Short communication

Re-defining historical geographic range in species with sparse records: Implications for the Mexican wolf reintroduction program

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ABSTRACT

Reintroduction is often the only remaining option for recovery of extirpated species. According to the U.S. Endangered Species Act, species should be reintroduced to suitable habitats within their probable historical range. However, accurately defining historical range often proves difficult, especially for taxa with limited historical information, and may represent a significant impediment for successful recovery. Here, we combine ecological modeling methods with morphometric and phylogenetic data from museum specimens to define a more biologically realistic historical distribution. We apply this approach to the Mexican wolf (*Canis lupus baileyi*), the most endangered and genetically distinct wolf subspecies in the New World. Our model substantially increases the potential geographic range of the Mexican wolf to include areas in southern California and Baja California, areas not previously recognized as part of the historical range. Motivated by this prediction, we reanalyzed morphometric data and genetically typed the only historical specimen known from southern California, which was previously assigned to another wolf subspecies. We found that the specimen was in fact of pure Mexican wolf ancestry and fell within our predicted range for this subspecies. Our findings provide an impetus for reconsidering reintroduction sites for the Mexican wolf and highlight how critical taxonomic assignment can be to reintroduction programs and species recovery. Re-analysis of potential range in other extirpated species that have ranges defined by antiquated taxonomic approaches used on a limited number of specimens could enhance the success of future reintroduction programs and restore historical processes such as admixture that can preserve the adaptive legacy of endangered species.

1. Introduction

Reintroduction is an important, often critical, conservation action for some threatened or endangered species that have been extirpated from significant parts of their geographic range. For taxa protected under the U.S. Endangered Species Act, recovery guidelines suggest that reintroduction efforts focus on suitable habitat within a defined historical range (U.S. Fish and Wildlife Service, 1992, 1993, 2012). However, defining past geographic range is not trivial given limited availability of historical distribution data for many species. Especially in the New World, historical ranges are primarily reconstructed from data collected in post-Columbian times gathered by antiquated methods. Consequently, the extent of any historical range is sample- and observation-dependent, and species for which there are limited historical data, or whose taxonomy is too narrowly defined, will likely have underestimated historical ranges. This underestimation may constrain recovery options by limiting consideration of potentially suitable reintroduction sites. Additionally, scientifically defensible delineations of historical ranges are crucial as recovery programs are frequently controversial and plagued with legal challenges (e.g. Zink et al., 2000; Vignieri et al., 2006; Frey, 2006; List et al., 2007). For example, the reintroduction of the Mexican wolf (*Canis lupus baileyi*) has been highly divisive, with the validity of the recovery plan recently being questioned in a lawsuit arguing that the U.S. Fish and Wildlife Service (USFWS) failed to create a scientifically grounded recovery plan (Center for Biological Diversity and Defenders of Wildlife v. Jewell., 2015).

The Mexican wolf is a genetically distinct subspecies that was once widespread throughout much of Mexico and southwestern U.S., but was extirpated in the wild by the early 1970s (Shaw, 1983; Leonard et al., 2005). The definitions of the historical range for this subspecies have varied due to conflicting taxonomic delineations (Shelton and Weckerly, 2007). Currently, the range limits defined by the USFWS incorporate an arbitrary 200-mile northward extension of the previously accepted range (Fig. 1; Parsons, 1996). Beginning in 1998, the USFWS initiated a reintroduction program from captive individuals to re-establish Mexican wolf populations (Hedrick et al., 1997). However, the reintroduced population remains fewer than 110 individuals despite the continued release of captive wolves (U.S. Fish and Wildlife Service, 2014a). This number stands in stark contrast to the successful reintroduction of gray wolves to Yellowstone National Park (USA) and central Idaho (USA) where the population size is now greater than 1100 individuals (U.S. Fish and Wildlife Service, 2014b). The Mexican wolf population has been constrained primarily due to human–wildlife conflicts, such as control efforts related to livestock loss within the recovery area (Wayne and Hedrick, 2011; Turnbull et al., 2013). Additional recovery locations for the Mexican wolf, which are currently limited by anthropogenic disturbance and the defined historical geographic range limit, may be imperative for successful re-establishment of this keystone predator to arid lands of the U.S. (Smith et al., 2003; Ripple et al., 2014, 2015).

Several lines of evidence suggest that the USFWS-defined historical range for the Mexican wolf is underestimated. First, the delineation of historical range is based on traditional morphological analysis of a relatively small number of historical specimens (18–21 cranial specimens; Young and Goldman, 1944; Bogan and Mehlhop, 1983; Nowak, 1995), which all post-date 1890, a period of time when the subspecies was already in decline (Shaw, 1983). Second, haplotypes belonging to the "southern clade" ecotype (a monophyletic clade consisting of the mitochondrial haplotype of extant Mexican wolves and closely-related haplotypes found in museum specimens; Leonard et al., 2005) have been found well outside of the range delineation, consistent with a larger historical geographic range. Third, the USFWS-delineated historical range boundaries did not include an estimation of ecologically suitable habitat that likely extends beyond the current range (Carroll et al., 2014). The genetic structure of North American gray wolves is strongly influenced by habitat distribution and is divided into distinct ecotypes (Geffen et al., 2004; Pilot et al., 2006, 2010; Carmichael et al., 2007; Musiani et al., 2007; Koblmüller et al., 2009; Muñoz-Fuentes et al., 2009; vonHoldt et al., 2011; Stronen et al., 2014) with the Mexican wolf representing a smaller form (Nowak, 1995) inhabiting more arid ecosystems. Lastly, wolves often have a long tenure in their birth pack before dispersing and may exhibit natal homing, whereby they disperse over large distances until they encounter habitats with a similar prey base and context to their natal habitat (Geffen et al., 2004). Thus, previous geographic boundaries for the subspecies are less realistic than those based on habitat distributions. Consequently, estimating suitable habitat based on ecological models is predicted to provide a more comprehensive
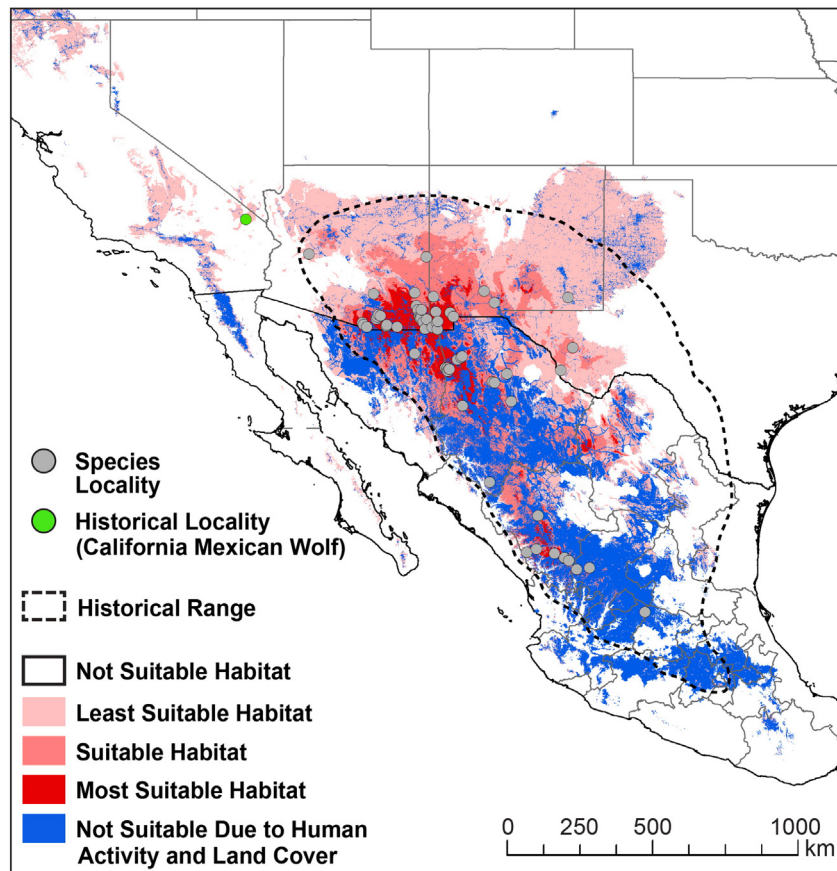

Fig. 1. Comparison of species distribution model and previously defined historical range of the Mexican wolves (*Canis lupus baileyi*). MaxEnt modeling identified areas with suitable abiotic conditions only (shades of red). Areas unsuitable due to modern human habitat alterations are shown in blue. Differences between the distribution of suitable habitat and the previously defined historical range (dashed lines) may represent inaccuracies in the previously defined historical range, which were verified through historical location records (gray circles) and new genetic data (green circle). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

estimate of potential areas inhabited historically by the Mexican wolf.

We employ a scientifically rigorous and pragmatic approach that more fully utilizes historical information to estimate the historical range of the Mexican wolf. Similar to a recent study that delineates subspecies/conservation units in tigers (*Panthera tigris*; Wilting et al., 2015), our methodology uses data sets of morphological, ecological, and molecular traits. First, we use presence only location data as input for a species distribution model (MaxEnt (Phillips et al., 2006)) to predict a suitable habitat. We show that the historical range of Mexican wolf likely extended beyond the boundary currently recognized by the USFWS (Parsons, 1996). We found that one historical specimen from southern California, previously classified as another subspecies of wolf (*Canis lupus youngi*; Grinnell et al., 1937), was captured within an area we projected as Mexican wolf habitat. To determine its correct subspecies designation, we applied modern morphological and genetic methods to taxonomically assign the museum specimen and genetically confirmed Mexican wolf ancestry. Second, we utilized these new data as well as previous genetic analysis of historic wolf museum specimens to produce a genealogically-based distribution model. This approach provides a direct insight into the distribution of lineages defining the historical legacy of the Mexican wolf and captures the likely distribution it occupied prior to its dramatic decline over the last century. Together, the distribution of specimens assigned by modern morphologic techniques to the Mexican wolf, combined with those assigned by phylogenetic analysis of historical specimens, defines a range of environments inhabited historically by the subspecies. Additionally, we identify areas where the likelihood of human disturbances of wolf populations is limited and should be considered high priority for reintroduction site reassessment. This comprehensive strategy, which combines phenotypic, genetic, and habitat suitability analyses, can readily be applied to other species with limited historical records, allowing for identification of additional suitable habitat that may have been missed by more traditional, taxonomic analysis of museum specimens.

2. Materials and methods

2.1. Distribution models

We compiled localities for Mexican wolf (*C. l. baileyi*) occurrence from the Global Biodiversity Information Facility (GBIF) data portal (www.gbif.org; Table A.1), as well as restricted data from museums for which verifiable specimens were available (see Appendix A for details). A total of 64 non-duplicate points were included in this "typological" subspecies distribution model using MaxEnt (version 3.3.3k) (Phillips et al., 2006), a niche modeling algorithm that consistently ranks high in inter-model comparisons (Elith et al., 2006; Diniz-Filho et al., 2009; Harrigan et al., 2014). MaxEnt offers a particular advantage in the study of endangered taxa (for which locality data may be sparse), in that it performs well with only a small number of point localities (Ng and Jordan, 2001; Hernandez et al., 2006; Wisz et al., 2008), and unlike many other algorithms, requires only presence data to assign spatially-explicit probabilities of occurrence (Phillips et al., 2006). For all models in this study, we used the MaxEnt default settings for function selection that fit environmental data to localities (see Appendix A for more detail). The minimum estimated habitat suitability estimates at known presence localities was used as the threshold for determining suitable habitat in all models and figures and subsequent divisions of habitat suitability were defined at equal intervals.

To determine the potential range limit of wolves sharing recent common ancestry or population history with extant Mexican wolves, we conducted additional analyses that included all "southern clade" wolves, comprised of the diagnostic mtDNA haplotype found in extant Mexican gray wolves as well as three closely-related haplotypes (Leonard et al., 2005). These genealogically-based analyses were performed using all previous 64 input data points and the addition of seven historical samples genetically identified as having "southern clade" haplotypes, but morphologically described as *Canis lupus nubilus* or *C. l. youngi* (Leonard et al., 2005). We used the MaxEnt default settings to fit a model of localities to environmental data, but used an increased regularization multiplier of 5, allowing for smoother response curves and a more generalizable model (Phillips et al., 2006). It should be noted here that given the few occurrence locations of the "southern clade" wolves (n = 7), the distribution of our model will be inherently biased towards the current extant Mexican wolf habitat, but we assume here that this habitat is most suitable for the species, and that the extended ranges represented by "southern clade" individuals represent more fringe habitats in terms of suitability for Mexican wolves.

The additional seven samples included in the genealogical-based model were located in Utah, New Mexico, Oklahoma, and Nebraska (USA; Fig. 1). The individuals from Utah and Nebraska represented the most northerly sample points in our dataset and include areas where admixture likely occurred historically between Rocky Mountain gray wolves and Mexican wolves (Leonard et al., 2005). The intent of including these range points was to provide a historic distribution that can restore admixture, a historic evolutionary process which may enhance the genetic variation of both subspecies. This approach emphasizes the lost component of ancestry contained by Mexican wolves before their extirpation in the wild and thus we consider it a more realistic population sampling than represented by the extant population or by the limited sampling of museum specimens and localities taxonomically assigned to the Mexican wolf. Essentially, this approach makes use of the historical relationships of mtDNA lineages to define an area with individuals sharing a common ancestry (e.g. evolutionary significant unit (ESU), see Moritz, 1994).

2.2. Post-modeling — defining unsuitable areas

To identify areas that fall within the ecological niche projections but are currently unsuitable for wolves because of human activity, we used two remote-sensing based data sets. First, pixels were designated as unsuitable when they were classified as "urban and built up" or "barren or sparsely vegetated" in the International Geosphere–Biosphere Programme (IGBP) land cover map for the year 2000, based on remotely-sensed data from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor onboard NASA's Terra satellite platform (Friedl et al., 2002). Second, we used the LandScan™ 2008 Global Population Database (Dobson et al., 2000; Oak Ridge National Laboratory, 2008) to identify as currently unsuitable those areas with human population density of >10 people/km^2. LandScan™ population estimates are based upon a variety of data sources including satellite estimates of nighttime lights, land cover, slope, and proximity to roads. Density estimates are generated with a separate area grid that corrects for latitudinal distortions in map pixel area. Several studies have documented decreases in wolf habitat suitability with increasing human population density (Mladenoff et al., 1995; Carroll et al., 2003; Oakleaf et al., 2006). We employed the 10 people/km^2 threshold for heuristic purposes, recognizing that regional thresholds may vary given ecological and anthropogenic factors.

2.3. Post-modeling — defining areas outside of historical range

After the typological- and genealogically-based environmental data were modeled using MaxEnt, we compared all pixels identified as ecologically suitable to those that only fell within the historical range (Parsons ,1996). We tabulated the percentages of pixels captured by

our models that fell within the defined historical range, and the percentage of pixels identified as suitable beyond the historical range. These percentages included pixels identified as both anthropogenically and non-anthropogenically altered (defined as those areas that were classified as suitable but excluded pixels that were identified as anthropogenically altered; see previous Materials and methods section). Additionally, we calculated the total percentage of non-anthropogenically altered suitable habitats as identified by the entire MaxEnt projection and that which only occurred within the U.S.

2.4. Morphometric analysis

Fifteen skull measurements from each of 161 male North American gray wolves were obtained from Young and Goldman (1944) and O'Keefe et al. (2013). We compared skull measurements using classification regressions and random forests (Breiman, 2001) as implemented in *tree* (Ripley, 1996) and *randomForest* (Liaw and Wiener, 2002; see Appendix A for details), respectively, within the R framework (R Development Core Team, 2011), to determine the cranial variables that best distinguished subspecies. *Tree* classifications were run using all 15 variables, of which four were most important (i.e., greatest length, condylobasal length, height of coronoid process, and squamosal constriction). Additionally, principal component analysis was performed using the package *pca* in R (R Development Core Team, 2011).

2.5. Genetic analysis

As previously described in Hendricks et al. (2014), DNA was obtained from six historical specimens of gray wolves (*Canis lupus* spp.) from the collections at University of California, Berkeley Museum of Vertebrate Zoology (MVZ). The specimens originated from southern California to the Pacific Northwest, USA (Table 1). Notably, one museum specimen (MVZ:MAMM:33389) collected in 1922 in southern California was previously identified as a Southern Rocky Mountain wolf (*C. l. youngi*) based on phenotypic and cranial morphometrics (Grinnell et al., 1937). However, this individual had a mtDNA haplotype only found in the Mexican wolf (lu33; Leonard et al., 2005; Hendricks et al., 2014). To verify the subspecific affiliation, we typed four autosomal ancestry informative markers (AIM), distinguishing North American gray wolf (*C. lupus*) from Mexican wolves (*C. l. baileyi*) (Table 1; vonHoldt et al., 2011, 2012). These four AIM markers were assayed using a High Resolution Melt (HRM) assay and Roche LightCycler 480 instrument (Indianapolis,

IN; see Appendix A for details). In addition to the six MVZ historical samples, a set of two known Mexican wolf and two western Canadian gray wolf samples were used as reference for allele calls.

3. Results

3.1. Distribution models

The model resulting from the typological MaxEnt analysis using 64 Mexican wolf locations differs substantially from the USFWS-defined historical range (Parsons, 1996), particularly with regard to the northern extent of suitable habitat (Fig. 1). The MaxEnt projection captures 80.2% of the defined historical range and suggests that the total suitable range is larger by 24.1%. Additionally, the projection extends into contiguous regions to the north and west, which overlaps with the distribution of genetically defined Mexican wolf historical specimens (Fig. 1; Leonard et al., 2005). The MaxEnt model predicts the capture site of the historical specimen from southern California (MVZ:MAMM:33389), to be suitable habitat for the Mexican wolf (green circle in Fig. 1).

The genealogically-based model resulting from the inclusion of additional individuals with genetic characteristics of the Mexican wolf ("southern clade"; Leonard et al., 2005) also suggests a much broader historic range that extended into parts of California, Baja California, Northern Arizona, Northern New Mexico, and Northwestern Texas. This model accounts for 71.4% of the historical range and extends beyond the defined historical range by 26.7% (Fig. 2).

Considering current urbanization and land use change, 30.5% of the projected genealogical Mexican wolf range currently consists of unsuitable habitat, primarily due to high human population density (Fig. 2). However, 90.4% of the projected range within the U.S. falls in areas that are not excluded due to human activity or unsuitable land cover (Fig. 2), which suggests alternative reintroduction sites within the U.S. may be feasible.

Model performance was evaluated by the area under the curve (AUC), which is often used to measure model performance (Rödder et al., 2009; Harrigan et al., 2010; Fourcade et al., 2014; Sesink Clee et al., 2015). All distribution models created in this study using MaxEnt performed better than distribution models produced using a random association between species localities and environmental variables (AUC of 0.5). All training and test AUC values for models were greater than 0.97, which suggests that the models were highly informative.

Table 1

Ancestry informative SNP loci and high resolution melting assay results. A set of four Mexican/North American gray wolf ancestry informative markers (AIM) was assayed in the historical samples to further classify specimens to subspecies.

			Chr2.42367520[a]	Chr3.40205690[a]	Chr5.15975864[a]	Chr34.43739502[a]
MVZ33389	San Bernardino, CA	1922	AC	TT	AG	TT
MVZ34228	Lassen, CA	1924	AC	GG	GG	CC
MVZ29771	Curry, OR	1918	–	GG	–	–
MVZ86874	Douglas, OR	1931	AC	H_1[c]	AG	CC
MVZ59682	Douglas, OR	1933	CC	H_2[c]	–	TC
MVZ33424	Elko, NV	1922	AC	–	AG	TC
Fst[b]		0.931	0.948	0.931	1
Canis lupus baileyi Allele		A	T	A	T
Canis lupus Allele		C	G	G	C

[a] CanFam2 SNP Collection (www.broadinstitute.org/mammals/dog/snp2).

[b] Pairwise Fst between 9 reference captive colony Mexican wolves and 48 reference western North American gray wolves (vonHoldt et al., 2011).

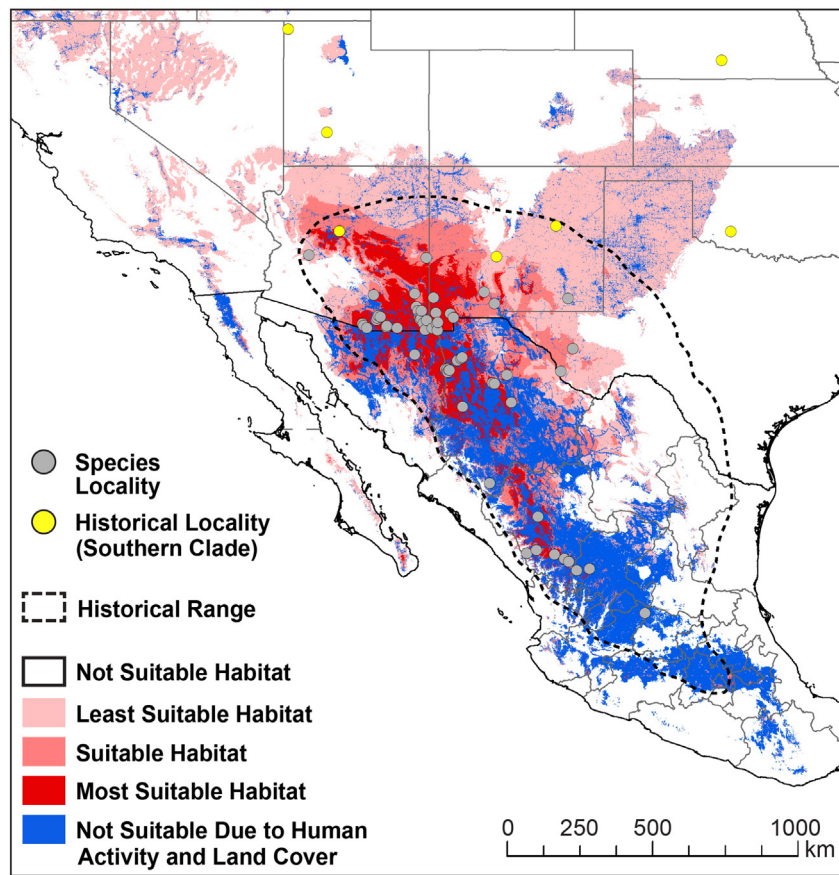[c] H_1 and H_2 represent alleles not found in modern Mexican or gray wolf genotypes.

Fig. 2. Genealogical species distribution models of Mexican wolves (gray circles) and closely-related ("southern clade" lineage) wolves (yellow circles). Areas unsuitable due to modern human habitat alterations are shown in blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Morphologic analysis of MVZ:MAMM:33389

The skull of the southern California wolf (MVZ:MAMM:33389) is morphometrically most similar to the smaller North American wolf subspecies, *C. l. nubilus* and, wolves of the "southern clade" (Appendices B and C; Young and Goldman, 1944; O'Keefe et al., 2013). Despite our low out-of-bag (OOB) error rate (13%) in identifying species using random forest analysis, the eleven *C. l. baileyi* specimens were incorrectly identified as another subspecies 45% of the time. The other subspecies used in this study, *C. l. nubilus* and *Canis lupus occidentalis*, had even lower OOB error rates of 6% and 10%, respectively. Morphometric data was collected in 1944 before genetic tools were available to verify the subspecies or admixed status of these individuals, potentially limiting the accuracy of the analysis. Nonetheless, these results imply greater heterogeneity within *C. l. baileyi* than in the other western subspecies. In fact, three of the specimens examined by Young and Goldman (1944), USNM 221961, USNM 147703, USNM A884 were morphologically *C. l. nubilus*, but were found to have "southern clade" haplotypes by Leonard et al. (2005). By our analysis, these specimens also morphologically fall within the *C. l. nubilus* grouping (Appendices B and C) as does MVZ:MAMM:33389, despite it having a Mexican wolf mtDNA haplotype (Hendricks et al., 2014). These results suggest the possibility of admixture among wolf subspecies or that the taxonomic designation of the Mexican wolf based on morphology is too limited and imprecise to be used as the sole criteria for defining the past geographic range of the subspecies.

3.3. Genetic analysis of MVZ:MAMM:33389

Genetic results showed that the southern California wolf specimen had six of eight *C. l. baileyi* specific nuclear alleles (75%; Table 1). The two known Mexican wolf controls genotyped had eight of eight *C. l. baileyi* specific alleles, whereas the two known North American wolf controls genotyped had private alleles not found in the Mexican wolf. Only two of the other five museum specimens, MVZ:MAMM:34228 and MVZ:MAMM:86874 (both morphologically and genetically identified as North American gray wolves), were successfully amplified for all four loci. MVZ:MAMM:34228 displayed one Mexican wolf specific allele (12.5%) in the heterozygous state for locus Chr2.42367520 (Table 1). MVZ:MAMM:86874 displayed two Mexican wolf specific alleles (25%) both in the heterozygous state at loci Chr2.42367520 and Chr5.15975864 (Table 1). The high percentage of *C. l. bailey* specific alleles typed in MVZ:MAMM:33389 support Mexican wolf ancestry.

4. Discussion

Defining the historical range of a taxon is critical for estimating a wide diversity of biological factors that may help inform conservation efforts, such as extinction probabilities, ecological requirements, and species interactions. We show here that the traditional specimen-driven and taxonomically oriented approaches may substantially underestimate the historical range of the Mexican wolf, the most

endangered gray wolf subspecies in the New World. We suggest a comprehensive genealogically-based approach, which captures a more biologically realistic projection of past range and explicitly includes environmental factors known to provide habitat suitable for the Mexican wolf ecotype. The genealogically-based approach uses information from the phylogenetic relationship of lineages that define groups of individuals with common ancestry. Our approach is likely to reduce the potential bias of range underestimation caused by limited temporal sampling and a rigid typological approach to defining subspecies boundaries that do not consider admixture.

Based on our multi-trait data set and topological distribution model, we suggest areas in western states that have not previously been considered in USFWS reintroduction plans and may potentially be suitable for Mexican wolf reintroduction. Several lines of evidence support this conclusion. First, we have identified a historical wolf specimen from southern California with a diagnostic Mexican wolf mtDNA haplotype and SNP markers suggesting a high proportion of Mexican wolf ancestry, which contrasts with the Southern Rocky Mountain wolf ancestry previously reported (Grinnell et al., 1937). Unfortunately, this is the only museum specimen known from this area, and it may have been a migrant rather than resident wolf. However, independent of the genetic data, our ecological models under current climate conditions identify this specimen's locality as suitable habitat (green circle on Fig. 1). Given that this specimen was collected prior to extirpation (1922; Grinnell et al., 1937), evidence suggests that this habitat was both historically and currently suitable for Mexican wolves. Second, previous research has shown that there was historically a wide distribution of the "southern clade" in the American West (Leonard et al., 2005), lending support to the idea that these areas may represent appropriate habitats for wolves with Mexican wolf ancestry. Finally, due to climate change, increasing aridity in the southwestern U.S. is projected (Notaro et al., 2012). Consequently, the establishment of populations at or beyond the northern limit of the historical range may be an appropriate plan to increase recovery success and metapopulation resilience (Carroll et al., 2014). Furthermore, most of the historic range in Mexico is currently unsuitable due to human activity (blue areas in Figs. 1 and 2) and the probability of anthropogenic wolf mortality is high (Araiza et al., 2012). This supports our suggestion to consider additional U.S. reintroduction sites, despite most of the historic range occurring within Mexico borders. We note that numerous abiotic and biotic factors such as prey base and land use patterns should be investigated before reintroductions are implemented (e.g. Carroll et al., 2014), but several locations identified as suitable by our models have already been shown to have abundant prey, appropriate habitat, low human density, and high connectivity to additional suitable habitat identified by spatially-explicit population models (Sneed, 2001; Carroll et al., 2006, 2014).

Given the close proximity of Mexican wolf habitats to a southern-expanding population of Northern gray wolves (Canis lupus irremotus) now in the U.S., admixture zones may develop between these subspecies. Such admixture occurred historically as shown by genetic analysis (Leonard et al., 2005) and is allowable under an approach such as ours that is inclusive of past historical processes at the population level. Despite a recent ruling that extends the Mexican Wolf Experimental Population Area (U.S. Fish and Wildlife Service, 2015), the USFWS prohibits natural reintroduction and expansion of Mexican wolves to areas in northern Arizona and New Mexico as well as southern California and western Texas. This limits the movement of a subspecies that had historically and naturally occurred across much of the southwestern U.S. and inhibits admixture for the foreseeable future. Importantly, admixture may lead to enhanced opportunities for selection to craft appropriate phenotypes. For example, in the Great Lakes area extensive admixture has resulted in phenotypic variety and maintenance of wolves better adapted to smaller prey size (Koblmüller et al., 2009; Nowak, 2009). The preservation of admixture may enhance adaptation to transitional environments (Allendorf et al., 2001), but is missing from

recovery considerations (U.S. Fish and Wildlife Service, 2015). Finally, our results support the findings of Carroll et al. (2006, 2014), which identify areas of habitat connectivity between the existing reintroduction area (Zone 1 (formerly the Blue Range Wolf Recovery area of New Mexico and Arizona); U.S. Fish and Wildlife Service, 2015) and potential restoration areas in northern (Grand Canyon Ecoregion) and central (Mogollon Rim) Arizona. Although the Zone 1 reintroduction area contains suitable habitat, recovery there has been unsuccessful due to much higher levels of human–wolf conflict than in Yellowstone National Park and central Idaho (Wayne and Hedrick, 2011; Turnbull et al., 2013). In contrast to the Zone 1 reintroduction area, the Grand Canyon Ecoregion has suitable habitat, low anthropogenic activity, connectivity with other suitable areas and protected habitat within a U.S. National Park (Sneed, 2001; Carroll et al., 2006, 2014). Our application of multiple, robust analyses for defining historical geographic range and identifying reintroduction areas for the Mexican wolf may assist in reversing the decline of this critically endangered species.

5. Conclusions

Underestimation of historical range can be a factor limiting the success of recovery programs, prolonging species endangerment and the expense of recovering them. Our results suggest that historical ranges of extirpated taxa, especially in the New World, should not be defined solely on past observations or phenotypic characteristics of historical specimens, both of which are subject to strong sampling biases that tend to underestimate range. Instead, estimates of historical range should also consider other factors such as the phylogenetic relationships of lineages defined by a population of historical specimens, including those not assigned taxonomically to the protected taxon, and appropriate habitats within dispersal proximity of the supposed historical geographic range. Moreover, even endangered taxa with good historical records may have experienced range expansions and contractions in the pre-Columbian era, and such demographic dynamics could be inferred from genetic data (e.g. vonHoldt et al., 2011; Freedman et al., 2014) and used to inform historical range designations. Our approach can readily be applied to a diversity of species, which have recently declined over a substantial part of their geographic range, such as Canadian lynx (Lynx canadensis), wolverine (Gulo gulo), and fisher (Martes pennanti). The ranges of many highly mobile organisms are dynamic, and estimates of historical range are likely to be most informative when they utilize both current and historical population genetic information, morphological and environmental data, and acknowledge potential admixture with related subspecies. Our results support reconsideration of some historical range delineations, and our methods may be used to identify additional reintroduction locations and thus help recover many species of concern.

Appendix A. Detailed description of methods

A.1. Species locality data

When available, we used geographic coordinates for specimens provided by the data source. Otherwise, we used location names provided with the sample to georeferenced individuals. Localities for which

Table A.1
List of data sources utilized with the Global Biodiversity Information Facility data portal search engine (www.gbif.org) for Mexican wolves (*Canis lupus baileyi*) on 04/07/2008, and the number of non-duplicate records used from each source for ecological niche modeling.

Source	Number of non-duplicate records
Museum of Vertebrate Zoology, UC Berkeley	15
University of Alaska Museum of the North	2
Michigan State University Museum	3
Field Museum of Natural History	1
California Academy of Sciences	3
University of Kansas Biodiversity Research Center	3
UNIBIO, IBUNAM; Coleccion Nacional de Mamiferos	5
Smithsonian National Museum of Natural History	32

geo-referencing could not be defined more precisely than the level of county or similar administrative unit were excluded. This level of spatial precision is consistent with that typically encountered in climate data applied to characterize potential distribution of species. The previous historical range limit of the Mexican wolf was based on the most current and accepted published historical range map of the species (Parsons, 1996).

A.2. Environmental data

From WorldClim (version 1.4) (Hijmans et al., 2005), 19 bioclimatic variables at a 1 km-resolution were selected according to their roles in determining the physiological limits of species (Nix, 1986) (i.e., variation in annual means, extremes and seasonality of temperature and precipitation). These metrics are derived from monthly-interpolated temperature and rainfall climatologies spanning the years 1950 to 2000 (Hijmans et al., 2005). ENMtools (Warren et al., 2010) was used to perform pairwise Pearson correlation tests between all 19 bioclimatic variables clipped to the extent of the study area. Clusters of highly correlated variables were identified and used in conjunction with initial distribution model results to trim variables that were not contributing to the model. The final eight variables used in Mexican wolf distribution models were: isothermality, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation of the driest month, precipitation seasonality, precipitation of the warmest quarter, and precipitation of the coldest quarter. We did not include current vegetation data in this analysis, since vegetation patterns are more severely influenced by anthropogenic activities (e.g., deforestation, land cover conversion, urban development, and road network intensification).

A.3. Distribution models

The MaxEnt approach is based on a probabilistic framework. Its main assumption is that the incomplete empirical probability distribution (which is based on the species occurrences) can be approximated by a probability distribution of maximum entropy (the MaxEnt distribution) subject to certain environmental constraints, and that this distribution approximates a taxon's potential geographic distribution (Phillips et al., 2006). In this analysis, the study area over which the potential distribution is computed, and from which the MaxEnt algorithm samples "background" points to train the model are substantially larger than the known historical ranges of the species (Mexican wolf, 134°–84° W, 13°–49° N). We verified that modeling results were insensitive to the choice of study area size by building models with progressively larger study areas, increased at an increment of 5° latitude and longitude (data not shown). Models included linear, quadratic and hinge

functions. Regularization attempts to balance model fit and complexity, with the default setting multiplying each automatic regularization parameter by 1. Additional multiplication of these parameters tends to smooth (make the model more generalized) at the expense of model fit (Elith et al., 2011). For comparisons of models, we chose to leave parameters the same across all runs, particularly because default settings have been successfully implemented in other comparisons (Elith et al., 2011), and represent a conservative approach to estimating species distributions based on occurrences. MaxEnt produces a continuous prediction with values ranging from 0 to 1 (in units of probability of occurrence) indicating least suitable to most suitable conditions for the taxa under consideration (Phillips et al., 2006). The cutoff for 'unsuitable'–'least suitable' habitat used is the minimum estimated suitability of known presence localities used in each model. Consecutive divisions of 'suitable' and 'most suitable' were set by equal intervals. Final models were created using the average of 100 replicates for each instance. To convert this continuous output into a binary prediction that approximates the potential distribution, we used a probability threshold equivalent to the minimum predicted probability of occurrence at actual occurrence localities used to train the model (Phillips et al., 2006).

A.4. Morphometrics analysis

Random forests were run using all 15 variables and 2000 iterations of trees, which randomly chose both records and predictor variables for use in training. Each response record was left out of training approximately 36% of the time, and the remaining records were then used to construct a training model. This training model was tested on the withheld records, and the resulting error rate is reported as the OOB, or out-of-bag estimate, of error. The OOB represents the error rate of the random forest model tested against withheld data records that the model had not observed (Breiman, 2001). Only male specimens were included as MVZ:MAMM:33389 was reported as male.

A.5. Genetic analysis

The polymerase chain reaction (PCR) consisted of a reaction volume of 10 μl containing 2× High Resolution Melt Master Mix (Roche Applied Science, Mannhein, Germany), 4 mM $MgCl_2$, 0.1 μM primer mix and genomic DNA (50 ng). The qPCR cycle consisted of an initial denaturing step of 95 °C for 10 min, followed by 60 cycles of amplification starting at an annealing temperature of 65 °C for 15 s, dropping by 0.5 °C/cycle to 53 °C, with denaturation at 95 °C for 10 s and extension at 72 °C for 10 s/cycle. After amplification, a melt assay step was implemented of 95 °C for 1 min, 40 °C for 1 min and 65 °C to 95 °C at 0.02 °C/s with 25 fluorescent signal acquisitions per °C. HRM melt temperatures were analyzed using Roche LightCycler 480 Software v1.5.0.

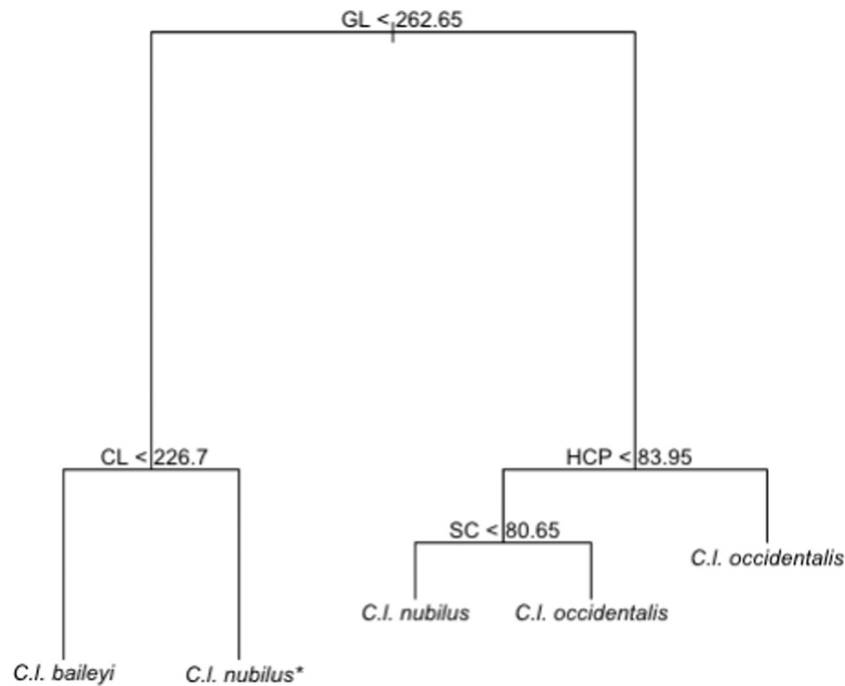**Appendix B. Decision tree for classifying North American wolf subspecies**

Fig. B. Decision tree for classifying North American wolf subspecies using skull measurements from Young and Goldman (1944). GL: greatest length, CL: Condylobasal length, HCP: height of coronoid process, SC: squamosal constriction. The asterisk (*) indicates the placement of MVZ:MAMM:33389 according to measurements from Young and Goldman (1944).

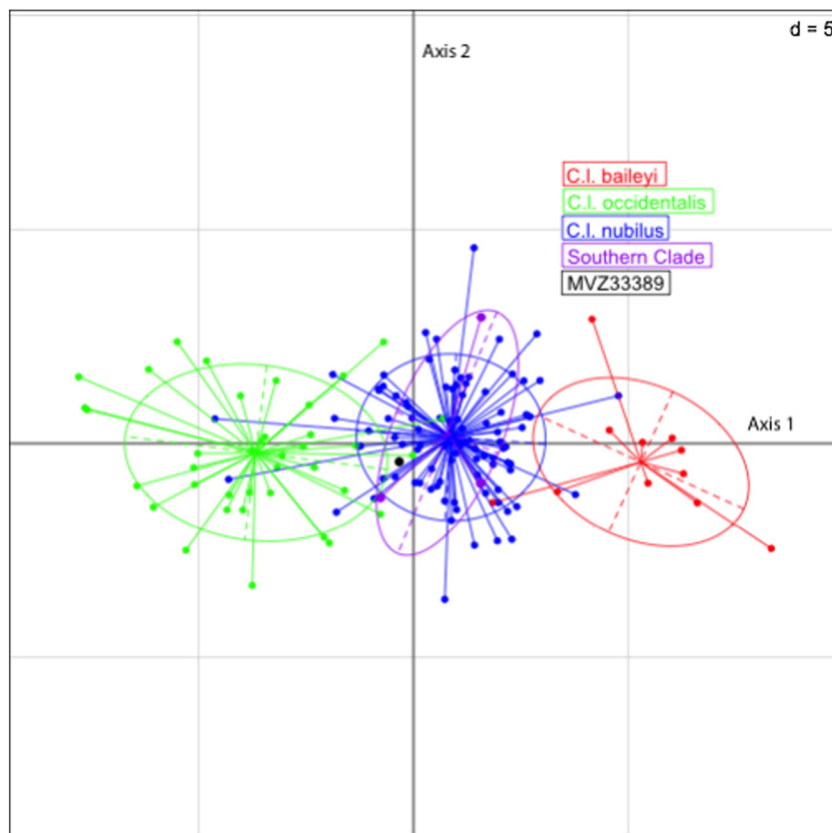**Appendix C. Principal component analysis results for classifying North measurements**

Fig. C. Principal component analysis results for classifying North American wolf subspecies using skull measurements. 144 male wolves from three North American subspecies, *Canis lupus baileyi* (red), *Canis lupus occidentalis* (green), *Canis lupus nubilus* (blue and purple), were used to identify the placement of MVZ:MAMM:33389. Three morphologically identified *Canis lupus nubilus* individuals (USNM 221961, USNM 147703, USNM A884; Young and Goldman, 1944) have southern clade haplotypes (purple). These individuals cluster within the broader *Canis lupus nubilus* morphological cluster. MVZ:MAMM:33389 falls within the *Canis lupus nubilus*/southern Clade morphotype cluster.

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