Rangewide habitat suitability analysis for the Mexican wolf (Canis lupus baileyi) to identify recovery areas in its historical distribution

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Abstract
Aim: To develop an updated distribution model and habitat suitability analysis for the Mexican wolf, to inform the recovery efforts in Mexico and the United States.
Location: Mexico and the southwestern United States.
Methods: We used an ensemble species distribution modelling (SDM) approach and a spatial analysis combining anthropogenic and ecological variables, including, for the first time, rangewide relative density estimates of wild ungulates, to determine the extent of suitable habitat for wolves within a region that includes the known historical range of the Mexican wolf and adjacent areas.
Results: The results showed that the modelled distribution of the Mexican wolf extended from central Arizona and New Mexico, and western Texas in the United States, southwards along the Sierra Madre Occidental and the Sierra Madre Oriental, to the high sierras of Oaxaca, in Mexico. The habitat suitability models indicated that large tracts (>81,000 km²) of high-quality habitat still exist for the Mexican wolf in the southwestern United States, and the Sierra Madre Occidental and the Sierra Madre Oriental in Mexico, which could ensure recovery within its historical range.
Main conclusions: The recovery of the Mexican wolf is a complex, multidimensional socio-ecological challenge, which requires binational cooperation guided by reliable information and robust scientific procedures. The next step is to carry out specific socio-ecological studies and actions for selected candidate sites to assess their viability for hastening its recovery.

KEYWORDS
Canis lupus baileyi, ecological niche modelling, habitat suitability, Mexican wolf, recovery, reintroduction

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INTRODUCTION

The Mexican wolf, *Canis lupus baileyi* (Nelson & Goldman, 1929), the smallest and genetically most distinct grey wolf subspecies in North America (Nowak, 1995), formerly inhabited the temperate forests of Mexico and the southwestern United States before being nearly extirpated during the 20th century (Gish, 1977; McBride, 1980). In 1976, the U.S. Fish and Wildlife Service (USFWS) listed the Mexican wolf as an endangered species (USFWS, 1976). At that time, there were fewer than 50 individuals in the wild, all in the Sierra Madre Occidental, Mexico (Brown, 1983).

In 1998, after a successful captive breeding programme (Siminski, 2016), the USFWS and its partners released the first wolves from captivity into central parts of Arizona and New Mexico (currently designated as the Mexican Wolf Experimental Population Area or MWEPA), to establish a self-sustaining wild population (USFWS, 1982). Currently, this area has a wild population of at least 163 individuals (USFWS, 2020). In the early 1980s, recovery efforts began in Mexico with initiatives to identify appropriate sites to establish a Mexican wolf population (CONANP, 2009). In 2011, the recovery programme released the first group of Mexican wolves to the wild in northern Sonora, Mexico (CONANP, 2011). Since then, 14 additional releases have occurred in the wild, with the first wild-born litter in 2014 (CONANP, 2016). Currently, an estimated 35 individuals are living in the wild in Mexico (CONANP, 2020). Additional releases in Mexico are necessary to secure the long-term persistence of the Mexican wolf in the wild.

In the last 20 years, several efforts, using information available at the time, have been undertaken to identify suitable areas for the recovery of the Mexican wolf. Most of these efforts have focused on specific regions of the United States and Mexico (Araiza, 2001; Araiza et al., 2012; Carnes, 2011; Carroll et al., 2003, 2006, 2014; Carroll et al., 2004; Martínez-Gutiérrez, 2007). One of the challenges to complete past rangewide habitat analyses has been the availability of reliable information spanning both countries, particularly on the availability of wild ungulate prey (Carroll et al., 2004). However, in recent years, regional and global databases have been available to help overcome this limitation. To our knowledge, only one study (Hendricks et al., 2016) has attempted a rangewide analysis to redefine the historical distribution of the Mexican wolf and to identify suitable areas in its expanded range to guide recovery. Unfortunately, their analysis contains critical methodological flaws for delineating suitable areas that render their results and conclusions questionable for informing recovery planning (Heffelfinger et al., 2017a).

Here, we present the modelled distribution and habitat suitability analysis for the Mexican wolf that was developed for, and integrated into, the Revised Mexican Wolf Recovery Plan (USFWS, 2017). This analysis used a niche-based species distribution modelling approach and incorporated natural and anthropogenic factors, derived from global databases, that previously were identified as influencing wolf population establishment and persistence, including land cover and vegetation, human population density and road density (Carroll et al., 2014; Jedrzejewski et al., 2004; Oakleaf et al., 2006). Working with the agencies responsible for the management and monitoring of wild ungulate populations, we included information on relative wild prey density for the first time, one of the key factors influencing wolf population success (Fuller et al., 1992, 2003).

METHODS

We carried out the analysis in four steps: (1) modelled the distribution of the grey wolf in the southwestern United States and Mexico using an ensemble niche-based modelling approach; (2) compiled and standardized ecological and anthropogenic habitat variables for Mexico and the United States; (3) modelled the habitat suitability for the Mexican wolf throughout the modelled distribution; and (4) quantified the largest, continuous high-quality habitat patches across its modelled distribution. We describe each step below and include details in the Appendix S1, Detailed methodology.

2.1 | Modelling the distribution of the grey wolf in Mexico and the southwestern United States

The delineation of the historical distribution of Mexican wolves has been controversial during the last two decades of recovery planning (Heffelfinger et al., 2017a; Heffelfinger et al., 2017b; Hendricks et al., 2016, 2019; Leonard et al., 2005). For our analysis, we designated the extent of the modelling area (“M” sensu Barve et al., 2011) from central Utah and Colorado in the United States to southern Mexico (Figure 1). In this way, we included an area beyond the historical distribution of the subspecies and the expanded distribution recognized by Parsons (1996) adopted by the USFWS.

To model the distribution of the grey wolf in the southwestern United States and Mexico, we followed a niche-based species distribution modelling (SDM) approximation. Niche modelling algorithms characterize the ecological niche (sensu Hutchinson, 1957) of a taxon by looking for non-random associations between a collection of occurrence records and environmental conditions of the region where this taxon occurs. Then, similar conditions across the study region are identified and potential distribution is mapped (Guisan & Thuiller, 2005; Guisan et al., 2017; Pearson & Dawson, 2003; Peterson et al., 2011).

2.1.1 | Input data

We established an area (“operational area”; Figure 1) that not only included the geographic delineation of the Mexican wolf historical range proposed by Goldman (1944), Hall (1981) and Nowak (1995), but also the expanded delineation used by the USFWS (Parsons, 1996), based on Bogan and Mehlhop (1983), who incorporated *C. l. monstrabilis* and *C. l. mogollonensis* into *C. l. baileyi*. Therefore, we included the totality of records of specimens recognized as *Canis lupus baileyi*.
by all the authors, but also the records within the operational area of specimens classified as *C. l. baileyi*, *C. l. mogollensis*, *C. l. nubilus*, *C. l. youngi* or *C. l. monstrabilis*, depending on the author. We acknowledge that our operational area includes areas of intermixing between the Mexican wolf and its neighbouring subspecies, but because range limits are not rigid and our knowledge of them is incomplete, any delineation will be somewhat imprecise.

We gathered grey wolf occurrences within this operational area from the literature (Araiza et al., 2012; Brown, 1983; Goldman, 1944; Hall, 1981; Martínez-Meyer et al., 2006; Nowak, 1995), electronic databases (i.e., GBIF, VertNet) and oral records from local trappers (Brown, 1983; Servín et al., 2007), from 1848 to 1980. We excluded existing records for the Mexican wolf after 1980 because these correspond exclusively to individuals reintroduced or born in the areas designated for its recovery in the United States and Mexico. We reviewed each record and discarded those for which location description was too ambiguous for accurate georeferencing. Next, we divided the records according to their reliability into primary (specimens preserved in natural history collections) and secondary (observations or interviews with no physical evidence). We used only the primary records to calibrate ecological niche models and secondary records for model validation. Due to the strong clustering observed in the primary records in some areas, we filtered occurrences at 25 km separation distance, that is, we eliminated records that were <25 km apart, aiming to reduce clustering and thus over-representing in the model the environmental conditions of such areas (Boria et al., 2014). To do so, we used the thin function in the spThin R package (Aiello-Lammens et al., 2015). Our final data set consisted of 41 primary and 296 secondary spatially unique occurrences (Figure 1).

We used 19 bioclimatic variables obtained from the WorldClim database (Hijmans, Cameron, et al., 2005; Table S1) and three topographic variables: elevation, slope and topographic heterogeneity from the HYDRO1k database (USGS, 2001). To avoid model overfitting, we used only the most informative variables (>1% contribution) selected via the permutation method implemented in the Maxent program (Phillips et al., 2004, 2006; Searcy & Shaffer, 2016). The final set included 15 variables at 30 arc seconds (approx. 1 km²) spatial resolution (Table S1).

### 2.1.2 Ecological niche and distribution modelling

Considering that no single niche modelling algorithm performs better under any condition (Qiao et al., 2015), we tested eight algorithms under default settings: 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). We ran all algorithms in the R packages sdm (Naimi & Araújo, 2016) and dismo (Hijmans, Phillips, et al., 2005), except Maxent, for which we used its stand-alone interface (Phillips et al., 2006; see Detailed methodology in Appendix S1). All models had a final spatial resolution of 30 arc seconds.
We converted the resulting continuous maps into binary (presence–absence, Figure S1) based on a 10-percentile threshold value to account for undetected uncertainty/error in occurrences (Liu et al., 2005), and validated each model using 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 a chi-square test (Allouche et al., 2006; Fielding & Bell, 1997). Then, we generated a consensus map with the four algorithms that performed best by summing each binary map, selected the areas where two or more models coincided and converted that into a binary map, resulting in the modelled distribution map (i.e., areas where suitable climatic conditions for the Mexican wolf exist, Figure S2). We approximated the historical distribution of Mexican wolves from the modelled distribution map (Figure S2) by clipping off climatically suitable areas in biogeographic provinces with no historical occurrence records of the subspecies, that is Mediterranean

![Figure 2](https://example.com/figure2.png)

**Figure 2** Individual suitability maps of environmental and anthropogenic variables rescaled to generate the composite habitat suitability model, (a) climate, (b) land cover, (c) human density, (d) road density, and (e) Ungulate Biomass Index (UBI)
California (Comer et al., 2003) and Baja California (Morrone, 2005), assuming that such biogeographic boundaries have represented barriers to the dispersal or establishment.

Finally, we characterized climatic suitability across our modelled distribution of Mexican wolves based on the notion that optimal conditions for a species prevail towards the ecological centroid of its multidimensional niche (Hutchinson, 1957; Maguire, 1973). We estimated the distance to the ecological niche centroid as a biologically meaningful measure of environmental suitability (Manthey et al., 2015; Martínez-Meyer et al., 2013; Osorio-Olvera et al., 2019, 2020; Yañez-Arenas et al., 2012). To do so, we calculated the multivariate Euclidean distance of each pixel to the multidimensional mean in environmental space (i.e., the niche centroid). Then, we rescaled these distances from 0 to 1, where 0 corresponded to the least climatically suitable areas and values near one corresponded to pixels with the highest suitable conditions (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2012).

2.2 | Environmental and anthropogenic habitat variables

We considered the following natural variables for the habitat analysis: (1) the climatic suitability score described above; (2) land cover and vegetation types; and (3) ungulate biomass. The anthropogenic variables considered were as follows: (1) human population density and (2) road density. All variables were clipped to our modelled distribution map of the Mexican wolf (Figure 2a) and resampled from their native spatial resolution to 30 arc seconds (approx. 1 km²) to have the same extent and spatial resolution for further analysis.

2.2.1 | Land cover and vegetation types

We used land cover information for the entire study region generated by the European Space Agency (CCI-LC, 2015). This map represents the major land cover and vegetation types of the world produced for 2015 at a spatial resolution of 300 m. We performed a use/availability analysis for the Mexican wolf via a chi-square test (Table S2). Finally, the land cover layer was standardized to values from −1 to 1 based on the proportional occurrence of wolf records in the different land cover classes in the raster calculator of ArcGIS 10.2 (ESRI, 2014; see Appendix S1).

2.2.2 | Human population density

We used the Gridded Population of the World, ver. 4 (GPWv4) raster map (CIESIN-FAO-CIAT, 2005) at 1-km resolution. We rescaled the original density values from −1 to 1 using the raster calculator of ArcGIS 10.2 (Figure S3). Negative values represent human population densities unfavourable for the Mexican wolf under three scenarios (optimistic, intermediate and pessimistic). Threshold values for those scenarios were defined by experts participating in the Mexican wolf Recovery Workshop in April 2016. Based on Mladenoff et al. (1995), we established a threshold value of 1.52 humans/km² for the pessimistic scenario, so we rescaled pixel values below this density from 0 to 1 (with 1 being a human population density = 0), and we rescaled values above this threshold from 0 to −1 (where −1 was the maximum population density in the region). We calculated 1 and 2 SE above the pessimistic threshold resulting in a human population density of 3.13 humans/km² and 4.74 humans/km², which corresponded to the threshold values of the intermediate and optimistic scenarios, respectively. Then, these layers were also rescaled from −1 to 1.

2.2.3 | Road density

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 we complemented this information with a road map for Mexico at a scale of 1:250,000 (INEGI, 2015). From these two maps, we selected paved roads and dirt roads suitable for two-wheel-drive vehicles and combined them into one consistent layer. From the unified, binational map we calculated road density (linear km/km²) using the Line Density function in ArcGIS 10.2. Previous studies have found that wolves can persist in human-dominated landscapes with varying road density thresholds, ranging from 0.15 to 0.74 km/km² before wolf populations are affected (Fuller et al., 1992; Mladenoff et al., 1995, 2009; Szatatornil et al., 2016; Thiel, 1985; Vickery et al., 2001). Road density values were rescaled from −1 to 1 in the same way as we did with the human density map to construct pessimistic, optimistic, and intermediate scenarios (Figure S4) using the following threshold values: 0.74 km/km² for the optimistic, 0.15 km/km² for the pessimistic and the average of these two values, 0.445 km/km², for the intermediate.

2.2.4 | Ungulate density

We used ungulate density estimations in the United States and Mexico to calculate an Ungulate Biomass Index (UBI) across wolf modelled distribution (Table S3). The UBI is a standardized value that uses a weighting factor based on mean animal mass to compare relative biomass available across different predator-prey systems (Fuller et al., 2003). Ungulate density estimates in the United States came from aerial surveys of elk (Cervus canadensis), mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus) in 23 Game Management Units (GMUs) in Arizona and seven in New Mexico. In New Mexico, survey observations of mule and white-tailed deer were aggregated and could not be used for species-specific analysis. For Mexico, we used white-tailed deer density estimates from camera-trap surveys conducted from 2012 to 2014 in Sonora and Chihuahua (López-González, García-Chávez,
et al., 2014; López-González et al., 2012, 2013, 2015) and 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 (Servín et al., 2008, 2018). We also used camera-trap surveys for mule deer density estimates in northern Mexico (López-González, Lara Díaz, et al., 2014).

After preliminary analyses to model the UBI across the study area, we made several adjustments to improve the accuracy of our predictions for each species (see Appendix S1). We analysed range-wide density estimations for the three ungulate species using a generalized linear model (GLM) and random forest (RF) modelling to establish the best parameters to estimate UBI. For calibrating the model, we used 15 climatic, topographic and ecological variables (selected from an initial set of 27 based on their levels of significance; Table S4). We measured the reliability of individual species’ models with a Pearson correlation analysis (r²) and Akaike’s information criterion (AIC). We calculated the UBI within the modelled distribution considering the ungulate abundance/density information and a weighting factor (β) for each species (see Appendix S1). We built the UBI distribution maps of each species across the whole study area in QGIS (QGIS Development Team, 2016) 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; Figure S5). The three individual UBI maps were summed together in QGIS to produce a combined UBI map (Figure S6), which was then clipped to our modelled distribution and finally rescaled from 0 to 1 to match the other layers for the habitat suitability model. This map represented the first spatial layer ever developed to estimate relative ungulate biomass available to Mexican wolves across their range.

### 2.3 Habitat suitability models

We implemented an additive model with the rescaled variables to produce two sets of habitat models, with and without the UBI map, to assess the sensitivity to this variable. For models without UBI, we summed the climatic suitability model (with values from 0 to 1) + land cover + human density + road density maps (all with a scale of −1 to 1) using the raster calculator in ArcGIS 10.2; hence, values of the resulting map could range from −3 to 4. For models including the rescaled UBI map (with values from 0 to 1), we added this variable to the previous maps; thus, the resulting maps could hold values from −3 to 5. Consequently, values lower than zero represented unsuitable areas, whereas positive values represented progressively higher habitat quality.

We built pessimistic, intermediate and optimistic scenarios based on the three versions of human and road density maps, whereas climatic suitability and land cover maps were fixed for all scenarios. We present results for the intermediate scenario (optimistic and pessimistic scenarios can be found in Appendix S1, Figures S7 and S8). Finally, we identified and quantified the areas of high-quality habitat across the modelled distribution of the Mexican wolf in each scenario using the aggregate polygons tool of ArcGIS 10.2. To identify large areas of high-quality habitat, we selected groups of pixels in the upper quartile for each scenario with and without UBI (≥3.57 and ≥2.513, respectively) that represented areas ≥2,500 km² in which high-quality pixels were not separated by more than 10 km.

### 3 RESULTS

#### 3.1 Distribution modelling of the grey wolf in the southwestern United States and Mexico

According to validation metrics, the niche modelling algorithms that performed best were Maxent, RF, CART, and GAM (Table 1). The resulting ensemble model showed that the ecological conditions defining the modelled distribution of the grey wolf in this region extended from central Arizona and New Mexico and western Texas in the United States, southwards to Mexico along the Sierra Madre Occidental and in scattered mountain ranges in the Sierra Madre Oriental, along the Transvolcanic Belt, and in the high sierras of Oaxaca (Figure 1).

#### 3.2 Environmental and anthropogenic habitat variables

The climatic suitability map showed that the highest suitability scores were found in the western portion of the modelled distribution
TABLE 2 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                     |

(Sierra Madre Occidental) and in smaller scattered areas in the Sierra Madre Oriental, in northeastern Mexico (Figure 1).

The resulting land cover preference map shows that the largest areas with adequate natural vegetation cover for the Mexican wolf were in the Mogollon Rim area in Arizona and New Mexico and in the Sierra Madre Occidental, in Mexico (Figure 2b). Those were also the areas with the lowest human population density (Figure 2c) and road density (Figure 2d). Other minor areas with similar conditions were scattered in southern Arizona, southern New Mexico and northeastern Mexico.

Ungulate density estimations were affected by methodological differences between sources of data. In general, the variance explained with the RF regression models was relatively high for elk but low for the mule deer and white-tailed deer (Table 2). Low $r^2$ values for deer data were a consequence of the large dispersion of density data values, where wide variability existed within and among similar climate and topographic conditions. Despite this, we found a relationship with predictor variables, which suggests that the model conservatively estimates the central tendency for the broader landscape of interest here. The pattern reflected by the combined UBI maps of the three species showed that UBI values were much higher where elk occurred in Arizona and New Mexico than in the rest of the modelled distribution. Elk is the largest of all three ungulates and is naturally absent in Mexico (Carrera & Ballard, 2003), so it was not a natural prey item throughout most of Mexican wolf historical range (Figure 2e).

3.3 | Habitat suitability without the Ungulate Biomass Index (UBI)

Results of the additive habitat suitability models excluding the UBI for the intermediate scenario indicated that large areas (>98,000 km$^2$) of high-quality habitat exist for Mexican wolves mainly in Arizona and New Mexico in the United States and the Sierra Madre Occidental, with scattered smaller suitable areas in the Sierra Madre Oriental, in Mexico (Table 3). Although high-quality patches remain in the Mexican Transvolcanic Belt and southwards, these are not large enough or sufficiently connected to form continuous areas, and thus are not suitable to maintain long-term Mexican wolf populations (Figure 3a). In the United States, high-quality areas were located in the MWEPA. In Mexico, the Sierra Madre Occidental held large areas of high-quality habitat concentrated in two main regions, one in western Chihuahua and eastern Sonora, and the other in Durango southwards to western Zacatecas and northern Jalisco. The Sierra Madre Oriental held high-quality areas, but mountain ranges in that region are naturally more fragmented than in the Sierra Madre Occidental (Figure 3a).

We calculated the area of high-quality habitat patches (upper quartile) in the four regions with the largest contiguous areas: (1) Arizona and New Mexico, (2) Northern Sierra Madre Occidental, (3) Southern Sierra Madre Occidental and (4) Sierra Madre Oriental (Table 3). Individually, the Southern Sierra Madre Occidental region held the largest amount of high-quality habitat, followed by the Arizona–New Mexico region, the Northern Sierra Madre Occidental and Sierra Madre Oriental (Table 3). The two large areas of suitable habitat in the Sierra Madre Occidental, although presented separately, are extensively connected by suitable habitat of variable quality, forming the largest continuum of habitat for the Mexican wolf (Figure 3a).

3.4 | Habitat suitability including the Ungulate Biomass Index (UBI)

When the UBI layer was included in the model, the general geographic patterns remained unchanged, but the estimated amount of high-quality habitat changed in most areas (Figure 3b). The Arizona–New Mexico region maintained almost the same amount (>33,000 km$^2$) of high-quality habitat as the scenarios without UBI, but Northern and Southern Sierra Madre Occidental and Sierra Madre Oriental had relatively smaller areas of high-quality habitat (Table 3). This is not surprising as the Arizona–New Mexico region held the highest UBI due to the presence of all three ungulate species. In contrast, only white-tailed deer occur naturally in most wolf habitat in Mexico. The addition of UBI data changed the amount of high-quality habitat in Mexico in a relative sense because rangewide values were rescaled, thereby reducing the relative proportion of high-quality habitat in Mexico compared to the United States.
The recovery of Mexican wolves has been a tremendous endeavour undertaken by governments, scientists and conservation agencies in the United States and Mexico over the last 40 years (CONANP, 2009; Moctezuma-Orozco et al., 2011; Servín et al., 2008; Siminski, 2016; USFWS, 1982). Today, more than 190 Mexican wolves roam free in two areas designated for their recovery, with at least 163 individuals in the United States (USFWS, 2020) and about 30 in Mexico (CONANP, 2020). However, the long-term persistence of this subspecies will be enhanced with additional recovery areas, highlighting the need for a comprehensive analysis of habitat suitability for the Mexican wolf throughout its historical range to identify potential areas to conduct specific investigations of local conditions, both ecological and sociological, to select suitable release sites.

We first determined the geographic extent of ecological conditions that potentially could have supported the Mexican wolf. Different niche-based distribution models concordantly identified a region that included central Arizona and New Mexico southwards into Mexico. This area was then the logical focus of the subsequent evaluation of habitat suitability to refine the areas that meet the ecological conditions that could maximize the probability of successful recovery. Therein, we identified large enough areas (>81,000 km²) of highly suitable habitat to support the recovery of the Mexican wolf, both in Mexico and in the United States (Figure 3, Table 3).

4.1 | Habitat suitability for the Mexican wolf

One of the limitations to evaluate habitat suitability for the Mexican wolf has been a lack of information on prey availability (Araiza et al., 2012; Carroll et al., 2003, 2014). In this analysis, we addressed this limitation for the first time by modelling relative ungulate density across the entire range of the Mexican wolf using empirical data to calculate an Ungulate Biomass Index (UBI, Fuller et al., 2003). Ungulate density is higher at the northern periphery of suitable range in central Arizona and New Mexico primarily because of the presence of elk and mule deer (Figure 2e), and more effective protection and management of ungulate populations than in Mexico. Elk did not historically occur in Mexico (Carrera & Ballard, 2003), and desert mule deer occur mainly at lower elevations. Therefore, wolves in Mexico have historically had a more diverse diet of smaller prey items (Saldivar Burrola, 2015) and thus suitability of Mexican wolf habitat there may not have been so closely related to ungulate density as it was in the United States. Regardless, based on our field knowledge of the study region, we consider that the habitat suitability model including the UBI is more realistic, so we focus our discussion based on this scenario (Figure 3b).

Highly suitable areas are concentrated in four main regions: (1) the Mogollon Rim and areas to the south (MR; where the MWEPA is located); (2) Northern Sierra Madre Occidental (NSMOcc); (3) Southern Sierra Madre Occidental (SSMOcc); and (4) Sierra Madre Oriental (SMOr; Figure 3b). These areas maintain habitat connectivity within and among them, but all have different ecological, social and political landscapes that may favour or limit Mexican wolf recovery.

The MR holds the largest contiguous area of high-quality habitat when all factors are considered together (climate, land cover, human population, roads and UBI; Table 3). Despite its geographic location on the northern edge of suitable habitat for the Mexican wolf (Figure 1), the high density of elk, as well as habitat and ungulate management practices in the MWEPA has made this area conducive to successful recovery of Mexican wolves. Interestingly, not all the MWEPA is occupied by the subspecies; there are extensive areas in MR adjacent to the current distribution where wolves have not established. The ecological reasons for this lack of expansion are unknown, but some plausible, non-exclusive hypotheses include: (1) wolf densities and prey availability within core area have not reached
the point to force expansion; (2) high mortality rates in areas where people are unaccustomed to wolves; (3) high mortality rates of dispersing wolves; (4) lack of detection of a small number of wolves; and (5) this northern ecological zone represents environmental conditions that are peripheral to those in which the Mexican wolf evolved. Our analyses partially support hypothesis (5), but further data and analyses are needed to clarify this intriguing question.

The NSMOcc and SSMOoc also hold extensive areas of highly suitable habitat interspersed in a mosaic of varying quality habitat (Figure 3). The smaller Mexican wolf evolved preying on Coues' white-tailed deer (*Odocoileus virginianus couesi*) and smaller mammals and birds (Brown, 1983), but seems to have benefited from the multispecies ungulate guild in the northern periphery of its historical range. Finally, the SMOc holds patches of high-quality habitat and may also play a role in the recovery of wolf populations, but the mountain ranges in that region are naturally smaller and more sparsely distributed than in the SMOc (Figure 3). This analysis shows that there is ample high-quality habitat in Mexico for the Mexican wolf to be recovered in its historical range.

### 4.2 Comparison with other habitat suitability analyses

Most previous habitat suitability analyses have focused only on select geographic areas in the United States or Mexico, in part because of the lack of comparable source data for the two relevant countries (Araíza et al., 2012; Carroll et al., 2004, 2006, 2014). Carroll et al. (2004) used what geospatial data and tools were available at the time to evaluate habitat throughout the Mexican wolf’s historical range and extralimital areas to the north, prior to wolves being released in Mexico. However, their analysis was influenced by the application of a differential spatial adjustment to base mortality risk that decreased the suitability of most habitat in Mexico and boosted suitability of extralimital areas, such as the privately owned Vermejo Park Ranch and Grand Canyon National Park. Despite these adjustments, they concluded that Mexico had suitable quality habitat to sustain 2,600 Mexican wolves (Carroll et al., 2004). On the other hand, the work of Araíza et al. (2012) was not intended to be a comprehensive analysis of Mexican wolf historical range, but rather an evaluation of six areas identified by knowledgeable biologists as holding potential for wolf recovery in Mexico. Unfortunately, this analysis has been portrayed inaccurately (Carroll et al., 2014; Hendricks et al., 2017) as evidence that Mexico does not have enough suitable habitat for wolf recovery.

Hendricks et al. (2016) addressed the question of the historical distribution of the Mexican wolf under an ecological niche modelling approach and analysed habitat suitability across the entire range, integrating land cover and human population density information. However, their results differed substantially from ours and warrant further discussion.

We found problems in several steps taken by Hendricks et al. (2016) to produce their niche models that we detail in Appendix S1. Extended discussion. First, the authors built two different niche models with Maxent (Phillips et al., 2004, 2006), one “typological,” using occurrence records from individuals morphologically recognized as Mexican wolves, and another “genealogical,” in which they included additional occurrences from individuals belonging to a genetic cluster referred to as the “southern clade” (Hendricks et al., 2016, 2019; Leonard et al., 2005), but morphologically recognized as a different subspecies. The records used for the typological model were highly clustered and did not include available records associated with museum specimens in the southern portions of the historical distribution of the Mexican wolf. Because the authors did not reduce the sampling bias, the resulting model included areas that the Mexican wolves rarely occupied, such as the lowlands of the Chihuahuan Desert (Brown, 1983; Gish, 1977; McBride, 1980). Furthermore, the genealogical model was more problematic. Besides including seven additional northern wolf samples—including one from Nebraska and two from Utah—Hendricks et al. (2016) changed the parameterization of Maxent without explanation to produce a more widespread distribution (Merow et al., 2013), resulting in a misleading model extending far to the north of the known historical and extended distribution, even as far north as Oregon (Goldman, 1944; Hall, 1981; Heffelfinger et al., 2017a; Nowak, 1995; Parsons, 1996). Nonetheless, even with these changes, the resulting model still did not capture the locations of four of the seven “southern clade” northern wolf records. In our analysis, we used similar sources to obtain the occurrence records, but we avoided these pitfalls and obtained a distribution model that better resembles the historical and extended distribution of this subspecies (Figure 1). Another substantial difference between our results and those of Hendricks et al. (2016) was that they determined habitat in Mexico, changing abruptly at the international border with the United States, to be mostly unsuitable (Heffelfinger et al., 2017a). The starkly artificial difference at a political boundary and their general depiction of “not suitable” habitat on the Mexican side of the boundary is inconsistent with recent human impact analyses, such as the global data set of the Human Influence Index (WCS-CIESIN, 2005) and two recent countrywide assessments of the human footprint (González-Abraham et al., 2015) and ecological integrity (CONABIO, 2018; Mora, 2017) in Mexico (Figure S9). These independent sources represent a unifying theme that are in agreement with our finding that the Sierra Madre Occidental and the Sierra Madre Oriental currently present mostly high to medium levels of ecological integrity with few heavily impacted areas. In sum, the overly simplistic modelling strategy of Hendricks et al. (2016) and the unexplained inconsistencies in their suitability analysis raise concerns about the reliability of their results for inferring the historical distribution and habitat suitability of the Mexican wolf.

### 4.3 Informing recovery actions

Our geographic description of ecological conditions associated with the Mexican wolf’s historical occurrences coincides with all historical range delineations, as summarized by Heffelfinger...
et al. (2017a), but made before the more recent advocacy of an expanded range to facilitate recovery only in the United States (Carroll et al., 2014; Hendricks et al., 2016, 2017, 2019; Leonard et al., 2005). The latter position seems especially incongruous because the greater part of the historical range of the Mexican wolf was in Mexico (Heffelfinger et al., 2017a; Parsons, 1996). Some have suggested that a significant portion of the subspecies’ range must be occupied before delisting (Vucetich et al., 2006); if such a position were adopted, the Mexican wolf could not be recovered without extensive efforts in Mexico. Furthermore, the recovery of a subspecies outside of the ecological conditions in which it evolved is fraught with legal and ecological concerns (Odell et al., 2018).

The Mexican wolf was extirpated both in Mexico and in the United States mainly because of conflicts with livestock operations and not because of habitat destruction. Nonetheless, in past analyses Mexico has been marginalized or parameterized in such a way as to make it appear unsuitable (Carroll et al., 2014; Hendricks et al., 2016, 2019). In contrast, we found that abundant high-quality habitat still exists across the historical range of the Mexican wolf to ensure recovery and allow Mexico to play a vital role in this endeavour.

Until now, all efforts to recover the Mexican wolf in Mexico have focused on the northern portion of the Sierra Madre Occidental (SMOcc). Here, we demonstrate that the alternatives are much broader as large tracts of highly suitable habitat remain in the southern SMOcc and to a lesser extent in the Sierra Madre Oriental. In fact, there is a continuum of suitable habitat among the four regions that we identified in our analyses (Table 3): the SMOcc connects with the Mogollon region through the Madrean Sky Islands; the SMOcc and the Sierra Madre Oriental are connected from the south across the mountains of the states of Jalisco, Zacatecas and San Luis Potosí. Likewise, a connection between the Sierra Madre Oriental and the suitable habitat available in western Texas exists in the Big Bend region, closing the circuit across eastern New Mexico (Figure 3).

Recovery efforts for the Mexican wolf must favour a collaborative process of common conservation interests to strengthen the currently successful binational effort to return Mexican wolves to the landscape where they can play their historical ecological role. Therefore, we suggest building on the present analysis to identify additional candidate areas to implement detailed local ecological and social analyses, including prey availability assessments, potential conflicts with livestock, social tolerance, safety issues for the field teams and the ability to maintain a long-term monitoring programme, all with the inclusion of stakeholders in the process.

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DATA AVAILABILITY STATEMENT

The occurrences data base and environmental layers used for modelling are available in CyVerse https://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/MartinezMeyer_et_al_DivDist_2021

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**BIOSKETCH**

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Author contributions: E.M.M. and A.G.B. conceived the idea and strategy of analysis. E.M.M., A.G.B., J.V., T.L.S. and Z.Y.G.S. designed the study and developed the analysis. J.S., C.A.L.G., J.K.O., S.L. and J.R.H. collected data and developed different parts of the analysis. E.M.M. led the writing. All authors contributed substantially to discussions, ideas and revisions to the text and approved the submission.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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