the need to define the environmental and social variables that promote territorial pack stability. As many as 31 wolves run free in the mountains of the Sierra Madre Occidental as of April 2017.

Previous habitat suitability analyses for the Mexican wolf

Increasing human pressure constrains remaining habitat for wolves (Thiel 1985), thus an analysis of the available habitat for the reintroduction of the Mexican wolf (*Canis lupus baileyi*) both in Mexico and in the US is a key element for the recovery of the species in the wild. In the last 15 years there has been several efforts to identify suitable areas for the recovery of the Mexican wolf in either the US or Mexico (Araiza 2001; Martínez-Gutiérrez 2007; Araiza et al. 2012; Carroll et al. 2003; 2004, 2013; Hendricks et al. 2016), but only one published study (Hendricks et al. 2016) has attempted an analysis across the historic range of the Mexican wolf. For instance, Araiza et al. (2012) was not intended to be a comprehensive analysis of all potential habitat in Mexico, but rather an exercise to identify the highest priority areas to begin restoration. Others have used the best information available at the time (Carroll et al. 2003; 2004; Martínez-Gutiérrez 2007), but there have been advances in recent years in the type and quality of data available. The most recent analysis (Hendricks et al. 2016) produced an ecological niche model across the whole historical range of the Mexican Wolf and this potential distribution map was then refined with global land cover and human density maps, but the aim of the study was primarily to redefine the historical distribution of the Mexican wolf, rather than a habitat suitability analysis. Thus, there is an opportunity to increase our understanding of available wolf habitat across the historic range of Mexican wolf.

In order to support the recovery of the Mexican wolf it is important to base the geography of recovery on the best science available. With recovery planning currently underway, a habitat analysis becomes an urgent necessity. To fill this gap, we carried out a habitat suitability analysis aiming to identify areas holding favorable conditions for the reintroduction and recovery of the Mexican wolf across its historical range, in order to provide authorities of the two countries with reliable information for decision-making. Thus, the main goals of the present study were:

1) Identify suitable, high-quality habitat areas to carry out recovery actions of Mexican wolf populations in Mexico.

2) Estimate the potential number of wolves in those areas to serve as input for a Population Viability Analysis (PVA).

Methods

Analyses were carried out in six steps: (1) reconstruct the historical distribution of the Mexican wolf via ecological niche modeling; (2) compilation, organization and standardization of compatible environmental and anthropogenic habitat variables for the two countries; (3) estimate ungulate density across the historic range of the Mexican wolf; (4) model the habitat suitability across the historic range of the Mexican wolf; (5) identify the largest, continuous patches through a landscape fragmentation analysis; and (6) estimate the possible number of wolves in those suitable areas. Each phase is described below.

1. Reconstructing the historical distribution of the Mexican wolf

To infer the historical distribution of the Mexican wolf we followed an ecological niche modeling (ENM) approach. The ecological niche of a species is defined by a set of abiotic (e.g., climatic, topographic) and biotic (e.g., food, predators, pathogens) variables that fulfill the ecological requirements of a species (Hutchinson 1957; Soberón & Peterson 2005). However, its modeling and representation in a geographic fashion has often been constrained by our knowledge of the ecological requirements of species and, most importantly, by the available spatial information to construct the niche model. Partial data of ecological requirements or spatial information results in a partial representation of the ecological niche, generally the abiotic portion of it, because information of climatic and topographic features is broadly available worldwide (Soberón 2007).

Ecological niche modeling is a correlative approach between the occurrence records of a species and a set of environmental variables that define the scenopoetic niche of that species (*sensu* Hutchinson 1957). Niche modeling algorithms look for non-random associations between the environmental conditions of a region and the presence of the species; once these conditions are identified (*i.e.*, the scenopoetic niche), similar conditions are searched for across the study region and a map of the potential distribution of the species is produced (Peterson et al. 2011).

For these analyses, the first challenge was to define the historical limits of the Mexican wolf (*Canis lupus baileyi*) in order to select the records to model its niche. In the original description of the gray wolf (*Canis lupus*), 24 subspecies were recognized for North America (Goldman 1944; Hall & Kelson 1959). Further studies considering cranial morphometry and genetic analyses (Nowak 1995, 2003) reduced the number of subspecies to five, namely *C. l. arctos* (Arctic wolf), *C l. lycaon* (Eastern timber wolf), *C. l. nubilus* (Great Plains wolf), *C. l. occidentalis* (Rocky Mountain wolf), and *C. l. baileyi* (Mexican wolf), but all agree that the Mexican wolf is the most differentiated both genetically and morphologically (Heffelfinger et al. 2017).

Participants of the Mexican wolf recovery workshop in April 2016 in Mexico City, agreed the northern extent of the analysis area should include central Arizona-New Mexico up to the I-40 (in order to include all of MWEPA), continuing south to the southernmost occurrence records in Oaxaca, Mexico, and east to include western Texas and the Sierra Madre Oriental in Mexico (Fig 1).

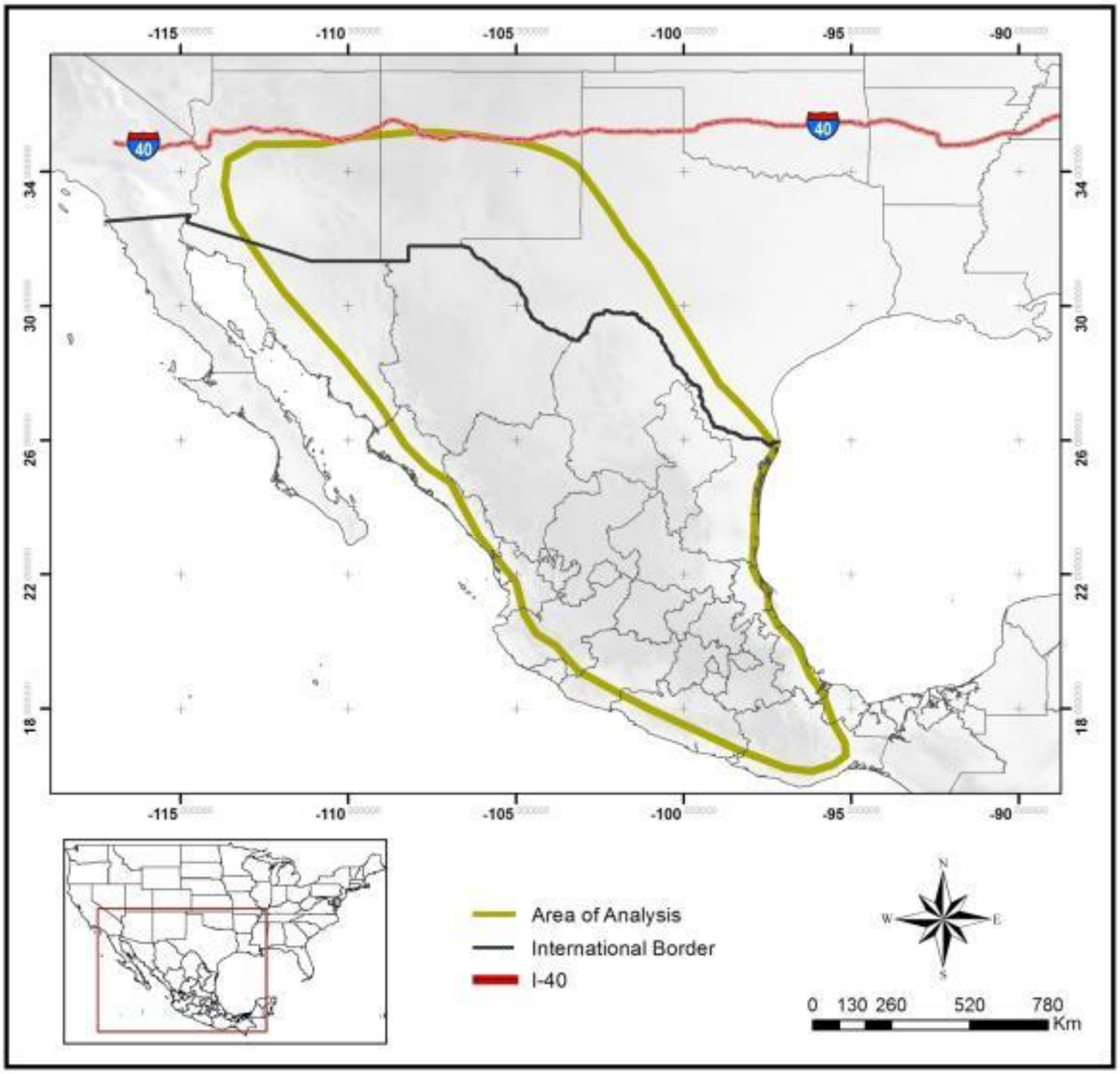

Figure 1. Map depicting the area of analysis.

Occurrence records

We compiled all occurrence records of the gray wolf (*Canis lupus*) available in the literature (Hall 1981, Brown 1983, Nowak 1995, Martínez-Meyer et al. 2006, Araiza et al. 2012), electronic databases (i.e., GBIF, Vertnet) and oral records from local trappers (from Brown 1983 and fieldwork of Jorge Servín), extending from 1848 to 1980. For those records within the polygon of analysis corresponding to the

Mexican wolf (Figure 1), we reviewed each record to accept or discard them based on the georeferencing accuracy. We divided the records according to their reliability into primary (i.e., those with skin or skull specimens preserved in a natural history collection) and secondary (i.e., those from observations or interviews). Only primary records were used to calibrate ecological niche models and secondary records were used for model validation. To avoid over-representation of particular environments due to sample bias that would result in model overfitting and bias, we filtered primary records to ensure a minimum distance of 25 km between each primary record (Boria et al. 2014). Thus, all records used for calibration were separated by a distance of at least 25 km to avoid clusters of points in areas where sampling effort has been higher. Validation records were filtered at a distance of 1 km. Filtering was conducted using the *thin* function in the spThin R package (Aiello-Lammens et al. 2015). Our final dataset to model the geographical distribution of the Mexican wolf consisted of 41 primary occurrences and included all historical records from the Blue Range Wolf Recovery Area (BRWRA) to the south (Fig. 2).

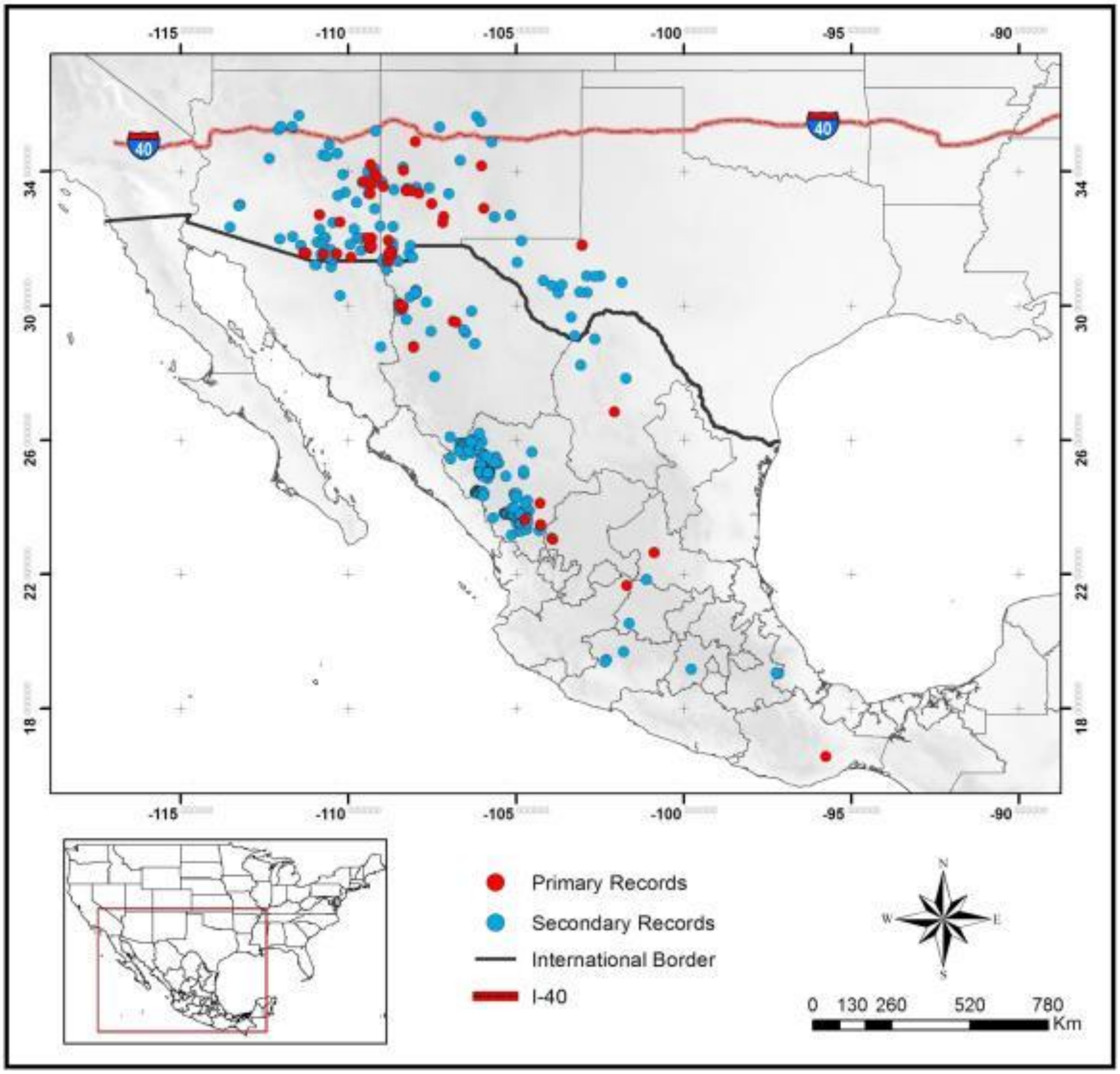

Figure 2. Occurrence records used for the construction of niche models. Primary records (for calibration) are shown in red and secondary records (for validation) are shown in blue. See text for details.

Environmental layers

We used 19 climatic variables obtained from the WorldClim database (Hijmans et al. 2005; Table 1) that have been extensively used in the ecological niche modeling field for thousands of species worldwide, including the Mexican wolf (Hendricks et al. 2016). We also included three topographic variables: elevation, slope and topographic heterogeneity (calculated as the standard deviation of elevation) from the Hydro 1k database (USGS 2008). To avoid model overfitting we used only the most informative variables. We reduced the number of variables using the MaxEnt program, which has implemented a permutation method to identify the relative contribution of all variables to model performance (Phillips et al. 2004; 2006; Searcy & Shaffer 2016). Thus, we selected only those variables with a relative contribution to model performance >1% (Table 1). The resolution of all variables was set to 0.008333 decimal degrees, which corresponds approximately to 1 km^2.

Table 1. Environmental abiotic variables selected (X) for building ecological niche models for the extended and restricted sets of occurrence data.

Variable	**Selected**
Elevation	X
Slope	X
Topographic Index	X
bio 1: Annual Mean Temperature	X
bio 2: Mean Diurnal Range	X
bio 3: Isothermality	X
bio 4: Temperature Seasonality	
bio 5: Max Temperature of Warmest Month	
bio 6: Min Temperature of Coldest Month	X
bio 7: Temperature Annual Range	X
bio 8: Mean Temperature of Wettest Quarter	X
bio 9: Mean Temperature of Driest Quarter	X
bio 10: Mean Temperature of Warmest Quarter	
bio 11: Mean Temperature of Coldest Quarter	X
bio 12: Annual Precipitation	
bio 13: Precipitation of Wettest Month	X
bio 14: Precipitation of Driest Month	X

bio 15: Precipitation Seasonality	X
bio 16: Precipitation of Wettest Quarter	
bio 17: Precipitation of Driest Quarter	
bio 18: Precipitation of Warmest Quarter	
bio 19: Precipitation of Coldest Quarter	X

Ecological niche and distribution modeling

Niche modeling algorithms perform differently depending on the type (i.e., presence-only, presence-absence, presence-pseudoabsence, or presence-background), amount and spatial structure (e.g., aggregated, biased) of occurrence data (Elith et al. 2006). There is not a single algorithm that performs best under any condition (*i.e.*, Qiao et al. 2015); therefore, it is advisable to test more than one algorithm and evaluate the results to select one or more with the best performance (Peterson et al. 2011). Hence, to model the ecological niche and potential distribution of the Mexican wolf we used the following algorithms: Bioclim, Boosted Regression Trees (BRT), Classification and Regression Trees (CART), Generalized Additive Model (GAM), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MaxEnt), Random Forest (RF), and Support Vector Machine (SVM). These models were implemented using the R packages *sdm* (Naimi & Araújo 2016) and *dismo* (Hijmans et al. 2005), and MaxEnt was used in its own interface (Phillips et al. 2006). For those algorithms based on presence and absence data (e.g., GLM, GAM, MARS), we generated pseudo-absences randomly across the geographical region with the same minimum distance as presences (*i.e*., 25 km). The number of pseudo-absences used was based on the prevalence, i.e., the proportion of sites in which the species was recorded as present (Allouche et al. 2006; Peterson et al. 2011); however, prevalence usually is unknown and depends on the size of the analysis area (Peterson et al. 2011). We defined prevalence based on the results of the first niche model performed in MaxEnt, where it was of 0.3.

Thus, we multiplied the number of calibration and validation presences by three to get the number of absences according to prevalence (Table 2).

Table 2. Number of presences and pseudo-absences for calibration and validation used for ecological niche modeling.

Calibration		**Validation**	
Presences	**Pseudo-absences**	**Presences**	**Pseudo-absences**
41	123	296	888

We used calibration data to produce niche models for each algorithm under default settings. Potential distribution maps produced with these algorithms represent either an estimation of the probability of presence of the species or a suitability score, both in a continuous scale from 0-1. To make them comparable, we converted continuous maps into binary (presence-absence) based on a 10-percentile threshold value (i.e., we allowed 10% of the presence records fall outside the prediction map). We chose a 10-percent threshold value to account for some inaccuracy in the original collection locations (*e.g.*, locality description: “Chiricahua Mountains”).

Model validation

We validated each model using a set of metrics based on the models performance in correctly predicting presences and absences (Fielding & Bell 1997; Allouche et al. 2006). We selected the best models according to a combination of four metrics: omission and commission errors (i.e., the number of presences predicted as absences and vice versa), True Skill Statistic (TSS), and chi-squared values.

Niche models produced results with large variation. BRT and GLM produced overpredicted distributions (Fig. 3); according to the validation metrics, the algorithms that performed better were MaxEnt, RF, CART, and GAM (Table 3).

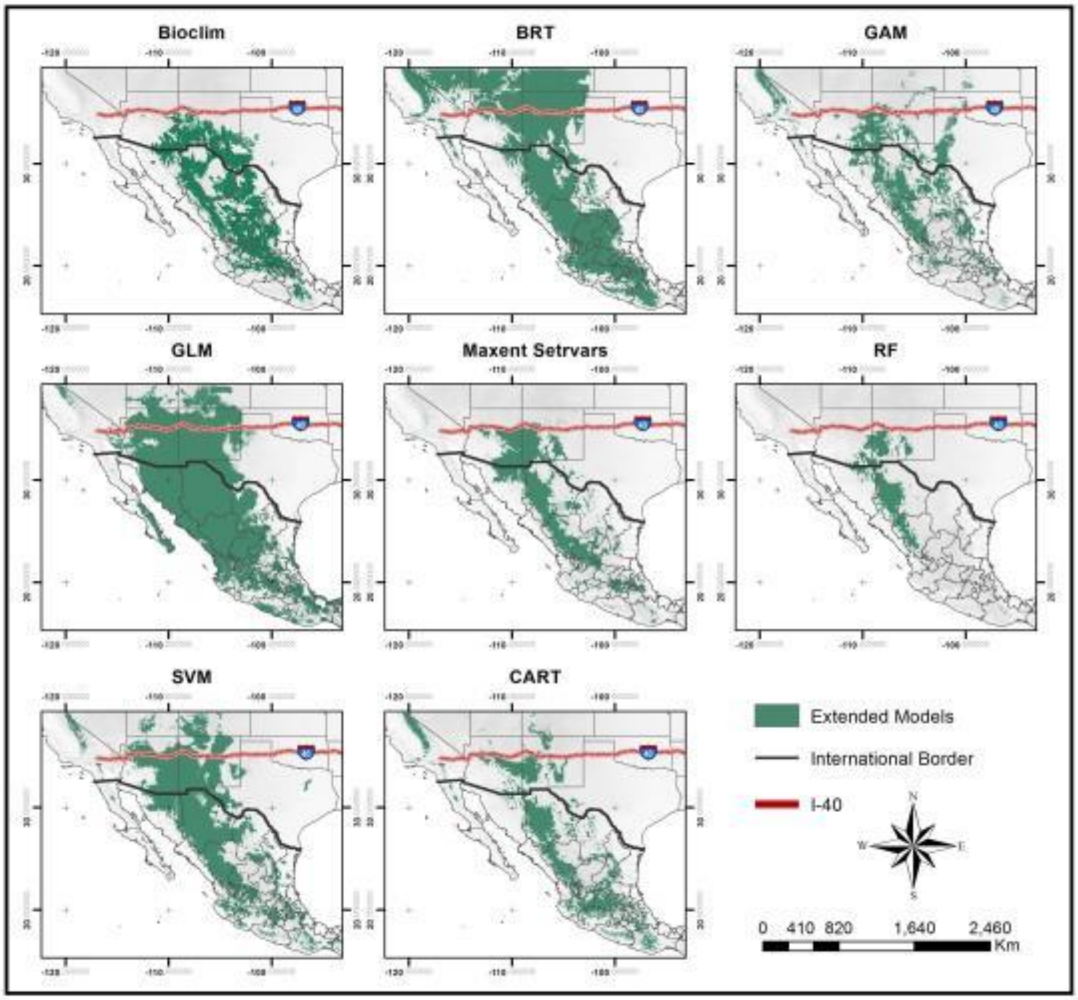

Figure 3. Binary maps of the potential geographical distribution of the Mexican wolf (*Canis lupus baileyi*) for each ecological niche modeling algorithm. Bioclim; BRT: Booted Regression Trees; GAM: Generalized Additive Model; GLM: Generalized Linear Model; Maxent: Maximum Entropy; RF: Random Forest; SVM: Support Vector Machines; CART: Classification and Regression Trees.

Table 3. Model performance metrics for binary predictions generated by each ecological niche modeling algorithm. In bold the selected binary predictions.

Metrics	Bioclim	BRT	CART	GAM	GLM	Maxent	RF	SVM
Omission error rate	0.23	0.06	**0.15**	**0.13**	0.02	**0.07**	**0.19**	0.03
Commission error rate	0.18	0.38	**0.14**	**0.13**	0.42	**0.12**	**0.04**	0.27
TSS	0.60	0.56	**0.72**	**0.74**	0.55	**0.81**	**0.77**	0.70
Chi-squared	928.88	402.05	**1513.69**	**1312.72**	352.03	**1768.84**	**4091.42**	753.43
p-value	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001

TSS: True Skill Statistic

Model assembling

We generated a consensus map with the four algorithms that performed better by summing each binary map. A consensus map expresses the areas where one, two, three, or four algorithms predicted the presence of appropriate abiotic conditions for the Mexican wolf. We selected the areas where two or more models coincided to predict the presence of the Mexican wolf and converted that in a binary map, representing the potential distribution of the subspecies. To approximate the historical distribution of the Mexican wolf from the potential distribution map, we discarded those climatically suitable areas within biogeographic regions that do not contain historical occurrence records of the species (e.g., Baja California), assuming that those regions have not been inhabited by Mexican wolves at least in the last two-hundred years (Anderson & Martínez-Meyer 2004) (Fig. 4).

The model shows that suitable climatic niche conditions for the Mexican wolf exist in central Arizona and New Mexico, The Sky Islands in southwestern US and northwestern Mexico, central-south New Mexico and western Texas in the US, and in the Sierra Madre Occidental, scattered mountain ranges in the Sierra Madre Oriental, along the Transvolcanic Belt in Mexico, and in the higher sierras of Oaxaca

(Fig. 4). This geographic description of the historical range of the Mexican wolf shows strong phylogeographic concordance with the distribution of the Madrean pine-oak woodlands and other endemic subspecies concomitant with this vegetation association, such as Mearns' quail (*Cyrtonyx montezumae mearnsi*), Coues' white-tailed deer (*Odocoileus virginianus couesi*), Gould's turkey (*Meleagris gallopavo mexicana*) and several others (Brown 1982; Heffelfinger et al. 2017).

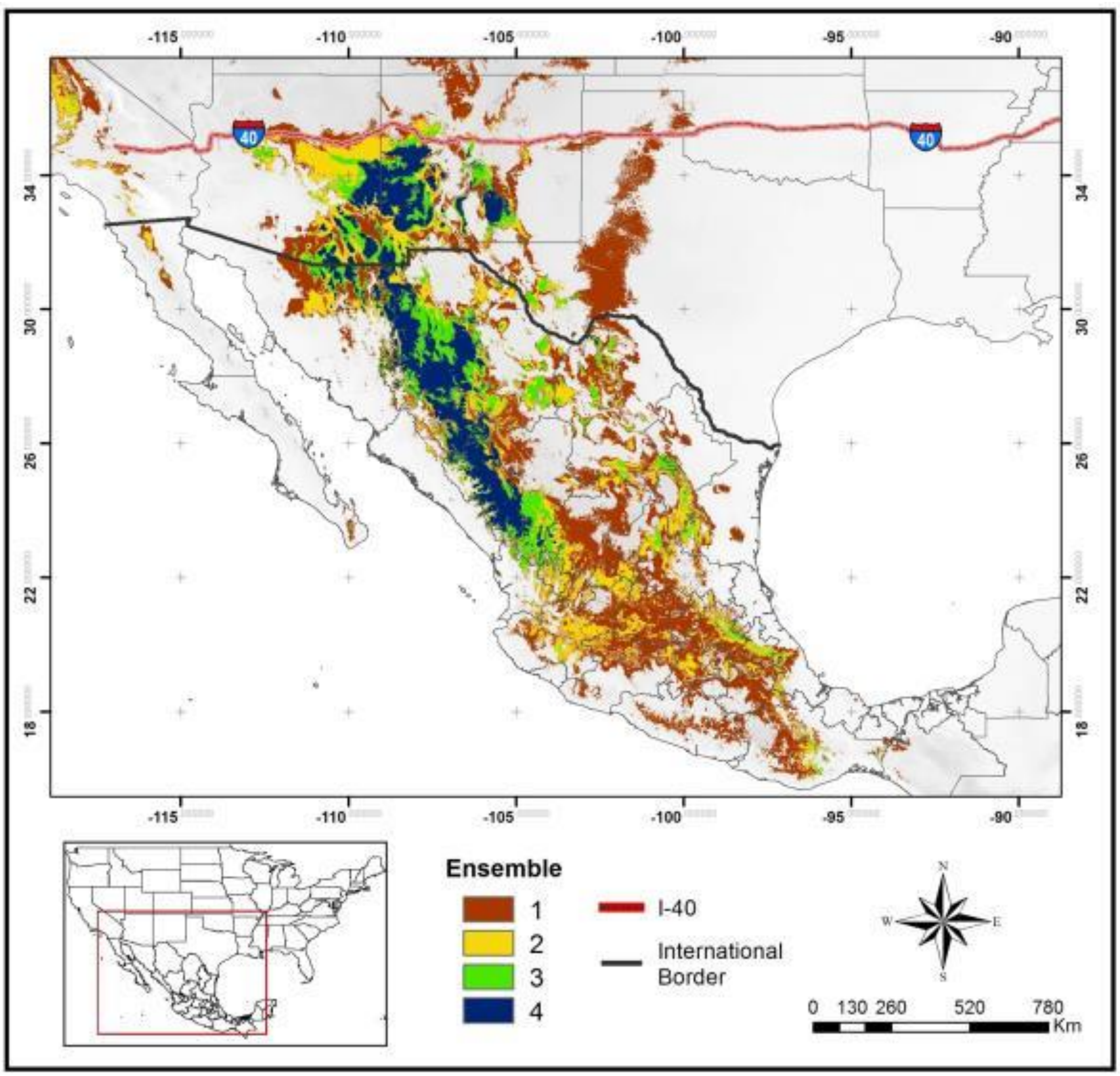

Figure 4. Consensus map representing the ensemble of four individual best models (see text for

details).

Climatic suitability

Based on the final ensemble, we characterized the climatic suitability across the geographical distribution based on the notion that optimal conditions for a species is towards the ecological centroid of its niche in multidimensional space (Hutchinson 1957; Maguire 1973). We followed the methodological approach proposed by Martínez-Meyer et al. (2013) to estimate the distance to the ecological niche centroid as an estimation of environmental suitability. To do so, for all grid cells defined as presence, we extracted the climatic values of the bioclimatic variables used in the modeling (Table 1), we *z*-standardized the values in a way that mean is 0 and standard deviation 1. For each pixel, we calculated the Euclidean distance to the multidimensional mean and finally rescaled these distances from 0-1, where 0 corresponds to the least climatically suitable areas (*i.e.*, farther away from the niche centroid) and values near 1 correspond to pixels with the highest suitable climates.

The resulting map indicates that the highest values of climatic suitability are in the western portion of the distribution (the Sky Islands, southwestern Texas, Sierra Madre Occidental [including western Sonora, Chihuahua, Durango, and Zacatecas]). In the eastern portion of the distribution there are scattered areas in Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí. Interestingly, there are three connections between the two Sierras Madre, one is from Chihuahua-Coahuila to Nuevo León, the other from the middle of the Sierra Madre Occidental via Durango-Zacatecas-Coahuila to Nuevo León, and finally, from Zacatecas-San Luis Potosí to Tamaulipas (Fig. 5).

In contrast, the least suitable niche conditions for the Mexican wolf are at the northern, southern and western edges of the distribution, as well as in the eastern edge of southern Sierra Madre Oriental (Fig. 5). The MWEPA generally resulted climatically-lower suitability, presumably because it is less like the conditions in the core of Mexican wolf historical range.

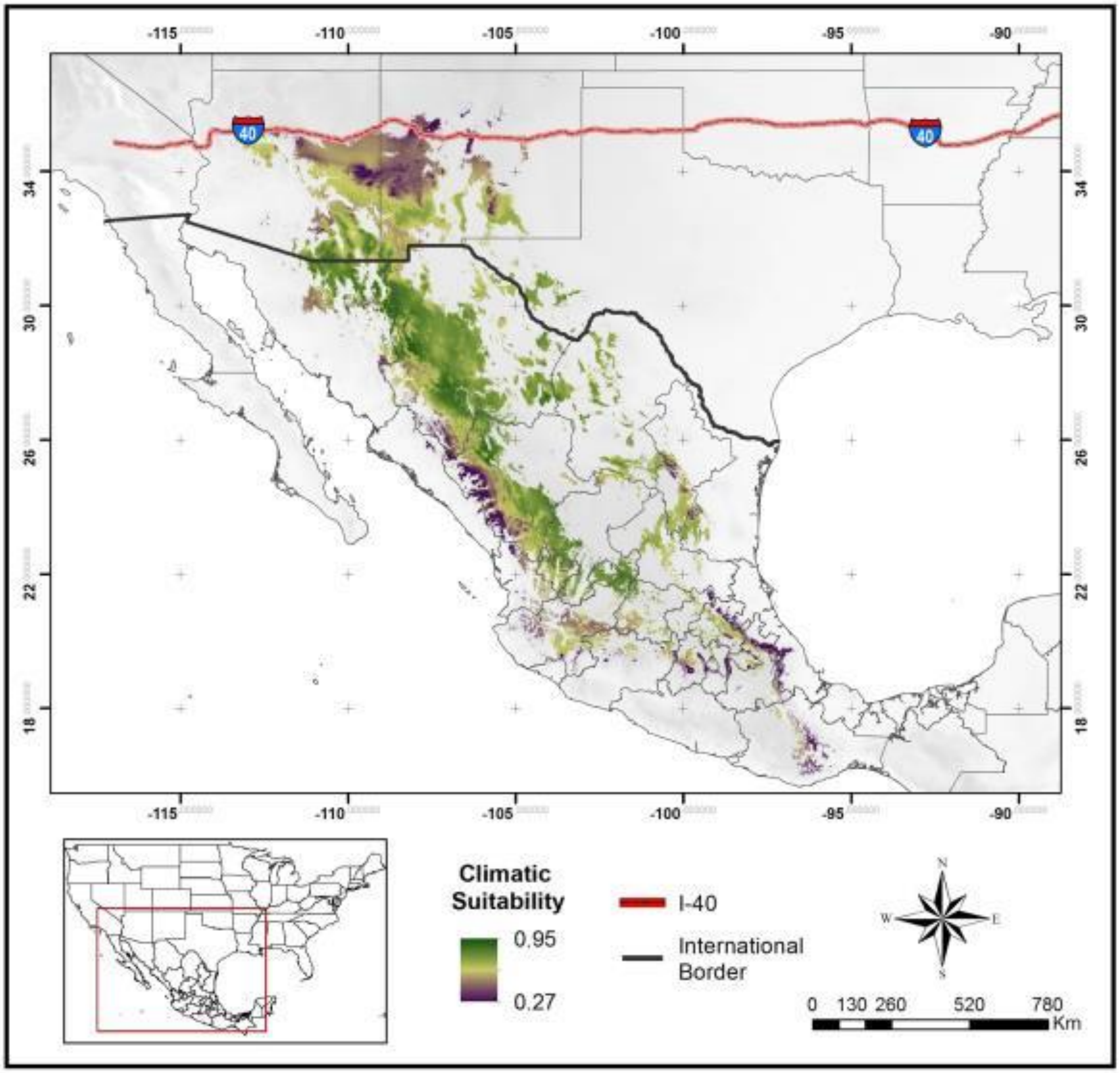

Figure 5. Climatic suitability map of the Mexican wolf based on the distance to the niche centroid approach (Martínez-Meyer et al. 2013) (see text for details). This map represents the historical distribution of the Mexican wolf.

2. Environmental and anthropogenic habitat variables

One of the main limitations of habitat analyses for the Mexican wolf in the past has been the asymmetry of environmental and anthropogenic variables between the

US and Mexico, thus concordant information of critical habitat variables for the two countries is necessary. Natural factors, including vegetation and prey density (Chambers et al. 2012), and anthropogenic factors, such as human population density, infrastructure (e.g., roads, settlements), land tenure and protection are key factors to consider relative to wolf population establishment (Jedrzejewski et al. 2004; Oakleaf et al. 2006; Carroll et al. 2013). In the US, high-quality or high-resolution information exists for all of these factors. Mexico information is quite reliable for some factors (e.g., land cover or population density), but is low-quality or lacking for many regions within the distribution of the Mexican wolf for other factors (e.g., prey density). An additional problem has been the difference in the classification scheme of the vegetation types in the two countries that makes it difficult to homogenize.

To overcome this limitation, we utilized regional or global information produced under the same criteria and methodological approach that covers the two countries. For the habitat model we considered the following natural variables: (1) the abiotic niche model expressed as the suitability score described above, (2) land cover and vegetation types and (3) ungulate biomass. The anthropogenic variables considered were: (1) human population density and (2) road density. All variables were clipped to the potential distribution map of the Mexican wolf (Fig. 5) and resampled from their native spatial resolution to 1 km pixel size. These methodologies allowed all maps to have the same extent and spatial resolution for further analysis. The ecological niche model was described above; below is a description of the remaining variables.

Land cover and vegetation types

Wolves are generalist and use a great variety of land cover and vegetation types. Preference for certain types of vegetation varies across areas and regions as a response to local differences in prey density and/or human tolerance levels (Oakleaf et al. 2006). Land cover has been used for suitability analysis in several studies (Mladenoff et al. 1995; Gehring & Potter 2005; Oakleaf et al. 2006; Carnes 2011; Fechter & Storch 2014; García-Lozano et al. 2015), mainly because it has proven important in different aspects of the ecology of wolves and a good predictor of wolf habitat (Mladenoff et al. 1995; Oakleaf et al. 2006). Vegetation types have also been considered an important factor in permeability for dispersing individuals (Geffen et al. 2004) and for predation (Kunkel et al. 2013). For instance, in reproduction periods, vegetation cover has been associated with the selection of denning sites (Kaartinen et al. 2010). For the Mexican wolf, previous studies have shown that it prefers certain types of vegetation cover, like Madrean evergreen and pine forests at altitudes above 1370 m, where they can find timber and bush cover (McBride 1980). Also, certain types of vegetation present barriers for dispersal. Historical reports indicate that Mexican wolves rarely denned or established a territory in desert-scrub habitats or below 1000 m elevation (Gish 1977) and were absent from desert and grasslands, except when dispersing (Brown 1983). Vegetation cover has also been used in other habitat analyses for the recovery of the species (Carroll et al. 2004, Araiza et al. 2012).

For these analyses, we used the land cover information for the entire study region (southern US and Mexico) provided by the European Spatial Agency (http://maps.elie.ucl.ac.be/CCI/viewer/). This map represents the major land cover and vegetation types of the world produced in 2010 at a spatial resolution of 300 m. We clipped the land cover layer to our study region (Fig. 7) and performed a use/availability analysis as follows: we used all available records of the Mexican wolf (primary and secondary) and also included records from free-ranging individuals in the US. GPS records from free-ranging individuals in the US wild population were generously provided by the Fish and Wildlife Service, which were selected randomly (one location/pack/month) since 1998, totaling 2190 records. In order to avoid over-representation of certain types of vegetation due to the large amount of records in the US, we reduced the number of records by selecting only those from 2011-2013 and only one record per year per pack, resulting in a total of 45 records. The final database for the use/availability analysis consisted of 421 occurrences including historical and GPS records. This database was transformed to a GIS shapefile and used ArcMap 10.0 to extract the cover type for each point record. We considered the vegetation cover from a surrounding area to each point equal to the average home range size of wolves in the US wild population (ca. 462 km^2) and extracted the vegetation types within this buffer area. We summed all areas of the same land cover class to obtain the proportional area available of each class and contrasted that information with the frequency of records in each land cover class, obtaining a score of frequency/availability, and a chi-squared test was performed (Araiza et al. 2012).

However, there is an effect of overestimating the importance of those cover classes that have a reduced distribution and very few occurrences (Table 4). Therefore, to obtain the relative importance of each land cover class we simply obtained the proportional number of records in each class (no. of records in class x / no. of records outside class x). Most records were in the ‘needleleaf evergreen closed to open forest’ class, followed by ‘shrublands’ (Table 4). However, shrublands apparently is a vegetation type that wolves do not prefer (Gish 1977; McBride 1980), but is so extensive in the area that wolves necessarily use it, mainly for dispersal (Brown 1983).

Finally, the land cover layer was standardized based on the proportional occurrence using the following conditional formula in the raster calculator of ArcGIS 10.1:

`Con("x"<=a,(1*(("x" - a)/a)),(1*("x"/b)))` Equation 1;

where ***x*** refers to the land cover layer; ***a*** is the threshold value which was defined based on the ‘Proportion In’ column (Table 3) and ***b*** refers to the maximum value of the land cover layer **x**. Values greater than ***a*** were considered classes positively used by wolves and values lower than ***a*** were classes not used or avoided by wolves. The threshold value (***a***) corresponded to the shrubland, thus its value was 0. The only land cover class above zero was needleleaf forest, so its rescaled value was 1 and the remaining classes had values below 0 (Table 4; Fig. 7). The land cover classes “Urban areas” and “Water bodies” were manually set to -1.

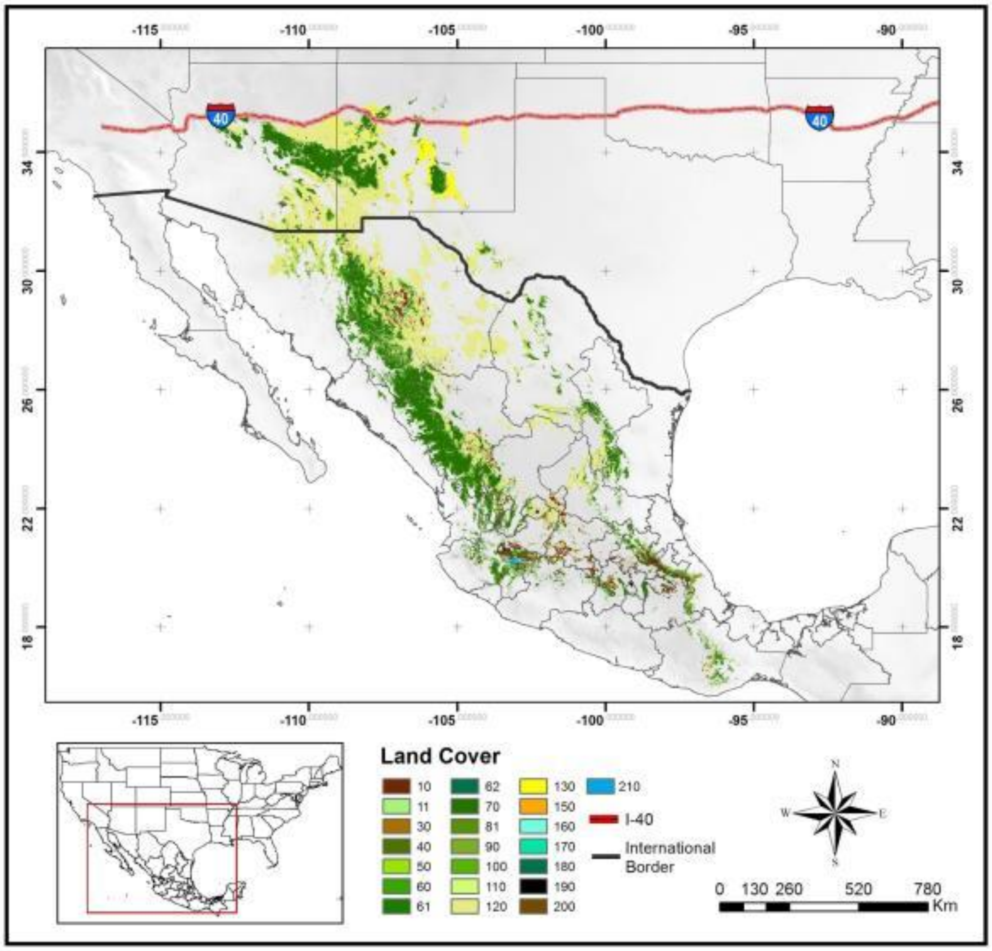

Figure 6. Landcover map for the study region from the European Spatial Agency (http://maps.elie.ucl.ac.be/CCI/viewer/). Codes are as follows: (10): Cropland rainfed, (11) Herbaceous cover; (30) Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous); (40) Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%); (50) Tree cover, broadleaved, evergreen, closed to open (>15%); (60) Tree cover, broadleaved, deciduous, closed to open (>15%); (61) Tree cover, broadleaved, deciduous, closed (>40%); (62) Tree cover, broadleaved, deciduous, open (15-40%); (70) Tree cover, needleleaved, evergreen, closed to open (>15%); (81) Tree cover, needleleaved, deciduous, closed (>40%); (90) Tree cover, mixed leaf type (broadleaved and needleleaved); (100) Mosaic tree and shrub (>50%) / herbaceous cover (<50%); (110) Mosaic herbaceous cover (>50%) / tree and shrub (<50%); (120) Shrubland; 130) Grassland; (150) Sparse vegetation (tree, shrub, herbaceous cover) (<15%); (160) Tree cover, flooded, fresh or brakish water; (170) Tree cover, flooded, saline water; (180) Shrub or herbaceous cover, flooded, fresh/saline/brakish water; (190) Urban areas; (200) Bare areas; (210) Water bodies.

Table 4. Frequency of Mexican wolf occurrences in land cover classes. The ‘Proportion In’ column was used to produce the rescaled values. Codes are as follows: (10): Cropland rainfed, (11) Herbaceous cover; (30) Mosaic cropland (>50%) / natural vegetation; (40) Mosaic natural vegetation (>50%); (50) Tree cover, broadleaved, evergreen, closed to open (>15%); (60) Tree cover, broadleaved, deciduous, closed to open (>15%); (61) Tree cover, broadleaved, deciduous, closed (>40%); (62) Tree cover, broadleaved, deciduous, open (15-40%); (70) Tree cover, needleleaved, evergreen, closed to open (>15%); (81) Tree cover, needleleaved, deciduous, closed (>40%); (90) Tree cover, mixed leaf type; (100) Mosaic tree and shrub (>50%) / herbaceous cover (<50%); (110) Mosaic herbaceous cover (>50%)/tree and shrub (<50%); (120) Shrubland; 130) Grassland; (160) Tree cover, flooded, fresh or brakish water; (170) Tree cover, flooded, saline water; (180) Shrub or herbaceous cover, flooded, fresh/saline/brakish water; (190) Urban; (200) Bare areas; (210) Water bodies.

Land cover	#Rec In	#Rec Out	Area (km^2)	Expected In	Expected Out	Proportion In	Chi^2	*P*-value	Rescaled value
10	3	418	17313	7.71	413.29	0.01	2.34	0.13	-0.98
11	1	420	956	0.43	420.57	0.00	0.01	0.91	-0.99
30	0	421	1032	0.46	420.54	0.00	0.00	0.95	-1.00
40	1	420	6105	2.72	418.28	0.00	0.55	0.46	-0.99
50	0	421	204	0.09	420.91	0.00	1.84	0.17	-1.00
60	1	420	4847	2.16	418.84	0.00	0.20	0.65	-0.99
61	0	421	286	0.13	420.87	0.00	1.09	0.30	-1.00
62	0	421	49	0.02	420.98	0.00	10.47	0.00	-1.00
70	290	131	405105	180.50	240.50	2.21	116.29	0.00	1.00
81	0	421	35	0.02	420.98	0.00	15.05	0.00	-1.00
90	0	421	96	0.04	420.96	0.00	4.89	0.03	-1.00
100	13	408	29834	13.29	407.71	0.03	0.01	0.94	-0.90
110	0	421	1590	0.71	420.29	0.00	0.06	0.80	-1.00
120	100	321	394987	175.99	245.01	0.31	56.38	0.00	0.00
130	7	414	20143	8.97	412.03	0.02	0.44	0.51	-0.95
160	0	421	29	0.01	420.99	0.00	18.36	0.00	-1.00
170	0	421	2	0.00	421.00	0.00	279.55	0.00	-1.00
180	0	421	89	0.04	420.96	0.00	5.34	0.02	-1.00
190	4	417	6392	2.85	418.15	0.01	0.15	0.70	-0.97
200	0	421	247	0.11	420.89	0.00	1.38	0.24	-1.00
210	1	420	237	0.11	420.89	0.00	1.47	0.22	-0.99

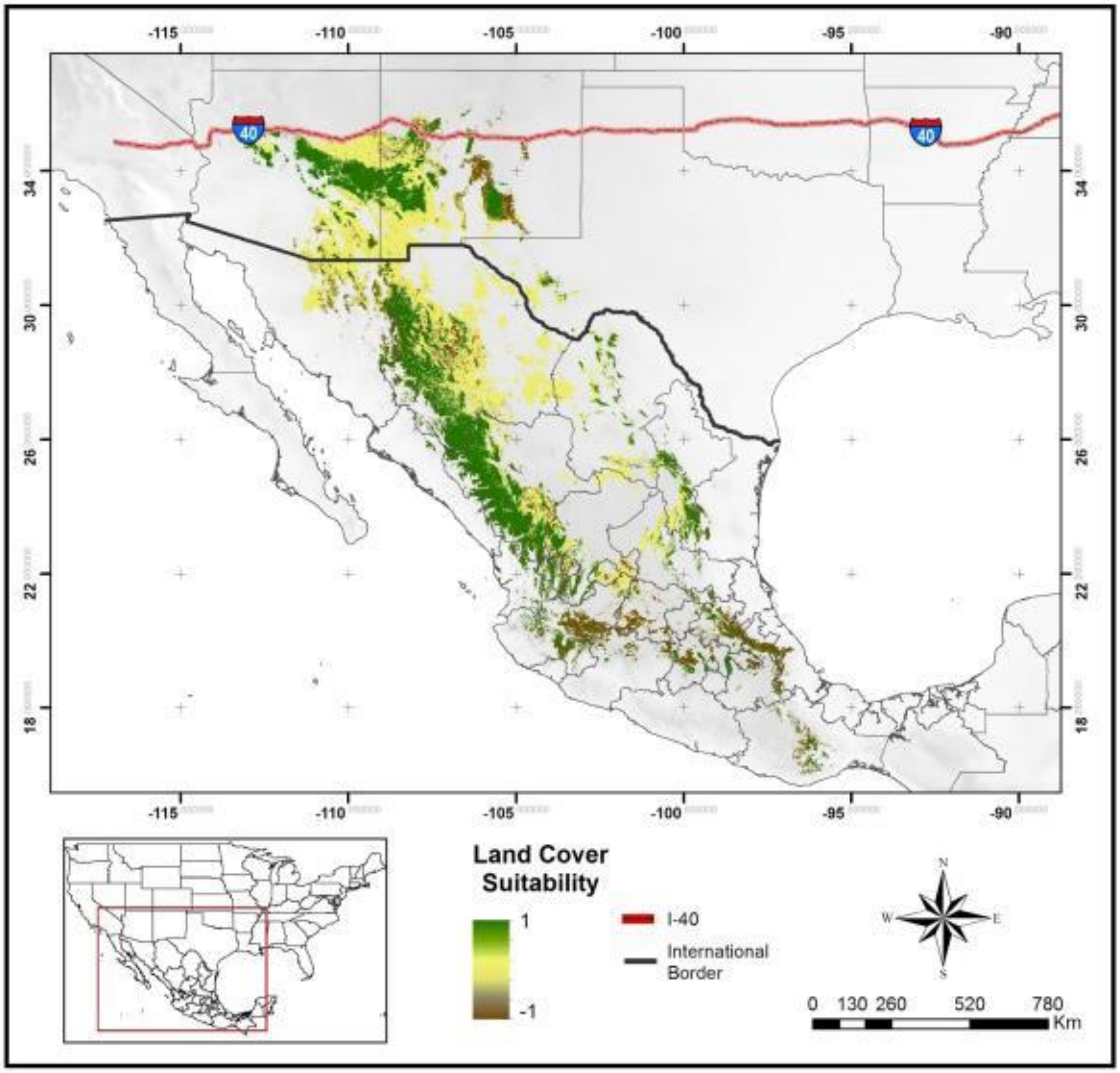

Figure 7. Standardized land cover map according to the habitat use/availability ratio (see text for details).

Human population density

The conflicts between humans and wildlife are one of the leading factors encroaching populations of large mammals (MacDonald et al. 2013), especially carnivores (Dickman et al. 2013). Particularly for wolves, previous studies have found that humans can have a strong influence in wolf ecology, behavior and mortality rates (Creel & Rotella 2010). For instance, human disturbance influence wolves' den selection and home range establishment (Mladenoff et al. 1995; Sazatornil et al. 2016). As well, a negative relationship between density of humans with wolf abundance has been documented, detecting critical thresholds of wolf tolerance to human presence, ranging from 0.4 to1.52 humans/km^2 (Mladenoff et al. 1995; Jedrzejewski et al. 2004; Oakleaf et al. 2006, Carroll et al. 2013). Therefore, human density is one of the key aspects to be considered for an analysis of suitable habitat for the wolf (Mladenoff et al. 1995; Kuzyk et al. 2004; Gehring & Potter 2005; Larsen & Ripple 2006; Belongie 2008; Jędrzejewski et al. 2008; Houle et al. 2009; Carnes 2011; Araiza et al. 2012; Fechter & Storch 2014; Bassi et al. 2015).

For this analysis we obtained a global human population density (individuals/km^2) raster map sampled at 1 km resolution from the Gridded Population of the World, version 4 (GPWv4) web page (CIESIN-FAO-CIAT 2005): http://sedac.ciesin.columbia.edu/data/collection/gpw-v4 and clipped to our study region (Fig. 9). Then, the original values of the raster were rescaled from -1 to 1 using the following conditional formula in the raster calculator of ArcGIS 10.1:

Con(**"x"**<=**a**,(-1*((**"x"** - **a**)/**a**)),(-1*(**"x"/b**))) Equation 2;

where ***x*** refers to the human population density layer; ***a*** is the threshold value and ***b*** refers to the maximum value of layer **x**. In this scale negative values represent human population densities unfavorable for the wolf and positive values favorable under three scenarios (optimistic, intermediate and pessimistic). Threshold values were defined at the Wolf Recovery Workshop in April 2016 based on Mladenoff (1995), who reports a value of 1.52 humans/km^2 (1.61 SE). We established that value for the pessimistic scenario, thus pixel values below this density were rescaled from 0 to 1 and above this value were rescaled from 0 to -1. We calculated 2 SE above the pessimistic threshold for the optimistic scenario, resulting in a human population density of 4.74 humans/km^2, which was used to rescale the map in the same way as in the previous map. Finally, for the intermediate scenario we simply averaged these two values, resulting in 3.13 humans/km^2 and then rescaled (Figs. 8 and 9).

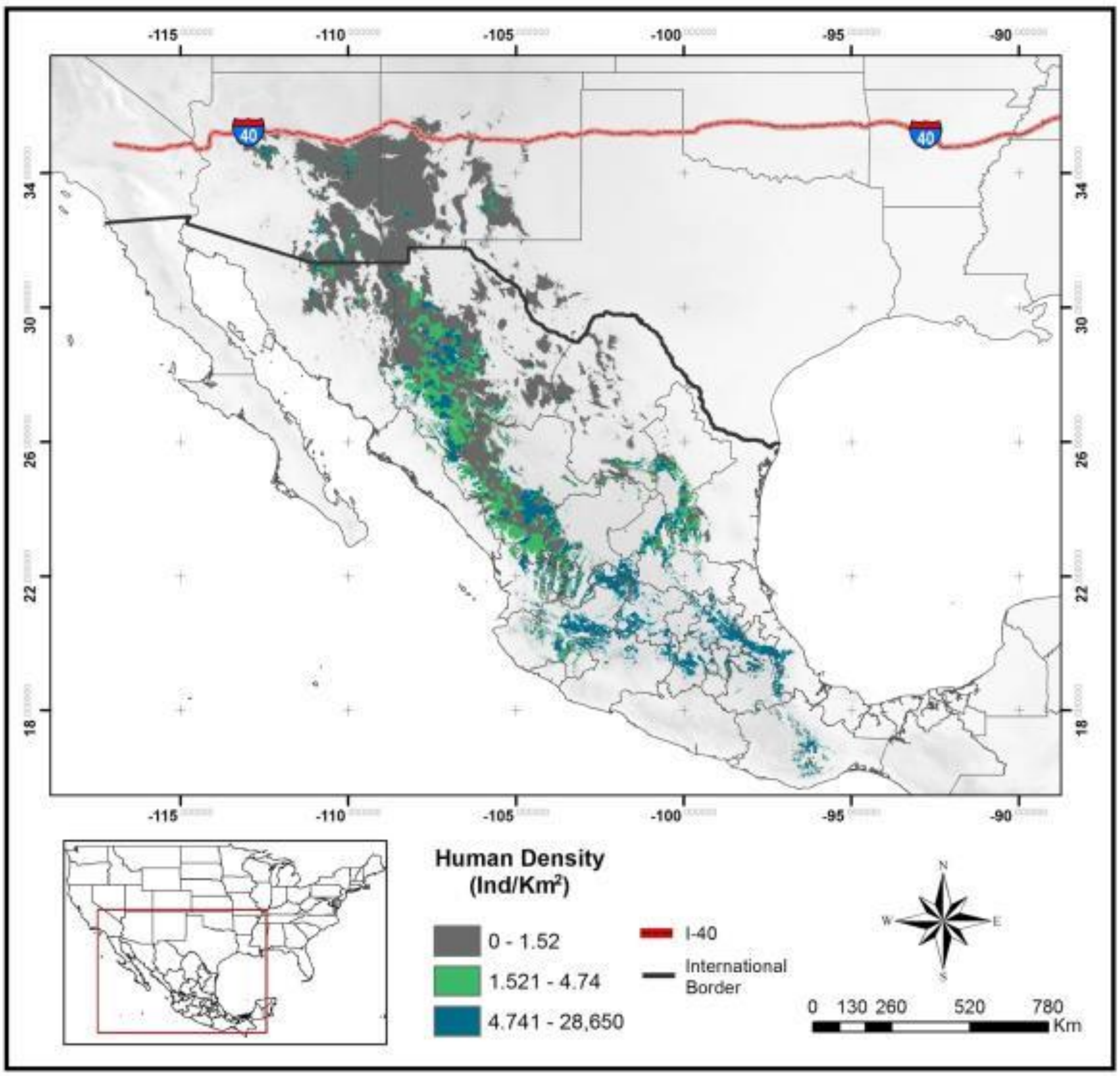

Figure 8. Human population density map in the inferred historic distribution of the Mexican wolf obtained from the Gridded Population of the World, version 4 (GPWv4).

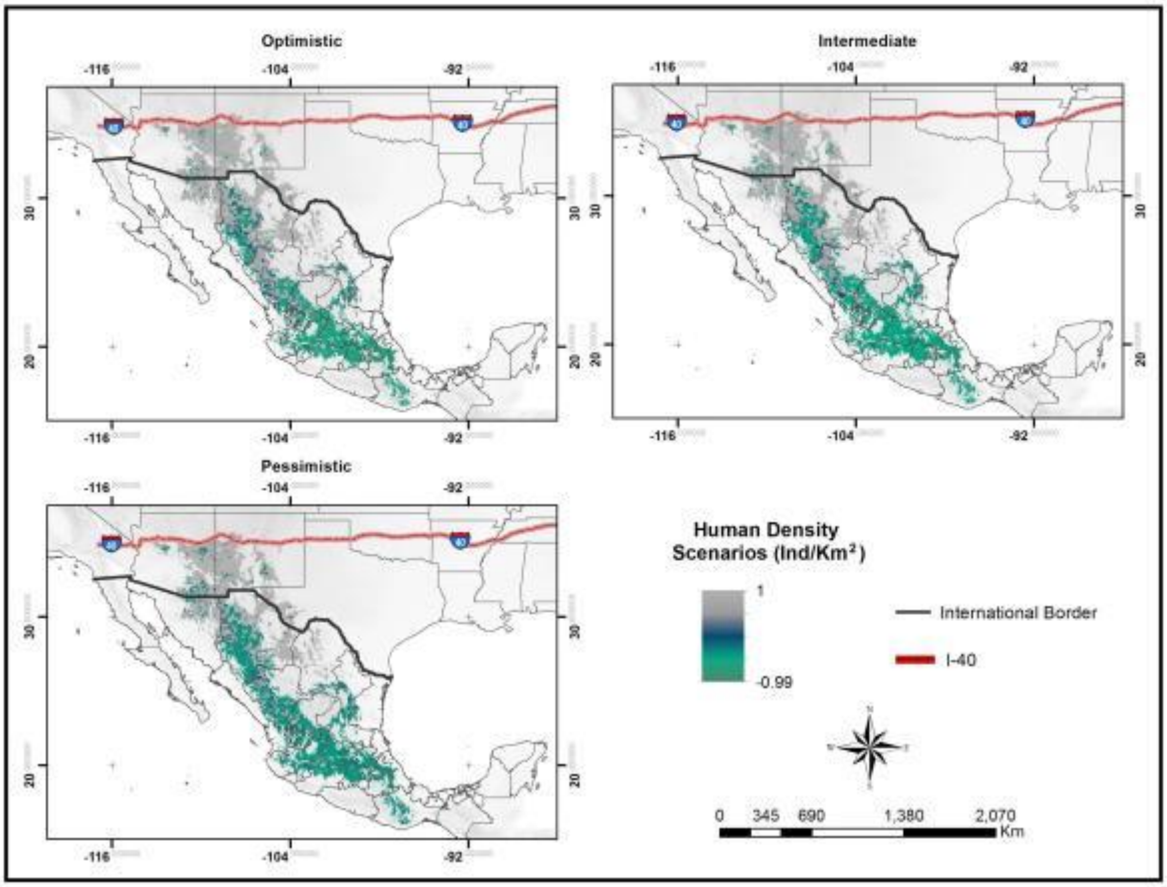

Figure 9. Rescaled human population density scenarios in the historic distribution of the Mexican wolf.

Road density

Road density has been recognized by several authors as one of the limiting factors in habitat suitability of carnivores, specially for wolves (Mladenoff et al. 1995; Jedrzejewski et al. 2004; Oakleaf et al. 2006; Basille et al. 2013; Dickson et al. 2013; Bassi et al. 2015; Angelieri et al. 2016). Different studies have found that wolves can persist in human-dominated landscapes with road density thresholds varying from 0.15 to 0.74 km/km^2, preventing colonization, den establishment and intensive use of the habitat, showing that wolves preferably select areas isolated from human influence, including roads (Thiel 1985; Fuller et al. 1992; Mladenoff et al. 1995; Vickery et al. 2001; Mladenoff et al. 2009; Sazatornil et al. 2016). It has been advised that road density should be monitored in wild areas to prevent exceeding limiting thresholds (Fuller et al. 1992). Several studies have included this variable in habitat suitability analysis for the wolf (Mladenoff et al 1995; Gehring & Potter 2005; Larsen & Ripple 2006; Mladenoff et al 2009; Carnes 2011; Carroll et al. 2013).

For this analysis we used two data sources for roads: OpenStreetMap (http://www.openstreetmap.org/), downloaded from Geofabrik (http://download.geofabrik.de/), which is a vector map of the roads of the world at a maximum scale of 1:1,000 in urban areas, and because the roads from Mexico in this database were not complete we complemented the information with a road map for Mexico at a scale of 1:250,000 (INEGI 2000). From these two maps we selected paved roads and dirt roads suitable for two-wheel drive vehicles. From the unified map we calculated road density (linear km/km^2) using the Line Density function in ArcGis 10.0 (Fig. 10).

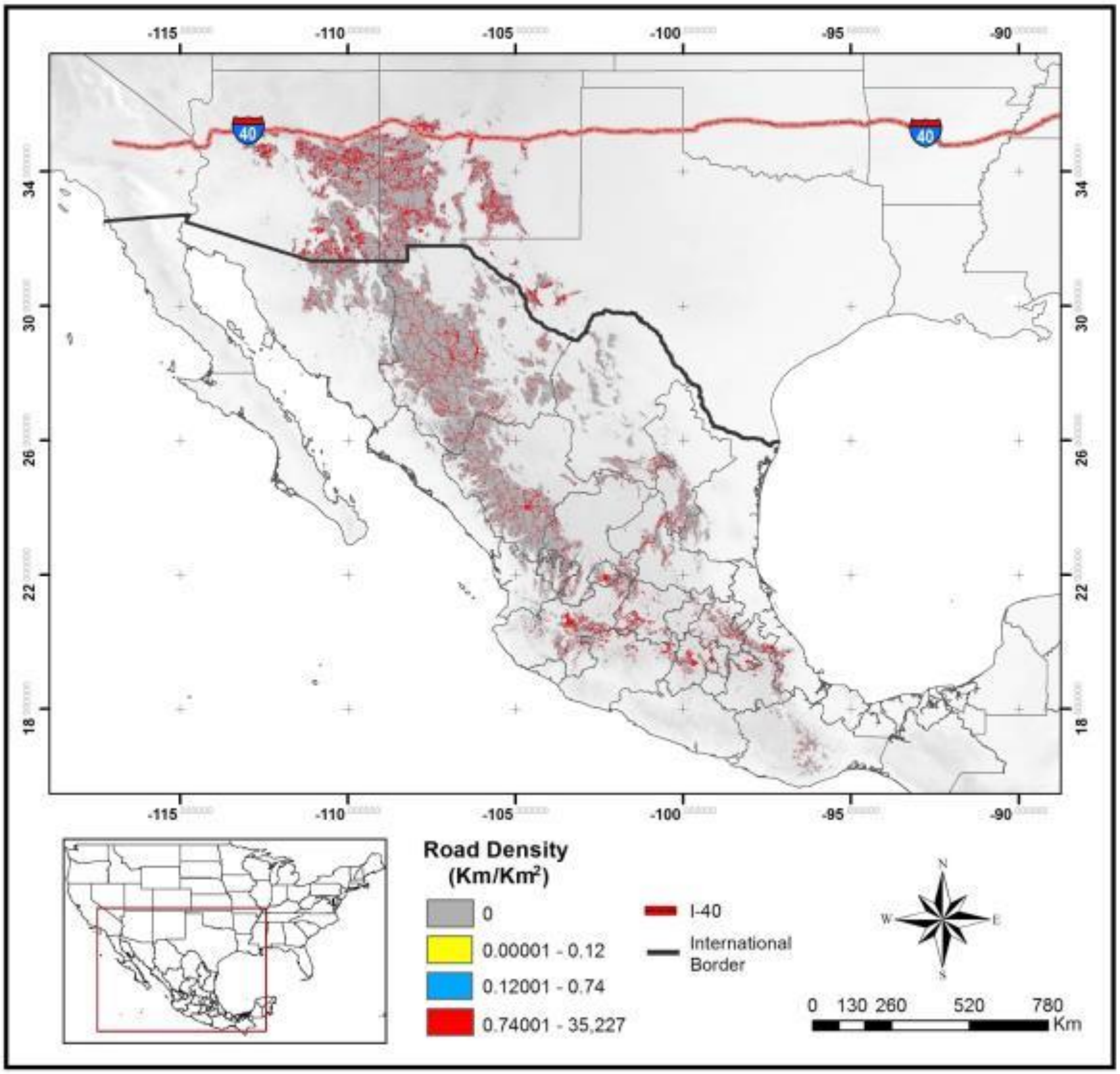

Figure 10. Road density map in the historic distribution of the Mexican wolf obtained from a combination of the OpenStreetMap database and INEGI (2000).

Road density values were rescaled to -1 to 1 using Equation 1 in the same way as we did with the human density map to construct the pessimistic, optimistic and intermediate scenarios, using the following threshold values: for the optimistic scenario it was 0.74 km/km^2, for the pessimistic 0.15 km/km^2, and for the intermediate 0.445 km/km^2 (Fig. 11).

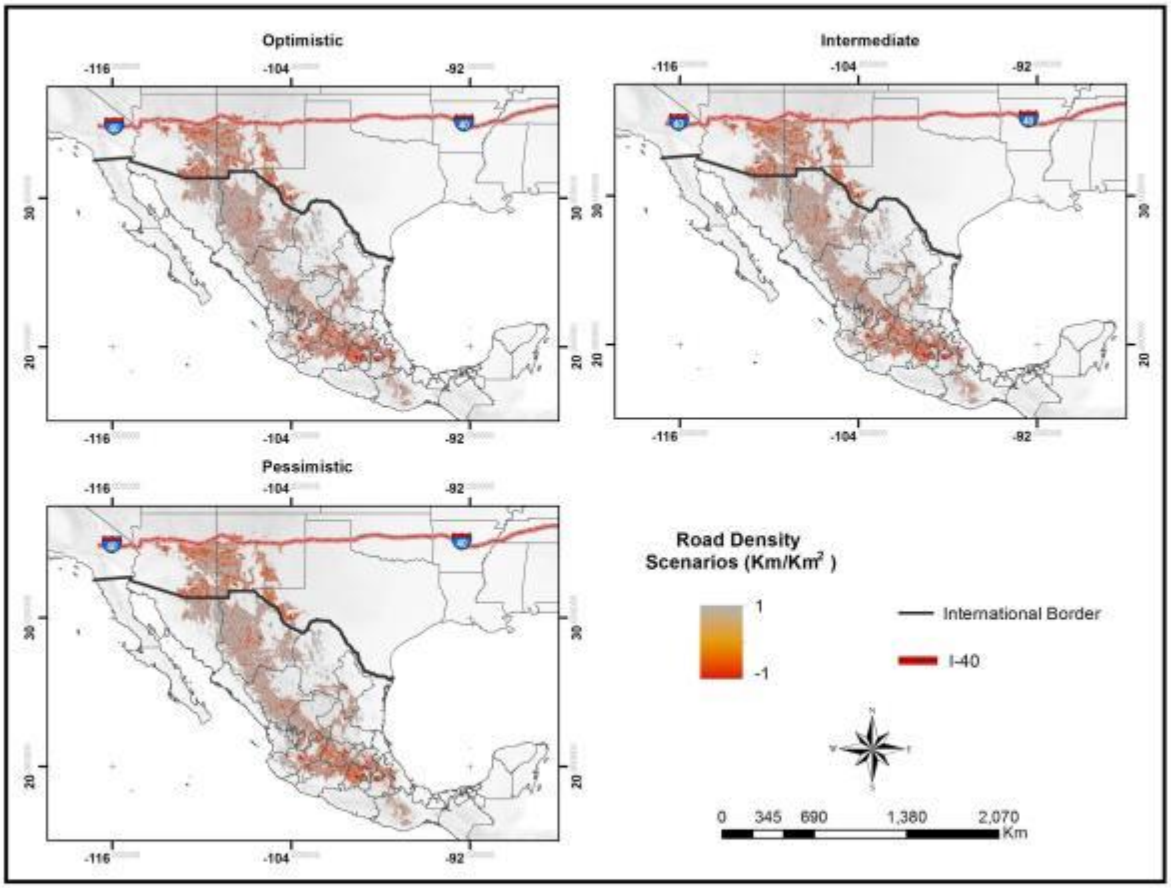

Figure 11. Rescaled road density scenarios in the historic distribution of the Mexican wolf.

3. Ungulate density estimation

Demography of wolves, as many other carnivores, strongly depends on the availability of their prey (Fuller et al. 1992). For instance, density of primary prey species has been identified as an important factor promoting wolf survival, recruitment and habitat use (Oakleaf et al. 2006). In contrast, the effect of wolf predation on wild prey largely depends on the number of wolves, kill rates and the response of prey to other predators (Seip 1995). For these reasons, prey densities have been used as a key predictor of wolf population and for habitat analysis (Fuller et al. 1992, 2003; Oakleaf et al. 2006; Belongie 2008; Moctezuma-Orozco et al.

2010). Based on this knowledge, we used ungulate field density estimations in the US and Mexico to calculate an ungulate biomass index (UBI) (Fuller et al. 2003) across wolf historical distribution (according to Fig. 5).

Ungulate field density estimates in the US come from aerial counts of elk, mule deer and white-tailed deer at 23 Game Management Units (GMUs) in Arizona and 7 in New Mexico. In the case of New Mexico, counts for mule and white-tailed deer were aggregated, so it was not possible to estimate an UBI value for each species thus this information was not used. For Mexico, we had two sets of white-tailed deer density estimates: (1) from wildlife surveys carried out in 2009 by Carlos López and his team using 30 sites with camera-traps (around 30 camera traps per site) across the state of Chihuahua. Details on the sampling scheme and density estimations can be found in Lara-Díaz et al. (2011). (2) White-tailed deer density from 193 Unidades de Manejo para la Conservación de la Vida Silvestre (UMAs) in four states of Mexico: Sonora, Chihuahua, Durango, and Sinaloa from 1999 to 2010 (Fig. 13). UMA data were gathered and organized by Jorge Servín, but the original source came from UMAs' field technicians that estimated deer density under different sampling techniques (e.g., direct, tracks and fecal pellets counts), but reliability has not been thoroughly evaluated, thus there is some uncertainty in these estimates. Importantly, all these data do not account for the high frequency (annual to semi-decadal) changes in ungulate populations that are influenced by a myriad of factors including prior harvest, drought, disease, or habitat degradation. Ideally, we would use a long-term average which would indicate the central tendency for the UMA or GMU areas.

After preliminary analyses to model the UBI across the Mexican wolf range we made several decisions for each species. For elk, we used the 30 available density data obtained from the GMUs (23 from Arizona and 7 from New Mexico) because elk do not occur in Mexico. The New Mexico data for elk are at a large regional GMU level. This leads to two results: (1) the variability in the environmental signatures is very small, and (2) the non-linearity in habitat quality may be hidden;

however, the estimates were very similar to the Arizona GMU data in most cases. For mule deer we used survey data for the Arizona GMUs, Mexican UMAs and camera trap data from Chihuahua. We discarded the UMA data from the UBI modeling because values reported in the Sonora and Chihuahua UMAs were up to 10 times greater than the average values in Arizona and New Mexico. Therefore, for this analysis we used 67 point estimates of density data from GMU and camera-trap surveys. For the analysis we initially split the data into two subspecies of mule deer (Desert and Rocky Mountain), but this proved uninformative so we combined both types into a single UBI model. Finally, for the white-tailed deer, we decided to use only density data from within the historical range of the wolf in the Sierra Madre thus excluding several UMAs located in the desert lowlands in western Sonora. This resulted in 90 point estimates of whitetail density data to build the UBI model.

Methodological differences between sources of data had an effect on density estimation. UMA data come from the annual reports of management units which, in turn, also have different methodologies to estimate densities. Also, UMAs primary source of income come from hunting tags, thus different management practiced in ranches caused important variability in the data. Aerial counts for ungulates in Arizona may be more accurate in open areas, but in dense forested areas –where white-tailed deer usually prefer– counts may be less reliable. All these factors contributed to differences in density estimations from the three sources.

Rangewide density estimations for the three ungulate species were explored under a Generalized Linear Model (GLM) and Random Forest (RF) modeling. The last approach was also implemented for the mule deer and elk. The GLM/RF approach was implemented to establish the critical parameters for the best estimate of the Ungulate Biomass Index (UBI) (Fuller et al. 2003).

UBI modeling

The Ungulate Biomass Index (UBI) (Fuller et al. 2003) is a standardized value which uses a weighting factor based on mean animal biomass (Table 6) to make body mass of different ungulate species comparable. For the purpose of the habitat model, we used the density estimates described above to build a UBI model across the historical range of the Mexican wolf under the GLM/RF approach. The UBI model was then included in some habitat suitability scenarios.

Table 6. Description of the Ungulate Biomass Index (UBI) factor for white-tailed deer, mule deer and elk.

Dependent parameter	**ID**	**Units**	**UBI factor**	**Density data source**
White-tailed deer density	WT	Individuals/km^2	0.6	GMU, CAMSURV, UMA
Mule deer density	MD	Individuals/km^2	1	GMU, CAMSURV
Elk density	ELK	Individuals/km^2	3	GMU

In general, ensemble modelling using machine learning and data-driven tools, such as RF, use non-linear and non-parametric data with numerous hidden interactions, thus, they are likely to violate most statistical assumptions and traditional parametric statistical approaches. RF can be used for prediction, bagging (decision-trees) can be used for assessing stability, and a single decision tree is used for interpreting results if stability is proven. The RF model helps to establish which model parameters are useful. In our case, we used RF with the density data from GMU, CAMSURV and UMA for regression modelling. We also used climatic, topographic, and ecological variables available for calibrating models. Reliability of individual species' models were measured via r^2 and the Akaike Information Criterion (AIC).

For the analyses we compared the response of ungulate density to 15 variables selected from an initial set of 27 based on their levels of significance versus the UBI: (1) monthly climate data archive (DAYMET v2, Thornton et al. 2014); (2) NASA SRTM (90m) digital elevation model and derivative products including the topographic wetness index and slope; (3) EarthEnv.org suite of habitat types (Tuanmu & Jetz 2014); (4) global cloud cover layers from MODIS (Wilson & Jetz 2016); and population density (CIESIN-FAO-CIAT 2005) (Table 7).

Table 7. Independent parameters used for the GLM/RF modeling.

Independent Parameters	**ID**	**Units**	**Scale**	**Source**
Slope	SLP	radians	90 m	Calculated using the patched SRTM DEM with SAGA-GIS
Mean Annual Precipitation	MAP	millimeters (cm)	1 km^2	DAYMET v2
Mean Annual Temperature	MAT	degrees Celsius (C)	1 km^2	DAYMET v2
Net Primary Productivity	NPP	kg C m2	1 km^2	MODIS MOD17A3
Forest Canopy Cover	FORCOVER	%	1 km^2	NASA (Hansen et al. 2013)
Forest Canopy Height Model	CHM	meter	1 km^2	NASA (Simard et al. 2011)
Topographic Wetness Index	TWI	index (unitless)	90 m	NASA SRTM, TauDEM (OpenTopo metadata job 1, job 2)
Digital Elevation Model	DEM	meters (m)	90 m	NASA SRTM, TauDEM (OpenTopo metadata job 1 , job 2)
Vegetation Types:		%	1 km^2	Tuanmu & Jetz 2014.

Herbaceous; Cultivated; Evergreen-deciduous-needleleaf	HERB CULTIV EVDECNEED			Data available on-line at http://www.earthenv.org/.
Population Density	POPDENS	Individuals/ km^2	1 km^2	CIESIN-FAO-CIAT 2005. Data available on-line at http://dx.doi.org/10.7927/H4639MPP.
MODIS Cloudiness: Mean annual; Inter-annual SD; Intra-annual SD	CLDANN CLDINTER CLINTRA	Mean, Inter-annual Standard Deviation,	1 km^2	Wilson & Jetz 2016. http://www.earthenv.org/cloud

We used the shapefiles for the current distribution of white-tailed deer, mule deer, and elk for Arizona in each GMU and the perimeter boundaries of the UMAs to calculate the mean value for each species habitat distribution area with the QGIS Raster Zonal Statistics. The input variable for ungulates was the Ungulate Biomass Index (UBI). To calculate the UBI within the total suitable habitat area we used the following function:

$$UBI = n * B / area \qquad \text{Equation 3;}$$

where n is the observed number of individuals in the GMU, B (beta) is a weighting factor, and area is square kilometers of suitable habitat in the GMU or UMA.

For the UMAs we had the total number of individuals per km only, so we weighted this using the B factor to derive the UBI for Mexico, as follows:

$$UBI = (n / area) * B \qquad \text{Equation 4;}$$

All calculations were made in RStudio (Rstudio Team 2016). The script loads the data, calculates a series of GLM models, and then produces variable importance models and figures of the Random Forest outputs.

In general, for elk, the variance explained with the RF regression models was relatively good, but low for the mule deer and white-tailed deer (Table 8). Low R^2, particularly for deer data, is a consequence of the large dispersion of density data values, where wide variability exists within and amongst identical climate and topographic areas. Despite this, a relationship with predictor variables exists, which suggests that the model conservatively estimates the central tendency for the broader landscape.

Table 8. Percentage of the UBI variance explained and Mean of Squared Residuals of the GLM/RF models for the three ungulates.

Species	**% of variance explained (R^2)**	**Mean of Squared Residuals**
Elk	43.5	9.33
Mule deer	25.49	0.2
White-tailed deer	9.39	1.94

Rangewide UBI map

UBI distribution maps of each species across the whole study area were built in a GIS using the best fit GLM/RF models. Then, the UBI map of each species was clipped to its known distribution using the IUCN polygon maps (IUCN 2016) (Fig. 12). Finally, the three individual UBI maps were summed together in a GIS to produce a combined UBI map, which was clipped to match the historical distribution of the Mexican wolf (Fig. 13). This map represents the estimated ungulate biomass available for Mexican wolf populations. Finally, the UBI map was rescaled from 0-1 to match the other layers for the habitat suitability model (Fig. 14).

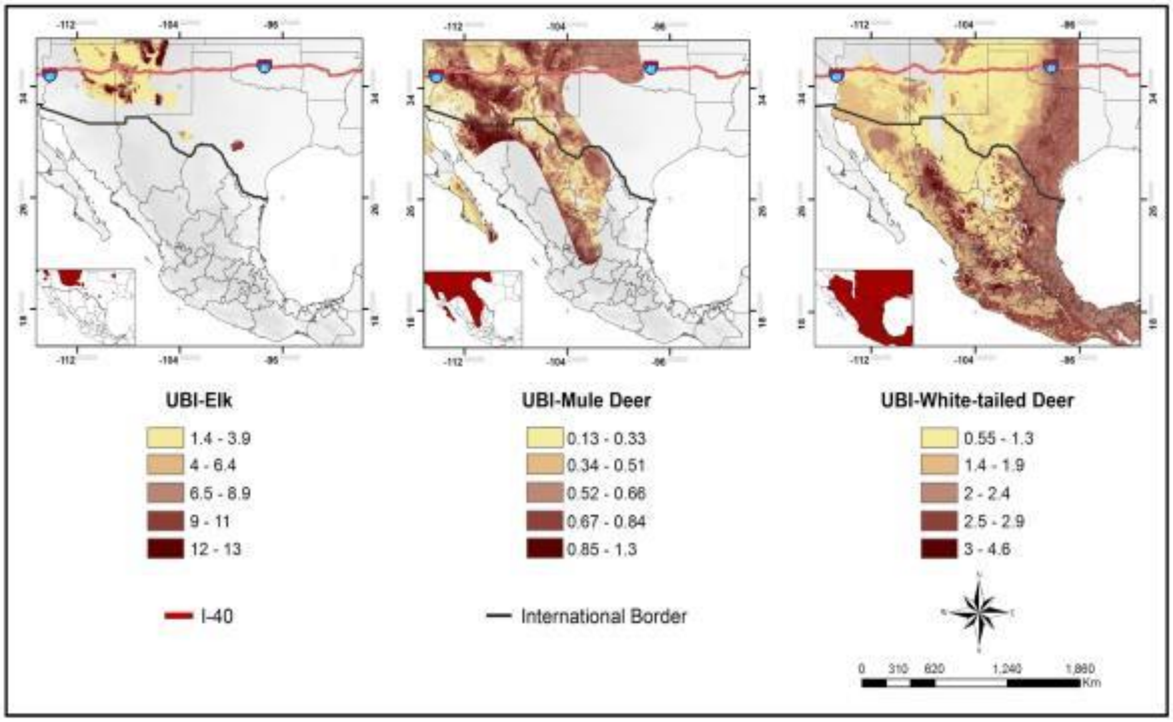

Figure 12. Ungulate Biomass Index (UBI) map for the elk, mule deer and white-tailed deer. Inset images represent the known distribution of species according to IUCN (2016).

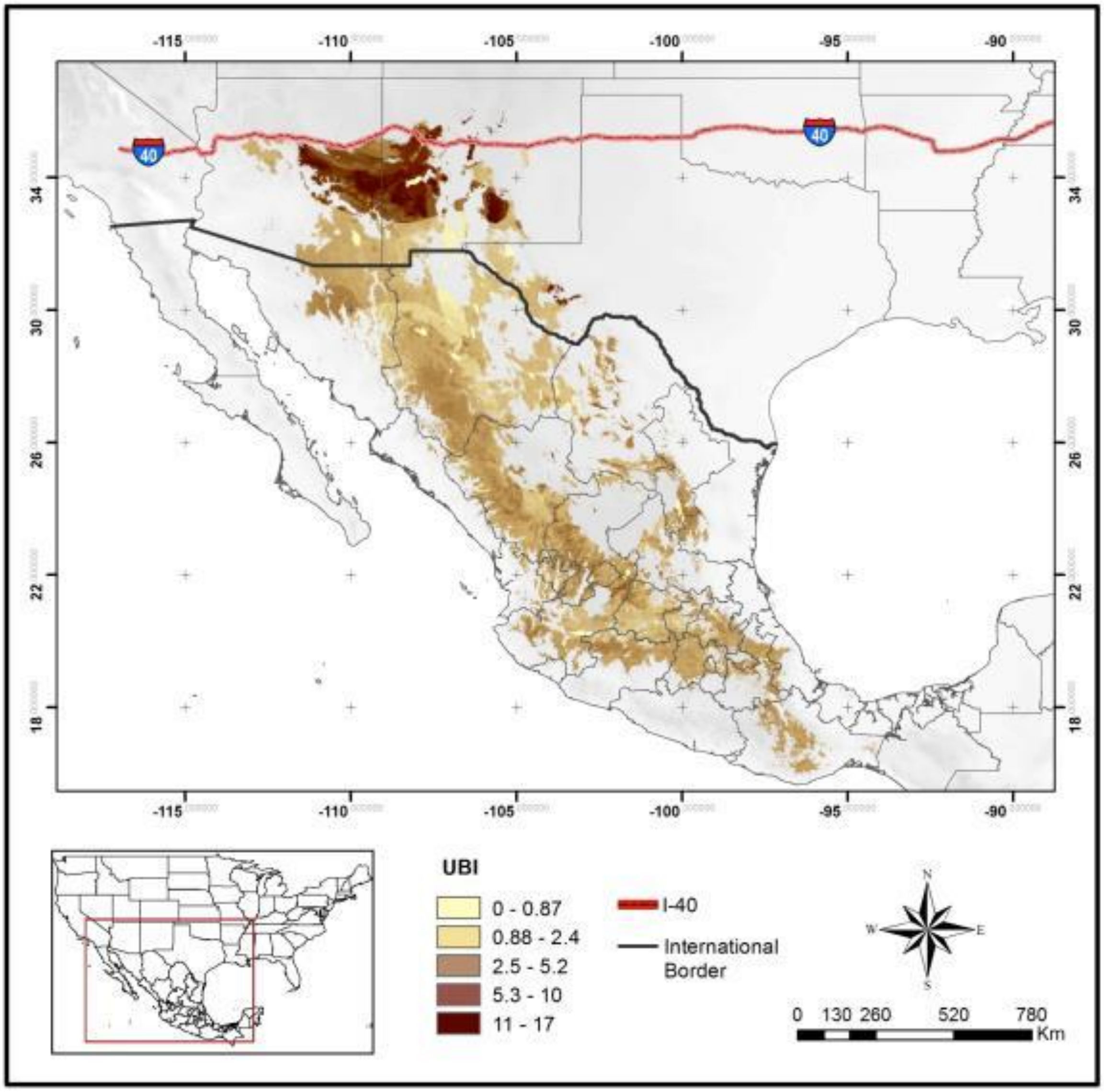

Figure 13. Combined Ungulate Biomass Index (UBI) map for the elk, mule deer and white-tailed deer across the Mexican wolf historical range.

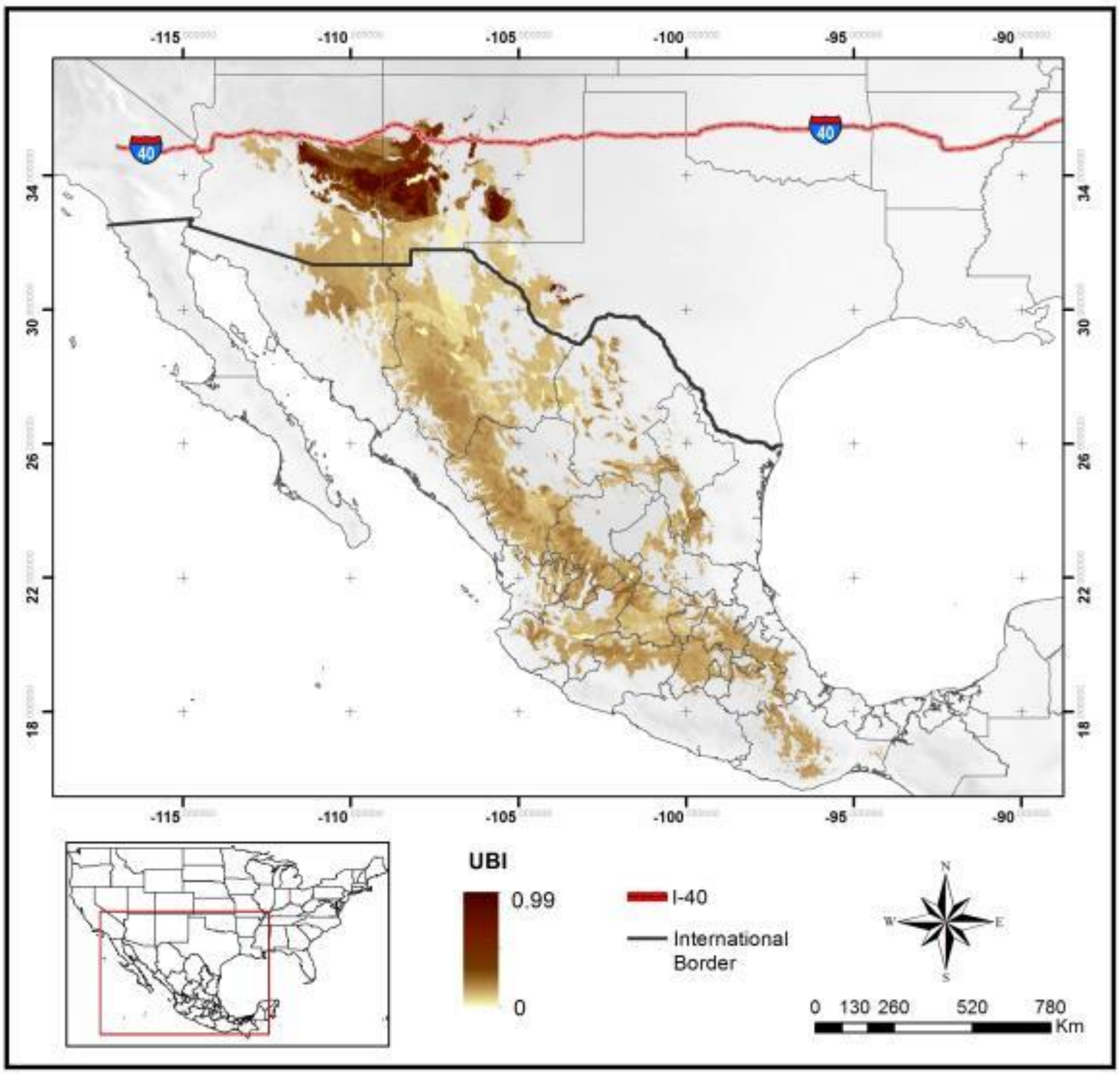

Figure 14. Rescaled Ungulate biomass index (UBI) map.

4. Habitat suitability modeling

We produced two sets of habitat suitability scenarios, with and without the Ungulate Biomass Index (UBI) map. This is because our geographic estimations of the UBI are less reliable than the other habitat variables, therefore its inclusion may mislead the habitat models.

To produce all habitat suitability scenarios for the Mexican wolf we implemented an additive model with the rescaled variables. For the set of scenarios without UBI information we summed: the niche model (with values from 0-1) + land cover + human density + road density maps (all with a scale from -1 to 1) using the raster calculator in ArcGis 10.0; hence, the resulting map may have values ranging from -3 to 4. For the set of scenarios including the UBI variable (with values from 0-1) we simply summed this variable to the rest as described above, thus potentially holding values of -3 to 5. The niche model and land cover were fixed factors for all scenarios (pessimistic, intermediate and optimistic), whereas human and road densities varied depending on the scenario: in the pessimistic scenario habitat suitability is more strongly impacted by anthropogenic variables (human and road densities), whereas for the optimistic scenario wolves tolerate higher values of these two variables. The intermediate scenario is simply the mean value of the two anthropogenic variables between these two extremes.

In order to identify the areas of the highest habitat quality for the wolf, we reclassified each scenario as follows: for the set of scenarios without UBI, values lower than zero were coded as unsuitable, values between 0-3 were coded as low quality, and values >3 were coded as high quality. Therefore, pixels classified as high quality corresponded to areas with a combination of high climatic suitability, in needleleaf forests and with low human impact. For the set of scenarios with UBI, unsuitable areas corresponded to values lower than 0; values between 0-3.2 were considered low quality; pixel values between 3.2-3.95 were classified as high quality and pixels >3.95 were coded as highest quality, indicating that ungulate density in those areas is highest.

5. Identification of suitable areas for future recovery actions

High-quality pixels in each scenario were converted to vector format to carry out a connectivity analysis using Fragstats ver. 4 (McGarigal et al. 2012), in order to identify continuous or aggregated patches across the geographic distribution of the Mexican wolf. Then, we identified geographical units in the US and Mexico containing these habitat clusters. Finally, polygons representing the protected areas of the US and Mexico were overlaid on the habitat suitability scenarios and high-quality patches, as well as the map of the municipalities of Mexico to identify potential areas for future releases.

6. Estimation of Mexican wolf population size in suitable areas

There are two fundamental approaches that have been previously used to estimate wolf population size: (a) based on home range size of wolf packs and calculate the number of wolves in the available area, and (b) based on the relationship of prey density with wolf density and then extrapolate to the available area (Bednarz 1988; Fuller 1989; Messier 1995; Mladenoff 1997; Paquet et al. 2001; Table 10). Despite the fact that all of them estimate the number of wolves per 1000 km^2, not all of the formulas use the same input units. For instance, Bednarz (1988) uses number of prey per 100 km^2, Fuller (1989) and Messier (1995) use units of prey (equivalent to 1 white-tailed deer), whereas Paquet (2001) uses average biomass.

Mladenoff et al. (1997) used the Fuller (1989) model and a home range-based model to estimate eventual wolf populations for Wisconsin and Michigan about 20 years ago, when about 99 wolves existed in Wisconsin (Wydeven et al. 2009), and 116 in Michigan (Beyer et al. 2009). The Fuller (1989) model estimated an eventual population of 462 for Wisconsin (90% confidence interval [CI]: 262-662), and 969 for Michigan (90% CI: 581-1357). A home range/habitat area-based model estimated potential population of 380 for Wisconsin (90% CI: 324-461) and 751 for Michigan (90% CI: 641-911). In recent years, the maximum population count achieved in Michigan was 687 in 2011, 71% of estimate by Fuller (1989) model and 91% of home range model estimate, and both estimates were within 90 CI of both models. The maximum count in Wisconsin was 866 in 2016, 187% of the Fuller (1989) model estimate and 228% of the home range model, and the recent count excedes the 90% CI of both methods. Thus, these two methods made reasonable estimates of potential wolf population for Michigan, but underestimated wolf numbers for Wisconsin, suggesting that the methods are reliable but somewhat conservative.

For this analysis we used and compared available methods to estimate wolf numbers (Table 9). In all cases, an estimation of the available suitable area was necessary, so for the scenarios not including the UBI layer, we used the high-quality patches and calculated their areas, and for the scenarios with the UBI layer we used the high- and highest-quality patches to obtain area calculations, and from these calculations we estimated wolf numbers.

Table 9. Equation and it author to estimate wolf numbers. y= number of wolves /1000km2; x= number of prey/biomass.

Author	**Formula**
Bednarz 1988	y = 14.48 + 0.03952x
Fuller 1989	y = 3.34 + 3.71x
Messier 1995	y = 4.19x
Paquet 2001	y = 0.041x
Home-range-based	764 km^2 / pack (4.19 wolves)

For estimations of wolf numbers based on the home range size, we used the average size reported for the wolf packs in the US for the last two years of 764 km^2 and an average of 4.19 wolves per pack (USFWS 2014, 2015). For wolf numbers estimations based on deer density, we obtained UBI values directly from the ungulate density map (see 'Ungulate density estimation' section) and averaged all pixel values from the same geographic unit (e.g., Arizona-New Mexico, Northern Sierra Madre Occidental, etc.), and finally those values were used in the equations of Table 9.

In sum, we generated two sets of wolf population size estimations for each scenario: (1) using the habitat suitability map with the UBI in the additive model and UBI averaged across geographic units from the GLM/RF model; and (2) using the habitat suitability map without the UBI in the additive model and UBI was also averaged across geographic units from the GLM/RF model.

Results and Discussion

Habitat suitability scenarios without the Ungulate Biomass Index (UBI) map

Results of the additive habitat suitability models excluding the Ungulate Biomass Index (UBI) map indicate that relatively large areas of high-quality habitat exist for the Mexican wolf in southwestern US, Sierra Madre Occidental and Sierra Madre Oriental even under the pessimistic scenario (Fig. 15). Although high-quality patches still remain in the Mexican Transvolcanic Belt and southwards, these are not large enough by themselves or are not connected to form continuous areas, thus they are unsuitable to maintain a large population of wolves, even in the intermediate (Fig. 16) and optimistic (Fig. 17) scenarios.

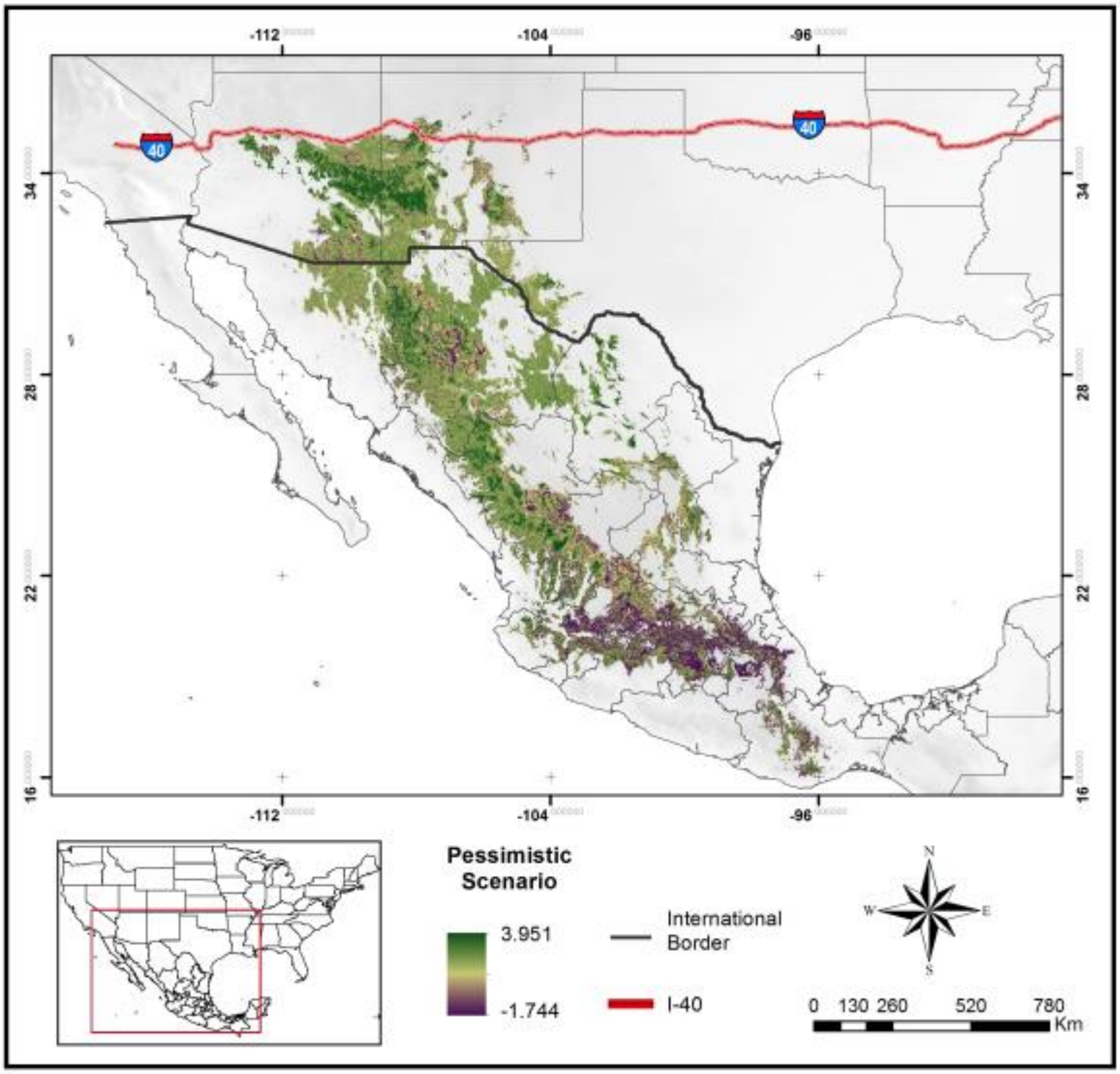

Figure 15. Pessimistic habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

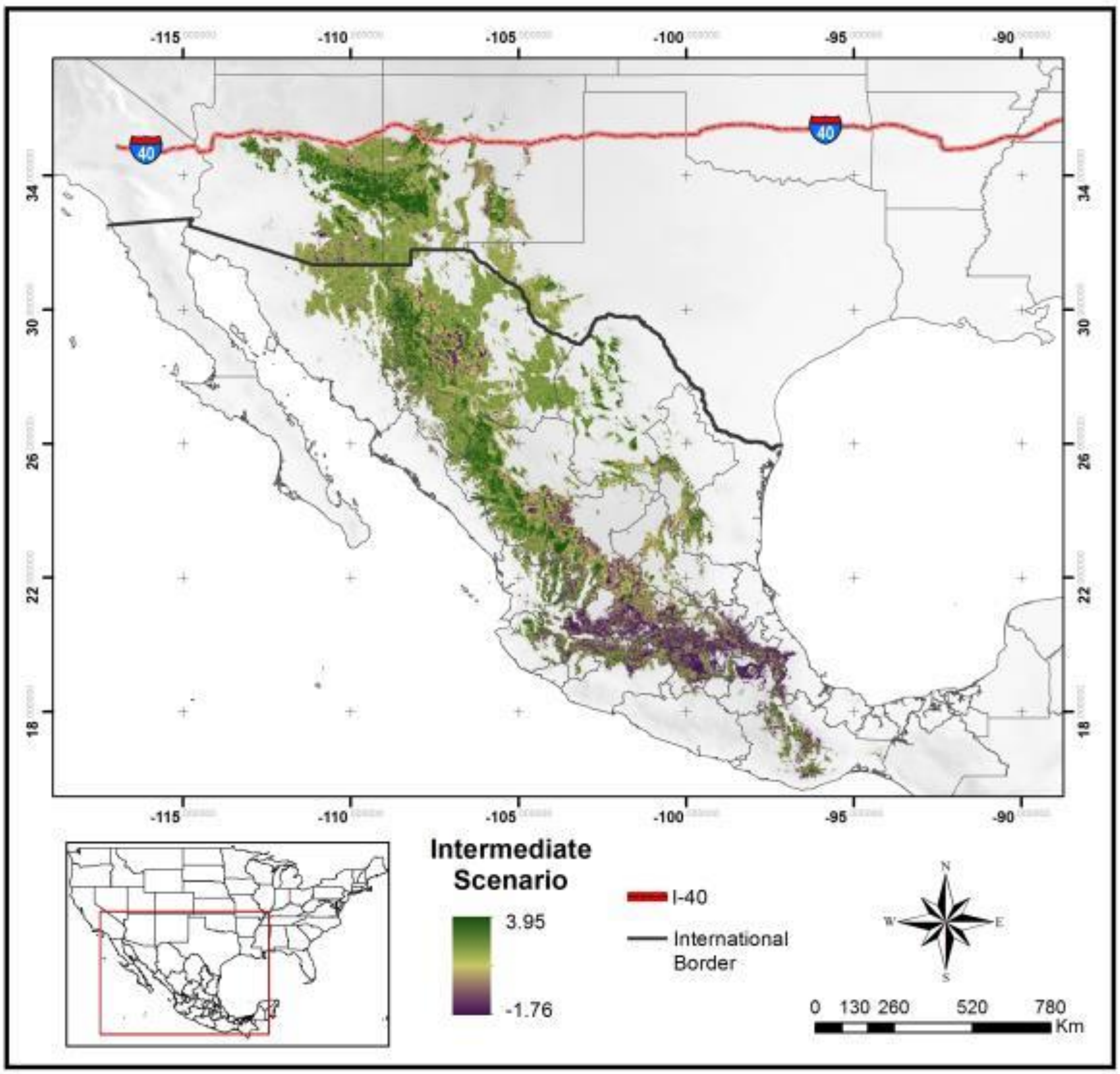

Figure 16. Intermediate habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

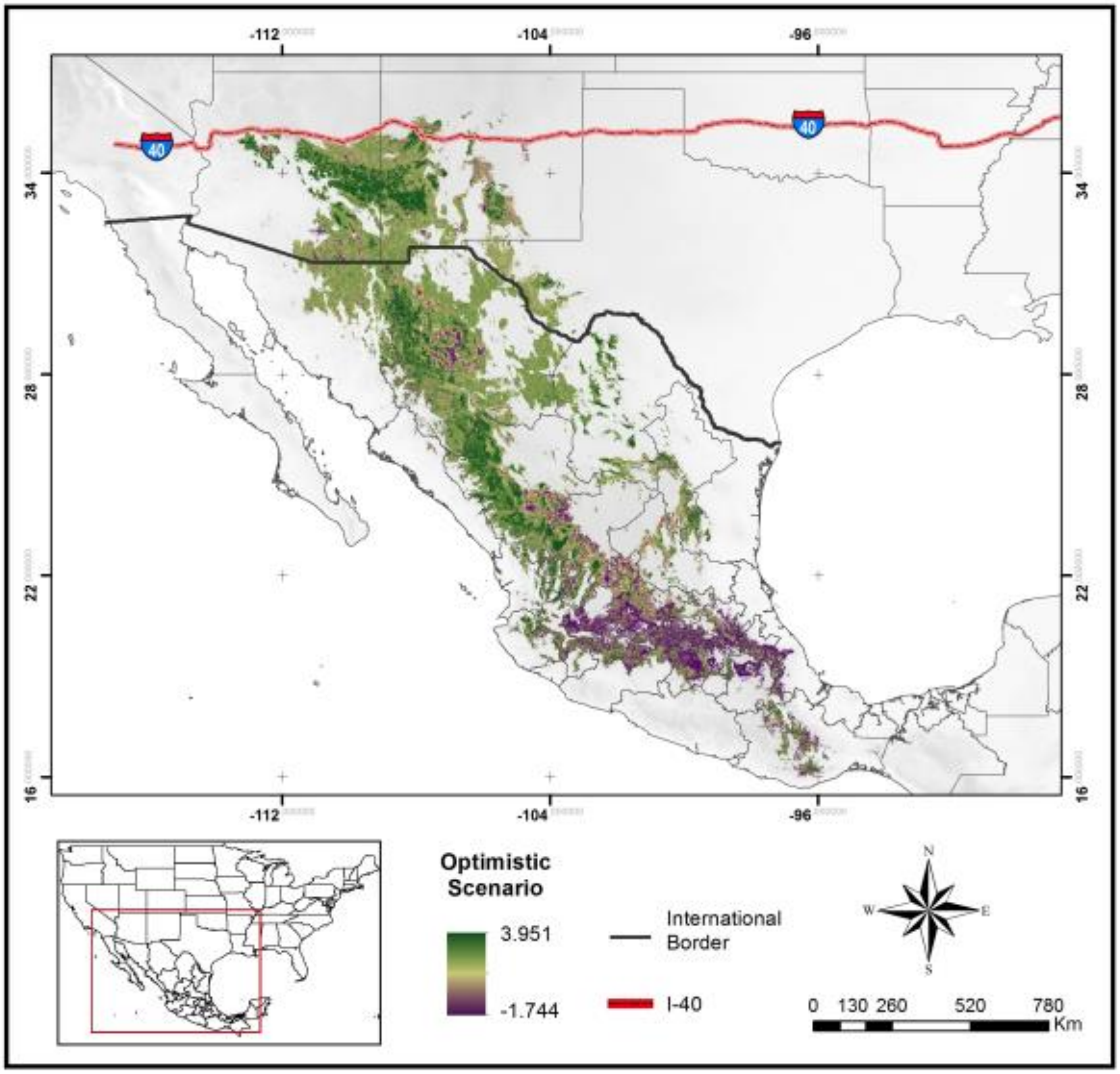

Figure 17. Optimistic habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Reclassified continuous maps into unsuitable, low-quality and high-quality habitat indicate that remaining high-quality areas exist in the two countries. In the US, highest-quality areas are located in and around the MWEPA and in southern New Mexico in the three scenarios (Figs. 19-21). In Mexico, the Sierra Madre Occidental holds large areas of high-quality habitat concentrated in two main areas, one in northern Chihuahua running along the border with Sonora, and the other one in Durango down to western Zacatecas and northern Jalisco. The Sierra Madre Oriental holds significant high-quality areas in Tamaulipas, Nuevo León and Coahuila, but mountain ranges in that region are naturally more fragmented than in the Sierra Madre Occidental (Figs. 18-20).

Potential connectivity between the two Sierras Madre mountain ranges is detected in at least three regions: at the north via eastern Chihuahua and Coahuila; in the center, from Durango to Nuevo León crossing through southern Coahuila, and in the south from Durango-Zacatecas to Tamaulipas via San Luis Potosí (Figs. 18-20).

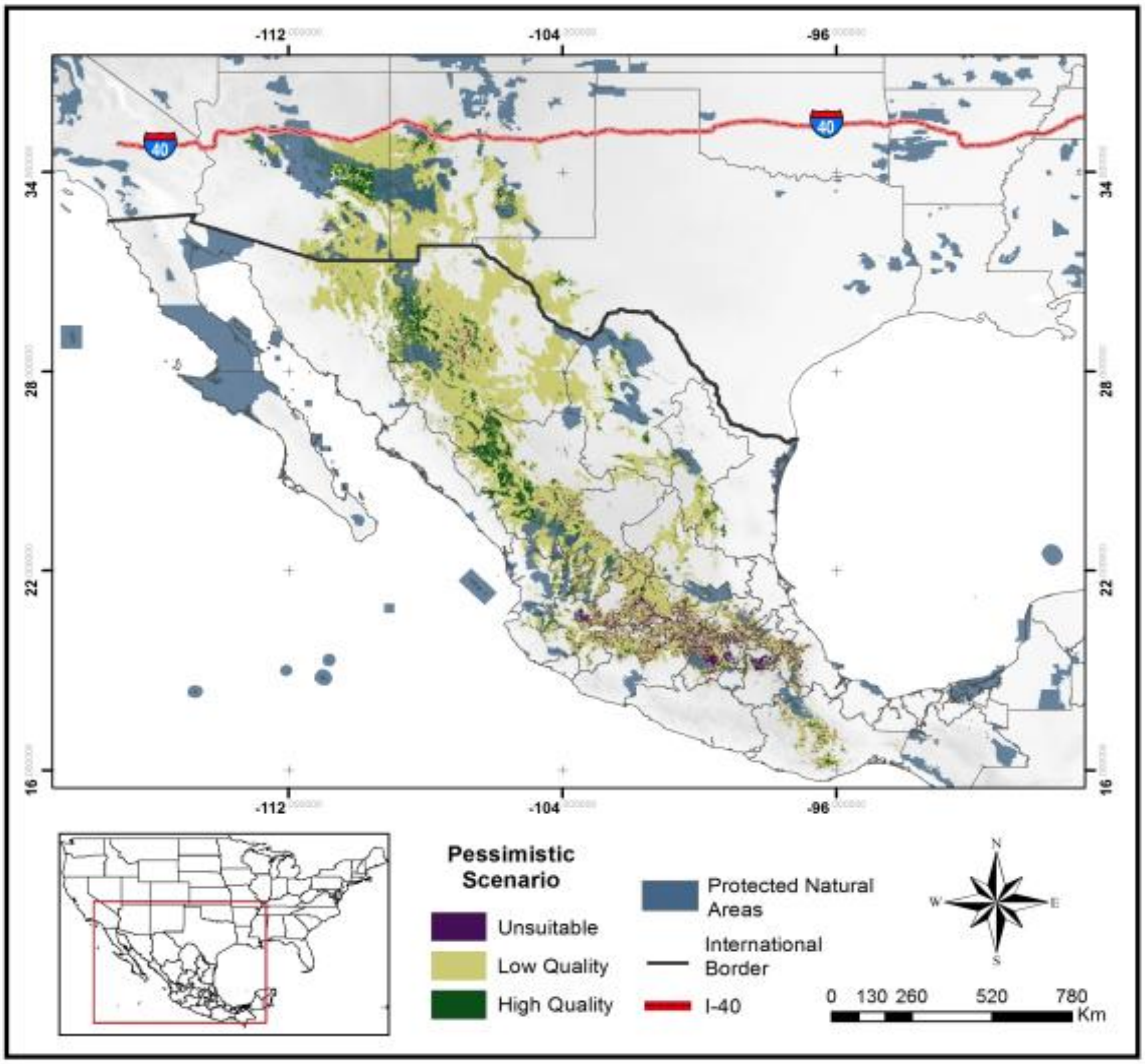

Figure 18. Reclassified pessimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

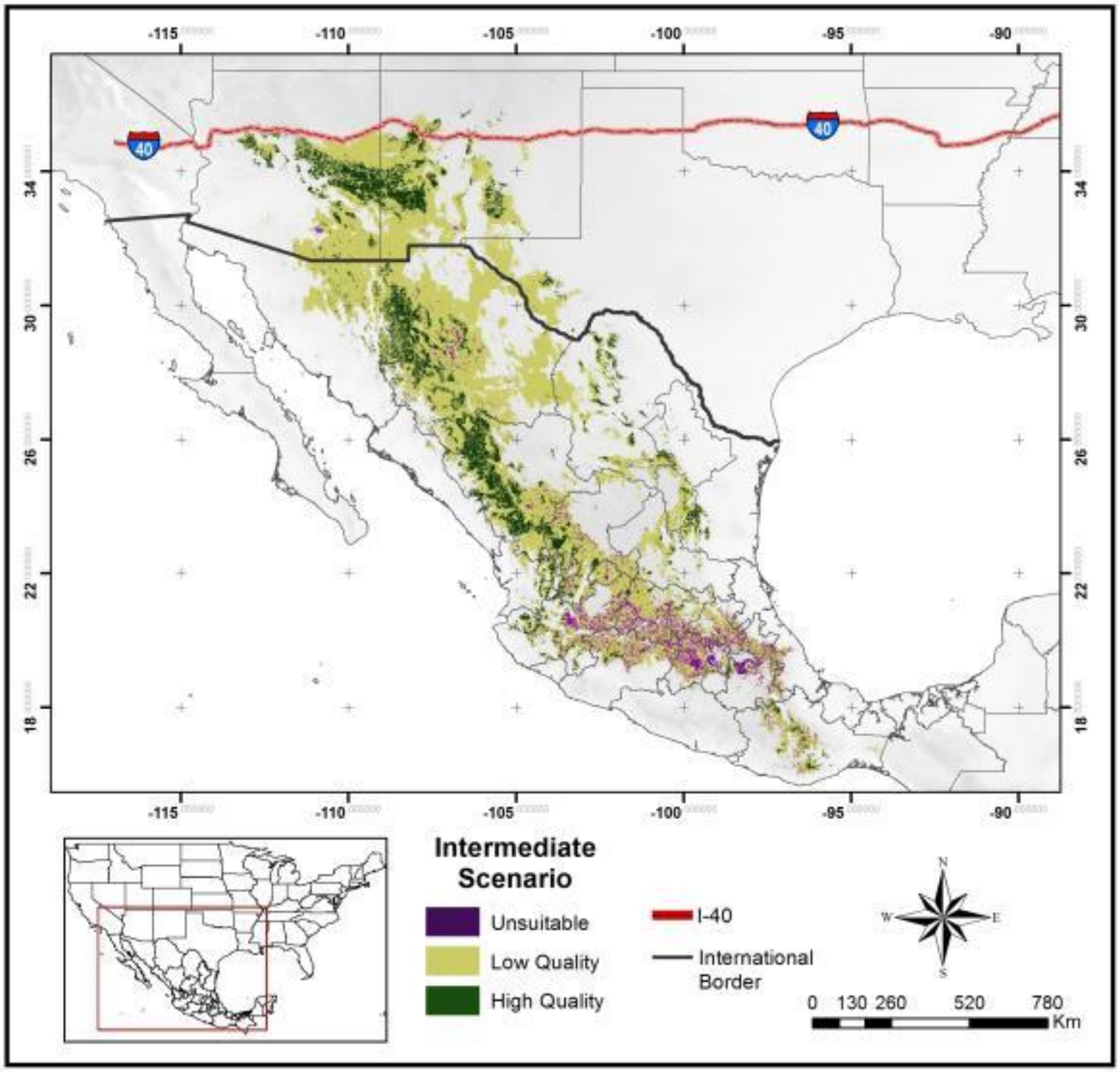

Figure 19. Reclassified intermediate habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

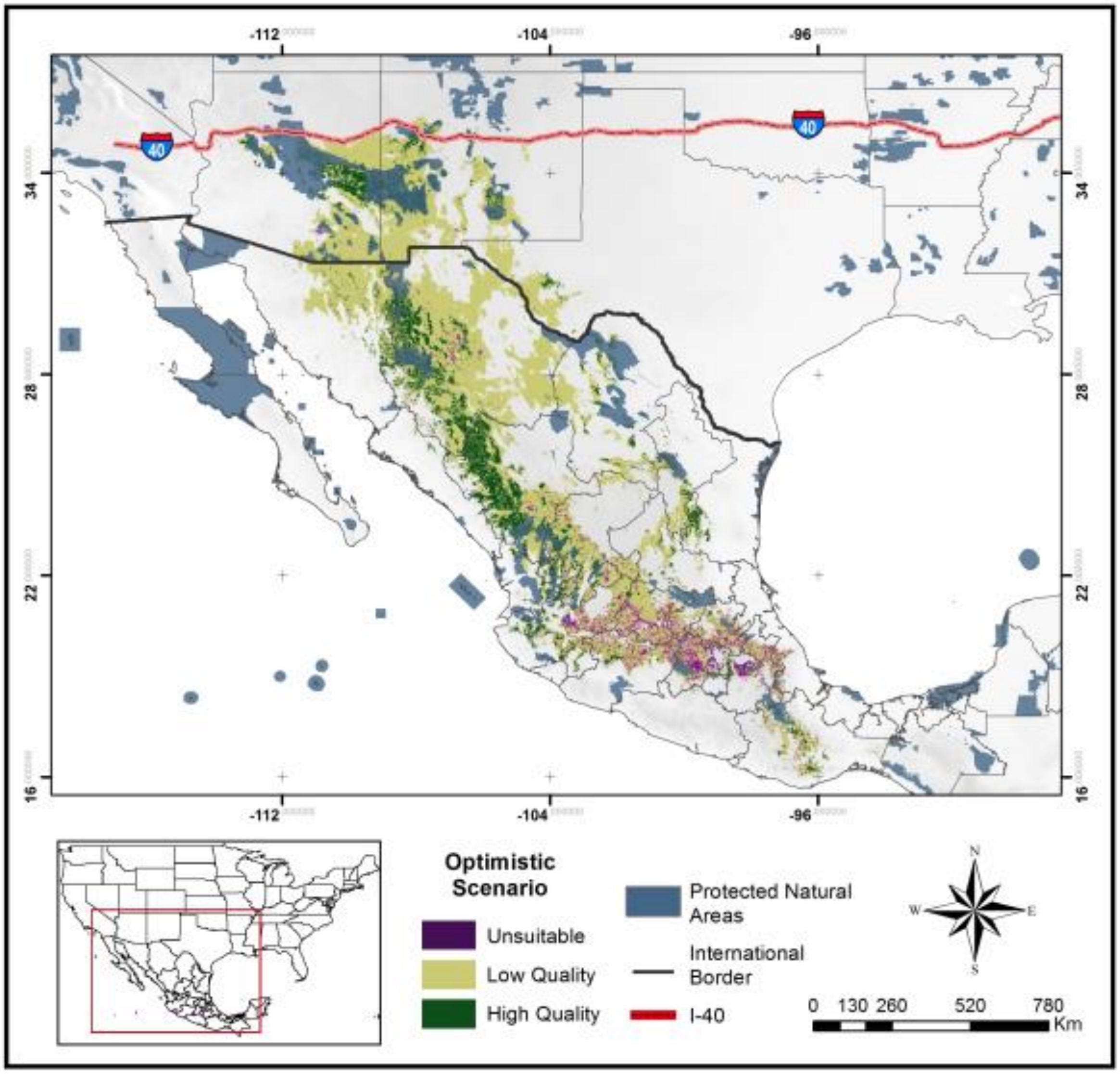

Figure 20. Reclassified optimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

We calculated the area of all high-quality habitat patches for the reclassified maps for each scenario (Figs. 18-20) in the four regions with largest continuous areas: (1) Arizona-New Mexico, (2) Northern Sierra Madre Occidental, (3) Southern Sierra Madre Occidental, and (4) Sierra Madre Oriental. Individually, the Arizona-New Mexico area holds the largest amount of high-quality habitat in the intermediate, followed by Northern Sierra Madre Occidental, Southern Sierra Madre Occidental, and Sierra Madre Oriental (Table 10). However, the two large areas of habitat of the Sierra Madre Occidental are not completely isolated, they are extensively connected by suitable habitat of variable quality, even in the pessimistic scenario, conforming the largest continuum of habitat for the Mexican wolf (Fig. 18).

Table 10. Area estimates of high-quality patches for the intermediate scenario without UBI.

Intermediate Scenario	***Area (Km2)***
Region	**108,522**
1. Arizona-New Mexico	44,477
2. Northern Sierra Madre Occidental	21,538
3. Southern Sierra Madre Occidental	34,540
4. Sierra Madre Oriental	7,967

Habitat suitability scenarios with the Ungulate Biomass Index (UBI) map

When the UBI layer was added to the habitat suitability model, an additional quality category was included (highest quality) to identify the areas with highest prey density. Comparing the two habitat models (with and without the UBI information), we observe that geographic patterns of the highest quality areas are maintained: Arizona-New Mexico, Sierra Madre Occidental and Sierra Madre Oriental regions hold large high-suitable areas in the three scenarios (Figs 21-23). However, the highest-quality areas were found in large patches only in the Arizona-New Mexico and in a much lesser extent in the two Sierras Madre (Figs 21-23); this is particularly conspicuous in the pessimistic scenario (Fig. 21). This is an expected result as the Arizona-New Mexico area holds the highest UBI (Fig. 14) due to the presence of the three ungulate species, whereas in most of the Mexican portion of the wolf distribution, there is only white-tailed deer and smaller mammals (Fig. 13). Examining the intermediate scenario, the extent of habitat increases dramatically on the Mexican side of the distribution when the high- and highest-quality patches are combined (Table 11). This is not so dramatic for the Arizona-New Mexico region because most of the habitat of this area is of the highest quality (Fig. 22).

Table 11. Area estimates of the highest-quality patches and high- and highest-quality patches combined for the intermediate scenario with UBI.

Intermediate Scenario	***High and Highest quality patches (Km^2)***	***Highest quality patches (Km^2)***
Region	**108,722**	**51,829**
1. Arizona-New Mexico	44,477	30,255
2. Northern Sierra Madre Occidental	21,538	8,073
3. Southern Sierra Madre Occidental	34,540	8,689
4. Sierra Madre Oriental	7,967	4,782

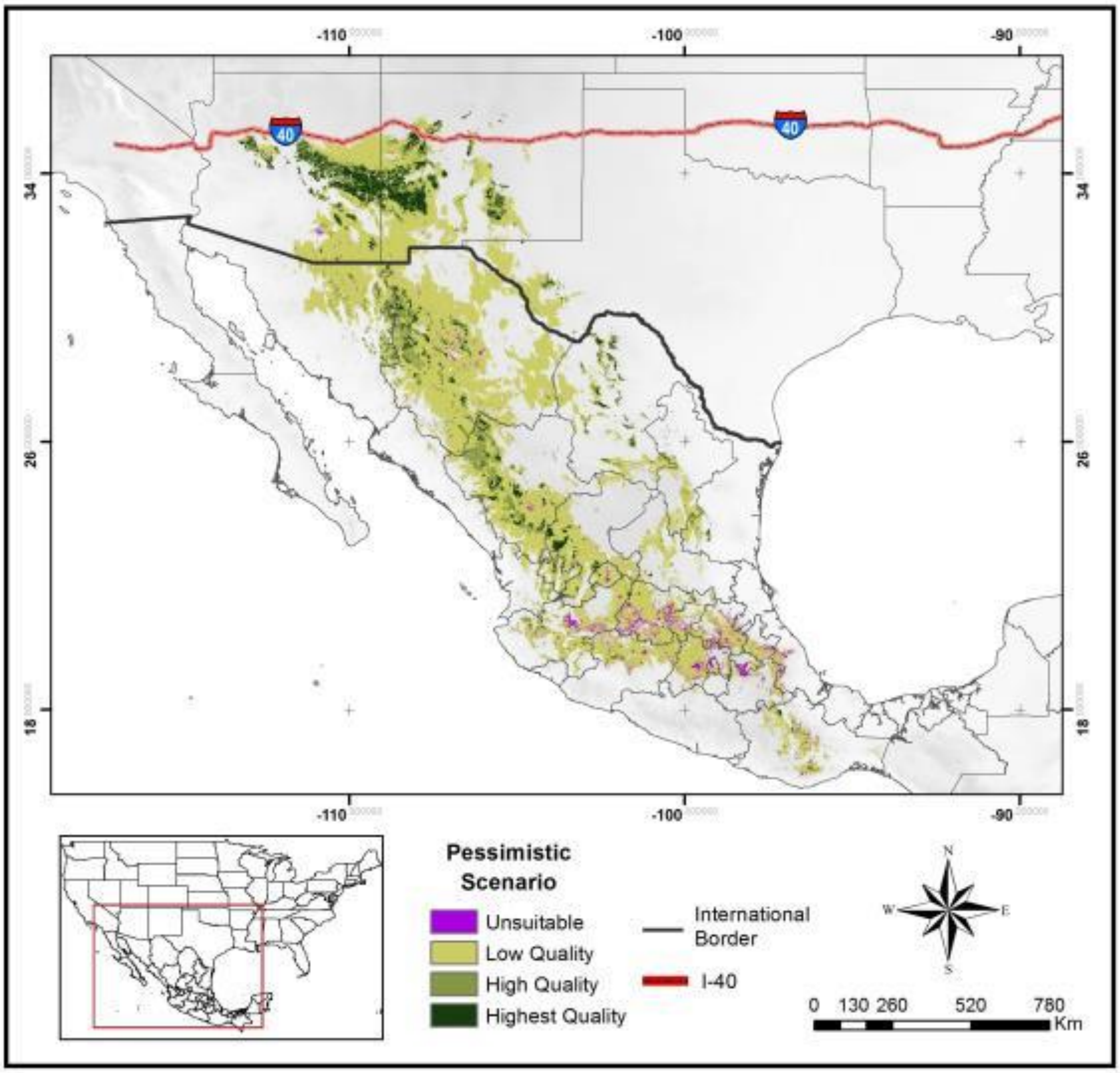

Figure 21. Rescaled pessimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

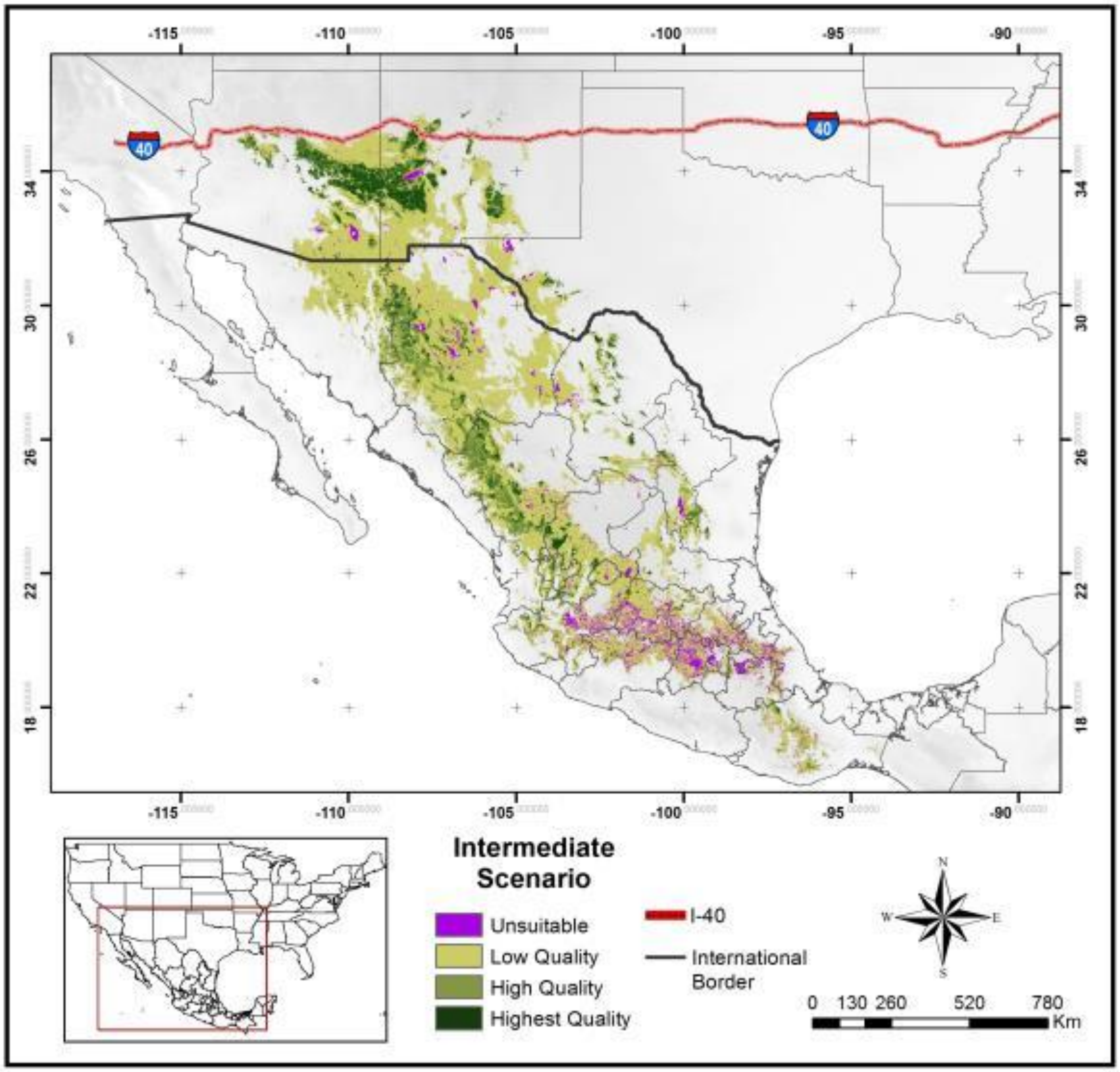

Figure 22. Rescaled intermediate habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

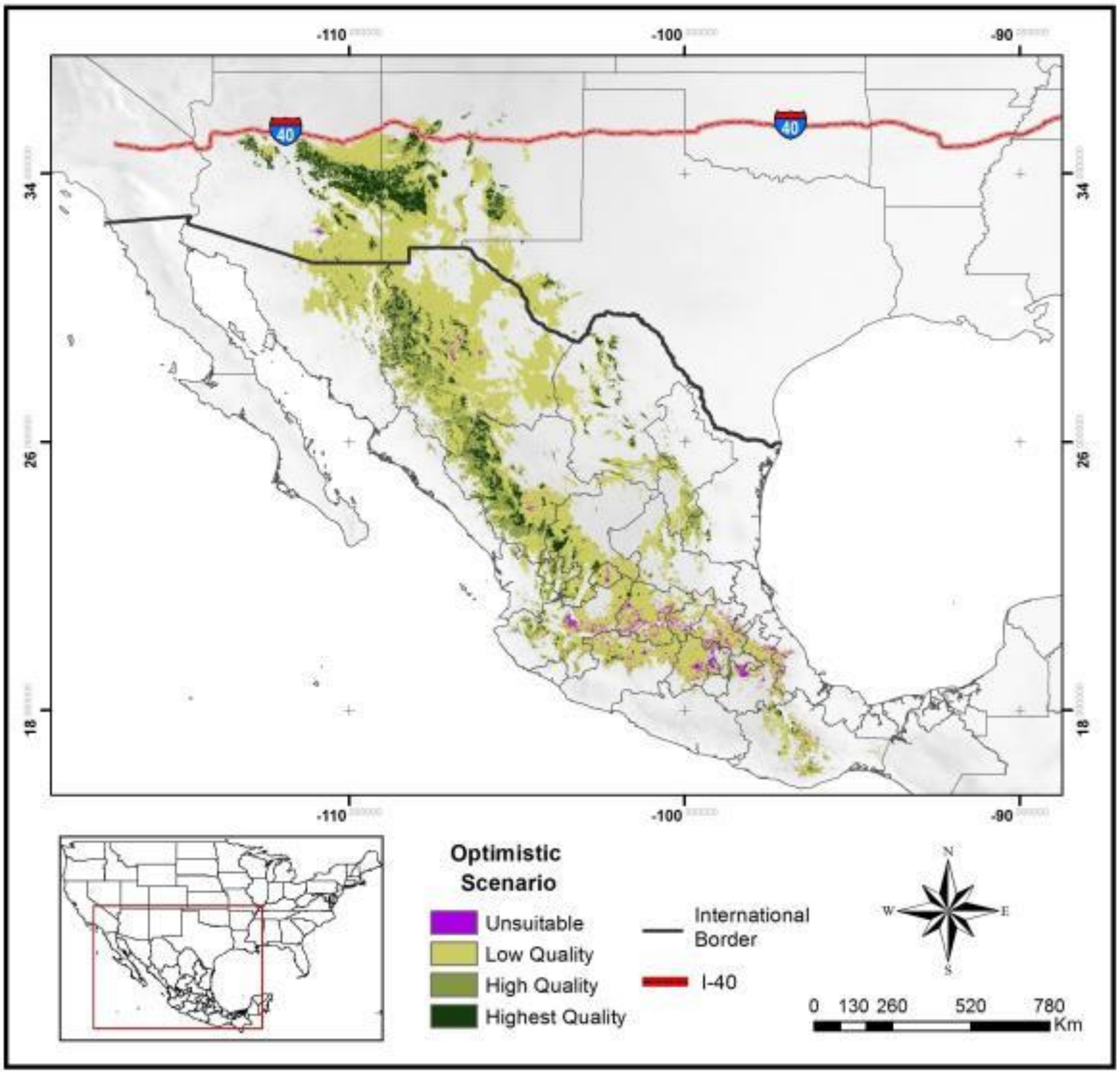

Figure 23. Rescaled optimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

Goal 1: Potential areas for undertaking recovery actions in Mexico

We consider that recovery efforts should focus in areas where conditions – both environmental and social– are favorable. This habitat suitability analysis is only the first of a series of steps that should be considered to select specific sites for further releases. Therefore, the scope of this study is to identify those areas in which suitable habitat conditions prevail and thus fieldwork should be initiated to evaluate environmental parameters like prey and cattle density, habitat condition, and social aspects such as land tenure, attitude towards the presence of wolves, and safety conditions for field teams, among others.

To be conservative, we carried out this analysis for the scenarios obtained from the habitat model without UBI information, as we are concerned about the reliability of this map. From the patch analysis and for each scenario we identified the largest, continuous patches. In the intermediate scenario, the largest patch was located in the Arizona-New Mexico region with an extension of 33,674 km^2. The other two were located in the Sierra Madre Occidental, one in the north, in Chihuahua-Sonora covering 25,311 km^2 and the other one in Durango with an expanse of 39,610 km^2 (Table 10). No continuous patches larger than 1,500 km^2 were identified in the Sierra Madre Oriental, suggesting that forests in this area are fragmented and connectivity is probably lower than in the Sierra Madre Occidental; nonetheless, scattered patches combined cover 9,259 km^2. Several small patches exist along and between the two Sierras Madre, in Coahuila and San Luis Potosí, and also between the Northern Sierra Madre Occidental and the MWEPA, in the Sky Islands, that might serve as stepping-stones for dispersing individuals across big patches (Fig. 25). It is important to highlight that as we move towards optimistic scenarios, change in total suitable area, especially in the south of the Sierra Madre, increases disproportionately compared to other areas, including those in the United States (Figs. 24-26). This suggests that if conditions in the field are more similar to optimistic scenarios, available area for the wolves will be much higher. Also, with habitat restoration and appropriate social conservation programs, the potential for wolf recovery in Mexico greatly increases.

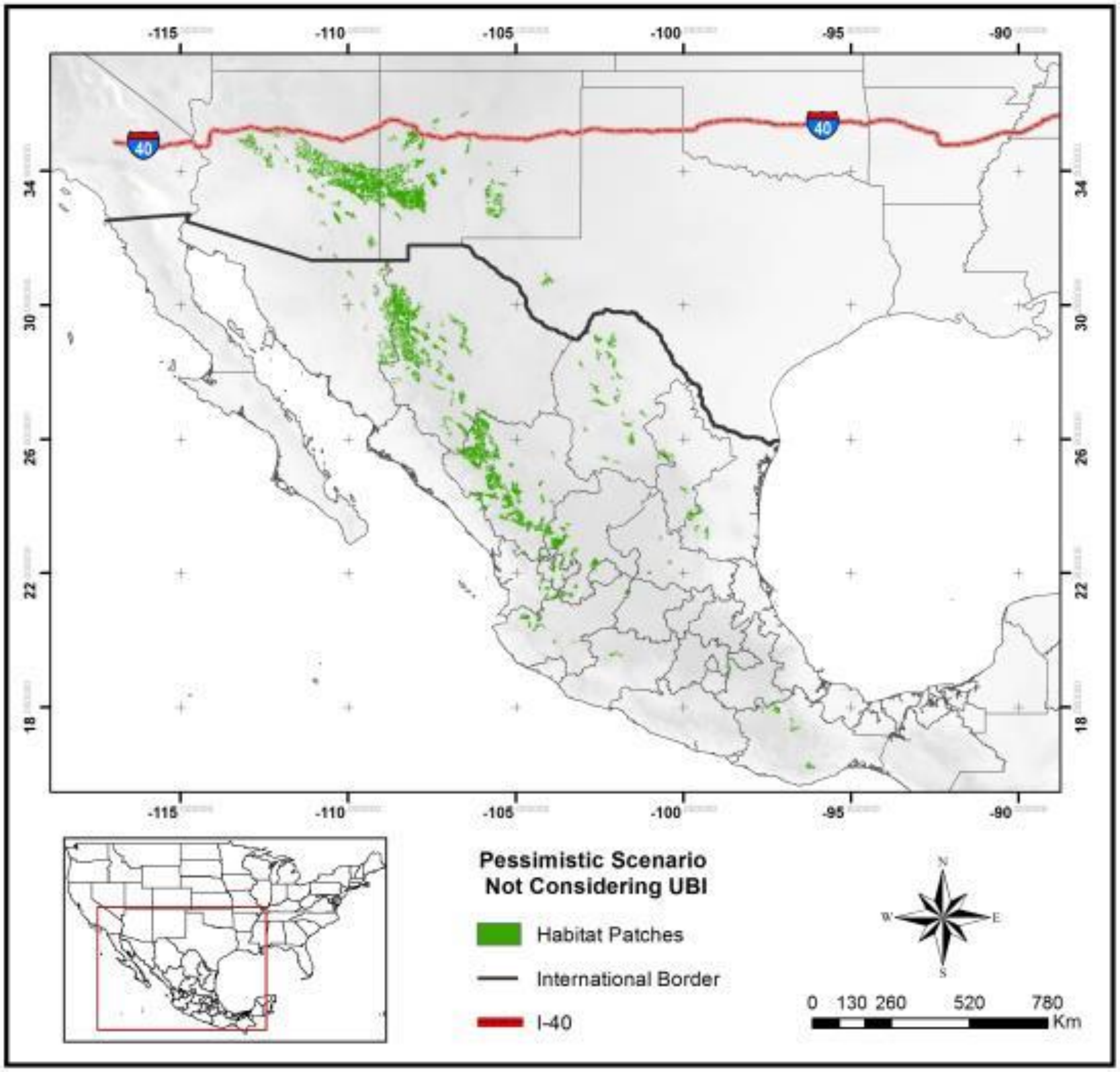

Figure 24. Depiction of only the contiguous patches of high-quality habitat under the pessimistic scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

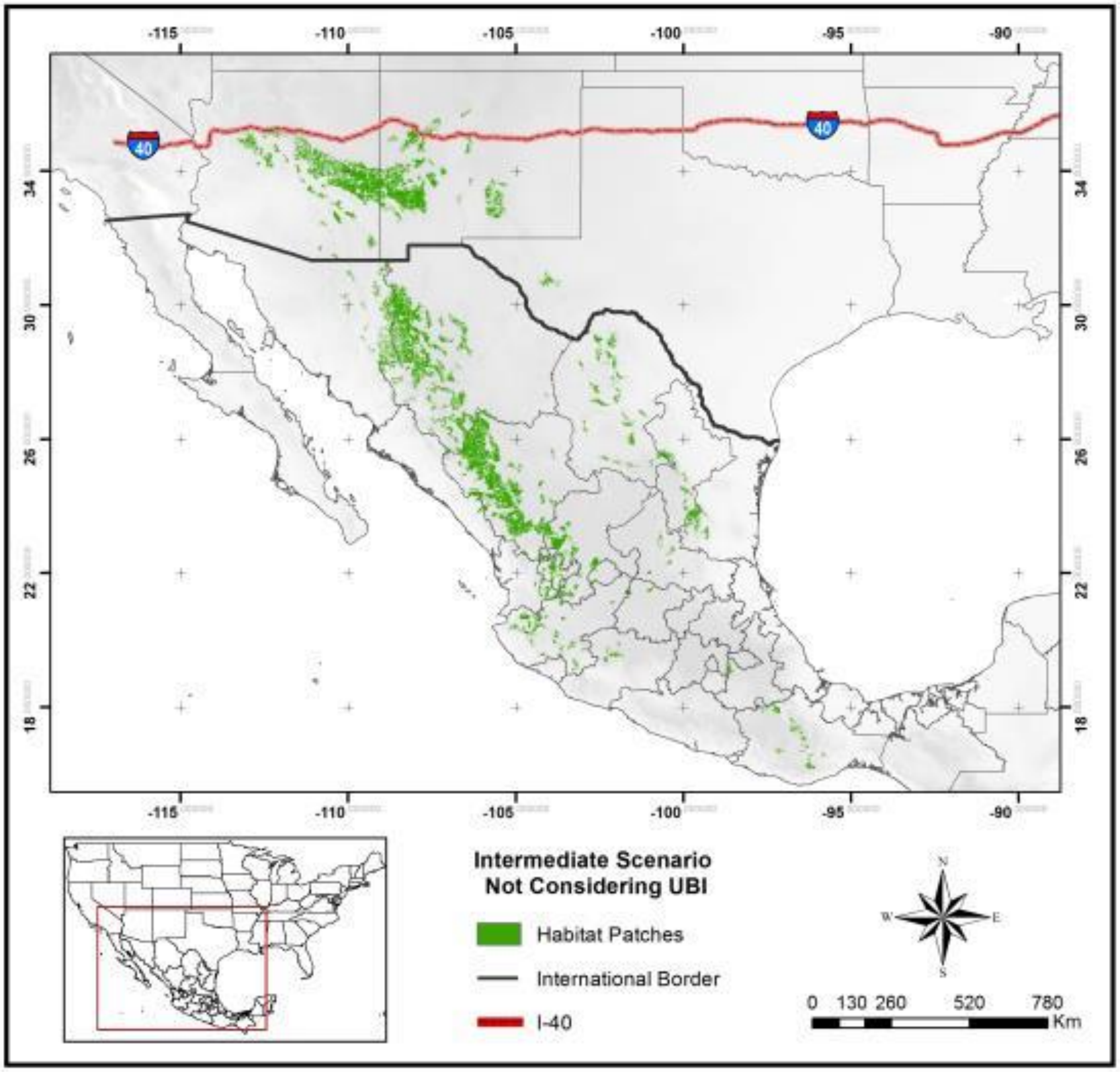

Figure 25. Depiction of only the contiguous patches of high-quality habitat under the intermediate scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

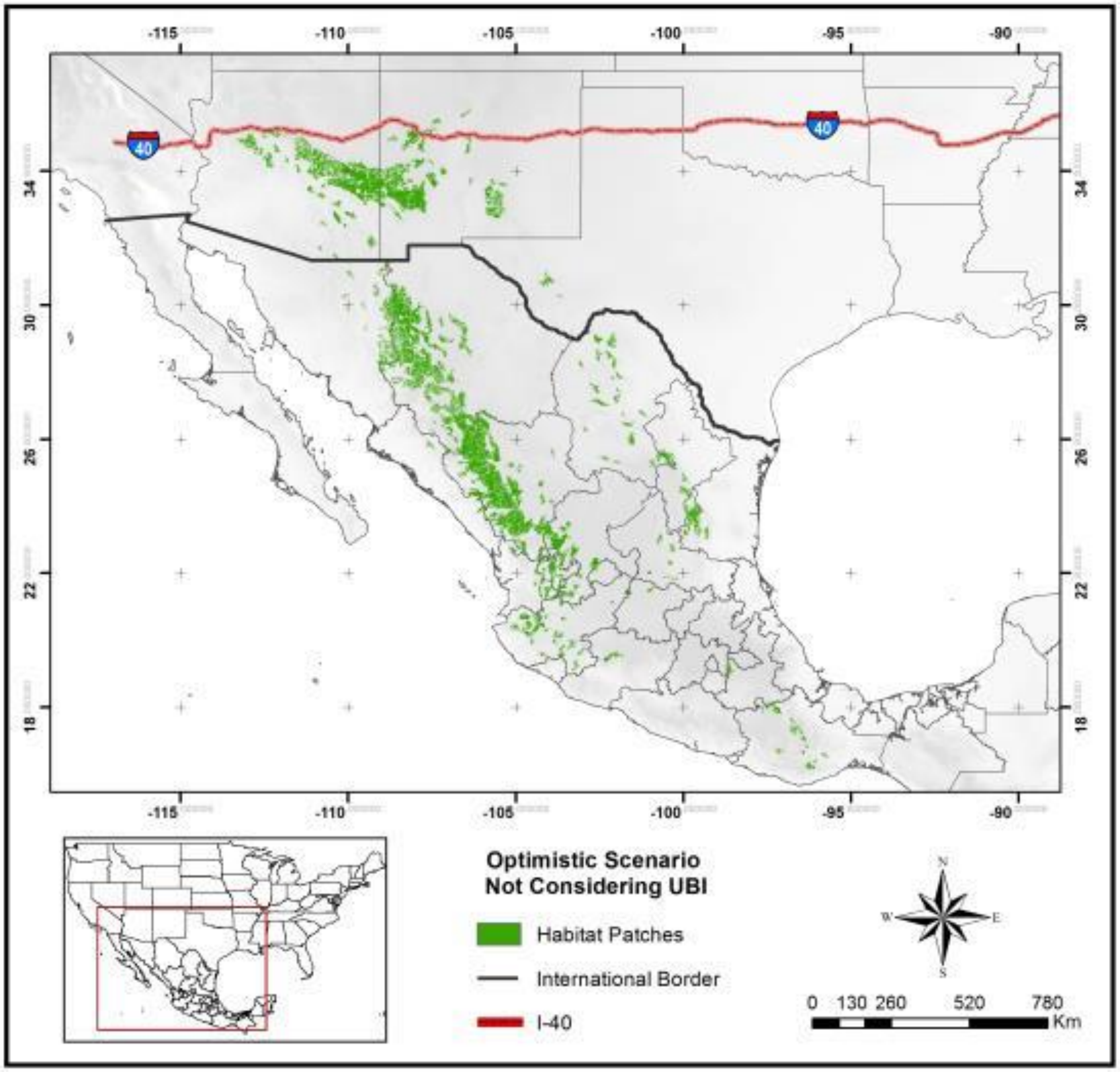

Figure 26. Depiction of only the contiguous patches of high-quality habitat under the optimistic scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Three natural protected areas in Chihuahua (Tutuaca-Papigochi, Campo Verde and Janos), one in Sonora (Ajos-Bavispe) and one in Durango (La Michilía, as well as the proposed protected area Sierra Tarahumara) cover part of the largest high-quality habitat patches in the Sierra Madre Occidental, as exemplified with the intermediate scenario (Fig. 27). In the Sierra Madre Oriental, Maderas del Carmen in Coahuila and Cumbres de Monterrey in Nuevo León are two federal protected areas that hold wolf high-quality habitat (Fig. 27). Hence, an opportunity to merge efforts among authorities from different government agencies at the federal and state levels seems feasible.

Regarding the results in the United States, we obtained several patches including the largest one in Arizona-New Mexico (in the MWEPA and surrounding area), which comprises several national forests parks that combined reaches ~33,000 km^2. This includes areas located in Lincoln National Forest and along the Cibola National Forest, in New Mexico (Figs. 27).

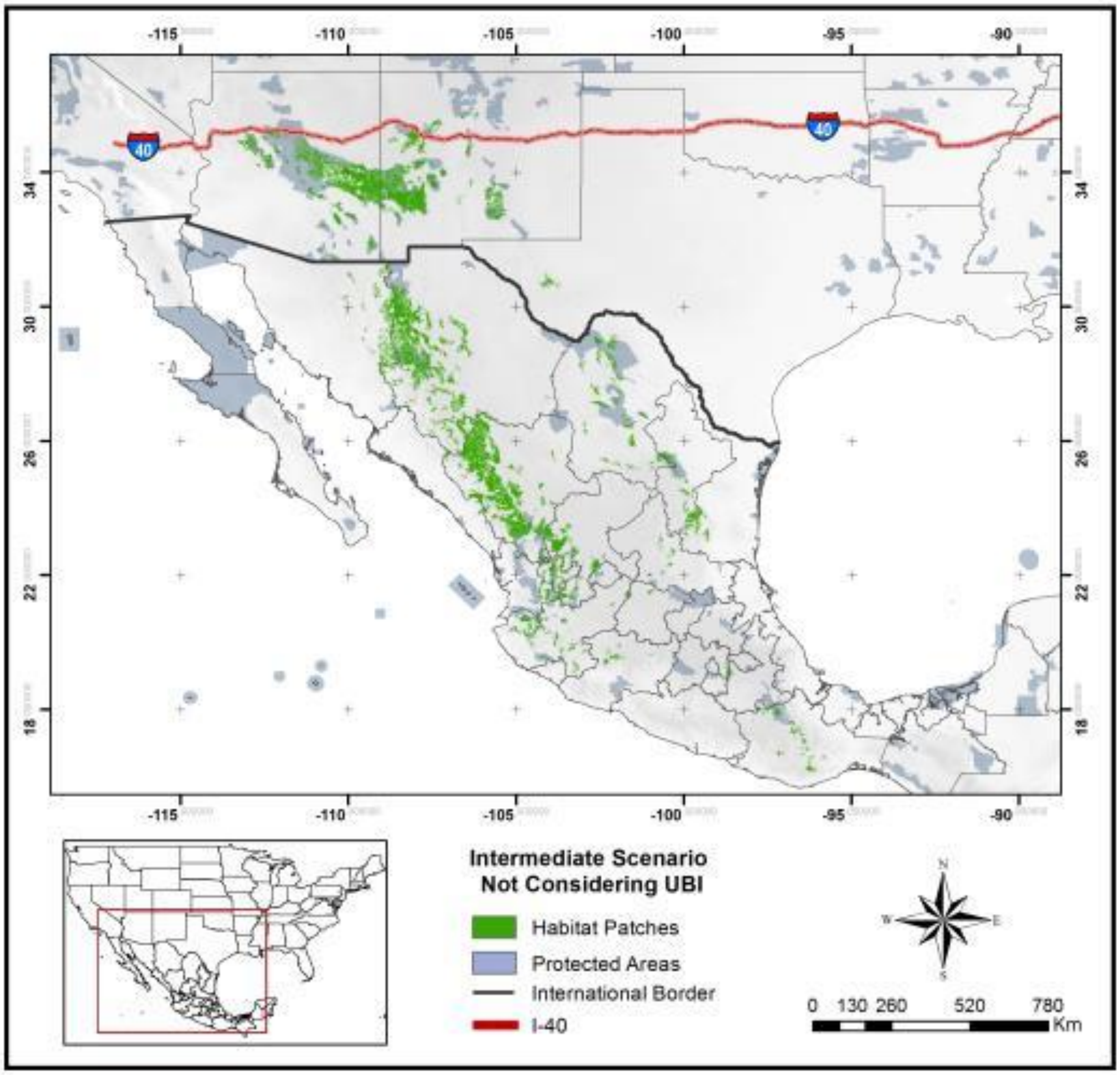

Figure 27. High-quality habitat patches and protected areas in the intermediate scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Finally, we overlaid the municipal boundaries map of Mexico on the intermediate scenario to identify the municipalities that hold significant area of high-quality habitat. In the northern Sierra Madre Occidental, 13 municipalities were identified, 15 in southern Sierra Madre Occidental 15, and 9 in the Sierra Madre Oriental (Table 12).

Table 12. Municipalities with high-quality habitat under the intermediate scenario for the Mexican wolf.

State	Municipality
Sierra Madre Occidental North	
Chihuahua	Carichi
Chihuahua	Casas Grandes
Chihuahua	Guerrero
Chihuahua	Ignacio Zaragoza
Chihuahua	Janos
Chihuahua	Madera
Chihuahua	Maguarichi
Chihuahua	Temosachi
Sonora	Bacerac
Sonora	Huachinera
Sonora	Nacori Chico
Sonora	Sahuaripa
Sonora	Yécora
Sierra Madre Occidental South	
Chihuahua	Balleza
Chihuahua	Guadalupe y Calvo
Durango	Canatlan
Durango	Durango
Durango	Guanacevi
Durango	Mezquital
Durango	Ocampo
Durango	Otaez

Durango	San Bernardo
Durango	San Dimas
Durango	Santiago Papasquiaro
Durango	Suchil
Durango	Tepehuanes
Zacatecas	Jimenez del Teul
Zacatecas	Valparaiso
Sierra Madre Oriental	
Coahuila	Acuña
Coahuila	Múzquiz
Coahuila	Ocampo
Coahuila	San Buenaventura
Nuevo León	Doctor Arroyo
Nuevo León	General Zaragoza
Tamaulipas	Jaumave
Tamaulipas	Miquihuana
Tamaulipas	Palmillas

Goal 2: Estimates of Mexican wolf population sizes

There are at least five methods to infer the potential number of wolves in an area (Bednarz 1988, Fuller 1989, Messier 1995, Paquet 2001, and based on average home range). The first four methods rely directly on the estimation of prey abundance or biomass in a simple multiplication with a constant factor (i.e., Paquet 2001) or in a regression equation (i.e., Bednarz 1988, Fuller 1989, Messier 1995). The home-range-based method is an extrapolation of the home range size and the mean number of wolves in the packs of a site or region to a given area. This method also relies, but indirectly, to prey density, because the home range and pack sizes depend on availability of prey (Fuller et al. 1992; Oakleaf et al. 2006; Belongie 2008).

Our estimates of prey density and UBI come with significant uncertainty, mainly for the Mexican portion of the distribution of the wolf. In Mexico the only wild ungulate that is a primary prey for the Mexican wolf is the Coues white-tailed deer and our analysis revealed the density modeling for this species is the weakest. The difficulty in modeling prey density and an Ungulate Biomass Index across a broad landscape is due to the large range of variation in estimated ungulate densities among sample points with similar environmental conditions. Also, in some cases there is wide environmental variation among ungulate management areas with similar ungulate densities. Trying to model these conflicting parameters resulted in poor model fit. Nonetheless, it is important to note that our relative ungulate density results for this species do capture the general geographic patterns of density known for this species in the US (J. Heffelfinger [AZGFD] and S. Liley (NMDGF]) Despite this general agreement with known variations in elk, mule deer, and white-tailed density, the UBI values for any given pixel may not accurately represent the actual biomass at that location.

Currently, there is no better information available on prey density, so it is clear that an urgent next step is to carry out a coordinated effort to gather updated, systematic field data that fulfills the needs for robust rangewide ungulate density estimations. In the meantime, we present biological carrying capacity estimations for the Mexican wolf in the different areas where suitable habitat exists, according to our geographical analyses.

We observed large variations in the wolf numbers depending on the method; estimations under Paquet (2001) and Bednarz (1988) methods were consistently higher, and the home-range-based approach is consistently lower –as much as one order of magnitude– than Fuller's (1989) and Messier (1995) methods, irrespective of the scenario analyzed (Tables 13-14). For instance, in the intermediate scenario of the habitat model for which the UBI layer was not included, the number of wolves estimated under Paquet's (2001) method is 1925, and with the home-range-based method is 184 (Table 13).

Another general result is that the largest estimated wolf population sizes were consistently from the Arizona-New Mexico region, in the MWEPA area; at least two or three times larger than Southern Sierra Madre Occidental, the next region in carrying capacity, again, irrespectively of the scenario (Tables 13-14). In turn, the Northern and Southern Sierra Madre regions have more similar numbers between them than to the other areas, and Sierra Madre Oriental always showed the lowest numbers. This relationship among regions seems very reasonable, since the MWEPA and surrounding areas holds the largest areas of highest quality habitat, according to our models, due to the high availability of ungulates, particularly elk (Figs. 22-24).

Table 13. Mexican wolf carrying capacity estimates in high-quality patches under the intermediate scenario for the habitat suitability model without the UBI layer. Deer densities were obtained from the GLM/RF model. In parenthesis are the estimates under the pessimistic and optimistic scenarios, respectively.

Intermediate (Pessimistic-Optimistic) scenarios without the UBI layer				
Carrying capacity estimation method	**Region**			
	Arizona-New Mexico	*SMOcc North*	*SMOcc South*	*SM Oriental*
Bednarz 1988	1798 (1624-1818)	579 (444-762)	982 (584-1072)	248 (159-256)
Fuller 1989	1343 (1217-1361)	284 (216-387)	516 (308-562)	138 (88-141)
Messier 1995	1390 (1261-1913)	225 (171-317)	433 (260-471)	121 (83-123)
Paquet 2001	1925 (1747- 1954)	312 (236-439)	600 (361-653)	168 (115-171)

Home range-based	184 (164-186)	138 (107-165)	217 (128-237)	50 (34-52)

Interestingly, there is not much variation in the carrying capacity between scenarios. Numbers remain relatively constant in the optimistic, intermediate and pessimistic scenarios for the habitat model with (Table 13) and without (Table 14) the UBI layer. Furthermore, it is important to emphasize that although we treated here the four regions as independent units to facilitate calculations, these areas may not be isolated from each other. Actually, there is extensive connection between the northern and southern portions of the Sierra Madre Occidental (Fig. 28), which may, in effect, be a single unit. Likewise, movements between the existing US wild population and Northern Sierra Madre Occidental are very possible due to the high mobility of wolves as evidenced by exploratory travels of US wolves and the released wolves in Mexico (Carlos López, pers. obs.).

Table 14. Mexican wolf carrying capacity estimates in high- and highest-quality patches under the intermediate scenario for the habitat suitability model including the UBI layer. Deer densities were obtained from the GLM/RF model. In parenthesis are the estimates under the pessimistic and optimistic scenarios, respectively.

Intermediate (Pessimistic-Optimistic) scenarios with the UBI layer				
Carrying capacity estimation method	**Region**			
	Arizona-New Mexico	*SMOcc North*	*SMOcc South*	*SM Oriental*
Bednarz 1988	2487 (2427-2534)	495 (443-672)	858 (547-1024)	222 (190-240)
Fuller 1989	1880 (1836-1911)	244 (195-337)	452 (290-538)	127 (97-136)
Messier 1995	1954 (1910-1986)	194 (171-272)	380 (245-452)	113 (88-121)

Paquet 2001	2708 (2646-2752)	269 (236-377)	527 (340-626)	157 (121-168)
Home range-based	243 (236-250)	122 (106-157)	212 (128-237)	50 (34-53)

The question that arises is, which of all these estimations is reliable? Unfortunately, the wolf-ungulate system in the Southwest has never been studied and all these methods based on ungulate biomass use formulas developed with data from northern ecosystems with different assemblages of ungulate and non-ungulate prey. These methods were also merely descriptive, that is they were published to describe the density of wolves experienced throughout a range of ungulate biomass indices. None were intended to predict the number of wolves one could expect when recovering a population from extirpation (especially not in the Southwestern US). The only reference point we have for comparison is the number of wolves in the US population which in 2016 was estimated to have a minimum of 113 individuals (J. Oakleaf, pers. comm.). However, we do not know the number of wolves that this area can actually support because the current population is growing.

In the Mexican side of the border, numbers are more uncertain. Currently, there are around 31 wolves distributed in three packs, but the level of human intervention is quite high, supplementing at least two of the packs (C. Lopez, pers. comm.). The reintroduction efforts are still in an early stage making it impossible to draw any conclusions regarding the potential carrying capacity in Mexico. The Mexican wolf is widely assumed to have evolved on a more diverse diet of smaller prey items in addition to white-tailed deer, indicating these estimates based solely on ungulate biomass may be biased somewhat lower if smaller prey items contributed substantially to maintaining wolves and increasing wolf densities.

Conclusions

The analyses presented here allow drawing some preliminary conclusions. First, under any scenario generated, results suggest that there is still sufficient habitat remaining in the US and Mexico to support viable populations of the Mexican wolf in the wild. Large, relatively continuous extensions of high-quality habitat remain mainly in the areas within and around the MWEPA and in Sierra Madre Occidental. High-quality habitat exists in Sierra Madre Oriental, but is naturally more fragmented than in Sierra Madre Occidental. Nonetheless, suboptimal habitat exists between high-quality patches within and between the two Sierras Madre, suggesting that dispersion of individuals is possible.

Second, information on ungulate density in Mexico is still poor. It is necessary to carry out systematic, extensive field surveys to produce reliable density estimates and rangewide models to be incorporated in the habitat suitability analysis.

Third, four natural protected areas cover portions of high-quality patches identified in the Sierra Madre Occidental. Most of high-suitable areas for wolves are under private lands, thus diversified conservation strategies are needed.

Finally, wolf number estimations showed a variation up to one order of magnitude, due to the estimation methods, input data and habitat scenario. The MWEPA region is the area overall with the highest-quality habitat due to the high availability of ungulate, particularly elk and therefore, with the highest estimation of Mexican wolf carrying capacity under any scenario. The Sierra Madre Occidental, both north and south, is the area with the potential to hold the largest number of wolves in Mexico.

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The Fish and Wildlife Service created an informational packet of the following materials related to the Draft Mexican Wolf Recovery Plan, First Revision. We have broken the packet into smaller sections to allow for easier readability.

The contents of the Packet are as follows:

- Draft Biological Report for the Mexican Wolf, May 1, 2017 version
- Population Viability Analysis for the Mexican Wolf (05/01/17) and Addendum (05/22/17)
- Mexican Wolf Habitat Suitability Analysis in Historical Range in Southwestern US and Mexico, April 2017 version
- 5 peer reviews received on the above documents

The U.S. Fish and Wildlife Service provided the above versions of the Draft Biological Report and two supporting analyses, "Population Viability Analysis for the Mexican Wolf" and "Mexican Wolf Habitat Suitability Analysis in Historical Range in Southwestern US and Mexico", followed by an addendum to the population viability analysis, for peer review from May 2, 2017 to June 2, 2017. Five peer reviewers provided comments to the Service through an independent contractor, Environmental Management and Planning Solutions, Inc.

FWS is providing this packet as supplemental background information to the public during the public comment period for the Draft Mexican Wolf Recovery Plan, First Revision. Peer reviews are anonymous at this time but FWS will provide peer reviewers names and affiliations when the recovery plan and biological report have been finalized.