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Range and niche shifts in response to past climate change in the desert horned lizard (*Phrynosoma platyrhinos*)

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Abstract

During climate change, species are often assumed to shift their geographic distributions (geographic ranges) in order to track environmental conditions – niches – to which they are adapted. Recent work, however, suggests that the niches do not always remain conserved during climate change but shift instead, allowing populations to persist in place or expand into new areas. We assessed the extent of range and niche shifts in response to the warming climate after the Last Glacial Maximum (LGM) in the desert horned lizard (*Phrynosoma platyrhinos*), a species occupying the western deserts of North America. We used a phylogeographic approach with mitochondrial DNA sequences to approximate the species range during the LGM by identifying populations that exhibit a genetic signal of population stability versus those that exhibit a signal of a recent (likely post-LGM) geographic expansion. We then compared the climatic niche that the species occupies today with the niche it occupied during the LGM using two models of simulated LGM climate. The genetic analyses indicated that *P. platyrhinos* persisted within the southern Mojave and Sonoran deserts throughout the latest glacial period and expanded from these deserts northwards, into the western and eastern Great Basin, after the LGM. The climatic niche comparisons revealed that *P. platyrhinos* expanded its climatic niche after the LGM towards novel, warmer and drier climates that allowed it to persist within the southern deserts. Simultaneously, the species shifted its climatic niche towards greater temperature and precipitation fluctuations after the LGM. We concluded that climatic changes at the end of the LGM promoted both range

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Supplementary Material Legends

Appendix S1. Descriptions of sampling sites for *Phrynosoma platyrhinos* species complex.

Appendix S2. Phylogenetic analyses of *Phrynosoma platyrhinos* species complex.

Appendix S3. Ecological niche modeling of *Phrynosoma Platyrhinos* species complex.

and niche shifts in this lizard. The mechanism that allowed the species to shift its niche remains unknown, but phenotypic plasticity likely contributes to the species ability to adjust to climate change.

Keywords

niche assessment; Great Basin; Last Glacial Maximum; niche shift; non-analog climate; range expansion

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Introduction

The escalating awareness of global climate change has focused attention on modeling species responses to past and predicted future climatic changes (Coetzee et al. 2009, Galbreath et al. 2009, Peterson et al. 2004, Sinervo et al. 2010, Thuiller et al. 2008). A general assumption underlying many of these models has been that the climatic niche of a species (that is the climate conditions under which a species can survive and reproduce) remains relatively stable through time; thus, as climate changes, a species' geographic range shifts to track suitable climatic conditions (Davis and Shaw 2001, Pearman et al. 2007, Wiens and Graham 2005). Accordingly, models often suggest extensive shifts and contractions of species' ranges in response to climate change (Galbreath et al. 2009, Hornsby and Matocq 2012, Jezkova et al. 2009). Increasing evidence, however, shows that niches of some species shift over even relatively short time scales, allowing species to persist within large portions of their ranges despite a climate change (Jezkova et al. 2011) or to expand into new areas as climate change opens novel niches (Guisan et al. 2014, Veloz et al. 2012). Thus, niche shifts should not be ignored when modeling species responses to environmental change (Ackerly 2003b, Guisan et al. 2014, Hill et al. 2013, Petersen 2013, Veloz et al. 2012).

A niche shift can result from a change in the fundamental niche of a species (the full spectrum of environmental factors that can be potentially utilized by an organism) or as a result of a change in the realized niche (a subset of the fundamental niche actually used by the organism, restricted by historical and biotic factors; Araújo and Guisan 2006, Pearman et al. 2007). Niche shifts resulting from an alteration of the realized niche do not require evolutionary adaptation (Jackson and Overpeck 2000, Jezkova et al. 2011, Rodder and Lotters 2009). Shifts in the realized niche may result from non-analogous climates between time periods (Rodder and Lotters 2009, Veloz et al. 2012), plasticity of traits (e.g., morphological, physiological, or behavioral) or through genotype sorting (spatial segregation of individuals with certain functional traits; Ackerly 2003a, Ackerly 2003b, Eiserhardt et al. 2013). Alternatively, the fundamental niche of a species may be shifted or become broadened to meet new environmental conditions through evolutionary (i.e., genetic) adaptation (Davis and Shaw 2001, Davis et al. 2005, Urban et al. 2007). A shift of the fundamental niche (evolutionary adaptation) can be difficult to distinguish from a shift in the realized niche as both can arise from the same underlying processes (e.g. climate change) and may even accompany each other (Csuti 1979, Jezkova et al. 2011).

Niche shifts can be triggered by changes in biotic interactions, such as ecological release from predators or competitors (Holt et al. 2005), or by access to novel combinations of abiotic environmental variables (Ackerly 2003b, Hill et al. 2013, Hill et al. 2012, Jackson and Overpeck 2000, Nogues-Bravo 2009, Rodder and Lotters 2009). Invasive species under such conditions often undergo niche shifts (Broennimann et al. 2007, Rodder and Lotters 2009, Urban et al. 2007). Populations of native species have also been shown to undergo niche shifts in response to climatic changes (Davis and Shaw 2001, Davis et al. 2005). Novel environmental conditions with no known historical analog are often formed during climate change, creating a spectrum of new conditions for populations capable of exploiting the new environment by shifting realized or fundamental niches. Environmental changes resulting from glacial-interglacial climatic oscillations throughout the Late Pleistocene are known to have had pronounced impacts on species ranges and genetic structure (Hewitt 1996, Hewitt 2000); however, relatively little is known as to the extent these climatic changes promoted niche shifts.

In this study, we assess the extent of range and niche shifts in the desert horned lizard (*Phrynosoma platyrhinos* species complex) in response to climatic changes at the end of the Last Glacial Maximum (LGM; ca. 21,000 years ago; Harrison 2000), which expanded arid environments within the western deserts of North America. We assess the phylogeographic structure of this species complex to evaluate the extent of population persistence within regions throughout the LGM and the extent of range expansions in response to warming climate after the LGM. We follow up on two previous studies of the species complex in which recent northward range expansion into the Great Basin was indicated from the more southern Mojave and Sonoran deserts (Jones 1995, Mulcahy et al. 2006). We then conduct climatic niche analyses based on temperature and precipitation variables to compare the climatic niche occupied by the species today with the niche it occupied during the LGM. We assess the directionality and extent of climatic niche shifts (Broennimann et al. 2007, Kozak and Wiens 2006, Warren et al. 2008), discuss possible mechanisms that facilitate niche shifts, and assess the biological consequences these shift might have had on populations and the species. We also assess whether the niche shift between LGM and current time was largely caused by the existence of non-analog climates between the two time periods (also called background environmental divergence; McCormack et al. 2010), or whether the niches shifted (at least partially) beyond what would be expected under background environmental divergence alone.

Materials and Methods

Study organism

Phrynosoma platyrhinos is part of a species complex with taxa currently distributed from the northwestern Sonoran Desert through the Mojave and Great Basin deserts (Fig. 1). Based on mitochondrial (mtDNA) sequence data and morphology, Mulcahy et al. (2006) found that southeastern populations of *P. platyrhinos* south of the Gila River represented a distinct lineage, which they referred to as *P. goodei*. Mulcahy et al. (2006) also identified another divergent population of *P. platyrhinos* from the Yuma Proving Ground (La Paz County, Arizona) along the east side of the Lower Colorado River Valley, but this lineage was not

assigned any particular taxonomic status. Herein, we use the name *P. platyrhinos* to refer to the group that includes *P. platyrhinos sensu stricto*, populations from Yuma Proving Ground, and *P. goodei*.

Taxon sampling

We acquired sequences or samples from 216 individuals of our target taxa from 104 localities (Fig. 1; Appendix S1, Supporting Information). Sequences representing 30 samples were acquired from GenBank (Mulcahy et al. 2006), 19 samples came from museums, and 70 samples were accessed from a study of Jones (1995). The remaining samples were obtained from specimens specifically captured for this study. In the field, we collected small samples of tail or toe and then released the animals at the capture site (following a protocol approved by the Animal Care and Use Committee, University of Nevada, Las Vegas).

Laboratory methods

We isolated total genomic DNA from tissues following a phenol-chloroform protocol or using a DNeasy Extraction Kit (Qiagen Inc.). We amplified and sequenced the mitochondrial NADH dehydrogenase subunit 4 (ND4) gene and adjacent tRNAs for all samples using primers ND4 and Leu (Arévalo et al. 1994). We also amplified and sequenced a portion of the Cytochrome B (cytB) gene using primers MVZ 49 and MVZ 14 (Roe et al. 1985) for a subset of samples used in phylogenetic analyses (see Appendix S2, Supporting Information). We updated amplification protocols through time, but most were accomplished at a 55°C annealing temperature using Takara Ex Taq Polymerase Premix (Takara Mirus Bio, Inc.) followed by purification using ExoSap-IT (USB Corp.). We conducted bi-directional cycle sequencing using fluorescence-based chemistry (BigDye Terminator v. 3.1 Cycle Sequencing Kit) with electrophoresis and visualization on an ABI Prism 3130 automated sequencer (Applied Biosystems, Inc.). We aligned sequences using Sequencher (v. 4.6; Gene Codes Corp.) and verified the alignments visually. Sequences are deposited in GenBank (KP776188 - KP776403).

Genetic analyses

We conducted Bayesian inference (BI) analysis using unique haplotypes from a concatenated dataset of 684 base pairs (bp) of ND4, and 128 bp of adjacent tRNAs (812 bp total). We also conducted BI and Maximum likelihood (ML) analyses on a combined dataset of 1089 bp of cytB, and 812 bp of ND4 and tRNAs. For this latter analysis, we used a subset of 27 samples representing all but one of the major clades of *P. platyrhinos* identified from ND4 and tRNA sequences. A sample of *P. mcallii* was included as an outgroup (see Appendix S2, Supporting Information for Methods and Results on the phylogenetic analyses).

We constructed a median-joining network (a maximum parsimony approach) using the concatenated ND4 and tRNA sequences in the program Network (v. 4.5.1.0; Bandelt et al. 1999) to visualize phylogeographic structure within *P. platyrhinos*. To construct the final network, we weighted transversions twice as high as transitions and employed the MP option (Polzin and Daneshmand 2003) to remove excessive links from the network.

We analyzed past demographic changes for *P. platyrhinos* from the concatenated ND4 and tRNA data using the Bayesian skyline plot (BSP) coalescent model (Drummond et al. 2005) implemented in the program Beast (v. 1.7; Drummond and Rambaut 2007). We employed the Bayes factor test (Newton and Raftery 1994, Suchard et al. 2001) implemented in Tracer (v. 1.5; Rambaut and Drummond 2007) to assess partitioning and chose to partition by genes and codon positions. Following assessment in MrModeltest, we selected substitution models GTR+I+ Γ for the 1st+2nd codon positions of ND4, GTR+ Γ for the 3rd codon position of ND4, and HKY+I for the tRNA. We used a strict molecular clock after assessing for clock-like behavior (Drummond et al. 2007), a general mtDNA substitution rate of 1% /lineage/ million years (Macey et al. 1999), 5 skyline groups, and a 2-year generation time (Pianka and Parker 1975). We conducted several independent Markov Chain Monte Carlo (MCMC) runs of 80 million generations, each with sampling every 8000 generations and a burn-in of 10%. For final analysis, four MCMC runs (all with similar results) were combined using Logcombiner (distributed with Beast). We checked convergence (effective sample sizes > 200) and visualized the median and 95% highest posterior density intervals using Tracer.

We assessed landscape patterns of genetic differentiation among populations of *P. platyrhinos* in order to identify areas of recent population expansion and distinguish these from areas where the species persisted throughout the LGM. Genetic differentiation among populations was represented by average pairwise genetic distances between sequences from neighboring sampling sites calculated in ALLELES IN SPACE v. 1.0 (Miller 2005). Residual values of pairwise genetic distances (derived from the linear regression of genetic versus geographical distance) were assigned to mid-points between sampling sites using the Delaunay triangulation-based connectivity network, imported into ARCGIS v. 9.2 (ESRI), and interpolated across uniformly-spaced 2.5 minute grids. We used the inverse distance weighted interpolation procedure (Watson and Philip 1985) in the Spatial Analyst extension and masked the interpolations to ecological niche models for current climatic conditions (see Appendix S3, Supporting Information, for the ecological niche modeling methodology).

Climatic niche assessments

We evaluated the extent of the climatic niche shift in *P. platyrhinos* between LGM and present time using multivariate methods (Kozak and Wiens 2006, McCormack et al. 2010). We first assigned each sampling locality to either a persistent or to an expanded group based on genetic patterns. We identified localities where our samples exhibited a genetic signal of a range expansion, that is, star-shaped haplotype structure across localities and low genetic distances among localities (See Results). The localities that exhibited high genetic differentiation from adjacent localities were assigned to the persistent group. From the localities identified as persistent, we removed 3 localities above 5,000 feet (Fig. 1), because we believe that *P. platyrhinos* did not occur at such elevations during the LGM. *Phrynosoma platyrhinos* currently appears to occur in low densities in upper elevations, and the elevation of 5,000 feet is approximately the upper limit for many Mojave and Sonoran warm desert taxa, such as creosote bush, *Larrea tridentata* (Hunter et al. 2001). We acknowledge that the 5,000 feet cutoff is quite conservative and that the upper elevational limit of *P. platyrhinos* in the southern deserts was likely lower during the LGM but we have no data to support a lower threshold selection.

The localities we identified as persistent were used to reconstruct the LGM niche, while all records were used to assess the current niche. From the occurrence records representing the current niche, we extracted values from 19 bioclimatic variables (Table S2; Kozak and Wiens 2006, Waltari et al. 2007) derived from the WorldClim dataset (v. 1.4) with resolution of 2.5 minutes (Hijmans et al. 2005). From the localities representing the LGM occurrence records (that is, from the persistent localities), we extracted the same bioclimatic variables derived from the coupled ocean-atmosphere simulations of the LGM climate (Harrison 2000) available through the Paleoclimatic Modeling Intercomparison Project (PMIP; Braconnot et al. 2007). PMIP has established a protocol followed by participating modeling groups for LGM simulations regarding concentration of greenhouse gases, ice sheet coverage, insolation, or change in topography caused by lowering sea levels. We used two models of the LGM climate: Community Climate System Model (CCSM v. 3; Otto-Bliesner et al. 2006) with a resolution of 1°, and the Model for Interdisciplinary Research on Climate (MIROC v. 3.2; Sugiyama et al. 2010) with an original spatial resolution of 1.4° x 0.5° (Braconnot et al. 2007). The original climatic variables used in these models have been downscaled to the spatial resolution of 2.5 minutes (under the assumption of high spatial autocorrelation) and converted to bioclimatic variables (Hijmans et al. 2005, Peterson and Nyari 2008).

We conducted a Principal Component Analysis (PCA) in Systat (v.12; Hilbe 2008) to reduce the bioclimatic variables (Table S2) to principal components (PCs). Factor scores of PCs with eigenvalues >1 were saved. After confirming that PC scores were normally distributed, we ran unbalanced ANOVA based on Type III sums of squares with PCA axis scores as dependent variables and the groups as fixed factors to test for the separation of population groups into different climatic niches. We used Post hoc Tukey tests to compare the least square means of each PC.

We also assessed the niche shift between LGM and current time while taking into consideration background environmental divergence (McCormack et al. 2010), that is, the difference in the climatic niche available to species between LGM and current time. The niche of a species is considered conserved if the mean background divergence between LGM and current climate is larger than the divergence between the LGM and current niches (McCormack et al. 2010). In order to assess the background divergence, we drew current and LGM bioclimatic values from 1000 random background points within the Basin and Range physiographic region (Olson et al. 2001). The variables from these random points, together with the occurrence records, were reduced with PCA as described above. On each PCA axis, we compared the observed difference in mean niche values to the difference in mean background values and assessed significance with 1000 jackknife replicates of the mean background values (McCormack et al. 2010).

Results

Assessing the range shift between LGM and present time using genetic analyses

We identified 121 unique haplotypes from 216 sequences in the *P. platyrhinos* species complex. Most haplotypes were represented by 1–4 samples with the exceptions of 4 abundant and widespread haplotypes (Hw1, Hw2, He1, and He2) which appear to have

given rise to numerous satellite haplotypes (i.e. newly evolved haplotypes surrounding a central abundant haplotype from which they are separated by one or a few mutational steps; Fig. 2a). From the phylogenetic analysis (Appendix S2 and Figure S1, Supporting Information), we identified 16 clades (Fig. 2). Most of the clades in the Mojave and northwestern Sonoran deserts exhibit numerous diverse and geographically restricted haplotypes and several clades overlap geographically (Fig. 2b). Conversely, only clade 3 was found in the western Great Basin with haplotype Hw2 and its satellite haplotypes comprising all individuals from the southwestern Great Basin, and haplotype Hw1 and its satellite haplotypes comprising all individuals in the northwestern Great Basin (Fig. 2). Similarly, only clade 11 extends from the eastern Mojave Desert into the eastern Great Basin with widespread haplotypes He1 and He2, and their satellite haplotypes, comprising individuals in the northeastern and southeastern Great Basin, respectively (Fig. 2). This haplotype structure is most likely indicative of a recent range expansion, where a subset of haplotypes expands across large areas from the source group followed by emergence of new mutations (see Discussion). Accordingly, these areas dominated by one of the abundant and widespread haplotypes were likely colonized by *P. platyrhinos* only recently.

The BSP plot (Fig. 3) indicates a rapid and recent increase in genetic diversity, which is consistent with recent geographic or demographic expansion. Under the general mutation rate, this increase in effective population size appears to have begun accumulating sometime during the latest glacial period, and we cannot rule out a post-LGM expansion.

Mean pairwise distances among sampling localities of *P. platyrhinos* interpolated across the species distribution (Fig. 4) show low values within the western and eastern Great Basin, which is consistent with a recent range expansion into these regions. The band of high genetic distances intersecting these two regions is concordant with the patterns identified from the haplotype network showing expansion into each region by a different haplotype group. Within the Mojave and Sonoran deserts, patterns of higher genetic distances among localities suggest that *P. platyrhinos* has persisted within these regions for some time.

Evaluating the niche similarity between LGM and present time using niche assessments

We assigned sampling locations within the geographic extent of haplotypes Hw1, Hw2 and their satellite haplotypes from clade 3, and haplotypes He1, He2 and their satellite haplotypes from clade 11 (Figs. 1, 2) to the expanded group. The areas containing these haplotypes correspond well with areas exhibiting low genetic distances among localities (Fig. 4). Localities 1, 81, and 104 (Fig. 1) were excluded from the analyses as they do not exhibit a signal of either stability or expansion. In particular, localities 81 and 104 belong to the clade 3 but do not exhibit either of the two abundant haplotypes that were used to define the expanded group. Locality 1 was represented by only a single, geographically isolated, sample (clade 10), from which we could not infer the demographic history of that population with any certainty. The other localities from the southern deserts that exhibit high genetic diversity and differentiation (Figs. 2, 4) were assigned to the persistent group (Fig. 1).

PCA reduced the 19 bioclimatic variables to 4 PCs with eigenvalues 1 that explained 45.1, 26.9, 11.6, and 6.3 percent of the total variance, respectively. The ANOVA and pairwise Tukey tests showed significant differences in least square means for all four PCs between the

current and CCSM model, and for the first three PCs when we used the MIROC model (Table 1). The scatterplot showed that the current niche expanded after the LGM along PC1 to include warmer and drier climate, and shifted along PC2 towards larger (broader) annual and diurnal temperature ranges and lower winter precipitation (Fig. 5a, PC2). The difference between the current and LGM niche was more extreme for the MIROC model than for the CCSM model.

When we compared the difference in climatic niche of *P. platyrhinos* between LGM and current time to the background climate divergence between the two time periods, we found support for niche conservatism in *P. platyrhinos* along the first and third PC axis for the CCSM model and along second axis for the MIROC model (Fig. 5b, Table 1). Conversely, we found support for niche divergence along the third PC axis of the MIROC model (Table 1). The remaining PC axes did not show significant support for either niche conservatism or divergence.

Discussion

Range shift between LGM and present time in *P. platyrhinos*

Our genetic assessments revealed that *P. platyrhinos* was likely quite widespread throughout much of the Mojave and northern Sonoran deserts during the latest glacial period, but was apparently absent from the Great Basin until relatively recently. The expansion of *P. platyrhinos* into the Great Basin likely followed the warming climate and desiccation of large pluvial lakes at the end of the LGM. Such post-glacial northward expansion has been documented or proposed in other warm-desert plant and animal taxa, and might have been a reoccurring event typical for interglacial periods of the late Pleistocene (Britten and Rust 1996, Graham et al. 2013, Hockett 2000, Mulcahy 2008, Pavlik 1989). The genetic evidence further suggests that *P. platyrhinos* expanded along two low elevation colonization routes into the Great Basin, one along an eastern corridor into the Bonneville Basin and the other along a western corridor into the Lahontan Basin. Below, we explain in detail how the genetic data support our major findings and address caveats associated with our approach.

The population history of *P. platyrhinos* left distinct evidence in the genome that allowed us to distinguish between populations that persisted in place throughout the latest glacial period (or longer) and those that recently expanded into new areas. Within the Mojave and Sonoran deserts, *P. platyrhinos* exhibits high genetic diversity and high genetic differentiation among populations (Figs. 2, 4) as evidenced by multiple divergent genetic clades (clades 1-16 in Fig. 2) inhabiting these two deserts. Each of these clades exhibits a large number of individual haplotypes (Fig. 2a) and high levels of genetic differentiation among populations (Fig. 4). These patterns are consistent with population stability through time, with enough time to allow accumulation of mutations and genetic divergence among adjacent populations (Castoe et al. 2007, Douglas et al. 2006, Jezkova et al. 2009, Jezkova et al. 2011, Murphy et al. 2006).

Conversely, populations of *P. platyrhinos* within the Great Basin exhibit little genetic structure and low genetic differentiation among populations (Figs. 2, 4). Only clades 3 and 11 are present in the western and eastern Great Basin, respectively. Within these clades, the

majority of individuals belong to one of four abundant and widespread haplotypes (Fig. 2) or their low frequency satellites (Fig. 2a). The close genetic relatedness among haplotypes within western and eastern Great Basin, respectively, results in low genetic differentiation within each region, but high genetic differentiation between the two regions (Fig. 4). These patterns are consistent with a recent range expansion of *P. platyrhinos* along two low elevation colonization routes, western and eastern, into the Great Basin.

From a population perspective, range expansion can be viewed as a series of founder events in which a subset of individuals from the colonization front disperses into new habitats. This leads to a process called thinning of genotypes (or, in case of mtDNA, thinning of haplotypes) in the direction of the expansion (Excoffier et al. 2009, Hampe and Petit 2005, Hewitt 1996, Hewitt 2000). The northward expansion in *P. platyrhinos* clearly exhibits this pattern with only haplotypes from clades 3 and 11 evident in samples from north of 38° latitude and only single ancestral haplotypes, Hw1 and He1, found north of 39° latitude along each of the two expansion routes (Fig. 2). Following establishment, populations grow exponentially and new private mutations (mutations restricted to a single population) typically appear in the newly invaded areas. Such newly evolved satellite haplotypes are indeed evident around each of the four ancestral haplotypes associated with the range expansions of *P. platyrhinos* (Fig. 2a).

Our coalescent assessment (Fig. 3) allowed us to assess whether the timing of the overall expansion was roughly consistent with a post-LGM process. The exact mutation rate for the *P. platyrhinos* ND4 gene region is unknown; however, assuming a general mutation rate estimate for mtDNA sequences in other reptile taxa (Macey et al. 1999), the expansion dates to the latest glacial period. The use of a slightly faster mutation rate of roughly 2% /lineage/ million years would be consistent with post-LGM expansion.

Mitochondrial DNA has been shown to be particularly sensitive for detection of historical range expansion due to small effective population size, maternal inheritance, and fast mutation rate (Hewitt 1996, Jezkova et al. 2015). Still, our approach has two main limitations. First, we were not able to address fine-scale elevational shifts within the southern deserts. These would require more detailed sampling to allow for population-level genetic assessments. We believe that this limitation did not affect the main conclusions of this study, but prevented us from a more detailed comparison between the LGM niche in the southern deserts and current niche in the Great Basin. Second, our genetic assessments did not allow evaluation of potential population extinctions in response to the climate change which could lead to an underestimation of the LGM niche. In particular, the sea level was lower during the LGM than it is today (Braconnot et al. 2007) which exposed large areas in the Gulf of California that are currently under water (Fig. 6). These areas were likely occupied by *P. platyrhinos* with subsequent extinction of populations when sea level rose in response to warming climate after the LGM. However, the CCSM and MIROC models suggest that during the LGM, even these areas did not reach the climatic extremes that the species experiences today (Fig. 6), and therefore we believe that our major conclusions remained unaffected by these population extinctions.

Niche shift between LGM and current time in *P. platyrhinos*

The climatic niche comparisons revealed that the niche of *P. platyrhinos* has shifted between LGM and current time (Fig. 5a). One dimension of this shift is an expansion of the species niche into overall warmer and drier climates after the LGM (Fig. 5a, lowest values along PC1). This niche expansion resulted from the persistence of *P. platyrhinos* populations in the low elevational areas of the Mojave and Sonoran deserts despite the warming and drying of climate. These areas now represent the hottest and driest parts of North America which had no analog during the LGM (Braconnot et al. 2007, Spaulding 1990).

In order to better understand this niche shift, we contrasted the difference between the current climate and the two models of the LGM climate for two bioclimatic variables (Hijmans et al. 2005): Bio 10 (mean temperature of warmest quarter) and Bio 16 (precipitation of wettest quarter) within the current range of *P. platyrhinos* and adjacent areas (Fig. 6a, b). Bio 10 and Bio16 were chosen because they were the most important temperature and precipitation variable, respectively, for the current ecological niche model (Table S2, Supporting Information).

The map in Figure 6a demonstrates that throughout large portions of the Mojave and Sonoran deserts, *P. platyrhinos* currently experiences mean temperatures during the warmest quarter of over 30°C. Accordingly, the response curve based on the current niche (see Appendix S3, Supporting Information for the ecological niche modeling methodology) indicates that occurrence probability increases with increasing values of mean temperature of the warmest quarter (Fig. 6a, inset). The high temperatures currently experienced, however, represent a novel niche that was nonexistent during the LGM when temperatures were below 27.5°C or 30°C (for the CCSM and MIROC models, respectively). The conditions below 30°C are considered suboptimal based on the current response curve of the species (Fig. 6a, inset), but represented the prime habitat for the species during the LGM and are similar to conditions that the species currently experiences in the Great Basin (Fig. 6a). Similarly, Figure 6b demonstrates that the southern deserts may have also shifted towards lower precipitation values after the LGM which would have exposed *P. platyrhinos* to values not experienced during the LGM. Precipitation of the wettest quarter is currently below 50 mm throughout most of the southern deserts while areas with such low precipitation were limited (CCSM model) or even non-existent (MIROC model) during the LGM (Fig. 6b).

Another dimension of the change in the niche of *P. platyrhinos* appears to be its post-LGM shift towards climate with higher fluctuations in temperature and precipitation (Fig. 5a, shift along PC2). This shift seems to be most prominent for the Great Basin populations and suggests that the expanding populations did not track a niche identical to what they had in the south during the LGM. Populations in the eastern Great Basin, especially, seem to experience the most extreme conditions with the lowest temperatures, largest annual temperature range, and highest precipitation (Fig. 5).

When we compared the LGM and current niche with respect to the background environmental divergence between the two time periods, we found little support for niche divergence between LGM and current time despite the post-LGM niche shift along multiple climatic axes (Table 1; Fig. 5b). These results seem contradictory, but the two analyses

aimed to assess different aspects of niche shifts. While the PCA analysis quantifies climatic differences, the background environmental divergence assesses whether the species occupies qualitatively the same niche between two time periods. Indeed, *P. platyrhinos* always inhabits the warmest and driest climate from the climate choices available to it. We can therefore conclude that the observed niche shift was caused largely by the existence of non-analog climates between the two time periods. These results are not surprising given that our assessment involved a short time period relative to the existence of the species and that niche conservatism relative to background environmental divergence seems to be common when comparing closely related species (Kozak and Wiens 2010, McCormack et al. 2010, Wiens et al. 2013). Our approach allowed us to assess niche changes across individual climatic axes, but there are approaches to quantifying overall niche shifts (Blonder et al. 2014, Broennimann et al. 2012, Warren et al. 2008). Such approaches may be more robust at assessing the degree of overlap between niches, allowing exact tests of niche similarity and equivalency. Given our rather rudimentary estimate of LGM range, however, we leave such assessments for future research.

Our niche shift assessments are critically dependent on accurate climatic reconstructions of the LGM. The two LGM simulation models (CCSM and MIROC) both indicate colder and wetter climate during the LGM (Figs. 5, 6). The CCSM model, however, predicts higher values across temperature variables whereas MIROC model predicts higher values across precipitation variables. These differences result in different levels of niche overlap and therefore niche shifts between each model and current time (Figs. 5, 6). Despite these discrepancies, our general results are consistent regardless of the model used, which indicates robustness in our interpretations of findings.

Additional uncertainty related to proposed niche shifts stems from different methodologies used to generate the current and LGM climate maps. The current climate maps (derived from the WorldClim datasets) were generated by interpolations of average monthly climate data from world-wide weather stations (Hijmans et al. 2005). The LGM climate maps were generated through climate simulations of the Earth's atmosphere known as Global Circulation Models (GCMs). GCMs are known to have regional biases (errors) that vary across individual models and that are generally larger for precipitation variables than for temperature variables (Hostetler et al. 2011). We believe that our use of two contrasting LGM models alleviated some of these biases.

Mechanism of niche shifts in *P. platyrhinos*

An important question to ask is whether the climatic niche shifts experienced by populations of *P. platyrhinos* after the LGM are biologically meaningful. The answer may lie in the latitudinal shifts in natural history traits observed in current populations. The populations of *P. platyrhinos* in the colder and wetter Great Basin exhibit increased sexual size dimorphism, shorter breeding season, fewer clutches per season, and possibly larger clutch size than the current populations within the southern deserts (Pianka and Parker 1975). Therefore, it is possible that populations in the southern deserts during the LGM exhibited natural history traits more similar to those currently found in the Great Basin populations. Indeed, shifts in morphological variables in response to the fluctuating climate of the late Pleistocene have

been documented in mammalian taxa (Smith and Betancourt 2003). Additionally, animals may now be compensating for a warmer climate behaviorally (Kearney et al. 2009) by shifting activity periods and occupying microhabitats with suitable thermal conditions (Lara-Resendiz et al. 2014), or physiologically by shifting active body temperatures (Monasterio et al. 2009).

Shifts in natural history traits could have been achieved through several (though not mutually exclusive) mechanisms: genetic adaptation, genotype sorting, or phenotypic plasticity. *Phrynosoma platyrhinos* could have adjusted to novel conditions after the LGM through genetic adaptation, thereby expanding its fundamental niche into conditions that had no analog during the LGM (Csuti 1979, Davis and Shaw 2001, Smith and Betancourt 2003, Urban et al. 2007). In the Mojave and northern Sonoran deserts the developing novel habitats may have been beyond the existing tolerance limits of the species which would have required genetic adaptation (Ackerly 2003b, Davis and Shaw 2001). Under the mechanism of genotype sorting, selection favors certain traits from the standing, genetically-based variation (Ackerly 2003b, Broennimann et al. 2007, Davis and Shaw 2001, Pearman et al. 2007). However, if adaptation or genotype sorting were the mechanism driving the observed niche shift, we would have expected a genetic signal of demographic expansion or shifts in genotype frequencies in the southern deserts, following selection on individuals better adapted to the new environment. We do not seem to have support in our data for such signal, although we acknowledge that our sampling and our choice of a molecular marker might not be sufficient to detect population-level demographic changes. Adaptation and genotype sorting, however, could have played a role in the range expansion of *P. platyrhinos* northwards as both evolutionary processes are consistent with a genetic signal of population expansion (Hahn et al. 2002).

Lastly, *P. platyrhinos* may exhibit broad phenotypic plasticity in various life history traits and could have simply expanded its realized niche to take advantage of changing environmental conditions that may well be within its existing range of tolerances (Jackson and Overpeck 2000, Rodder and Lotters 2009). Such plasticity would not have necessarily required any genetic changes, and could easily explain the persistence of the species within the changing climate of the southern deserts, as well as the expansions northwards into the Great Basin. Phenotypic plasticity as a mechanism for the niche shifts observed in *P. platyrhinos* seems to be supported by the persistence of many independent populations in the southern deserts in the face of the warming climate following the LGM. Species, like *P. platyrhinos*, appear to have been exposed to cycles of climatic oscillations throughout the Pleistocene which may have allowed them to evolve plasticity for niche shifts (Jezkova et al. 2011).

In any case, the pattern and scale of range and niche shift by *P. platyrhinos* are interesting when compared to other organisms within the region. Some species from the Great Basin are known to have shifted their ranges towards higher elevations and latitudes after the LGM (Smith et al. 2009), indicating that they were not capable of adjusting to the warming and drying climate after the LGM. Additionally, several lizards currently sympatric with *P. platyrhinos* within the Mojave Desert have not expanded into the Great Basin after the LGM (e.g., *Dipsosaurus dorsalis*, *Sauromalus obesus*, *Heloderma suspectum*; Stebbins 2003),

possibly indicating that not all species were capable of the range shift documented in *P. platyrhinos*.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Ackerly D. Canopy gaps to climate change - extreme events, ecology and evolution. *New Phytologist*. 2003a; 160:2–4.
- Ackerly DD. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*. 2003b; 164:S165–S184.
- Araújo MB, Guisan A. Five (or so) challenges for species distribution modelling. *Journal of Biogeography*. 2006; 33:1677–1688.
- Arévalo E, et al. Mitochondrial DNA sequence divergence and phylogenetic relationships among 8 chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*. 1994; 43:387–418.
- Bandelt HJ, et al. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*. 1999; 16:37–48. [PubMed: 10331250]
- Blonder B, et al. The n-dimensional hypervolume. *Global Ecology and Biogeography*. 2014; 23:595–609.
- Braconnot P, et al. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum - Part 1: experiments and large-scale features. *Climate of the Past*. 2007; 3:261–277.
- Britten HB, Rust RW. Population structure of a sand dune-obligate beetle, *Eusattus muricatus*, and its implications for dune management. *Conservation Biology*. 1996; 10:647–652.
- Broennimann O, et al. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*. 2012; 21:481–497.
- Broennimann O, et al. Evidence of climatic niche shift during biological invasion. *Ecology Letters*. 2007; 10:701–709. [PubMed: 17594425]
- Castoe TA, et al. Phylogeographic structure and historical demography of the western diamondback rattlesnake (*Crotalus atrox*): A perspective on North American desert biogeography. *Molecular Phylogenetics and Evolution*. 2007; 42:193–212. [PubMed: 16934495]
- Coetzee BWT, et al. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*. 2009; 18:701–710.
- Csuti BA. Patterns of adaptation and variation in the Great Basin kangaroo rat (*Dipodomys microps*). University of California Publications in Zoology. 1979; 111:1–73.
- Davis MB, Shaw RG. Range shifts and adaptive responses to Quaternary climate change. *Science*. 2001; 292:673–679. [PubMed: 11326089]
- Davis MB, et al. Evolutionary responses to changing climate. *Ecology*. 2005; 86:1704–1714.

- Douglas ME, et al. Evolution of rattlesnakes (Viperidae; *Crotalus*) in the warm deserts of western North America shaped by Neogene vicariance and Quaternary climate change. *Molecular Ecology*. 2006; 15:3353–3374. [PubMed: 16968275]
- Drummond AJ, et al. A rough guide to BEAST. 2007; 1.4. (http://beast-mcmc.googlecode.com/files/BEAST14_Manual_6July2007.pdf).
- Drummond AJ, Rambaut A. BEAST: Bayesian evolutionary analysis by sampling trees. *Bmc Evolutionary Biology*. 2007; 7:214. [PubMed: 17996036]
- Drummond AJ, et al. Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*. 2005; 22:1185–1192. [PubMed: 15703244]
- Eiserhardt WL, et al. Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. *Scientific Reports*. 2013; 3:1–8.
- Excoffier L, et al. Genetic consequences of range expansions. *Annual Review of Ecology Evolution and Systematics*. 2009; 40:481–501.
- Galbreath KE, et al. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution*. 2009; 63:2848–2863. [PubMed: 19663994]
- Graham MR, et al. Phylogeography of Beck's Desert Scorpion, *Paruroctonus becki*, reveals Pliocene diversification in the Eastern California Shear Zone and postglacial expansion in the Great Basin Desert. *Molecular Phylogenetics and Evolution*. 2013; 69:502–513. [PubMed: 23933071]
- Guisan A, et al. Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution*. 2014; 29:260–269. [PubMed: 24656621]
- Hahn MW, et al. Distinguishing between selection and population expansion in an experimental lineage of bacteriophage T7. *Genetics*. 2002; 161:11–20. [PubMed: 12019219]
- Hampe A, Petit RJ. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*. 2005; 8:461–467. [PubMed: 21352449]
- Harrison SP, Braconnot P. Palaeoenvironmental data sets and model evaluation in PMIP. *Proceedings of the Third PMIP Workshop*. 2000:9–25.
- Hewitt GM. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*. 1996; 58:247–276.
- Hewitt GM. The genetic legacy of the Quaternary ice ages. *Nature*. 2000; 405:907–913. [PubMed: 10879524]
- Hijmans RJ, et al. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*. 2005; 25:1965–1978.
- Hilbe JM. Systat 12.2: An overview. *American Statistician*. 2008; 62:177–178.
- Hill MP, et al. A predicted niche shift corresponds with increased thermal resistance in an invasive mite, *Halotydeus destructor*. *Global Ecology and Biogeography*. 2013; 22:942–951.
- Hill MP, et al. Understanding niche shifts: using current and historical data to model the invasive redlegged earth mite, *Halotydeus destructor*. *Diversity and Distributions*. 2012; 18:191–203.
- Hockett BS. Paleobiogeographic changes at the Pleistocene-Holocene boundary near Pintwater Cave, southern Nevada. *Quaternary Research*. 2000; 53:263–269.
- Holt RD, et al. Theoretical models of species' borders: single species approaches. *Oikos*. 2005; 108:18–27.
- Hornsby AD, Matocq MD. Differential regional response of the bushy-tailed woodrat (*Neotoma cinerea*) to late Quaternary climate change. *Journal of Biogeography*. 2012; 39:289–305.
- Hostetler SW, et al. Dynamically downscaled climate simulations over North America: Methods, evaluation, and supporting documentation for users. U.S. Geological Survey Open-File Report 2011-1238. 2011:1–64.
- Hunter KL, et al. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography*. 2001; 10:521–533.
- Jackson ST, Overpeck JT. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*. 2000; 26:194–220.
- Jezkova T, et al. Pleistocene impacts on the phylogeography of the desert pocket mouse (*Chaetodipus penicillatus*). *Journal of Mammalogy*. 2009; 90:306–320.

- Jezkova T, et al. Niche shifting in response to warming climate after the last glacial maximum: inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (*Dipodomys microps*). *Global Change Biology*. 2011; 17:3486–3502.
- Jezkova T, et al. Genetic consequences of a post-glacial range expansion in two co-distributed rodents (genus *Dipodomys*) depend on ecology and genetic marker choice. *Molecular Ecology*. 2015; 24:83–97. [PubMed: 25413968]
- Jones, KB. Phylogeography of the desert horned lizard (*Phrynosoma platyrhinos*) and the short-horned lizard (*Phrynosoma douglassii*): patterns of divergence and diversity. University of Nevada; 1995.
- Kearney M, et al. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*. 2009; 106:3835–3840. [PubMed: 19234117]
- Kozak KH, Wiens JJ. Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*. 2006; 60:2604–2621. [PubMed: 17263120]
- Kozak KH, Wiens JJ. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*. 2010; 13:1378–1389. [PubMed: 20875038]
- Lara-Resendiz RA, et al. Thermoregulation during the summer season in the Goode's horned lizard *Phrynosoma goodei* (Iguania: Phrynosomatidae) in Sonoran Desert. *Amphibia-Reptilia*. 2014; 35:161–172.
- Macey JR, et al. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: A molecular phylogenetic perspective and an area cladogram for Central Asia. *Molecular Phylogenetics and Evolution*. 1999; 12:320–332. [PubMed: 10413626]
- McCormack JE, et al. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation?: Insights from tests with niche models. *Evolution*. 2010; 64:1231–1244. [PubMed: 19922442]
- Miller MP. Alleles In Space (AIS): Computer software for the joint analysis of interindividual spatial and genetic information. *Journal of Heredity*. 2005; 96:722–724. [PubMed: 16251514]
- Monasterio C, et al. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *Journal of Biogeography*. 2009; 36:1673–1684.
- Mulcahy DG. Phylogeography and species boundaries of the western North American Nightsnake (*Hypsiglena torquata*): Revisiting the subspecies concept. *Molecular Phylogenetics and Evolution*. 2008; 46:1095–1115. [PubMed: 18226930]
- Mulcahy DG, et al. Phylogeography of the flat-tailed horned lizard (*Phrynosoma mcallii*) and systematics of the *P. mcallii*-*platyrhinos* mtDNA complex. *Molecular Ecology*. 2006; 15:1807–1826. [PubMed: 16689900]
- Murphy RW, et al. Conservation genetics, evolution and distinct population segments of the Mojave fringe-toed lizard, *Uma scoparia*. *Journal of Arid Environments*. 2006; 67:226–247.
- Newton MA, Raftery AE. Approximate bayesian inference with the weighted likelihood bootstrap. *Journal of the Royal Statistical Society Series B-Statistical Methodology*. 1994; 56:3–48.
- Nogues-Bravo D. Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*. 2009; 18:521–531.
- Olson DM, et al. Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience*. 2001; 51:933–938.
- Otto-Bliesner BL, et al. Last Glacial Maximum and Holocene climate in CCSM3. *Journal of Climate*. 2006; 19:2526–2544.
- Pavlik BM. Phytogeography of sand dunes in the Great Basin and Mojave deserts. *Journal of Biogeography*. 1989; 16:227–238.
- Pearman PB, et al. Niche dynamics in space and time. *Trends in Ecology and Evolution*. 2007; 23:149–158. [PubMed: 18289716]
- Petersen MJ. Evidence of a climatic niche shift following North American introductions of two crane flies (Diptera; genus *Tipula*). *Biological Invasions*. 2013; 15:885–897.
- Peterson AT, et al. Reconstructing the Pleistocene geography of the *Aphelocoma* jays (Corvidae). *Diversity and Distributions*. 2004; 10:237–246.

- Peterson AT, Nyari AS. Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the neotropics. *Evolution*. 2008; 62:173–183. [PubMed: 18005155]
- Pianka ER, Parker WS. Ecology of horned lizards: review with special reference to *Phrynosoma platyrhinos*. *Copeia*. 1975; 1975:141–162.
- Polzin T, Daneshmand SV. On Steiner trees and minimum spanning trees in hypergraphs. *Operations Research Letters*. 2003; 31:12–20.
- Rambaut, A.; Drummond, AJ. Tracer v1.4. 2007. <http://beast.bio.ed.ac.uk/Tracer>
- Rodder D, Lotters S. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography*. 2009; 18:674–687.
- Roe BA, et al. The complete nucleotide sequence of the *Xenopus laevis* mitochondrial genome. *Journal of Biological Chemistry*. 1985; 260:9759–9774. [PubMed: 4019494]
- Sinervo B, et al. Erosion of lizard diversity by climate change and altered thermal niches. *Science*. 2010; 328:894–899. [PubMed: 20466932]
- Smith FA, Betancourt JL. The effect of Holocene temperature fluctuations on the evolution and ecology of *Neotoma* (woodrats) in Idaho and northwestern Utah. *Quaternary Research*. 2003; 59:160–171.
- Smith FA, et al. A tale of two species: Extirpation and range expansion during the late Quaternary in an extreme environment. *Global and Planetary Change*. 2009; 65:122–133.
- Spaulding WG, Betancourt JL, et al. Vegetational and climatic development of the Mojave Desert: The last glacial maximum to the present. *Packrat middens: The last 40,000 years of biotic change*. 1990:166–199.
- Stebbins, RC. *A Field Guide to Western Reptiles and Amphibians*. Third Edition.. Houghton Mifflin Company; Boston: 2003.
- Suchard MA, et al. Bayesian selection of continuous-time Markov chain evolutionary models. *Molecular Biology and Evolution*. 2001; 18:1001–1013. [PubMed: 11371589]
- Sugiyama M, et al. Precipitation extreme changes exceeding moisture content increases in MIROC and IPCC climate models. *Proceedings of the National Academy of Sciences of the United States of America*. 2010; 107:571–5. [PubMed: 20080720]
- Thuiller W, et al. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics*. 2008; 9:137–152.
- Urban MC, et al. The cane toad's (*Chaunus* [Bufo] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B-Biological Sciences*. 2007; 274:1413–1419.
- Veloz SD, et al. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*. 2012; 18:1698–1713.
- Waltari E, et al. Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*. 2007; 2:1–11.
- Warren DL, et al. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 2008; 62:2868–2883. [PubMed: 18752605]
- Watson DF, Philip GM. A refinement of inverse distance weighted interpolation. *Geo-Processing*. 1985; 2:315–327.
- Wiens JJ, Graham CH. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics*. 2005; 36:519–539.
- Wiens JJ, et al. Diversity and niche evolution along aridity gradients in North American lizards (*Phrynosomatidae*). *Evolution*. 2013; 67:1715–1728. [PubMed: 23730764]

Fig. 1.

General sample sites of *Phrynosoma platyrhinos* species complex (*P. goodei* are represented in localities 7, 13–17, and 102 and *P. platyrhinos* from Yuma Proving Grounds in locality 2). Grey shadings represent the three main ecoregions of interest: Mojave Desert, Sonoran Desert, and the Great Basin (Olson et al. 2001). Pink and red circles represent localities above and below 5,000 feet, respectively, that were assigned to the populations that persisted throughout the LGM. Blue circles represent localities assigned to populations that expanded after the LGM. Grey circles were not included in either group due to unclear genetic signal.

Fig. 2.

(a) Median-joining network of mtDNA sequences of the *Phrynosoma platyrhinos* species complex nested into 16 clades. Clade 1 represents the Yuma Proving Ground haplotypes, Clade 2 represents *P. goodei*, and Clades 3-16 represent *P. platyrhinos*. Circle size and shading reflect the number of individuals exhibiting a given haplotype ranging from 1 to 4, with several abundant haplotypes indicated by large circles labeled internally. The length of connection lines between haplotypes is proportional to the number of mutational changes, with the shortest line representing a single mutational change. (b) Distribution of nested clades identified from the median-joining network. Pie graph sizes reflect the sample size at each location progressing from smallest ($n = 1$) to largest ($n = 6$). The clade numbers and color correspond to those on the median-joining network. The polygons represent extent of the expanding haplotypes in the western (Hw1, Hw2 and their satellites indicated in green) and eastern Great Basin (He1, He2 and their satellites indicated in pink).

Fig. 3.

Bayesian skyline plot derived from mtDNA sequences of the *Phrynosoma platyrhinos* species complex. The x-axis shows time and the y-axis shows effective population size of females. The black line is the median and the grey area represents the 95% upper and lower highest posterior density limits. The plot is presented truncated on the right as the missing region showed no evidence of change in effective population size.

Fig. 4.

Pairwise genetic distances among populations derived from mtDNA sequences and interpolated across landscape for the *Phrynosoma platyrhinos* species complex. The interpolation is restricted to the current distribution of the species complex approximated by a climatic niche model (Appendix S3, Supporting Information). The shading gradation progresses from green (lowest differentiation among populations) to white (highest differentiation among populations).

Fig. 5.

(a) Pairwise comparisons of the first three principal components representing the climatic niche of the *Phrynosoma platyrhinos* species complex. The red circles and red confidence ellipse represent the current niche, while the blue and green crosses and ellipses represent the LGM niche using CCSM and MIROC simulations, respectively. The black dashed circles in the first plot indicate confidence ellipses around localities belonging to the southern deserts, western Great Basin, and eastern Great Basin, respectively. The larger endpoints of the main loading variables of each principal component are listed along the axis of each principal component. (b) Current and LGM climatic niches of the *P. platyrhinos* complex with respect to the background points drawn from the respective climates. The niches are represented by ellipses while the background points are represented by symbols.

Fig. 6.

Values for (a) the mean temperature of the warmest quarter (Bio10) and (b) the precipitation of the wettest quarter (Bio16) for the current climate and two models of the LGM climate (CCSM and MIROC, respectively). The insets on the right represent a response curve for each variable reconstructed from the current occurrence records of *P. platyrhinos* using the methodology of ecological niche modeling (see Appendix S3, Supporting Information).

Table 1

Differentiation between the current and LGM climatic niche of *Phrynosoma platyrhinos* species complex reduced to four principal components (first column). The LGM climate is represented by two models, (a) CCSM and (b) MIROC. The second column shows the results of Tukey tests with significant differentiation between current and LGM niches indicated in bold. The third and fourth columns represent the low and high null values of the background environmental divergence, whereas the observed values of niche divergence for the species are in the fifth column. The last column summarizes whether the niche along each PC axis diverged (the observed value is larger than the high null value), remained conserved (the observed value is smaller than the low null value), or whether we failed to reject the null (NS; the observed value is between the low and high null values). The background divergence test was conducted for all PCs that showed a significant differentiation based on the Tukey test.

a. CCSM	Tukey test	Null low	Null high	Observed	Niche Conserved?
PC1	0.043	2.38	3.77	0.67	Conserved
PC2	0.000	0	0.46	0.28	NS
PC3	0.035	1.68	2.29	0.25	Conserved
PC4	0.039	0	0.55	0.13	NS
b. MIROC	Tukey test	Null low	Null high	Observed	Niche Conserved?
PC1	0.010	1.51	2.68	1.83	NS
PC2	0.000	1.63	2.75	1.01	Conserved
PC3	0.000	0	0.42	0.58	Diverged
PC4	0.081	N/A	N/A	N/A	N/A