DEFINING SUITABLE HABITAT AND CONSERVATION STATUS FOR THE TUCSON SHOVEL-NOSED SNAKE (*CHIONACTIS ANNULATA KLAUBERI*) IN THE SONORAN DESERT

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***Abstract**--The Tucson shovel-nosed snake (Chionactis annulata klauberi) is a small specialized colubrid associated with sandy loams of the elevated portions of the Lower Colorado River Valley Sonoran Desert in central Arizona. This taxon is a recently redefined subspecies based on genetic data, and may be extirpated in the Tucson region, including the type locality. A recent (USFWS 2014) decision against protecting it was based in part on an expansive definition of its geographic range and a habitat model. Here, we redefine the subspecies distribution by uniting published results of mitochondrial and nuclear DNA. We then present a new ecologically based model of its original and current habitat using the machine learning algorithm Random Forests. The new model accurately matches known and estimated presence-absence data for this taxon, and is consistent with morphometrics and, largely, with color pattern variation. It estimates 60% less available habitat than the USFWS model. We estimate that 39% of the 1,255,946 ha (3,103,505 ac) of original habitat has been converted to urban developments, roads, agriculture, or otherwise altered non-habitat. Of the remaining 770,971 ha (1,905,108 ac), 60% is susceptible to habitat conversion in the region, with only 10.9% of habitat having current legal protection. Ongoing and projected urbanization and energy development in its flatland desert habitat present a bleak future for this subspecies.*

INTRODUCTION

In recent decades, genetic data have greatly increased our understanding of the history and processes shaping populations, gene pools, and landscape relationships of species (Avise 2000). This revolution has reshaped concepts of speciation, species boundaries, subspecies, and appropriate targets of conservation and management (Avise and Ayala 2017). Earlier consensus regarding the "biological species concept" and subspecies have largely been supplanted by evolutionary and genealogical species concepts. Here taxa are considered species if they are on distinct evolutionary trajectories and have anciently differentiated genetically (De Quiroz 2007). Subspecies have become controversial, with some elevated to full species rank while others have been dismissed or remain in taxonomic limbo. However, adaptive subspecific differentiation may play a critical role in speciation (Gavrilets 2014), and subspecies may merit protected conservation status (Phillimore and Owens 2006).

Shovel-nosed snakes (genus *Chionactis*) present complexities with regard to identifying species, lineages, and significant conservation entities. Four taxa are currently recognized: the relatively divergent Sonoran shovel-nosed snake (*C. palarostris*) and three taxa in the geographically variable *C. occipitalis* complex (Wood et al. 2014). These include the Mojave shovel-nosed snake (*C. occipitalis*) and two subspecies of the Sonoran Desert shovel-nosed snake (*C. annulata*): the Colorado Desert shovel-nosed snake (*C. a. annulata*) and the Tucson shovel-nosed snake (*C. a. klauberi*). The *C. occipitalis* complex displays complicated geographic patterns of genetic differentiation (Wood et al. 2014) making definition of taxon boundaries (Wood et al. 2014; USFWS 2014) and conservation status challenging.

In the *C. occipitalis* complex, the head is morphologically specialized for burrowing in the sandy soils they inhabit (Ernst and Ernst 2003), more so than in the sister taxon *C. palarostris*. The body is slim and thus apparently adapted for rapid locomotion (Cundall 1987) compared to the stouter build of the closely related banded sand snake (*Chilomeniscus cinctus*), which is similarly specialized for burrowing (Ernst and Ernst 2003). Further, *Chionactis* in the Sonoran Desert have bold red and black crossbands over a cream or yellowish ground color, marking them as mimics of venomous coralsnakes, including the sympatric Sonoran coralsnake (*Micruroides euryxanthus*).

In 2004, *C. a. klauberi* was petitioned for listing as Threatened or Endangered under the US Endangered Species Act (ESA). This petition was based on its habitat specialization in desert flats subject to agricultural conversion and urban sprawl in central Arizona, and its apparent disappearance from the Tucson region (Center for Biological Diversity

2004), which includes the type locality (Stickel 1941). The subspecies was defined based on the strong infusion of black pigment on the red crossbands, which may enhance both coralsnake mimicry (Mahrdt *et al*. 2001) and background matching (via flicker-fusion: Titcomb et al. 2014). Its geographic range and the presence of intergrades with *C. a. annulata* were described by Klauber (1951) and Cross (1979). On the basis of morphological, mitochondrial and nuclear gene analyses, Wood et al. (2008, 2014) supported continued recognition of *C. a. annulata* and *C. a. klauberi* as a subspecies with "fuzzy" boundaries due to evidence of asymmetric gene flow between the recovered genetic entities that were largely consistent with the earlier concepts of the morphologically described subspecies (Stickel 1941; Klauber 1951; Mardt et al. 2001; Stebbins 2003). However, Wood et al. (2014) did not define distributional limits for *C. a. klauberi*. In rejecting *C. a. klauber*i for ESA protection the U.S. Fish and Wildlife Service (USFWS; 2014) adopted an expansive definition of the subspecies that included all geographic regions within *C. annulata* with any genetic connection to *C. a. annulata*. Herein we define operational boundaries consistent with the complex genetic variation known in *C. annulata* for analysis of the conservation status of *C. a. klauberi*. We then model the ecological distribution and habitat extent of *C. a. klauberi* and re-evaluate the geographic extent of threats to its habitat and its vulnerability to extinction.

METHODS

Occurrence records: *L*ocation data were coordinates for tissue sample records in Wood et al. (2014, Table 1). Delineating the geographic distribution of *C. a. klauberi* presented challenges associated with divergent geographic gradients in mtDNA and nuclear microsatellite data (Wood et al. 2008, 2014). We resolved this problem by using the intersection of the mitochondrial and nuclear DNA datasets from Wood et al. (2014), using individuals from microsatellite cluster C (red circles and half circles in Figure 1a, Wood et al. 2014) that were also contained in mtDNA clade C. This resulted in 44 locality points from which we added verified museum and published locality records that were within the previously delineated range of *C. a. klauberi* (Mahrdt et al. 2001) but not sampled by Wood et al. (2014). This included records from Santa Cruz Flats, Pinal County, and Avra Valley near Tucson, Pima County (including the type locality) that could be mapped with a precision of 0.161 km or better. We placed a grid of 1 km square cells over the points and randomly selected one occurrence per cell to remove repetitive records that likely reflect sampling bias and to reduce autocorrelation. The resulting dataset represented 53 C.a. klauberi "presence" records (Figure 1b) that were used as model inputs.

Absence records: We constructed model inputs of "absence" records based on paved road segments (the only way this subspecies was effectively sampled) that have been intensively searched without yielding records of *C. a. klauberi*. Points were placed along the paved road transects at 10 km intervals, excluding all areas within 10 km of a record of a *C. a. klauberi* record. Road transects are often in areas of low slope gradient, so we placed additional absence records on popular mountain ranges near Phoenix where there are no records of *Chionactis.* We placed an additional eleven absence records in western Arizona at localities representing microsatellite clusters A or B (Wood et al. 2014). The absence dataset thus included 74 locality records (Figure 1) yielding a balanced presence/absence dataset for use in our model.

Environmental Predictors: We assembled 38 explanatory (*x*) variables that literature (Klauber 1951, Cross 1979, Stebbins 2003, Ernst and Ernst 2003) and our field experience suggested as potentially important to the species (Table 1), with particular attention to soils. We extracted percent sand, silt, clay, rock fragments, and available water storage from the USDA's STATSGO2 database for Arizona (STATSGO 2016). We did not use the finer scale SSURGO database because it has significant data gaps and discontinuities within our study area. Soil map units were converted into a 90 m resolution grid for use in our model that appropriately represented the resolution of the original vector data. All subsequent raster datasets mentioned herein were resampled to match this 90 m resolution using bilinear interpolation for continuous data or majority filter for discrete data.

We represented vegetation with the Biophysical Settings, Vegetation Cover, and Existing Vegetation Type (EVT) datasets from LANDFIRE (LANDFIRE 2014). The Biophysical Settings maps depict the vegetation likely present before

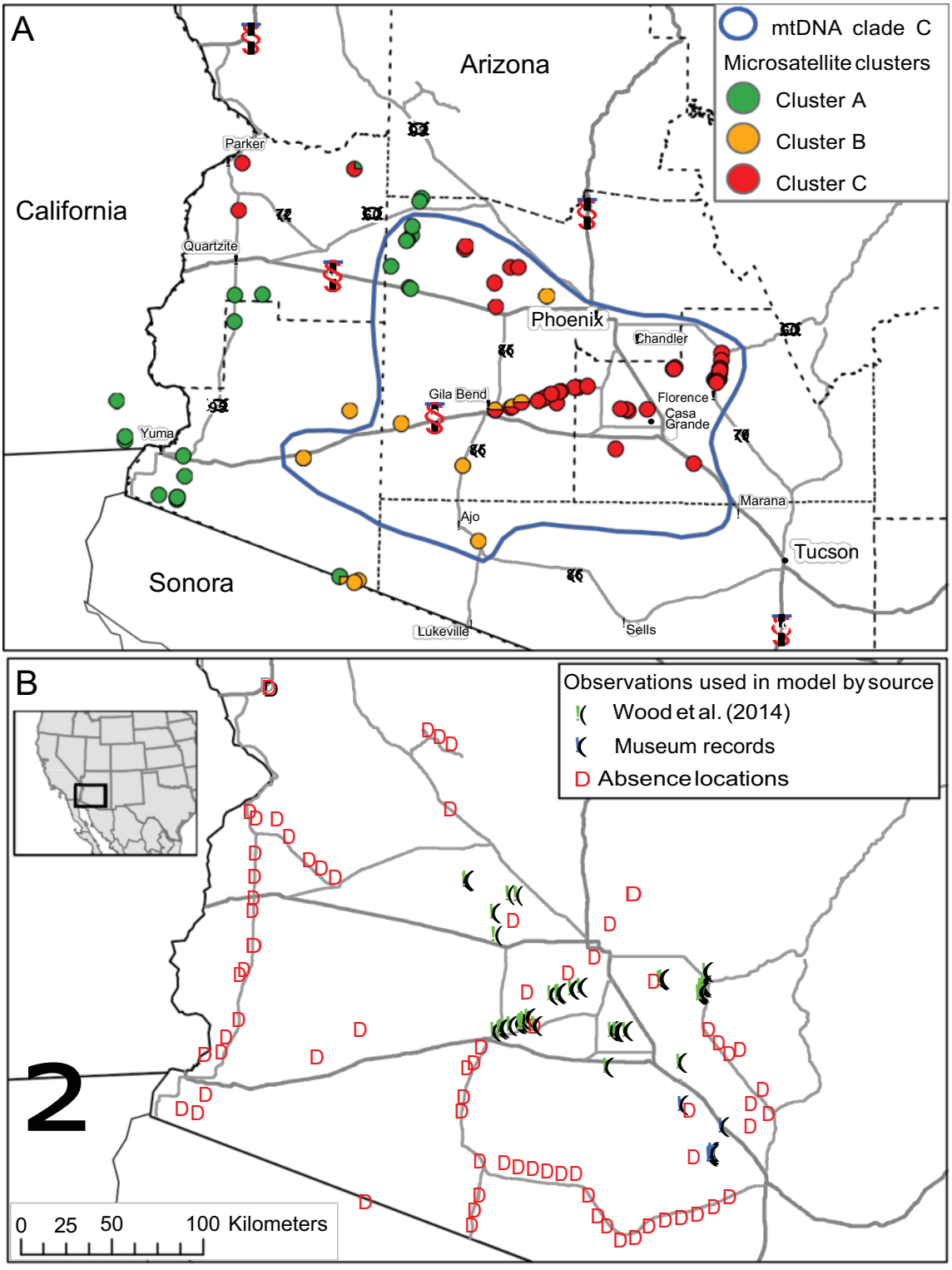

Figure 1--A) Microsatellite clusters and mtDNA clade C from Fig. 5 in Wood et al. (2014). The cluster C locations (red circles and half circles) within the mtDNA clade C are the basis for delineating *C. a. klauberi*'s distribution. B) Observations and assigned absence locations used in the species distribution model

Euro-American settlement and was used in our model because many observation records pre-date valley conversion to non-habitat. The Vegetation Cover dataset was modified to indicate the percent shrub cover. The EVT maps were used

Table 1— Explanatory variables evaluated for inclusion in the species distribution model for *C. a. klauberi*. Final variables used in the model are in bold. Variable importance rankings can be seen in Figure 5.

Variable	Description	Variable	Description
ELEV	**Elevation in meters**	bio_1	Annual mean temperature
Slope	**Slope (%)**	bio_2	Mean diurnal range
Slope2dir	Second derivative of slope	bio_3	Isothermality
HSP	Hierarchical slope position	bio_4	Temperature Seasonality
CTI	Compound topographic index	bio_5	Max Temperature of Warmest Month
Sand	Sand by weight (%)	bio_6	Minimum temperature of coldest month
Silt	Silt by weight (%)	bio_7	Temperature Annual Range
Clay	Clay by weight (%)	**bio_8**	Mean Temperature of Wettest Quarter
Frags	Rock fragments by weight (%)	bio_9	Mean Temperature of Driest Quarter
H2OStorage	Available water storage	bio_10	Mean Temperature of Warmest Quarter
BPS	Biophysical settings	bio_11	Mean Temperature of Coldest Quarter
PctShrubLFire	Shrub cover (%)	**bio_12**	**Annual precipitation**
LS8_B1	Landsat 8 band 1	**bio_13**	**Precipitation of wettest month**
LS8_B2	Landsat 8 band 2	bio_14	Precipitation of Driest Month
LS8_B3	Landsat 8 band 3	bio_15	Precipitation Seasonality
LS8_B4	Landsat 8 band 4	bio_16	Precipitation of Wettest Quarter
LS8_B5	Landsat 8 band 5	**bio_17**	**Precipitation of Driest Quarter**
LS8_B6	Landsat 8 band 6	bio_18	Precipitation of Warmest Quarter
LS8_B7	Landsat 8 band 7	bio_19	Precipitation of Coldest Quarter

to classify areas that have been converted to non-habitat such as agriculture, roads, urban and semi-urban development, quarries/mines, or otherwise altered habitat. To supplement our landcover datasets we acquired the most recent late spring, cloud-free Landsat 8 imagery, from 5/3/2017 to 5/21/2017. Land ownership data were obtained from the Arizona State Land Department to determine how much current habitat is vulnerable to future conversion.

Elevation, slope, and the topographic indices of hierarchical slope position, the second derivative of slope, and compound topographic index were derived from a 30 m digital elevation model. Bioclimatic variables, based on average monthly temperature and precipitation data of conditions between 1970 and 2000, were downloaded from WorldClim (Fick and Hijmans, 2017) at the 30 arc-second (~ 1km) resolution. These 19 variables are often used in species distribution modeling and represent annual means and ranges in temperature and precipitation as well as limiting environmental factors such as temperature of the coldest and warmest months.

Random Forest Model--We modeled resource selection using the data-mining algorithm Random Forests (RF) (Breiman 2001) in R (R Core Team 2013). RF is gaining prominence in ecology because of its ability to work with spatially autocorrelated data and requires no assumption of variable distributions (Cutler et al. 2007, Evans et al. 2011). We tested and removed any our 38 initial variables that were multi-collinear using the R package "rfUtilities" (threshold = 0.05; Evans and Murphy 2017). From the remaining explanatory variables, we selected the most parsimonious model that maximized the amount of explained variation while minimizing model error and the number of explanatory variables, resulting in six variables in the final model.

The RF algorithm samples approximately 66% of the data to build regression trees, and the remaining withheld data are a validation sample to assess error. We used the validation sample to determine the amount of variance explained and variable importance. The algorithm also produces individual variable importance measures by calculating differences in prediction mean square error before and after randomly permuting each dependent variable's values. Variable importance is a measure of how much each variable contributes to the model's overall predicative accuracy. Unlike linear models, RF does not produce regression coefficients to examine how a change in a predictor variable affects the response variable. The analogy to this in RF is the partial dependence plot which is a graphical depiction of how the probability of occurrence will change with a single predictor while averaging out the effects of the other predictors (Cutler et al. 2007).

The model predicted probabilities of habitat suitability on a raster map where each 90 x 90 m cell was assigned a probability ranging from 0 to 1, with higher values corresponding to higher habitat suitability. To differentiate between habitat and non-habitat we used a threshold value of equal sensitivity and specificity (the probability at which the false positive rate and the true negative rate are equal) based on Liu et al. (2005). The thresholding resulted in patches of habitat and non-habitat. We retained habitat patches that overlapped our occurrence records and considered this historic (original) habitat. We removed from historic habitat those areas that were converted to agriculture, urbanized, etc., to map the remaining available habitat.

Using land ownership, we determined how much remaining habitat is susceptible to habitat conversion: private, state trust, BLM lands outside of national monuments, tribal, and 'other' lands. National parks, national monuments, military, and city, county, and state parks were considered legally protected from habitat conversion.

RESULTS

Predicted probabilities for habitat suitability are shown in Figure 2. The model was well supported with low (8.59 %) error (Table 2). The observed versus expected accuracy of our model was 0.825 (Kappa statistic), which is considered "almost perfect agreement" (Landis and Koch 1977), and the AUC value of 0.976 also indicates a very good model fit.

The threshold value of 0.52 produced a nearly contiguous habitat patch that incorporated 52 of the 53 observation records. We determined that, historically, the snake's distribution included 1,255,946 ha (3,103,505 ac) of suitable habitat, of which 38.6% has been converted into non-habitat types (Table 3, Figure 3). Of the remaining 770,971 ha (1,905,108 ac), only 10.9% (84,041 ha, 207,669 ac) is afforded legal protection from habitat conversion (Table 4).

The variable importance plot (Figure 5) indicates that elevation was the most important variable in explaining the variation in the data, followed by three climate variables and a topographic variable: annual precipitation, precipitation of the driest quarter, precipitation of the wettest month and percent slope. All of the climate variables are linked to elevation, to some degree, but also to spatial variation of the summer monsoon rainfall pattern.

Table 2—Model error, sensitivity, specificity, Kappa, ROC area under curve (AUC), significance (P), and the threshold value of equal sensitivity and specificity (Threshold).

Model error (%)	Sensitivity	Specificity	Kappa	AUC	Threshold
8.590	0.926	0.905	0.825	0.976	0.52

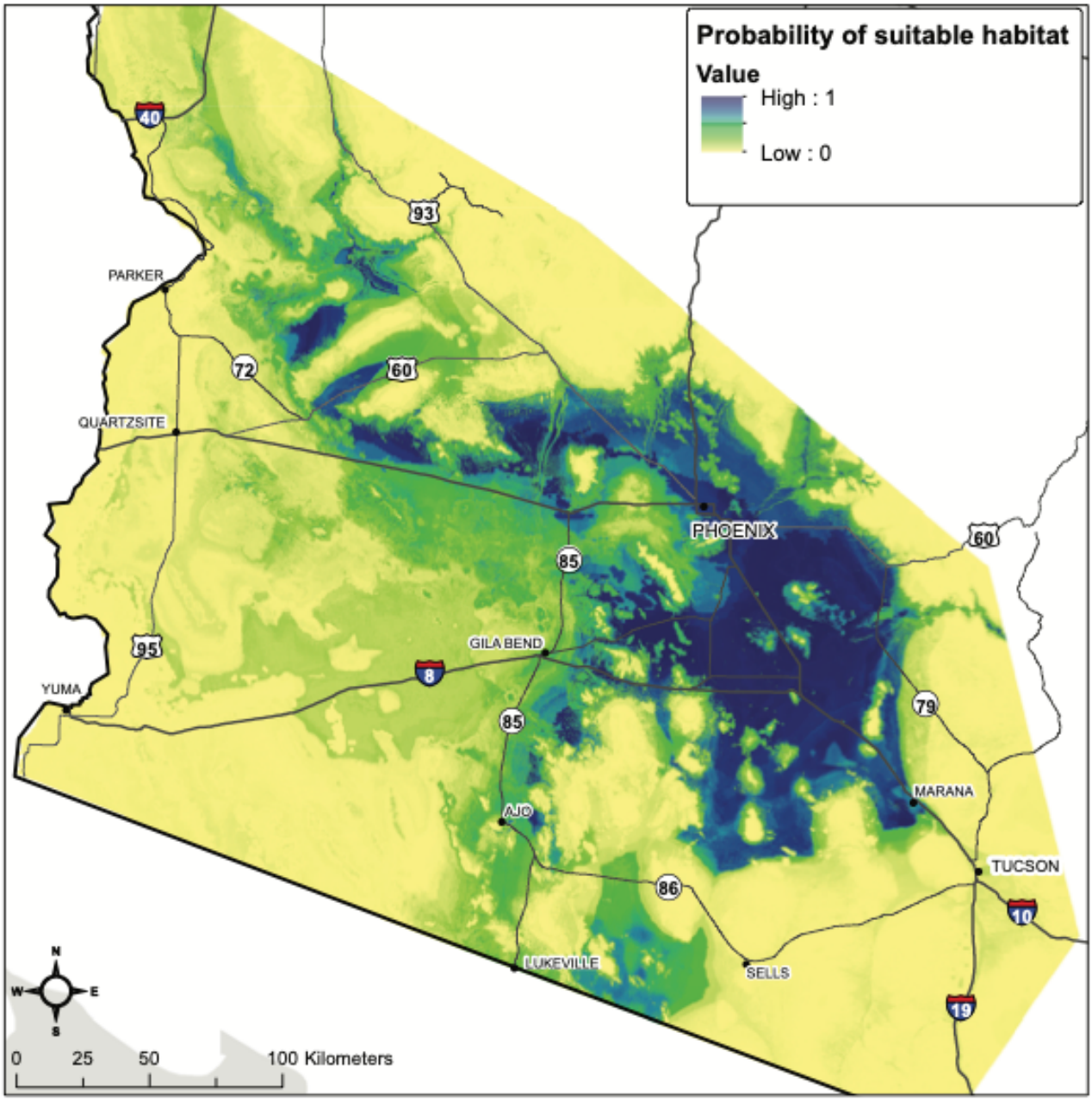

Figure 2--Estimated habitat suitability for the Tucson shovel-nosed snake in Arizona.

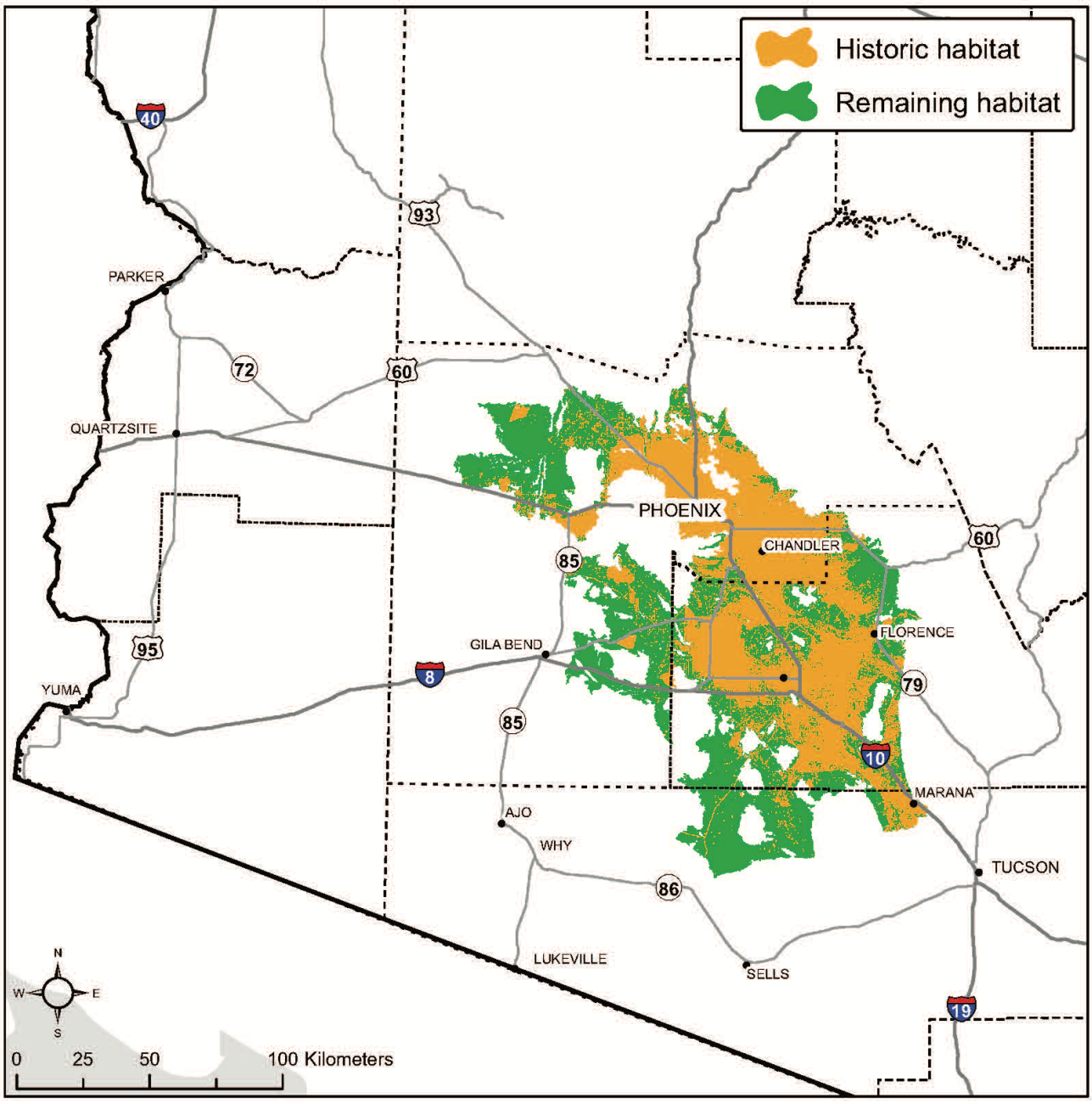

Figure 3--Currently suitable habitat and historic habitat that has been converted to urban development, roads, and agriculture within the distribution of *C. a. klauberi.*

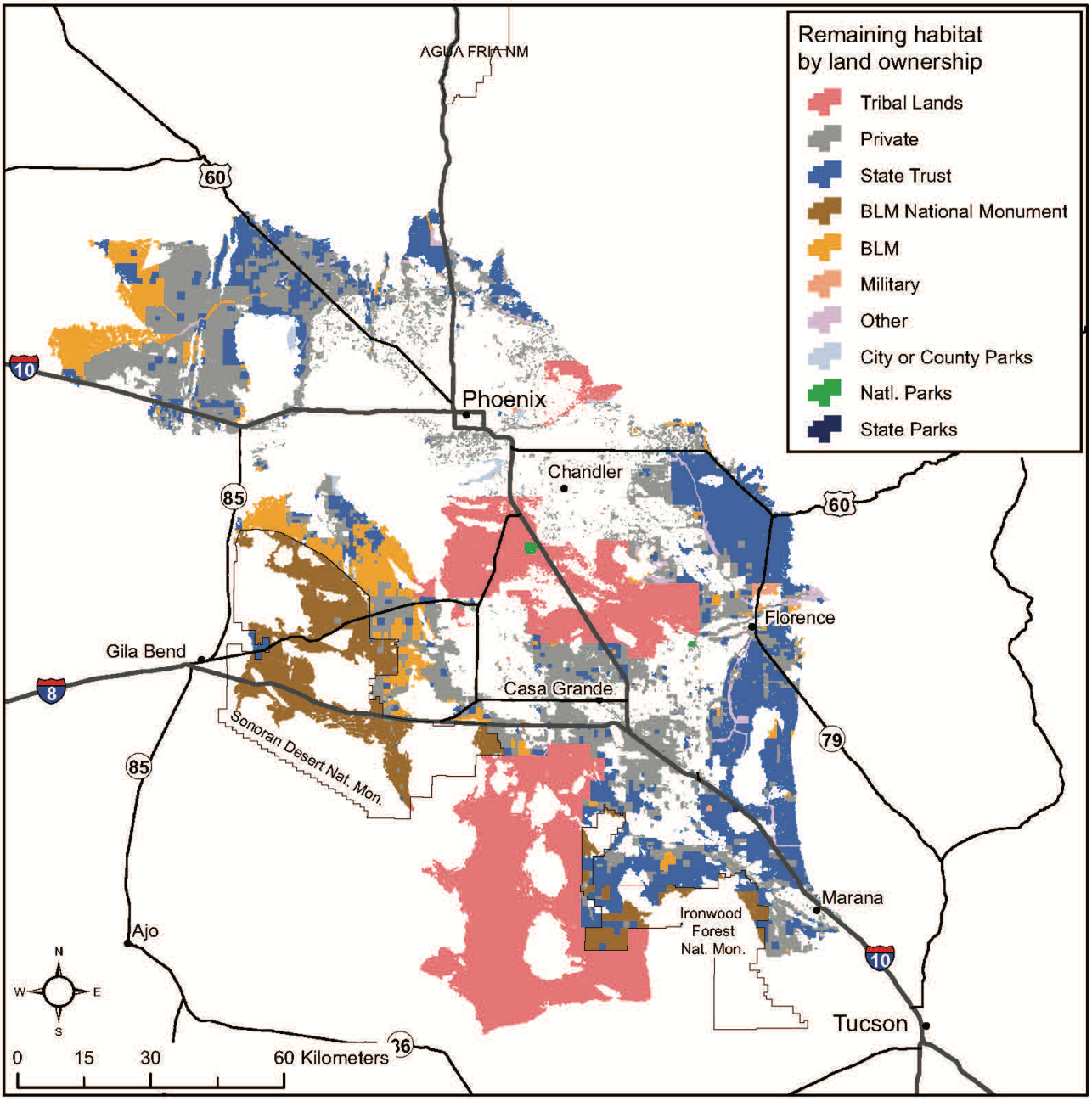

Figure 4--Land ownership of the currently suitable habitat of C. a. klauberi.

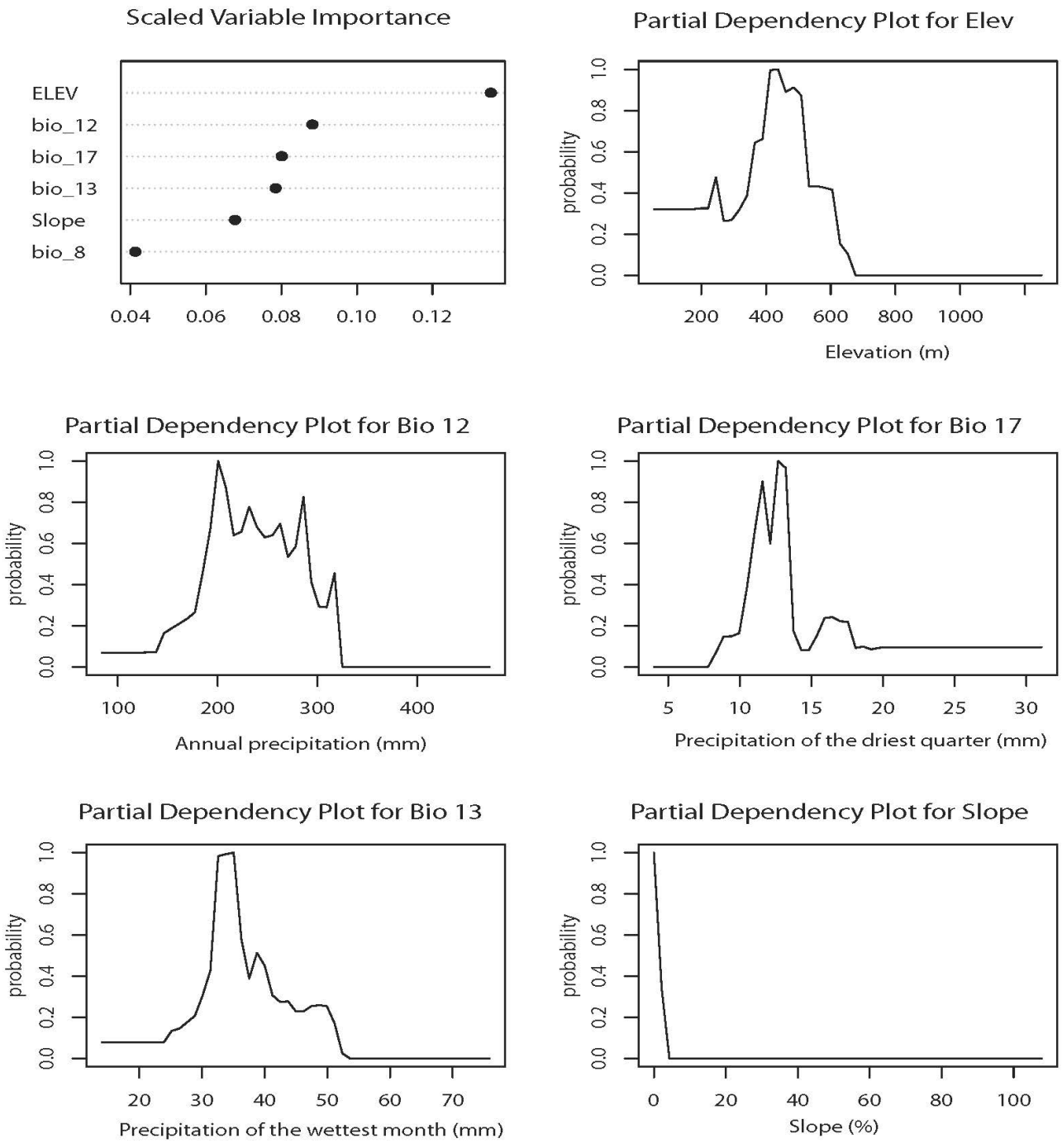

Figure 5--Variable importance plot and partial dependence plots of the top 5 independent variables in the species distribution model for C. a. klauberi: elevation (ELEV), annual precipitation (bio_12), precipitation of the driest quarter (bio_17), precipitation of wettest month (bio_13), and slope.

Table 3— Historic versus remaining habitat of *C. a. klauberi* by land ownership and protection class. Private, state trust, BLM lands outside national monuments, tribal, and 'other' lands are considered inadequately protected.

Category	Hectares	Acres		% of historic
Historic habitat	1,255,946	3,103,505		
Converted habitat	484,975	1,198,397		38.6
Remaining habitat	770,971	1,905,108		61.4
Remaining habitat by ownership	**Hectares**	**Acres**	**% of current**	**% of historic**
Tribal lands	222,407	549,580	28.8	17.7
Private	219,592	542,622	28.5	17.5
State Trust	185,081	457,345	24.0	14.7
BLM (national monuments)	75,036	185,418	9.7	6.0
BLM (other)	57,345	141,703	7.4	4.6
Military	6,617	16,352	0.9	0.5
Other	2,505	6,189	0.3	0.2
City or County Parks	1,563	3,863	0.2	0.1
National Parks	672	1,661	0.1	0.1
State Parks	152	375	0.0	0.0
Remaining habitat by protection class	**Hectares**	**Acres**	**% of current**	**% of historic**
Inadequately protected	686,930	1,697,438	89.1	54.7
Protected	84,041	207,669	10.9	6.7

DISCUSSION

The GIS-based habitat model used by USFWS (2014) in rejecting legal protection status for *C. a. klauberi* yielded an estimated area of suitable habitat 2.4 times greater (1,835,591 vs 770,971 ha) than what we estimated. The USFWS (2014) did not assess model sensitivity or specificity to report how well the model performed but we identified several reasons for the overestimation of habitat. First, the model included areas up to the 1500 m elevation which is over twice the maximum elevation for any *C. annulata* record (735 m) we can find in Arizona. Our analysis indicated an approximate elevational range of 350–625 m for *C. a. klauberi* (Figure 6). The elevation discrepancy may explain why well-sampled regions where the subspecies is unrecorded were included in the USFWS model, e.g., the region between Florence and Tucson along U.S. Highway 79 that supports strongly arborescent Arizona Upland Sonoran Desertscrub rich in saguaro cactus, and semi-desert grassland. Second, the USFWS (2014) model relied entirely on two variables, land cover and elevation, to predict *C. a. klauberi* habitat. We found elevation to be the most important habitat predictor while land cover was supplanted by climate variables and ultimately dropped from our model (Table 1). Third, the USFWS (2014) model included areas with limited nuclear and mtDNA representation associated with *C. a. klauberi* (Clade E, see Fig. 6), whereas we used a preponderance of genetic evidence approach to delineate the geographic distribution.

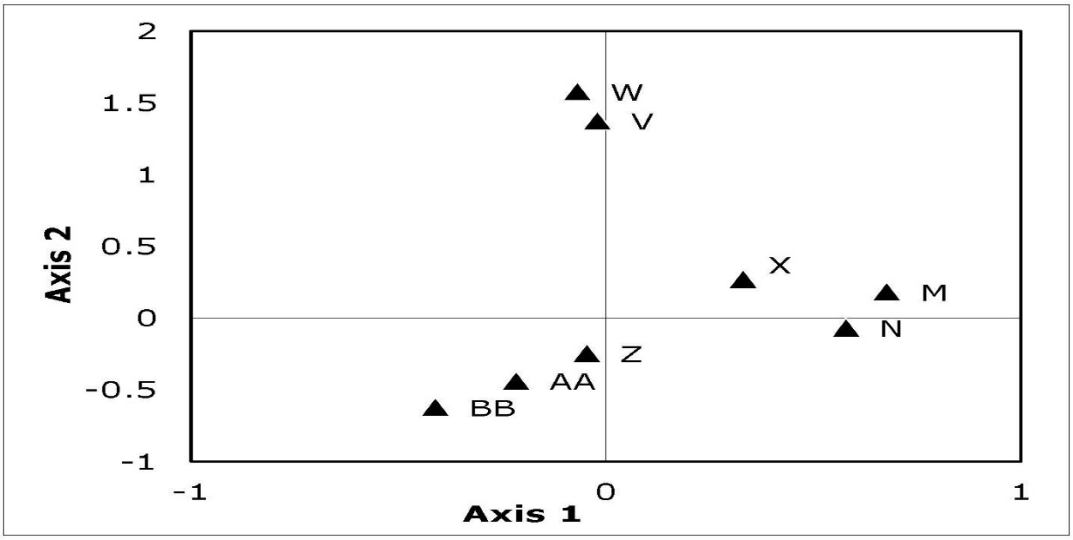

Figure 6--Locations of morphologicaly defined populations of C. annulata in Arizona designated by Cross (1979) and corresponding nonmetric mulitdeminsional scailing (NMS) ordination based on 14 morphological variables from Wood et al. (2008) (inset, modified with permission). USFWS (2014) range boundary shown in blue outline with mtDNA clade E specimens from Wood et al. (2014) shown as yellow dots.

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Figure 6 shows the results of Wood et al.'s (2008) nonmetric multidimensional scaling (NMS) ordination based on 14 morphological variables collected from Cross (1979), with population labeling added (D. Wood, pers. comm. 2018). Population M, included in the USFWS (2014) model, is morphometrically divergent from the *C. a. klauberi* populations located at AA and BB based on the NMS analysis (Figure 3 inset). Our genetics-based range interpretation also includes nearly all observation records classified using color pattern as either *C. a. klauberi* or intergrades with *C. a. annulata* (Cross 1979; Klauber 1951; Mahrdt et al. 2001) and excludes geographic populations that are markedly dissimilar to *C. a klauberi* on the basis of morphological characters (D. Wood, pers. comm. 2018). The new model we present is thus consistent with morphometric as well as genetic data and better represents the color pattern characteristic upon which the subspecies was originally based. Therefore, Figure 3 represents an improved estimate of the geographic extent of *Chionactis annulata klauberi*.

On this basis we found that 60.3% of remaining habitat (not already rendered unsuitable by agricultural conversion and urbanization) is vulnerable to loss from urbanization and other habitat uses, such as conversion to solar energy production facilities, in the coming five or so decades (or less). This dire scenario occurs as a result of the low slope values of occupied habitat, which is restricted to valley flats and lower bajadas with relatively simple perennial vegetation. These environments currently receive little protection, are rapidly being urbanized throughout central and southern Arizona, and are the typical siting for solar energy fields. Further, the lands we considered to have some reasonable chance of supporting natural environments in perpetuity may not actually do so. Both tribal and military lands could be used for energy production or other purposes destructive to natural environments. Recently, even national monument status may no longer be viewed as inviolate (Center for Biological Diversity 2017).

Explanatory bio-climatic variables estimating habitat availability for *C. a. klauberi* highlight its association with elevated portions of the highly arid Lower Colorado River Valley subdivision of the Sonoran Desert. These environments are higher in elevation, less arid, less sparsely vegetated, and less sand-dominated than those largely occupied by *C. a. annulata*. The weak predictive power of soil attributes in our model is likely due to the coarse scale of the STATSGO2 data. An earlier model for the Avra Valley population (Town of Marana 2004), for which the SSURGO soils data were usable, showed a strong association with loam- and sand-dominated soils. Thus, soil characteristics are likely critical for shovel-nosed snake conservation.

Despite extensive surveys from 1987-2017 (USFWS 2014; P. Rosen, unpublished), *C. a. klauberi* has not been found in formerly occupied, seemingly suitable habitat in the Avra Valley region, suggesting a range contraction of ca. 35 km since ca. 1979, facts dismissed by USFWS (2014). Urbanization in the Phoenix-Casa-Grande-Tucson-Florence corridor, comprising the genetic core of *C. a klauberi* and much of rest of the geographic distribution, is rapidly urbanizing (McClure et al. 2017) with no current prospect for substantial protection of valley habitats of *C. a. klauberi*. Although the relationship of recent regional climate change to range contraction of *C. a. klauberi* is unclear, climate acclimation via upward elevation range shifts would likely be blocked by anthropogenic land cover changes. *Chionactis annulata klauberi* may be significantly more threatened than foreseen by USFWS (2014), under both current and projected future climate and landscape regimes. As such, protection and restoration of sandy, saguaro-free, valley floor and lower bajada habitat in the northeastern Sonoran Desert of central Arizona may deserve higher priority than it is currently afforded.

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