Cytogeography of *Larrea tridentata* at the Chihuahuan-Sonoran Desert Ecotone

Robert G. Laport and Robert L. Minckley
Department of Biology, University of Rochester, Rochester, New York

Abstract—*The long separation of the Chihuahuan and Sonoran Deserts is reflected in the high species richness and endemism of their floras. Although many endemic species from both deserts reach their distributional limits where the Sierra Madre Occidental massif fragments into smaller mountain complexes in northern Mexico and adjoining areas of the United States, indicator species approaches to identify the boundary between the Chihuahuan and Sonoran Deserts are complicated by differences in physiology and morphology among species that independently influence their local occurrences. Here we use an alternate approach that examines distributional differences within a single species that is widespread in both deserts. We find that diploid and tetraploid Larrea tridentata occur sympatrically at an abrupt boundary in the low elevation areas of the Gila and San Pedro Rivers of southeastern Arizona. This cytotype boundary is correlated with climatic and vegetational transition, is consistent with a boundary between the Chihuahuan and Sonoran Deserts first suggested by Shreve, and raises interesting questions about the historical persistence of this contact zone.*

Introduction

The Chihuahuan and Sonoran Desert biomes of North America harbor species-rich, highly endemic floras that reflect a long isolation maintained along most of their boundary by the high elevations of the Sierra Madre Occidental. At present, species from both deserts come into contact only in the lowland areas where the Sierra Madre Occidental massif fragments into smaller mountain complexes in northern Mexico and adjoining areas of the United States (Warshall 1994). Species of plants (Henrickson and Straw 1976; Mabry and others 1977; McLaughlin 1986; Shreve 1942, 1951), mammals (Riddle 1998; Riddle and others 2000), reptiles (Morafka 1977), and bees (Danforth 1994; Rozen 1992) from each desert have been documented to reach their distributional limits in this area. These biological discontinuities coupled with abrupt changes in several climatological measures (Ackerman 1941; MacEwen and others 2005; Russell 1931; Schmidt 1979) support the presence of a transition zone between the Chihuahuan and Sonoran Deserts.

Although there is a general consensus that the boundary between the Chihuahuan and Sonoran Deserts occurs where vegetation transitions to a high elevation grassland community in southeastern Arizona, southwestern New Mexico, and northeastern Sonora, uncertainty persists over the formal location of the eastern boundary of the Sonoran Desert within this region (Gehlbach 1967; Schmidt 1979; Thornthwaite 1948; Weaver and Clements 1938). This uncertainty stems in part from the use of species assemblages, or select plant species to identify a boundary. However, different physiological and morphological traits among species invariably result in local differences in their occurrence, which are accentuated by the complex climatological and topographic variability of the "Sky Islands" area. Thus, the location of the eastern boundary of the Sonoran Desert has depended on the choice of indicator species and/or the definition of desert employed. For example, Shreve (1942, 1951) argued that the distributional limits of Saguaro Cactus (*Carnegiea gigantea*) and Ironwood (*Olneya tesota*) were closely associated with the edge of the Sonoran Desert as it transitions to the intervening grasslands currently separating the Chihuahuan and Sonoran Deserts. In contrast, Schmidt (1979) used measures of aridity to suggest the Chihuahuan and Sonoran Deserts were connected and shared a boundary in southeastern Arizona.

An approach not previously used to investigate the Chihuahuan-Sonoran Desert boundary is to examine genetic or distributional discontinuities within a single species of plant that inhabits both deserts. Single-species analyses should generally enjoy the advantage of controlling for the variable environmental effects on distantly related indicator species (Gleason 1926, 1939). Abrupt breaks in the distribution of a species, or discontinuities in DNA molecular markers, may indicate significant geological or environmental shifts. For example, Riddle (2000) demonstrated that species from multiple taxonomic groups in the North American deserts comprised divergent mitochondrial DNA lineages. Divergence of these phylogroups was found to correlate with past inundations that bisected the peninsula for species with distributions on the Baja Peninsula. We adopted a similar approach in this study using cryptic genetic variation to identify distributional shifts in the North American creosote bush (*Larrea tridentata* (DC) Coville; Zygophyllaceae).

Larrea tridentata is a ubiquitous shrub found throughout the Chihuahuan, Sonoran, and Mojave Deserts (Barbour 1969; Benson and Darrow 1981; Hunter and others 2001; Laport and others 2012; Lewis 1980; Turner and others 1995; Yang 1967, 1970; Yang and Lowe 1968). The distribution of *L. tridentata* has been used to define the extent of these deserts (Hastings and Turner 1965; Hunziker and others 1977; Shreve 1942) and its macrofossils are used to infer past desert conditions (Betancourt and others 1990). Yang (1967, 1970)

documented the existence of three chromosome races of creosote bush in North America. Recent analyses using guard cell measurements (Hunter and others 2001) and flow cytometry (Laport and others 2012) demonstrated that populations of tetraploids ($2n = 4x = 52$) and hexaploids ($2n = 6x = 78$) intermingle in the northern Sonoran Desert, while diploids ($2n = 2x = 26$) are limited to the Chihuahuan Desert and only hexaploids are known from the Mojave Desert.

As part of a broader study of cytotype distributions, Laport and others (2012) identified an abrupt transition between diploids and tetraploids near the classically defined boundary of the Sonoran Desert. However, it remains unclear if the diploid and tetraploid cytotypes are restricted to the Chihuahuan and Sonoran Deserts, respectively, due to the low resolution of prior sampling. Here, we describe additional sampling across this di ploid-tetraploid cytotype transition and examine evidence for the presence of a concordant ecological gradient supporting a transition from the Chihuahuan to Sonoran Desert. We measured plant community composition at sites spanning the cytotype transition and used multi-decadal climate data to determine if the cytotype transition is concordant with biotic and abiotic change. Finally, we constructed Ecological Niche Models, a widely used method for generating hypotheses of species distributions (Hijmans and others 2003; Kozak and Weins 2006; Oberhauser and Peterson 2003; Roura-Pascual and others 2004) to test if bioclimatic

data predict the boundary between *L. tridentata* cytotypes. These data were then used to discuss the potential relationship of this transitional area to the historical extent of the Chihuahuan and Sonoran Deserts.

Methods

Details of the cytotye distributions discussed here can be found in Laport and others (2012). Here, we employed 15 diploid and 13 tetraploid sites from areas surrounding the Gila and San Pedro River valleys of southeastern Arizona, USA (table 1; fig. 1). These sites, as reported in Laport and others (2012), were established in spring 2007 and 2008. The cytotype of 5-50 individuals per site was inferred using flow cytometry (Laport and others 2012). Discovery of the transition between diploid and tetraploid *Larrea tridentata* prompted the establishment of seven additional sites (T1Q1, T1Q2, T1Q3, T1Q4, T1Q5, T6Q1, T6Q2; table 1) along the Gila and San Pedro Rivers in 2008, creating two sampling transects between known diploid and tetraploid sites. Each plant (650 in total) was permanently marked with a numbered aluminum tag, and the GPS coordinates of each site were recorded (table 1).

To examine if other elements of the plant community changed in conjunction with the transition from diploid to tetraploid *Larrea tridentata*, we measured vegetation attributes at five sites along the

Table 1—*L. tridentata* collection sites and 30-year averages of NOAA climate data used in statistical analyses.

Ploidy	Number Plants Sampled	Site Name	Latitude	Longitude	Altitude (m)	January Max. (°C)	January Min. (°C)	July Max. (°C)	July Min. (°C)	Annual Precip. (cm)
2x	6	AZ07-B	31.816	-110.167	1216	15.28	2.28	34.06	19.17	35.81
2x	6	AZ07-G	33.341	-110.599	1027	15.17	0.83	37.89	22.72	40.31
2x	5	AZ07-J	32.258	-110.334	988	15.83	-2.39	35.11	17.67	33.91
2x	5	AZ07-K	32.153	-110.288	—	—	—	—	—	—
2x	5	AZ07-L	32.050	-110.327	1074	15.22	-1.22	33.94	17.83	33.55
2x	20	AZ07-M	33.162	-110.400	842	15.22	-2.22	36.00	20.17	26.16
2x	20	AZ07-N	33.174	-110.512	1027	15.22	-2.22	36.00	20.17	26.16
2x	8	AZ07-O	33.178	-110.530	—	—	—	—	—	—
2x	10	AZ07-T	32.493	-110.494	843	15.83	-2.39	35.11	17.67	33.91
2x	10	AZ07-U	32.269	-110.352	—	—	—	—	—	—
2x	10	AZ08-AI	31.905	-109.743	1330	16.78	-1.44	34.17	18.00	34.95
2x	5	AZ08-AX	31.934	-110.660	1183	14.61	0.17	32.11	16.06	53.80
2x	20	AZ08-H	32.838	-109.628	965	14.56	-2.67	35.67	18.17	27.08
2x	10	NM07-G	32.636	-109.024	1241	9.56	-10.89	28.44	7.94	44.63
2x	10	SN07-C	31.314	-109.317	1191	16.78	-1.44	34.17	18.00	34.95
2x	50	T1Q1	32.521	-110.504	—	—	—	—	—	—
2x	50	T1Q2	32.556	-110.516	—	—	—	—	—	—
2x/4x	50	T1Q3	32.596	-110.539	—	—	—	—	—	—
2x	50	T1Q5	32.540	-110.507	—	—	—	—	—	—
2x	25	T6Q2	33.189	-110.551	—	—	—	—	—	—
4x	6	AZ07-A	32.078	-111.259	789	18.78	0.72	37.22	21.06	32.03
4x	20	AZ07-F	33.020	-110.743	635	15.17	0.83	37.89	22.72	40.31
4x	8	AZ07-P	33.158	-110.805	846	15.17	0.83	37.89	22.72	40.31
4x	20	AZ07-Q	33.084	-110.715	634	15.17	0.83	37.89	22.72	40.31
4x	10	AZ07-R	32.749	-110.645	707	18.17	-0.78	37.61	18.44	36.40
4x	50	AZ07-S	32.633	-110.558	809	18.17	-0.78	37.61	18.44	36.40
4x	30	AZ08-AA	32.430	-111.360	605	19.22	1.44	38.17	22.11	31.50
4x	10	AZ08-AB	32.451	-111.480	753	18.89	5.50	38.06	24.67	30.48
4x	10	AZ08-AC	32.347	-111.459	761	19.22	1.44	38.17	22.11	31.50
4x	5	AZ08-AD	32.821	-111.204	724	13.44	1.67	33.39	19.33	63.30
4x	30	AZ08-AE	33.303	-111.372	576	16.11	6.06	36.72	24.11	51.41
4x	10	AZ08-AH	31.964	-110.926	839	14.61	0.17	32.11	16.06	53.80
4x	10	AZ08-AW	31.963	-110.728	1083	14.61	0.17	32.11	16.06	53.80
4x	50	T1Q4	32.616	-110.539	—	—	—	—	—	—
4x	25	T6Q1	33.021	-110.740	—	—	—	—	—	—
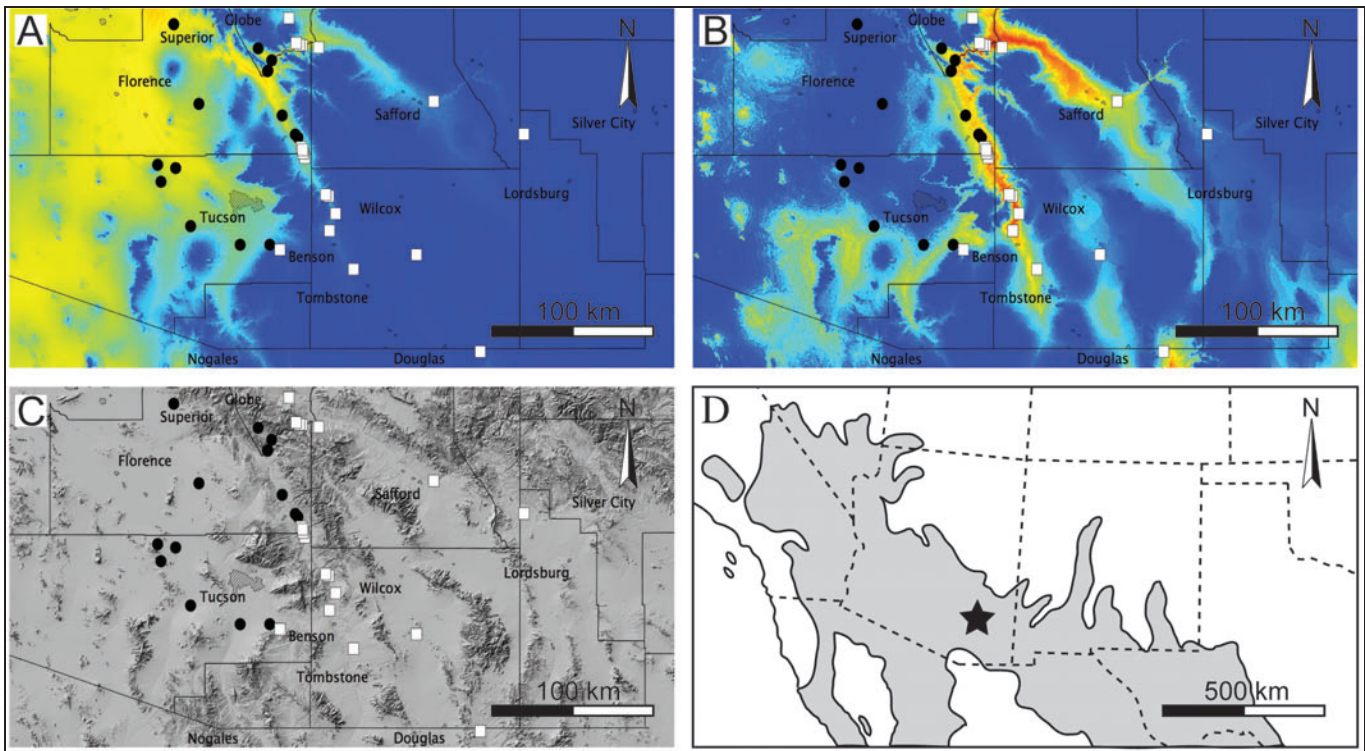
Figure 1—Ecological Niche Model projections of (A) tetraploid and (B) diploid *L. tridentata* based upon collections near the Chihuahuan/Sonoran Desert transition. Relief map (C) displaying *L. tridentata* collections in the San Pedro River and Gila River drainages of SE Arizona. Diploid sites are represented by white squares; tetraploid sites are represented by black circles. Warmer colors in the niche model projections represent higher predicted suitability. The northern range of *L. tridentata* (D) adapted from Hunziker et al. 1977. Star denotes location of study region.

San Pedro River and four sites along the Gila River (tables 1, 2). At each site, a representative 25 m x 25 m sampling plot was established in spring 2010 and the total number of each woody perennial species present was recorded (table 2). The vegan (v2.0.3) CRAN package for community ecology analyses implemented in the R statistical package (www.r-project.org) was used to conduct Nonmetric Multi-dimensional Scaling (NMDS) ordinations on the species density data. NMDS ordinations were implemented on square-root transformed and Wisconsin double standardized data. A two-dimensional solution with stress = 0.05192 was obtained using Bray-Curtis dissimilarities and 20 random starts. This solution was selected after inspection of a dimensionality vs. stress plot revealed that stress values reached

Table 2—*L. tridentata* sites and species density data used for species ordinations. San Pedro R. sites are listed north to south, Gila R. sites are listed west to east.

River Transect	Site Name	Larrea tridentata	Opuntia spp.	Cylindropuntia spp.	Prosopis velutina	Parkinsonia spp.	Carnegiea gigantea	Ferocactus wislizeni	Acacia greggii	Acacia spp.	Calliandra eriophylla	Encelia farinosa	Fouqueria splendens	Ephedra spp.	Simmondsia chinensis	Yucca spp.
San Pedro	AZ-S	50	0	9	8	0	1	0	0	0	0	0	0	0	0	0
	T1Q4	77	0	19	1	2	3	1	1	0	0	0	0	0	0	0
	T1Q3	81	6	5	4	17	4	2	2	3	4	0	2	0	0	0
	T1Q5	45	13	6	9	14	11	7	6	10	0	0	0	0	0	0
	T1Q2	27	1	2	7	23	14	1	5	4	0	0	0	0	0	0
Gila	AZ-F	19	2	0	3	14	1	0	1	0	0	1	1	0	7	0
	AZ-Q	27	0	8	9	10	3	4	13	1	2	13	0	1	0	0
	T6Q2	46	0	0	1	0	5	1	1	0	12	33	5	14	23	2
	AZ-N	20	9	1	6	4	1	1	12	0	0	0	0	0	0	2

an asymptote at solutions with higher dimensionality (McCune and Grace 2002).

To test if climate differed between diploid and tetraploid sites, we obtained climate values from the closest (mean 21.4 km, range 1–45 km) National Oceanic and Atmospheric Administration (www.noaa.gov) weather stations to 12 diploid and 13 tetraploid sites (table 1). Some sites could not be paired with unique weather stations and were excluded from climate analyses. We obtained 30-year averages (longest available for all sites) for January maximum temperature, January minimum temperature, July maximum temperature, July minimum temperature, and mean annual precipitation for Analysis of Variance (ANOVA) models and Principal Components Analysis (PCA) using the JMP statistical package (v9; SAS Institute, Cary, North Carolina, USA). Altitudes were obtained from the USGS National Map (www.nationalmap.gov), as were political boundaries and bedrock geology for qualitative assessments of cytotype distributions in Quantum GIS (www.qgis.org) (fig. 1).

We modeled cytotype distributions using the occurrence data in table 1 to examine if niche models supported the observed boundary of diploid and tetraploid *Larrea tridentata*. Altitude and climate variables at 30 arcsecond resolution ("bioclim") covering the geographic area of the *L. tridentata* localities listed in table 1 were obtained from Worldclim (www.worldclim.org; Hijmans and others 2005). To reduce inclusion of climate parameters from areas outside the distribution of *L. tridentata* and over-prediction of occurrence, the bioclim data were trimmed to encompass only the distribution of sampling localities detailed in table 1 (Pearson and others 2007; Stohlgren and others 2011). To minimize the high correlation among the 19 bioclim variables we reduced them to the six most dominant variables via Principal Component Analysis (PCA) on site-specific bioclim data (obtained using the "query" tool in Quantum GIS). The six variables retained were those most closely associated with the first six Principal Components: mean temperature of the wettest quarter, annual precipitation, mean temperature of the coldest quarter, precipitation of the driest quarter, temperature annual range, and seasonality of precipitation, respectively.

We used the program Maxent (v3.3.0b; www.cs.princeton.edu/~schapire/maxent/) with default parameter settings to construct a probabilistic niche model prediction for each cytotype (Phillips and others 2006). We ran 20 replicate models that were averaged via the crossvalidation method. Niche models for diploid and tetraploid *Larrea tridentata* were projected onto a broader region encompassing the "Sky Islands" and surrounding areas, and qualitatively reviewed in Quantum GIS (fig.1). Following Warren and others (2008) and Glor and Warren (2011), we also assessed the consistency and accuracy of the averaged predictions via the receiver operating characteristic (ROC) and the area under the ROC curve (AUC). High AUC values are generally indicative of models that predict occurrences well (Phillips and others 2006).

Results

Diploid and tetraploid sites were found in both the Gila and San Pedro River valleys. All individuals in four of the added transect sites (T1Q1, T1Q2, T1Q5, T6Q2) were diploid and all individuals in two of the sites (T1Q4, T6Q1) were tetraploid (table 1). A mixed site of 36 diploid and 14 tetraploid individuals was found near the center of the San Pedro River transect (T1Q3). Excluding this mixed-cytotype site (T1Q3), diploid and tetraploid sites were separated by ca. 7 km along the San Pedro River transect while diploid and tetraploid sites were separated by ca. 18 km along the Gila River transect.
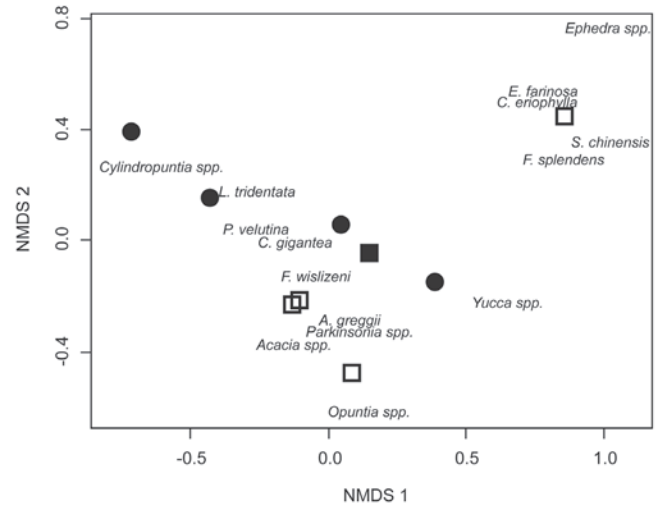

Figure 2—Non-metric Multi-Dimensional Scaling species density ordination of diploid and tetraploid sites. Diploid sites denoted by open squares, tetraploid sites denoted by black circles, the single mixed-cytotype site is denoted by a black square.

All plant species recorded in the Gila and San Pedro River transect sites had Sonoran Desert affinities (table 2) but vegetation ordination separated diploid and tetraploid sites (fig. 2). Tetraploid sites were associated with high densities of *Parkinsonia* spp., *Cylindropuntia* spp., *L. tridentata*, and *Prosopis velutina*. Diploid sites were associated with high densities of *Calliandra eriophylla*, *Carnegiea gigantea*, *Encelia farinosa*, *Ephedra* spp, *Fouqueria splendens*, *Acacia greggii*, *Opuntia* spp., *Prosopis velutina*, and *Simmondsia chinensis*. Diploid sites tended to have higher densities of Arizona Upland species than tetraploid sites.

Multiple ANOVA ($F = 3.257$, $P < 0.001$) and PCA using all climate data suggested diploid and tetraploid sites differed significantly (fig. 3).
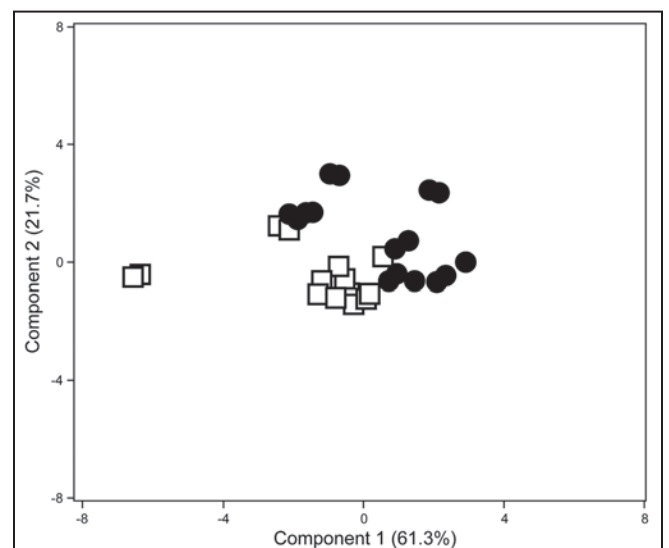
Figure 3—PCA of NOAA 30-year average climate data collected for diploid and tetraploid sites. Diploid sites denoted as open squares, tetraploid sites denoted as black circles.
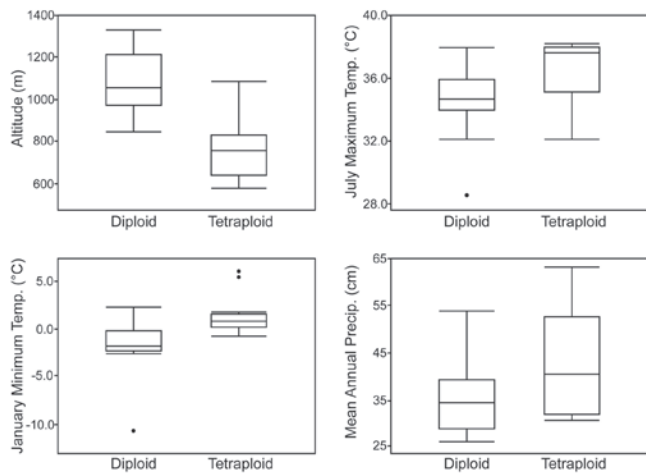
Figure 4—Boxplots of altitude and NOAA 30-year average climate data for diploid and tetraploid *L. tridentata* sites.

PC1 was associated with July maximum temperature (61.3% of variation), and PC2 was associated with mean annual precipitation (21.7% of variation). The first four Principal Components—July maximum temperature, mean annual precipitation, altitude, and January maximum temperature, respectively—accounted for 98.1% of the variation. Diploid sites tended to be at higher elevations ($F = 31.6203, P < 0.001$) and to have lower average temperatures (January minimum temperature, $F = 9.8483, P = 0.005$) (fig. 4).

Qualitatively, the niche models for diploid and tetraploid *Larrea tridentata* corresponded to the reported ranges for the individual cytotypes (Barbour 1969; Felger 2000; Hunter and others 2001; Hunziker and others 1977; Laport and others 2012; Turner and others 1995; Yang 1967; 1970). High average AUCs were obtained for both diploid (0.888, 0.178 s.d.) and tetraploid (0.893, 0.067 s.d.) niche models. The mean temperature of the wettest quarter made the largest contribution as an explanatory variable in the diploid model (39.8%), and mean temperature of the coldest quarter made the next largest contribution (29.8%). In the tetraploid model, mean temperature of the coldest quarter made the largest contribution (61.2%) and mean temperature of the wettest quarter made the next largest contribution (33.6%). Although diploids were predicted to have suitable habitat in some of the higher elevations of the Sonoran Desert, tetraploid suitability was essentially restricted to the Sonoran Desert (fig. 1). Nevertheless, diploid and tetraploid *L. tridentata* were predicted to share a boundary in the low elevations of the Gila and San Pedro River drainages, the same area where this transition is actually observed (fig. 1).

Discussion

Here, we documented an abrupt transition between diploid and tetraploid *Larrea tridentate*, a characteristic desert species, over the span of approximately 7-18 kilometers in the San Pedro and Gila River valleys of southeastern Arizona (fig. 1). A single site where diploids and tetraploids co-occur was discovered in the San Pedro River valley, an observation not previously reported. Although Yang (1970) reported the discovery of diploids and tetraploids within a. 5-mile radius near Mountain View, Arizona, it is not clear if they were growing sympatrically.

Differences in plant community suggest that our Gila and San Pedro River sites occurred near the eastern boundary of the Sonoran Desert (Bahre 1995; Betancourt and others 1990; McLaughlin 1986; Schmidt 1979; Shreve 1942, 1951; Turner and others 1995). Vegetation ordination results indicate diploid and tetraploid sites differ somewhat, though not strongly, in species composition. For example, tetraploid sites had higher densities of *Larrea tridentata*, while diploid sites tended to have higher densities of Arizona Upland species such as *Calliandra eriophylla*, *Encelia farinosa*, and *Simmondsia chinensis*. The mixed-cytotype site grouped with sites where tetraploids occur (fig. 2). Surprisingly, diploid sites also had higher densities of the Sonoran Desert endemic *Carnegiea gigantea*, a species typically used as an indicator of Sonoran Desert habitat (Shreve 1951; Soule and Lowe 1970). However, the study area is located only a few kilometers north and west of the documented range limit of *C. gigantea*, as the Chihuahuan endemic *Flourensia cernua* (Benson 1969; Benson and Darrow 1981; Brown 1994; Laport *personal observation*; Zimmerman 1969). These species have been used variously to denote the boundaries of the Sonoran and Chihuahuan Deserts, respectively (Shreve 1951; Zimmerman 1969). The higher densities of *C. gigantea* in diploid sites may be attributable to local variation in their occurrence, or the placement of sampling plots, which could be corrected with more intensive vegetation sampling. Nevertheless, these observations can be interpreted as indicating that the study area resides in an Arizona Upland plant association (*sensu* Brown 1994) near the boundary between the Sonoran Desert and a higher elevation grassland community (*sensu* Burgess 1995), and that the diploid cytotype may not be entirely restricted to the Chihuahuan Desert and its surrounding semidesert habitat.

Altitude, precipitation, and temperature data in addition to our ecological niche models constructed from bioclim variables indicate abiotic differences occur at or near the range limits of diploid and tetraploid *Larrea tridentata*. The northwestern part of the study area is at lower elevation than the southeastern part of the study area. Tetraploid *L. tridentata* predominate in the northern and western portion of the study region while diploids were found only on the southeastern portion of the study area. Although our niche models predict some overlap between the diploid and tetraploid ranges (figs. 1, 2, 3), the overall pattern obtained from the altitude/climate data and niche models suggests areas inhabited by these two cytotypes are abiotically unique with warmer temperatures prevailing in areas where tetraploids are found. The differences observed here presumably reflect more general climatic differences between the eastern Sonoran Desert and the adjacent high elevation grassland biomes, and concur remarkably well with prior investigations of climatic differences at the boundary of the Sonoran and Chihuahuan Deserts (Ackerman 1941; MacEwen and others 2005; Russell 1931; Schmidt 1979). Despite high AUCs indicative of "good" models, the diploid model under-predicts the actual range of *L. tridentata* in SE Arizona and SW New Mexico (fig. 1B). Pearson and others (2007) suggested that niche models with limited sampling might conservatively be interpreted as indicating areas of similar climatic conditions to the known localities, rather than a model of species range limits. Nevertheless, a broader scale analysis of *L. tridentata* spanning all three North American warm deserts recapitulates the niche model differences reported here, suggesting the limited sampling of this study does not overtly bias niche model construction and projection (Laport et al. *unpublished*).

The results of our analyses contribute to the body of literature investigating the limits of the Chihuahuan and Sonoran Deserts. The transition between diploid and tetraploid *Larrea tridentata* over a few kilometers is generally concordant with the distributional limits of some characteristic Chihuahuan and Sonoran endemic species (i.e.,

F. cernua, *C. gigantea*) as well as a subtle climatic gradient (Benson and Darrow 1981; Schmidt 1979). Given the patterns observed in this relatively small-scale analysis, it would be informative to include additional sites and their physical features in the transition area for future analyses. We doubt soils explain cytotype distributions in this study because of the predominance of unconsolidated alluvial substrates in these river valleys. However, prior studies have demonstrated significant effects of soil on the distribution of *L. tridentata* (Ignace and Huxman 2009; McAuliffe 1994). Moreover, limestone-containing soils are common throughout the Chihuahuan Desert (Brown 1994; Wentworth 1985) and many of the diploid sites in this study appear to occur upon underlying limestone-containing sedimentary series. This includes the unsampled, but probable, boundary between diploids and tetraploids (fig. 1) in the Needle's Eye Canyon along the Gila River (Richard and others 2000; www.nationalmap.gov).

If the within-taxon analysis presented here is a reasonable indicator of where the Chihuahuan and Sonoran Desert boundary occurs, the distributions of diploid and tetraploid *Larrea tridentata* (along with other plants) suggest the current boundary between these deserts occurs within the Gila and San Pedro River valleys.

The boundary between diploids and tetraploids identified in this study may imply that a previously unrecognized zone of contact has long persisted in the low elevations of the Gila and San Pedro Rivers. No paleovegetation records have been reported for low elevations in this area, though some historical records and photographs indicate limited pockets of desert vegetation occurred among grasslands in these areas within the last 200 years (Hastings and Turner 1965; Humphrey 1987). The steep alluvial slopes near the cytotype boundary in the Needle's Eye Canyon of the Gila River (Mescal Mts., Ryan 1985) are very similar to northern extralimital populations of *Larrea tridentata* that grow on the alluvial slopes of the Rio Grande valley south of Albuquerque, New Mexico (Wislizenus 1848). These climatic conditions have likely been present for thousands of years raising the possibility that *L. tridentata* has persisted for an extended period in this ancient drainage. Future efforts to obtain paleovegetation data from pack rat (*Neotoma*) middens at low elevations in the eastern Catalina, northwestern Galiuro, and southern Mescal Mountains would be particularly informative for determining ancient botanical communities of the area, which may help elucidate the importance and persistence of the Gila and San Pedro Rivers as corridors between the Chihuahuan and Sonoran Deserts.

References

Ackerman, E.A. 1941. The Köppen classification of climates in North America. *Geographical Review* 31: 105-111.

Bahre, C.J. 1995. Human Impacts on the Grasslands of Southeastern Arizona. In McClaran, M. P., and T.R. Van Devender, Eds., *The Desert Grassland*. Tucson: The University of Arizona Press, pp. 230-264.

Barbour, M.G. 1969. Patterns of genetic similarity between *Larrea divaricata* of North and South America. *American Midland Naturalist* 81: 54-67.

Brown, D.E., Ed. 1994. *Biotic Communities: Southwestern United States and Northwestern Mexico*. Salt Lake City: University of Utah Press.

Benson, L. 1969. The Cacti of Arizona. 3rd Ed. Tucson: University of Arizona Press.

Benson, L., and R.A Darrow. 1981. *Trees and Shrubs of the Southwest Deserts*. Tucson: University of Arizona Press.

Betancourt, J.L., T.R. Van Devender, P.S. Martin, Eds. 1990. *Packrat Middens: The Last 40,000 Years of Biotic Change*. Tucson: University of Arizona Press.

Burgess, T.L. 1995. Desert Grassland, Mixed Shrub Savanna, Shrub Steppe, or Semidesert Scrub? In McClaran, M. P., and T.R. Van Devender, Eds., *The Desert Grassland*. Tucson: The University of Arizona Press, pp. 31-67.

Danforth, B.N. 1994. Taxonomic review of *Calliopsis* subgenus *Hypomacrotera* (Hymenoptera; Andrenidae), with special emphasis on the distributions and host plant associations. *Pan-Pacific Entomologist* 70: 283-300.

Felger, R.S. 2000. *Flora of the Gran Desierto and Rio Colorado of Northwestern Mexico*. Tucson: University of Arizona Press.

Gehlbach, F.R. 1967. Vegetation of the Guadalupe escarpment, New Mexico-Texas. *Ecology* 48: 393-419.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7-26.

Gleason, H.A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21: 92-110.

Glor, R.E., and D. Warren. 2011. Testing ecological explanations for biogeographic boundaries. *Evolution* 65: 673-683.

Hastings, J.R., and R.M. Turner. 1965. *The changing mile. An ecological study of vegetation change with time in the lower mile of an arid and semiarid region*. Tucson: University of Arizona Press.

Henrickson, J.R. and R.M. Straw. 1976. *A Gazeteer of the Chihuahuan Desert Flora*. Los Angeles: California State University.

Hijmans, R.J., M. Jacobs, J.B. Bamberg, D.M. Spooner. 2003. Frost tolerance in wild potato species: Assessing the predictivity of taxonomic, geographic, and ecological factors. *Euphytica* 130, 47-59.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Hunter, K.L., J.L. Betancourt, B.R. Riddle, T.R. Van Devender, K.L. Cole, and W.G. Spaulding. 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology & Biogeography* 10: 521-533.

Hunziker, J.H., R.A. Palacios, L. Poggio, C.A. Naranjo, and T.W. Yang. 1977. Geographic distribution, morphology, hybridization, cytogenetics, and evolution. In *Creosote Bush: Biology and Chemistry of Larrea in New World Deserts*, US/IBP Synthesis Series 6. Stroudsburg: Dowden, Hutchison & Ross, Inc.

Humphrey, R.R. 1987. *90 Years and 535 Miles: Vegetation Changes Along the Mexican Border.* Albuquerque: University of New Mexico Press.

Ignace, D.D., Huxman, T.E. 2009. Limitations to photosynthetic function across season in *Larrea tridentata* (creosotebush) growing on contrasting soil surfaces in the Sonoran Desert. *Journal of Arid Environments* 73: 626-633.

Kozak, K.H., J.J. Wiens. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* 60, 2604-2621.

Laport, R.G., R.L. Minckley, J. Ramsey. 2012. Phylogeny and cytogeography of the North American Creosote Bush (*Larrea tridentata*; Zygophyllaceae). *Systematic Botany* 37: 153-164.

Lewis, W.H. (Ed.) 1980. *Polyploidy, Biological Relevance*. New York: Plenum Press.

Mabry, T.J., J.H. Hunziker, D.R. Difeo Jr. 1977. *Creosote Bush: Biology and Chemistry of Larrea in New World Deserts,* US/IBP Synthesis Series vol. 6. Stroudsburg: Dowden, Hutchinson & Ross, Inc.

MacEwen, R., R.S. Mann, A.M. Castillo, D.P. Guertin. 2005. Defining boundaries across borders: A case study extending a major land resource area into Mexico. RMRS-P-36. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

McAuliffe, J.R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64: 112-148.

McCune, B., and J.B. Grace. 2002. *Analysis of Ecological Communities*. Glen Eden Beach: MjM Software Design.

McLaughlin, S.P. 1986. Floristic analysis of the southwestern United States. *Great Basin Naturalist* 46: 46-65.

Morafka, D.J. 1977. Is there a Chihuahuan Desert? A quantitative evaluation through a herpetofaunal perspective. In Wauer, R.H. and D.H. Riskind, Eds., *Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region, U.S. and Mexico. Alpine, Texas*. USDI National Park Service Transactions and Proceedings Series 3, pp. 437-454.

Oberhauser, K., A.T. Peterson. 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences of the USA* 100, 14063-14068.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34: 102-117.

Phillips, S.J., R.P. Anderson, R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190: 231-259.

Richard, S.M., S.J. Reynolds, J.E. Spencer, and P.A. Pearthree, comps., 2000, Geologic Map of Arizona: Arizona Geological Survey Map M-35, 1 sheet, scale 1:1,000,000.

Riddle, B.R. 1998. The historical assembly of continental biotas: Late Quaternary range-shifting, areas of endemism, and biogeographic structure in the North American mammal fauna. *Ecography* 21: 437-446.

Riddle, B.R., D.J. Hafner, L.F. Alexander, and J.F. Jaeger. 2000. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceedings of the National Academy of Sciences of the USA* 97: 14438-14443.

Rozen, Jr., J.G. 1992. Systematics and host relationships of the cuckoo bee genus *Oreopasites* (Hymenoptera: Anthopheridae: Nomadinae). *American Museum Novitates* 3046: 1-56.

Roura-Pascual, N., A.V. Suarez, C. Gomez, P. Pons, Y. Touyama, A.L. Wild, A.T. Peterson. 2004. Geographical potential of Argentine ants (*Linepitherma humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271, 2527-2534.

Russell, R.J. 1931. *Dry Climates of the United States*. Berkeley: University of California Press Publications in Geography 5:1-41 + map.

Ryan, G.S. 1985. Mineral investigation of the Needle's Eye Wilderness Study Area, Gila County, Arizona. *U.S. Bureau of Mines Mineral Land Assessment MLA 9-85*. Denver: U.S. Department of the Interior Bureau of Mines.

Schmidt, Jr., R.H., 1979. A climatic delineation of the 'real' Chihuahuan Desert. *Journal of Arid Environments* 2: 243-250.

Shreve, F. 1942. The desert vegetation of North America. *The Botanical Review* 8: 195-246.

Shreve, F. 1951. *Vegetation and Flora of the Sonoran Desert. Volume I. Vegetation*. Carnegie Institution of Washington Publications 591.

Soule, O.H., and C.H. Lowe. 1970. Characteristics of tissue fluids in the Sahuaro Giant Cactus (*Cereus giganteus*). *Annals of the Missouri Botanical Garden* 57: 265-351.

Stohlgren, T.J., C.S. Jarnevich, W.E. Esaias, J.T. Morisette. 2011. Bounding species distribution models. *Current Zoology* 57: 642-647.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38: 55-94.

Turner, R.M., J.E. Bowers, T.L. Burgess. 1995. *Sonoran Desert Plants: An Ecological Atlas*. Tucson: University of Arizona Press.

Warshall, P. 1994. The Madrean Sky Island Archipelago: A planetary overview. Gen. Tech. Rep. RM-GTR264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Warren, D.L., R.E. Glor, M. Turelli. 2008. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* 62: 2868-2883.

Weaver, J.W. and F.E. Clements. 1938. *Plant Ecology*. New York: McGraw-Hill Book Co.

Wentworth, T.R. 1985. Vegetation on limestone in the Huachuca Mountains, Arizona. *The Southwestern Naturalist* 30: 385-395.

Wislizenus, A. 1848. *Memoir of a tour to northern Mexico, connected with Col. Doniphan's Expedition, in 1846 and 1847*. Washington: Tippin & Streeper.

Yang, T.W. 1967. Chromosome numbers in populations of creosote bush (*Larrea divaricata*) in the Chihuahuan and Sonoran subdivisions of the North American Desert. *Journal of the Arizona Academy of Science* 4: 183-184.

Yang, T.W. 1968. A new chromosome race of *Larrea divaricata* in Arizona. Western Reserve Academy Natural History Museum Special Publication 2: 1-4. Hudson, OH: Western Reserve Academy.

Yang, T.W. 1970. Major chromosome races of *Larrea divaricata* in North America. *Journal of the Arizona Academy of Science* 6: 41-45.

Yang, T.W., and C.H. Lowe. 1968. Chromosome variation in ecotypes of *Larrea divaricata* in the North American Desert. *Madroño*. 19: 161-164.

Yang, T.W., J.H. Hunziker, L. Poggio, and C.A. Naranjo. 1977. Hybridization between South American jarilla and North American diploid creosote bush (*Larrea*, Zygophyllaceae). *Plant Systematics and Evolution* 126: 331-346.

Zimmerman, R.C. 1969. Plant ecology of an arid basin, Tres Alamos-Redington area southeastern Arizona. U.S. Geological Survey Professional Paper, 485-D.