

Comparative phylogeography reveals deep lineages and regional evolutionary hotspots in the Mojave and Sonoran Deserts

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ABSTRACT

Aim We explored lineage diversification within desert-dwelling fauna. Our goals were (1) to determine whether phylogenetic lineages and population expansions were consistent with younger Pleistocene climate fluctuation hypotheses or much older events predicted by pre-Pleistocene vicariance hypotheses, (2) to assess concordance in spatial patterns of genetic divergence and diversity among species and (3) to identify regional evolutionary hotspots of divergence and diversity and assess their conservation status.

Location Mojave, Colorado, and Sonoran Deserts, USA.

Methods We analysed previously published gene sequence data for twelve species. We used Bayesian gene tree methods to estimate lineages and divergence times. Within each lineage, we tested for population expansion and age of expansion using coalescent approaches. We mapped interpopulation genetic divergence and intra-population genetic diversity in a GIS to identify hotspots of highest genetic divergence and diversity and to assess whether protected lands overlapped with evolutionary hotspots.

Results In seven of the 12 species, lineage divergence substantially predated the Pleistocene. Historical population expansion was found in eight species, but expansion events postdated the Last Glacial Maximum (LGM) in only four. For all species assessed, six hotspots of high genetic divergence and diversity were concentrated in the Colorado Desert, along the Colorado River and in the Mojave/Sonoran ecotone. At least some proportion of the land within each recovered hotspot was categorized as protected, yet four of the six also overlapped with major areas of human development.

Main conclusions Most of the species studied here diversified into distinct Mojave and Sonoran lineages prior to the LGM – supporting older diversification hypotheses. Several evolutionary hotspots were recovered but are not strategically paired with areas of protected land. Long-term preservation of species-level biodiversity would entail selecting areas for protection in Mojave and Sonoran Deserts to retain divergent genetic diversity and ensure connectedness across environmental gradients.

Keywords

Biogeography, conservation planning, desert southwest, evolutionary potential, genetic diversity.

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INTRODUCTION

Comparative phylogenetic approaches are often used to uncover the historical processes that have shaped genetic structure for regional biotas (Avice, 1992; Humphries *et al.*, 1995; Moritz, 1995; Riddle & Hafner, 2006). Phylogeographic studies of the south-western deserts of North America have uncovered diverse historical processes, with two posed as most important for shaping genetic structure: Pleistocene climate fluctuations and pre-Pleistocene vicariance. Support for climate fluctuation hypotheses emerged from a historical understanding of Pleistocene vegetation patterns within North American deserts and from the perception that desert floras were relatively young (Savage, 1960; Findley, 1969; Morafka, 1977; Axelrod, 1983). Paleo-environmental reconstructions, based largely on analysis of packrat middens, have indicated that present distributions of the Mojave and northern Sonoran Desert biomes were largely comprised of mesic woodlands during the Last Glacial Maximum (LGM: 18,000–20,000 years ago, Betancourt *et al.*, 1990). Furthermore, these deserts only recently reached their current extents in the present interglacial period (Van Devender, 1977; Spaulding, 1991; Wilson & Pitts, 2010). Presumably, recent biotic responses of desert habitats to climatic change have also occurred during the repeated glacial/interglacial cycling throughout the Pleistocene (especially over the last 700,000 years; Clark *et al.*, 1999). As such, several studies have posited that arid-adapted species spanning multiple deserts would have been limited to isolated refugia within the Mojave and Sonoran Deserts during glacial periods, assuming that niche requirements remained the same over time (Ayoub & Riechert, 2004; Jaeger *et al.*, 2005). Repeated displacement and fragmentation of habitats during climatic fluctuations should have resulted in genetic lineage diversification between refugial populations. Similarly, evidence of demographic expansion within lineages should coincide with the end of the LGM, as desert habitats expanded to maximum distributions. Work describing diversification patterns in the desert southwest may support this prediction by revealing the presence of moderately divergent mtDNA lineages between Mojave and Sonoran Deserts (Ayoub & Riechert, 2004; Douglas *et al.*, 2006; Wood *et al.*, 2008a; Jezkova *et al.*, 2009), but whether the timing of these diversification events is consistent with Pleistocene glacial cycles is unclear. Furthermore, corresponding evidence of range expansion in lineages coinciding with the LGM remains to be tested.

Pre-Pleistocene vicariance hypotheses challenge the importance of Pleistocene lineage diversification (Riddle *et al.*, 2000; Riddle & Hafner, 2006). Although southwest deserts are recent ecological transformations (Axelrod, 1983; Betancourt *et al.*, 1990), evidence of their existence predating the Pleistocene has been used to implicate older Neogene (> 2.5 million years ago, Ma) events in shaping south-western desert biota. Much of the strength for pre-Pleistocene vicariance hypotheses came from a better understanding of the geophysical processes that impacted desert regions and empirical observations of phylog-

eographic patterns. Two inundation events are credited for divergence patterns across the Mojave and Sonoran Deserts. The oldest event, estimated around the Late Miocene-Early Pliocene (10–8 Ma), entailed marine extensions of the Gulf of California caused by tectonic development of the Baja California Peninsula (Ivo, 1979; Stock & Hodges, 1989; Holt *et al.*, 2000; Dorsey *et al.*, 2007). Marine inundations filled basins in the Colorado Desert region and established the Imperial Formation (Ivo, 1979; McDougall *et al.*, 1999). A more recent and more extensive inundation, known as the Bouse embayment, occurred around the Late Pliocene (6.0–5.3 Ma) and extended deeply into California and Arizona contributing to the formation of the early Colorado River system (Metzger, 1968; Buising, 1990; McDougall *et al.*, 1999). These embayments likely served as substantial east-west barriers to dispersal for many Sonoran and Mojave species, and opportunities for contact would not have occurred until these embayments receded around the mid-to-late Pleistocene. These vicariant hypotheses counter previous ideas that solely emphasized waves of expansion and contraction of species distributions mediated by Pleistocene climatic change as the dominant force in the evolution of arid-adapted species (Savage, 1960; Hubbard, 1973).

Understanding concordance in spatial patterns of vicariance and diversification among desert species can provide useful metrics for identifying regions of evolutionary significance to help prioritize lands for conservation (Moritz & Faith, 1998; Moritz, 2002). As diversity comprises the raw material for adaptation, protecting regions of high genetic diversity within species can maximize a species' evolutionary potential and resilience (Carvalho *et al.*, 2011; Sgrò *et al.*, 2011; Santamaria & Mendez, 2012). Likewise, geographic areas that contain high genetic divergence among populations may be important regions of evolutionary potential, because they often reflect secondary contact between divergent lineages (Stebbins & Major, 1965; Remington, 1968) or steep environmental gradients and other abiotic drivers of adaptation (Smith *et al.*, 2001; Davis *et al.*, 2008; Thomassen *et al.*, 2011). When multiple species show spatial concordance in patterns of high genetic diversity and divergence, and hence high evolutionary potential for lineage diversification and adaptation, these areas may be particularly important for maintaining regional biodiversity, and can be designated as evolutionary hotspots (Davis *et al.*, 2008; Vandergast *et al.*, 2008; Kraft *et al.*, 2010). The south-western deserts of the United States contain a large number of endemic species, and anthropogenic land-use activities have impacted biodiversity in this region (Dobson *et al.*, 1997; Chaplin *et al.*, 2000). Proposed development of utility-scale renewable energy facilities (Zweibel *et al.*, 2008; Fthenakis *et al.*, 2009; California Energy Commission, 2012) and ongoing ecoregional planning efforts to designate lands for development or conservation

(e.g. California Desert Renewable Energy Conservation Plan) necessitate an evaluation of land protection status in terms of evolutionary function throughout this region (e.g. Spencer *et al.*, 2010).

In this study, we investigated the phylogeographic history of the Mojave and Sonoran Deserts using a comparative approach. By examining spatial and temporal patterns of DNA sequence variation in 12 species, we evaluated the concordance of phylogeographic breaks and lineage diversification for both Pleistocene climate fluctuation hypotheses and pre-Pleistocene vicariance hypotheses. Multiple methods were used to test whether temporal patterns in divergence time and historical demographic expansion were consistent with a Pleistocene timeframe or whether lineages responded *in situ* to much older events (> 2 Ma). Next, we used visualization methods to assess the spatial pattern of genetic diversity and divergence across species and identify regional evolutionary hotspots. Finally, we examined the status of identified evolutionary hotspots in relation to land ownership and conservation.

METHODS

Study area

Our study region encompassed the Mojave and Sonoran Deserts in the United States, focusing on the junctures between the Mojave, Sonoran and Colorado Deserts (Fig. 1). We used the EPA Level III Ecoregions Mojave Basin and Range and Sonoran Basin and Range (U.S. Environmental Protection Agency, 2003) with a 10-km perimeter buffer to define our study region.

Compiling genetic data

We identified species for which regionally representative genetic data across the Mojave and Sonoran Deserts were published. The 12 species identified were small, terrestrial animals representing a wide taxonomic range (Table 1).

Available genetic data consisted mainly of mtDNA sequence data, with nuclear sequence data available only for three species (Table 1). Nuclear data were incorporated into genetic divergence and diversity landscape maps, but were not included in phylogenetic divergence estimates or demographic analyses due to comparatively low levels of variability and phylogenetic signal (Crews & Hedin, 2006; Leaché & Mulcahy, 2007). While there are limitations in using a single locus to study evolutionary and demographic history (Edwards & Beerli, 2000; Ballard & Whitlock, 2004), we rely upon multiple taxa rather than multiple loci to cross-validate observed patterns. This approach is consistent with our goal to uncover regional history, rather than any single species' history. Prior to genetic analyses, each dataset was aligned using CLUSTAL-W (Thompson *et al.*, 1994), as implemented in MEGA 4.0 (Tamura *et al.*, 2007) and adjusted by eye.

Phylogenetic gene tree and divergence estimates

We used BEAST v1.6.1 (Drummond & Rambaut, 2007) to estimate phylogenetic trees and divergence times for mtDNA sequence data for each species. This program uses a Markov Chain Monte Carlo (MCMC) algorithm to estimate tree topology, model parameters and the timing of divergence events. For each species, we identified the best-fitting models of nucleotide substitution with the Bayesian information criterion (BIC) using JMODELTEST 0.1.1 (Guindon & Gascuel, 2003; Posada, 2008). We estimated posterior distributions of model parameters and genealogies by sampling from the MCMC posterior distribution every 1000th generation for 20–30 million generations, discarding the first 10% of samples as burn-in. All analyses were conducted with a constant population tree prior, assuming uncorrelated and log-normally distributed evolutionary rates across the tree branches. We assessed convergence using AWTY (Nylander *et al.*, 2008).

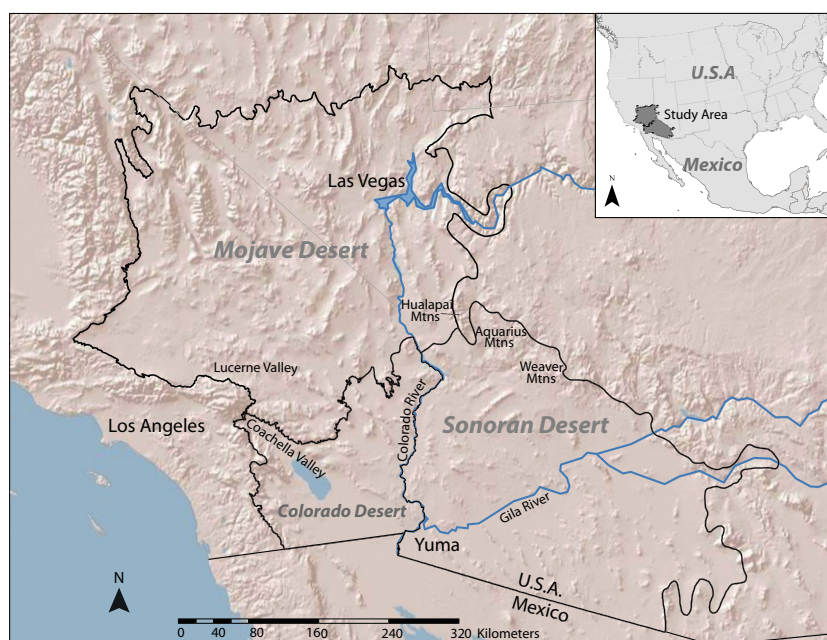


Figure 1 Map of the study region (black outline) within the Mojave, Sonoran and Colorado Deserts of the south-western United States and other geographic features mentioned in the text. Our study region boundaries were based on the EPA Level III Ecoregions Mojave Basin and Range, and Sonoran Basin and Range (U.S. Environmental Protection Agency, 2003) with a 10 km buffer.

Table 1 Taxa and genetic datasets examined across the Mojave and Sonoran Deserts. Number of sampling locations and mean sample size (*N*) for diversity estimates are shown in parentheses. Species contributing strongly to divergence and diversity hotspots are denoted with a + symbol. Grey boxes indicate no overlapping coverage, and NI denotes not included

Species	No. sampling locations	Mean <i>N</i>	Divergence hotspots			Diversity hotspots		
			Lucerne Valley (A)	Colorado Desert (B)	Colorado River (C)	Coachella Valley (A)	So. Colorado and Gila Rivers (B)	Hualapai – Weaver Mtns (C)
Herpetofauna								
<i>Anaxyrus punctatus</i> – red-spotted toad‡	38 (19)	2.11 (3.79)						
<i>Chionactis occipitalis</i> – shovel-nosed snakes§	131 (26)	1.12 (5.46)		+	+		+	
<i>Crotaphytus bicinctores</i> – collar lizard¶	50 (10)	1.02 (4.2)						
<i>Crotalus cerastes</i> – sidewinder**	50 (17)	1.44 (2.88)	+	+	+	+		
<i>Lichanura trivirgata</i> – rosy boa††	29 (15)	1.93 (3.47)			+			
<i>Phrynosoma platyrhinos</i> – horned lizard‡‡	15	1.13			+	NI	NI	NI
<i>Sceloporus magister</i> – desert spiny lizard§§†	36 (14)	1.1 (2.57)	+			+	+	
<i>Xantusia vigilis</i> – desert night lizard¶¶	107 (40)	3.46 (9.8)	+		+	+		
Invertebrates – ground dwelling spiders								
<i>Homalonychus selenopoides</i> ****†	20	2.67			+		+	+
<i>Homalonychus theologus</i> ****†	28	2.61			+	+		
Mammals								
<i>Chaetodipus penicillatus</i> – pocket mouse†††	41 (31)	4.34 (6.58)	+		+			+
<i>Thomomys bottae</i> – pocket gopher‡‡‡	24	1	+	+	+	NI	NI	NI

† Indicates species in which both mtDNA and nuDNA were available.

‡ Jaeger *et al.*, 2005.§ Wood *et al.*, 2008a.¶ McGuire *et al.*, 2007.

** Pece, 2004.

†† Wood *et al.*, 2008b.‡‡ Mulcahy *et al.*, 2006.

§§ Leaché & Mulcahy, 2007.

¶¶ Leavitt *et al.*, 2007.

*** Crews & Hedin, 2006.

††† Jezkova *et al.*, 2009.

‡‡‡ Álvarez-Castaneda, 2010.

Lineages with posterior probabilities (Pp) of ≥ 0.95 were considered strongly supported.

To estimate the divergence time of each regional lineage, we used published mutation rates where available (e.g. *Anaxyrus punctatus*, Jaeger *et al.*, 2005; *Chaetodipus penicillatus*, Jezkova *et al.*, 2009). When this was not possible, we chose widely used rates specific to taxon group (1.0×10^{-8} substitutions per site per year for invertebrates, Brower, 1994; 6.6×10^{-9} substitutions per site per year for reptiles, Zamudio & Greene, 1997; 5.0×10^{-8} substitutions per site per year for mammals, Nabholz *et al.*, 2008). When a range of rates were previously reported, we chose the faster rates to be conservative with respect to our hypothesis – slower mutation rates would only increase divergence time estimations leading to older inferred divergence and demographic estimates. To assess whether diversification occurred prior to the Pleistocene (> 2 Ma), we examined the 95% posterior distribution of divergence dates for each species and lineage. If the distribution of dates included 2 Ma or later, then we could reject the pre-Pleistocene divergence hypothesis. Lineage and divergence time estimations for the closely related sister species *Homalonychus selenopoides* and *H. theologus* were combined in a single analysis, because there was limited phylogenetic signal within each species (Crews & Hedin, 2006).

Historical demography

In general, mtDNA gene tree analyses revealed multiple regional lineages within each species (see Results). Therefore, demographic analyses were conducted separately for each recovered lineage to reduce the confounding impacts of subdivision. We performed a series of complementary analyses to characterize the relative magnitude and timing of population size changes. While our estimates of demographic history are limited by single-locus data, both simulation and empirical studies have shown that single-locus coalescent-based estimates contain ample information to detect general trends of demographic change (Drummond *et al.*, 2005; Heled & Drummond, 2008). Furthermore, population size change by lineage was verified with multiple analytical methods. First, we used site mismatch distribution analysis (MDA) in which the observed number of pairwise differences between haplotypes was compared with the distribution under a theoretical model of expansion using DNASP 5.0 (Librado & Rozas, 2009). A multimodal MDA profile signals populations at demographic equilibrium, while a smoother and unimodal MDA signals demographic expansion (Rogers & Harpending, 1992; Ray *et al.*, 2003). We estimated F_S (Fu, 1997) and R_2 (Ramos-Onsins & Rozas, 2002) in each clade and tested for significant departure from demographic stability with 10,000 coalescent simulations. We calculated coalescence time (the start of the population expansion) using the statistic τ with the formula $\tau = 2\mu t$, where t is the number of years since expansion and μ is the per locus per year mutation rate. Finally, we used Bayesian skyline plots

(BSP, Drummond *et al.*, 2005) to examine changes in demography over time. This method considers the coalescent history of gene lineages to characterize change in effective population size (N_e) through time. Plots include credibility intervals of N_e through time, which provide an indication of both phylogenetic and coalescent uncertainty of the mtDNA-based estimate. For each clade, the time axis was scaled using species-specific DNA substitution rates. All coalescent analyses were implemented in BEAST version 1.6.1 (Drummond & Rambaut, 2007) using uniform prior distributions for model parameters and 10 specified coalescent intervals. BSP posterior distributions were estimated by sampling the MCMC every 1000th generation for 20 million generations with the first 10% discarded as burn-in. BSP plots and credible intervals were calculated from posterior probability distributions using TRACER 1.5 (Rambaut & Drummond, 2007).

Creating divergence and diversity landscapes

We mapped genetic divergence between samples and genetic diversity within groups of individuals using the GENETIC LANDSCAPES GIS TOOLBOX (Vandergast *et al.*, 2011) in ARC GIS 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Genetic divergence was calculated as D_A (Nei & Li, 1979), which corrects for multiple samples at a site. For datasets where multiple loci were sequenced, pairwise divergences were averaged across loci after normalization. Using IBDWS 3.16 (Jensen *et al.*, 2005), we tested for relationships between genetic divergence and geographic distance among samples (isolation by distance, IBD) using a Mantel test. Where IBD was significant, divergence landscapes were visualized using the residuals from reduced major axis reduction to remove the effect of geographic distance. Pairwise divergence values or residuals were mapped at the mid-points among collection locations and then calculated as continuous surfaces using inverse distance weighted interpolation (1 km² grid cell size). High values represent regions of high genetic divergence between sampled locations, and low values represent comparatively low levels of genetic divergence (or high genetic similarity) between locations.

Diversity landscapes were created from estimates of genetic diversity within pools of samples. As genetic diversity estimates are more dependent on sample size than divergence estimates, we grouped samples separated by 20 km or less that were not divided by apparent barriers (e.g. mountains, rivers). Remaining singleton sampling locations were excluded. Two species, *Phrynosoma platyrhinos* and *Thomomys bottae*, were excluded from diversity mapping because only singletons were sampled in disparate locations. Genetic diversity was calculated as the average sequence divergence among individuals π_i under the Tamura & Nei (1993) model of nucleotide evolution. For each species, genetic diversity estimates were mapped at the mid-points of combined collection locations and interpolated in the same manner as the divergence layer.

To highlight spatial congruence among species, genetic divergence and diversity landscapes were averaged across

species. We rescaled individual landscapes by dividing each cell value by the maximum, so that each species received equal weighting in the average landscapes. We defined diversity and divergence ‘hotspots’ as regions with average diversity and divergence values > 1.5 standard deviations from the mean (Vandergast *et al.*, 2008). We calculated the coefficient of variation among individual species landscapes to assess concordance in combined divergence and diversity landscapes, and visually examined all single-species landscapes to determine which species contributed to each hotspot.

Assessing relationship between divergence/diversity and land protection status

We assessed land status with management/ownership maps (i.e. U.S. Bureau of Land Management – BLM) for each state (i.e. California, Arizona, Nevada and Utah). We categorized public land status as: Protected, At Risk and Uncertain in relation to general stewardship mandates for each agency (see Appendix S1 for more detail). For each land status category, we calculated the percent area of average diversity and divergence landscapes and visually assessed the protected status of the hotspot regions.

RESULTS

Phylogenetic trees, divergence landscapes and divergence times

Bayesian inference of phylogenetic trees for each species supported regionally structured lineages (Mojave and Sonoran; posterior probabilities of 0.95–1.0). Genetic divergence maps based on pairwise genetic distances suggested that major lineage breaks occurred across the Colorado River and across the Mojave/Sonoran ecotone. *Crotaphytus bicinctores*, *Lichanura trivirgata* and the two *Homalonychus* species showed greatest genetic divergence across the Colorado River (e.g. Fig. 2A; Fig. S1). For these species, the Colorado River was a barrier between clades distributed in the Mojave Desert and Colorado Desert and clades in the Sonoran Desert east of the Colorado River, although some overlap occurred on either side of the river for *H. theologus* and *L. trivirgata*. Conversely, for *Anaxyrus punctatus*, *Sceloporus magister* and *Xantusia vigilis*, genetic divergence was greatest across the Mojave/Sonoran ecotone (e.g. Fig. 2B; Fig. S1). For *A. punctatus*, greatest divergence was recovered along the eastern portion of the Mojave and Sonoran Desert ecotone, while *S. magister* and *X. vigilis* had greater divergence along the western axis of the ecotone (e.g. Lucerne Valley and surrounding region). Finally *Chaetodipus penicillatus*, *Chionactis occipitalis*, *Crotalus cerastes* and *Thomomys bottae* showed strong divergence across both the Mojave/Sonoran ecotone and the Colorado River (e.g. Fig. 2C; Fig. S1) providing support for further lineage divergence within the Colorado Desert. Three species had no significant spatial phyloge-

graphic structure (*P. platyrhinos*: Fig. S1; *H. selenopoides* and *H. theologus*: data not shown).

The majority of regional lineage divergence times for the 12 species examined significantly predated the Pleistocene (Table 2). Only *A. punctatus*, *C. penicillatus*, *L. trivirgata* and *T. bottae* had divergence estimates within the Pleistocene (≤ 2.0 Ma), while all others were estimated within the late Pliocene or earlier (3.0–15.7 Ma). In contrast, time to most recent common ancestor (tMRCA) estimates within regional lineages primarily fell within the middle to early Pleistocene (0.5–2.5 Ma), but still predated the LGM. Within *C. penicillatus*, however, tMRCA estimates differed by area, with Mojave lineages being consistent with the LGM in their 95% confidence intervals, and all the others substantially predating it.

Demographic summary statistics and expansion plots

Demographic population expansion was supported by multiple methods (F_s , R_2 , MDA, and BSP; Table 3) in seven of twelve species examined. A total of five species (*A. punctatus*, *C. bicinctores*, *H. theologus*, *P. platyrhinos* and *T. bottae*) lacked evidence of population expansion (i.e. no significant values for all statistics), but exhibited high genetic diversity and multimodal MDA plots (including bimodal), suggesting long-term demographic stability.

While MDA profiles varied considerably among the 12 species, indicating broadly variable histories, *C. penicillatus*, *C. occipitalis*, *C. cerastes*, *H. selenopoides* and *S. magister* had regional clade profiles consistent with population expansions (Fig. S2). The most common profile revealed haplotype distributions shifted to the right with non-zero mismatch values (Fig. 3A). Right-shifted profiles are consistent with older demographic expansion histories (e.g. *C. penicillatus* Sonoran, *H. selenopoides*, *S. magister*), indicating that enough time has passed to allow mutations to accumulate since the expansion occurred. In contrast, two MDA profiles exhibited near zero modal mismatch values (*C. penicillatus* northern and western Mojave clades), a distribution consistent with a more recent demographic history, because the majority of individuals possess the same haplotype (Fig. 3B).

After re-scaling τ from species mutation rates, we estimated the start of population expansions across regional clades within six of the 12 species where unimodal MDA distributions and significant departures from stability were inferred (F_s and R_2 ; Table 3). These estimates varied from a low of 58.6 ka (thousand years ago) in *C. occipitalis* (east Sonoran clade) to a high of 323 ka in *S. magister* (Sonoran clade). Overall population expansion times predated the LGM with most estimates between 90 and 200 ka. These dates provide further support for older temporal dynamics as opposed to a single expansion event at the end of the LGM. BSPs were generally consistent with results from the MDA analyses (Table 3; Fig. S3). Only four species (six regional lineages) possessed BSPs indicating population expansions occurring at or after 20 ka, consistent with the LGM: Mojave lineages in *C. occipi-*

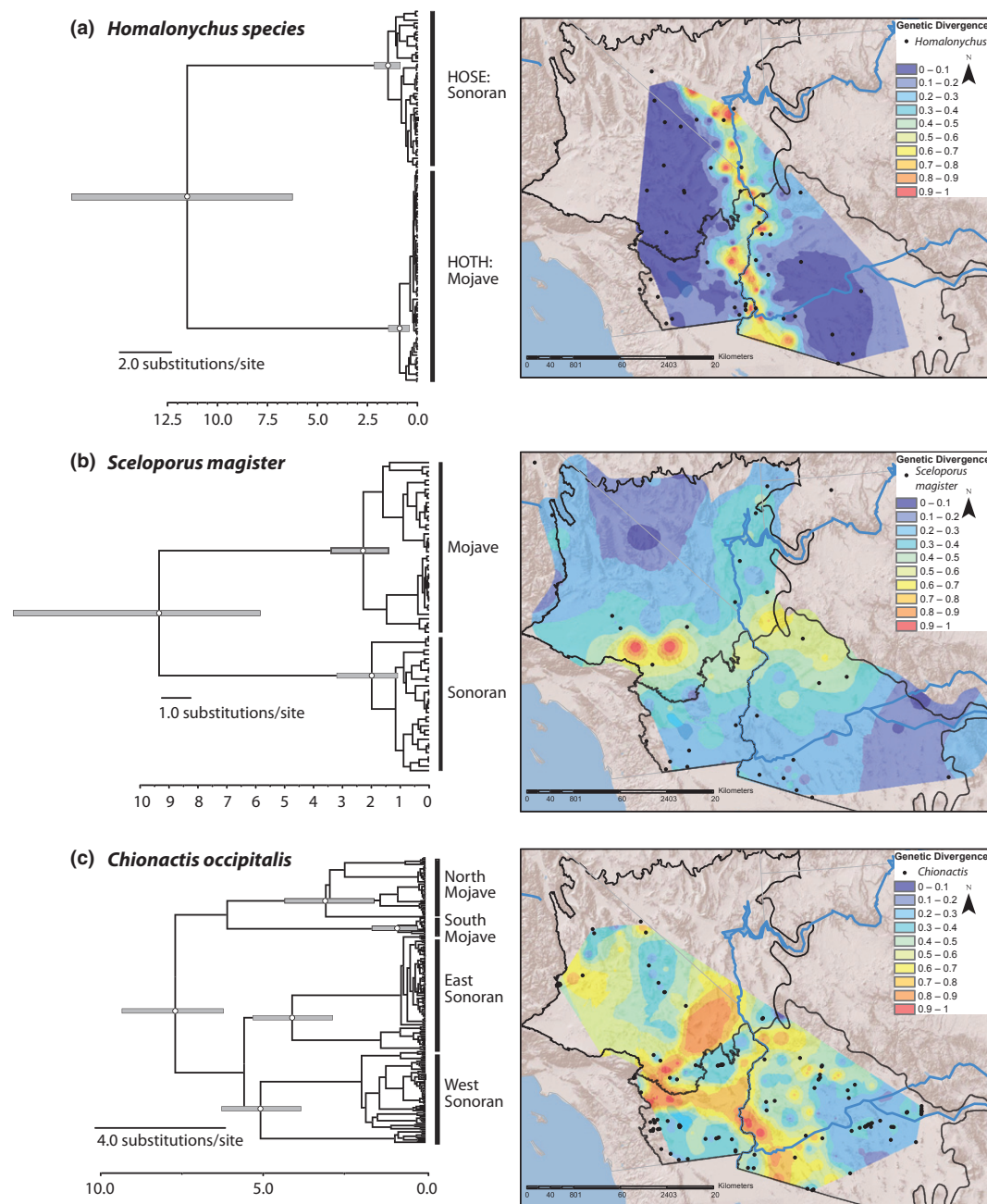


Figure 2 Examples of phylogenetic trees and genetic divergence landscapes highlighting three different spatial patterns of divergence found among species: (a) *Homalonychus* is representative of taxa with strongest divergence coincident with the Colorado River, HOSE = *H. selenopoides* and HOTH = *H. theologus*; (b) *Sceloporus magister* is representative of species with strong divergence along the Mojave/Sonoran ecotone and (c) *Chionactis occipitalis* is representative of species with strong divergence at the ecotone boundary and across the Colorado River.

talis, *S. magister*, and *X. vigilis*, and Sonoran lineages in *A. punctatus* and *C. occipitalis*. For the remainder of the regional lineages, evidence of either older episodes of population growth (pre-LGM) or demographic stability was revealed.

Genetic divergence and diversity hotspots

Average genetic divergence was highest at the Mojave and Sonoran Desert ecotone and the Colorado River, concordant

with inferred tree topologies (Fig. 4). Hotspots of genetic divergence were located in three main regions: (A) Lucerne Valley, (B) the Colorado Desert and (C) the Colorado River. Concurrence in divergence patterns was greatest at the Colorado River hotspot, where 10 of 12 species showed high divergence (Table 1). Five of seven species with samples across the Lucerne Valley were highly divergent, while only three of the 10 across the Colorado Desert showed high divergence (Table 1). Average divergence was lowest in the

Table 2 Divergence age estimates, 95% highest posterior densities (HPD) and time period of lineage divergence

Species/Clades	Age (Ma)	95% CI	pre-Pleistocene divergence	Time period
Herpetofauna				
<i>Anaxyrus punctatus</i>				
Mojave vs. Sonora	0.956	0.479–1.568	N	Late Pleistocene
Mojave	0.448	0.155–0.789		
Sonora	0.542	0.231–0.884		
<i>Chionactis occipitalis</i>				
Mojave vs. Sonora	7.706	6.251–9.371	Y	Miocene
Mojave: North	2.950	2.140–3.820		
South	1.380	0.812–2.010		
Sonora: West	1.971	1.490–2.480		
East	0.682	0.407–0.992		
<i>Crotaphytus bicinctores</i>				
Mojave vs. Sonora	15.731	12.099–19.756	Y	Miocene
Mojave: North	2.234	1.582–2.909		
South	3.063	2.455–3.665		
Sonora	4.735	3.477–6.004		
<i>Crotalus cerastes</i>				
Mojave vs. Sonora	3.280	2.29–4.27	Y	Pliocene
Mojave: North	1.185	0.661–1.758		
South	0.675	0.342–1.052		
Sonora: West	0.785	0.389–1.218		
East	0.386	0.178–0.622		
<i>Lichanura trivirgata</i>				
Mojave vs. Sonora	2.376	1.580–3.284	N	Early Pleistocene
Mojave (CA)	0.432	0.217–0.671		
Sonora (AZ)	0.873	0.4371–1.354		
<i>Sceloporus magister</i>				
Mojave vs. Sonora	9.717	5.844–14.390	Y	Miocene
Mojave	2.370	1.410–3.390		
Sonora	2.060	1.089–3.190		
<i>Xantusia vigilis</i>				
Mojave vs. Sonora	3.028	2.322–3.766	Y	Late Pliocene
Mojave: West	2.510	1.970–3.060		
East	2.189	1.631–2.772		
Sonora	2.220	1.720–2.770		
Invertebrates				
HOTH vs. HOSE: Mojave vs. Sonora	11.519	6.2508–17.298	Y	Miocene
<i>Homalonychus theologus</i>				
Mojave	0.890	0.395–1.447		
<i>Homalonychus selenopoides</i>				
Sonora	1.468	0.855–2.168		
Mammals				
<i>Chaetodipus penicillatus</i>				
Mojave vs. Sonora	0.536	0.274–0.872	N	Late Pleistocene
Mojave: North	0.076	0.033–0.127		
West	0.035	0.001–0.067		
South	0.115	0.048–0.194		
Sonora: North	0.149	0.089–0.219		
South	0.152	0.088–0.223		
<i>Thomomys bottae</i>				
Mojave vs. Sonora	2.258	1.541–2.957	N	Early Pleistocene
Mojave	0.704	0.427–1.02		
Sonora	0.994	0.669–1.342		

northern Mojave and south-eastern Sonoran Deserts, consistent with recent range expansions into these regions. Variation among divergence landscapes, however, was highest in

the northern Mojave and south-eastern Sonoran (Fig. 4 insert), indicating that not all species have high genetic similarity across these regions.

Table 3 MtDNA sample size (*n*), nucleotide diversity (π), haplotype diversity (*h*), Fu's F_S statistic, Ramos-Osins and Roza's R_2 statistic, mismatch distribution analysis profile shape (MDA), Bayesian Skyline plot results (BSP) of expansion (e) or constant demographic history (c), and values of τ estimated from a sudden expansion model

Species/Clades	<i>n</i>	π	<i>h</i>	F_S	R_2	MDA	BSP	τ	Expansion time
Herpetofauna									
<i>Anaxyrus punctatus</i>									
Mojave	48	0.005	0.795	−0.342	0.082	Bi-	c	—	
Sonora	43	0.003	0.636	−0.610	0.089	Bi-	e	—	
<i>Chionactis occipitalis</i>									
Mojave: North	38	0.021	0.892	6.370	0.175	Multi-	c	—	
South	16	0.007	0.992	−7.332	0.129	Multi-	e	—	
Sonora: West	50	0.016	0.972	−12.430	0.086	Multi-	e	—	
East	57	0.003	0.914	−26.730	0.035	Uni-	e	0.845	58,681
<i>Crotaphytus bicinctores</i>									
Mojave: North	8	0.022	1.000	−0.071	0.165	Multi-	c	—	
South	22	0.026	0.983	−0.750	0.105	Multi-	c	—	
Sonora	22	0.023	0.983	0.080	0.134	Multi-	c	—	
<i>Crotalus cerastes</i>									
Mojave: North	21	0.005	0.938	−6.782	0.087	Uni-	e	1.270	97,243
South	19	0.004	0.906	−3.995	0.093	Uni-	e	—	
Sonora: West	18	0.003	0.876	−3.076	0.102	Uni-	c	1.174	89,838
East	20	0.003	0.958	−9.730	0.081	Uni-	c	2.563	196,128
<i>Lichanura trivirgata</i>									
Mojave	24	0.004	0.830	−0.135	0.121	Uni-	c	3.415	234,129
Sonora	19	0.013	0.912	2.418	0.168	Multi	c	—	
<i>Phrynosoma platyrhinos</i>									
	17	0.030	0.985	−1.369	0.115	Multi-	e	—	
<i>Sceloporus magister</i>									
Mojave	39	0.016	0.943	−7.990	0.137	Multi-	e	—	
Sonora	31	0.013	0.983	−8.425	0.080	Uni-	e	6.842	322,748
<i>Xantusia vigilis</i>									
Mojave: West	50	0.018	1.000	−36.870	0.083	Multi-	e	—	
East	50	0.016	1.000	−39.030	0.077	Multi-	e	—	
Sonora	10	0.009	1.000	−3.269	0.155	Bi-	e	—	
Invertebrates									
<i>Homalonychus theologus</i>									
Mojave	73	0.005	0.724	−2.916	0.069	Multi-	c	—	
<i>Homalonychus selenopoides</i>									
Sonora	54	0.015	0.968	−9.457	0.072	Uni-	c	2.552	227,451
Mammals									
<i>Chaetodipus penicillatus</i>									
Mojave: North	51	0.002	0.809	−1.151	0.080	Uni-	e	—	
West	15	0.001	0.714	−0.154	0.179	Uni-	c	—	
South	26	0.003	0.942	−7.637	0.058	Uni-	c	2.121	77,223
Sonora: North	95	0.006	0.978	−54.573	0.044	Uni-	e	4.737	172,468
South	34	0.006	0.996	−32.516	0.067	Uni-	e	5.998	218,380
<i>Thomomys bottae</i>									
Mojave	8	0.031	1.000	−1.603	0.144	Multi-	c	—	
Sonora	11	0.053	1.000	−2.626	0.138	Multi-	c	—	

Statistical significance for F_S and R_2 was estimated using 10,000 replicates; bolded values indicate $P \leq 0.05$. The online spreadsheet tool of Schenekar & Weiss (2011) was used for all mismatch calculations.

Diversity hotspots were indicated in three main geographic regions: (A) the Coachella Valley, (B) along the southern Colorado and Gila Rivers and (C) along the eastern Mojave/Sonoran Desert ecotone (Fig. 5). Concordance among species was greatest in the Coachella Valley hotspot, with five of eight species sampled there containing high diversity (Table 1). Three of seven species present showed high

diversity across the southern Colorado and Gila Rivers, while only two of the six species present showed high diversity in the Mojave/Sonoran Desert ecotone (Table 1). Variation among diversity landscapes was lowest in the vicinity of the diversity hotspots, and highest in the northeast Mojave Desert (surrounding Lake Mead), in the southern Sonoran Desert and across Lucerne Valley (Fig. 5 insert).

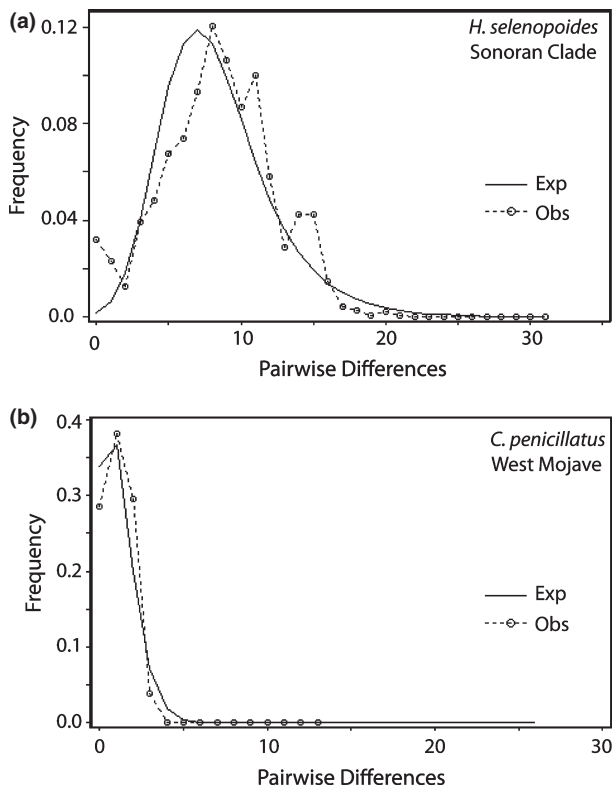


Figure 3 Examples of mismatch distribution (MDA) profiles (observed values shown with open circles; expected values shown with a solid line) that revealed relatively different temporal demographic expansion patterns: (a) older vs. (b) more recent demographic expansion history.

Approximately 32% of the area analysed was categorized as protected, 63% was categorized as at risk, and 5% was of uncertain status. At least some proportion of each of the identified divergence and diversity hotspots was categorized as protected. For divergence hotspots, gaps in protection occur in the southern portion of hotspot A, the northern portion of hotspot B and along the central portion of hotspot C where protected lands rarely encompass both sides of the lower Colorado River (Fig. 4). For diversity hotspots, more than half of diversity hotspot A was categorized as protected, while some portions of diversity hotspot B and large portions of hotspot C fell outside of protected lands (Fig. 5).

DISCUSSION

Previous comparative phylogeographic studies of the North American Deserts have focused on deep divergences between the eastern (Chihuahuan Desert) and western (Mojave + Sonoran) deserts and across central Baja California (Riddle *et al.*, 2000; Riddle & Hafner, 2006; Hafner & Riddle, 2011). Our analyses of lineage divergence indicate broad spatial divisions also exist across the Mojave and Sonoran deserts. Species can be categorized into three groups: (1)

those with lineage breaks across the Colorado River; (2) those with breaks along the Mojave and Sonoran Desert ecotone and (3) those with breaks at both. For all patterns, we found support for relatively ancient diversification of desert biota. Most lineage divergence estimates recovered were late Pliocene or older, with only three species having estimates only within the Pleistocene, suggesting stronger correspondence with pre-Pleistocene vicariance than Pleistocene climate fluctuation hypotheses. Additionally, most of the population expansion estimates significantly predated the LGM – a time when paleoenvironmental studies indicate that major range changes occurred (Spaulding, 1985; Van Devender, 1990). Most species had signatures of population expansion beginning between 100 and 200 ka. These estimates are congruent with Smith *et al.* (2011), which described similar demographic and phylogeographic patterns in Joshua trees (*Yucca brevifolia*) and their associated yucca moths (*Tegeticula* spp.). Although multiple events, both old and recent, have likely shaped the distribution and genetic diversity of desert biota, these results provide further evidence that population expansion in the deserts began long before the intense climate change at the end of the last pluvial period.

For lineages with divergence centered along the Colorado River, inundations of the Gulf of California and subsequent persistence of the Colorado River likely limited (and in some species prevented) dispersal between Sonoran and Mojave Desert biota. Several studies conclude that the influence of this barrier on gene flow was sufficient to cause vicariant speciation (e.g. spiders, Crews & Hedin, 2006; desert tortoise, Murphy *et al.*, 2011). While the Colorado River remains a barrier to gene flow for many species, this region may also represent a suture zone (area of re-contact between divergent lineages) for others. We recovered instances where lineages extended slightly on both sides of the Colorado River (e.g. *C. penicillatus*, *L. trivirgata*, *P. platyrhinos* and *T. botatae*), particularly along the southern portion of the river. This pattern has been observed in other studies (e.g. desert tortoise, McLuckie *et al.*, 1999; fringe-toed lizards, Trépanier & Murphy, 2001; flat-tailed horned lizards, Mulcahy *et al.*, 2006) where transfer across the Colorado River was evident among otherwise genetically differentiated groups of populations. Periodic avulsions during the Pleistocene shifted the flow of the Colorado River (Stokes *et al.*, 1997) and may account for the transfer of biotic components on opposite sides of the river, especially for species with weak dispersal capacities (McLuckie *et al.*, 1999; Wood *et al.*, 2008b). Accordingly, Colorado Desert biotas appear to be conglomerates of Sonoran and Mojave lineages where secondary contact is evident in the southern region of the Colorado Desert and in the north along the Coachella Valley. For species exhibiting lineage divergence along the Mojave and Sonoran Desert ecotone, it is more difficult to implicate the Colorado River as an isolating barrier, because most Sonoran lineages broadly transcend the Colorado River. Instead, earlier events (Late Miocene-Early Pliocene) associated with marine exten-

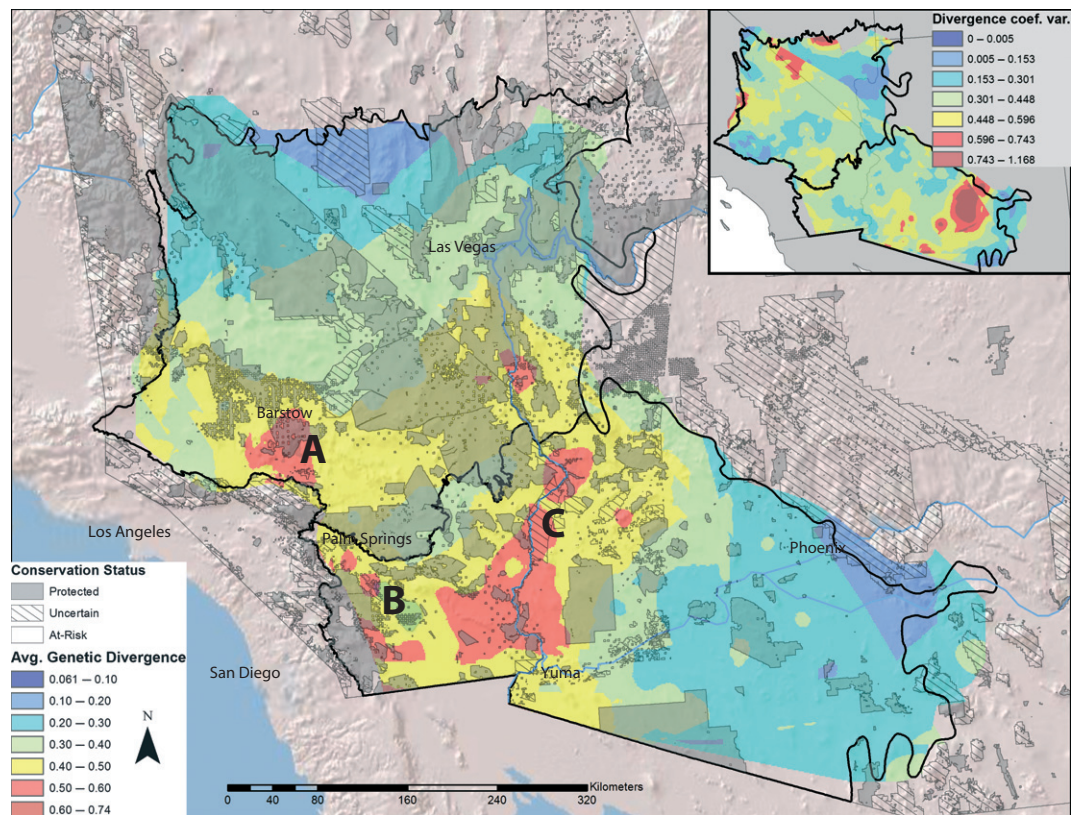


Figure 4 Average genetic divergence of 12 species overlaid with protected status. The three areas of relatively high genetic divergence (> 1.5 standard deviations from the mean value) are shown in red and denoted as (a) Lucerne Valley, (b) throughout the Colorado Desert and (c) along the Colorado River. The coefficient of variation among species landscapes is shown in the inset.

sions of the Gulf of California are more consistent with the older divergence estimates for these lineages. In addition to embayments, steep environmental gradients existing along the Sonoran/Mojave ecotone may maintain genetic structure. Previous analyses of *Chionactis occipitalis* found that the strongest environmental predictors of genetic divergence were elevation, temperature and desert assignment (Wood *et al.*, 2008a). The Mojave and Sonoran ecoregions are defined by a combination of temperature, precipitation, vegetation and terrain features (Bailey, 1995; McNab *et al.* 2005), and the Mojave Desert is generally higher in elevation than the Sonoran. Consequently, regional Mojave and Sonoran Desert lineages may not only be divergent at the molecular level in neutral loci but may also be locally adapted to specific Mojave and Sonoran environmental conditions (Wood *et al.*, 2008a; Wilson *et al.*, 2011).

Preserving evolutionary potential in a changing environment

Levels of lineage divergence, regional diversity of gene pools and concordance in diversity and divergence hotspots for an array of desert animals should inform biological conservation strategies and land management across the desert southwest. For instance, genetic divergence across the Colorado River

and the Mojave and Sonoran ecotone within multiple distantly related species indicates that biota in the Mojave and Sonoran Deserts should be treated separately for conservation. Protection of major historical lineages in each of these desert regions may be important for long-term conservation (Avice, 1992; Moritz & Faith, 1998; Moritz, 2002). Consequent to the extinction of historically divergent lineages is the loss of genetic diversity that can only be replaced with the accumulation of mutations over evolutionary time scales, greatly exceeding what can be recovered through habitat restoration and population re-establishment (Moritz, 2002).

Regions of lineage re-contact (Stebbins & Major, 1965; Remington, 1968) that occur across the Mojave and Sonoran ecotone and the Colorado River are also of particular conservation importance. Gene flow between previously isolated and divergent lineages can create novel gene combinations that facilitate speciation and adaptive evolution (Barton *et al.*, 1983; Barton & Hewitt, 1985; Turgeon *et al.*, 1999; Ebert *et al.*, 2002; Tallmon *et al.*, 2004; Lavergne & Molofsky, 2007), and protection of such diversity may be best achieved by maintaining viable populations across heterogeneous environments (Crandall *et al.*, 2000; Moritz, 2002). The Colorado Desert contains a mixture of both Sonoran and Mojave lineages/species and bridges these two regions (Riddle & Haf-

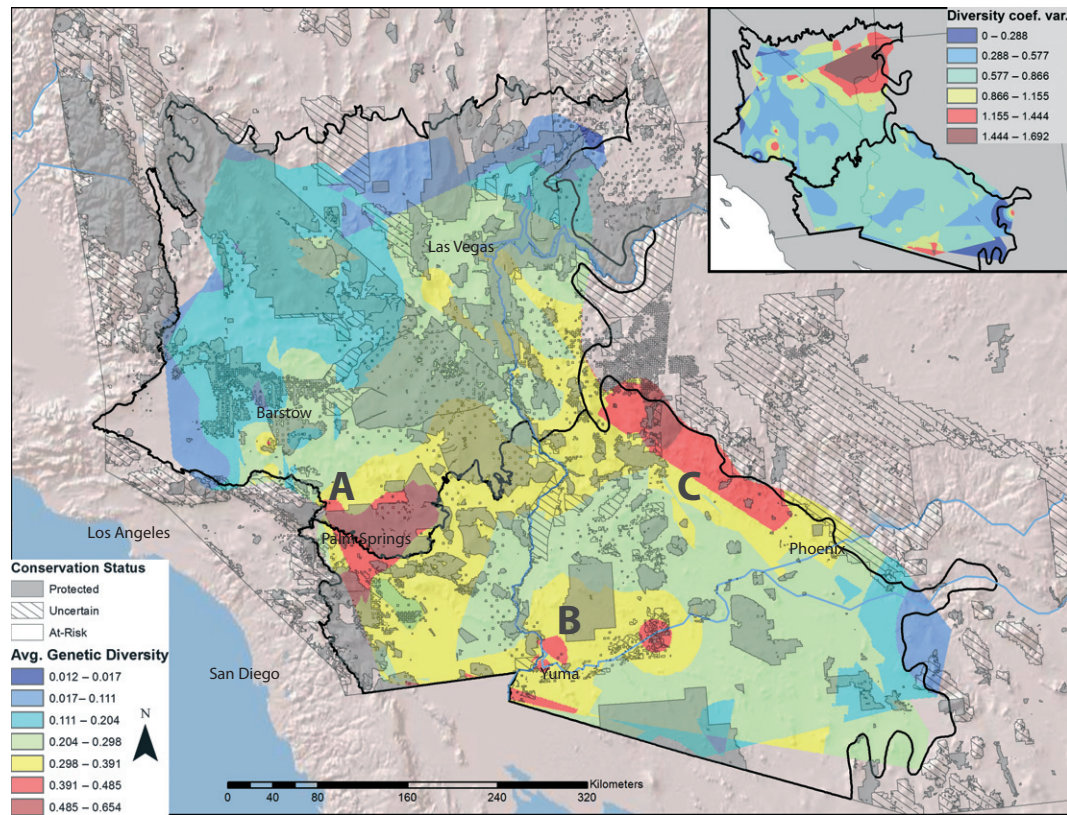


Figure 5 Average genetic diversity of 10 species overlaid with protected status. The three areas of relatively high genetic diversity (> 1.5 standard deviations from the mean) are shown in red and denoted as (a) the Coachella Valley, (b) along the southern Colorado and Gila Rivers and (c) along the Hualapai, Aquarius and Weaver Mountains at the eastern Mojave/Sonoran ecotone. The coefficient of variation among species landscapes is shown in the inset.

ner, 2006). Zones of apparent lineage re-contact (high divergence) and high diversity within lineages occur here in multiple species, particularly through the Coachella Valley and along the Colorado River. Protection of populations and habitat corridors through these regions as well as throughout ‘core’ Mojave and Sonoran Desert habitats may facilitate natural processes of range expansion and contraction, providing opportunity for both migration and *in situ* adaptation in response to changing environmental conditions (Heller & Zavaleta, 2009; Game *et al.*, 2011).

Generally, protected lands are more extensive and well-connected throughout the Mojave than in the Sonoran ecoregion (e.g. Death Valley and Joshua Tree National Parks, Lake Mead National Recreation Area, BLM wilderness lands; Fig. 4). Despite the existence of extensively protected areas in the Mojave, most identified evolutionary hotspots fell outside of their auspices. Additionally, four of the six genetic divergence and diversity hotspots overlap with major areas of human development: divergence hotspot A overlaps with Victorville and Barstow, California; diversity hotspot A and portions of divergence hotspot B overlap with Palm Springs and 29 Palms, California; and diversity hotspot B overlaps with Yuma, Arizona. The eastern Mojave and Sonoran Desert ecotone (diversity hotspot

C) is still relatively free of development, and land management plans could prioritize conservation here. Resource management planning efforts should take into account connectivity within and among hotspots whenever possible. This focus might be particularly relevant between the Hualapai-Weaver Mountains and Yuma, Arizona due to the large amount of protected area already available in the intervening areas.

This work provides GIS-based maps of genetic information that could be valuable for use in regional conservation planning initiatives such as the U.S. Department of the Interior – Bureau of Land Management Landscape Approach to Managing Public Lands (Abby, 2012), the Landscape Conservation Cooperatives (Salazar, 2009) and the Desert Renewable Energy Conservation Plan (Spencer *et al.*, 2010). These science-based initiatives, among others, are ongoing and may readily incorporate the information presented here. Ultimately, the best strategy for conservation of historical and adaptive diversity in the Mojave and Sonoran Deserts would entail strategically selecting areas for protection on the basis of genetic and ecological information for many species and ensuring connectedness across environmental gradients and variable habitats that may be under different selection regimes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 GIS sources and compilation of Land Protection Status.

Figure S1 Phylogenetic trees and genetic divergence landscapes.

Figure S2 Mismatch distribution plots for the 12 species examined.

Figure S3 Bayesian skyline plots (BSP) for the 12 species examined.

BIOSKETCH

Our research team seeks to understand the potential impacts of renewable energy development on wildlife habitat, connectivity and genetic diversity in the desert southwest (<http://www.werc.usgs.gov/Project.aspx?ProjectID=227>).

Author contributions: A.G.V., D.A.W., K.E.N., T.C.E. and R.N.F. conceived the ideas, K.R.B. compiled and verified genetic data, R.D.I. and K.E.N. gathered and coded land ownership data, D.A.W. and A.G.V. conducted analyses and led writing, K.E.N., K.R.B., R.N.F., T.C.E. and R.D.I. contributed to data interpretation and writing.

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