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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*)

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Abstract

During Pleistocene glacial-interglacial cycles, the geographic range is often assumed to have shifted as a species tracks its climatic niche. Alternatively, the geographic range would not necessarily shift if a species can adapt *in situ* to a changing environment. The potential for a species to persist in place might increase with the diversity of habitat types that a species exploits. We evaluate evidence for either range shift or range stability between the last glacial maximum (LGM) and present time in the chisel-toothed kangaroo rat (*Dipodomys microps*), an endemic of the Great Basin and Mojave deserts. We modeled how the species' range would have changed if the climatic niche of the species remained conserved between the LGM and present time. The climatic models imply that if *D. microps* inhabited the same climatic niche during the LGM as it does today, the species would have persisted primarily within the warm Mojave Desert and expanded northwards into the cold Great Basin only after the LGM. Contrary to the climatic models, the mitochondrial DNA assessment revealed signals of population persistence within the current distribution of the species throughout at least the latest glacial-interglacial cycle. We concluded that *D. microps* did not track its climatic niche during late Pleistocene oscillations, but rather met the challenge of a changing environment by shifting its niche and retaining large portions of its distribution. We speculate that this kind of response to fluctuating climate was possible because of 'niche drifting', an alteration of the species' realized niche due to plasticity in various biological characters. Our study provides an example of an approach to reconstruct species' responses to past climatic changes that can be used to evaluate whether and to what extent taxa have capacity to shift their niches in response to the changing environment – information becoming increasingly important to predicting biotic responses to future environmental changes.

Keywords: climate change, climatic niche, Great Basin, last glacial maximum, niche shift, phylogeography, range expansion

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Introduction

When climate changes beyond the existing tolerance limits of individuals, species can persist either by shifting their geographic distributions (ranges) to locations that remain suitable, or by staying in place and adapting to novel environmental conditions (Vrba, 1992; Parmesan *et al.*, 1999; Pounds *et al.*, 1999; Barnosky *et al.*, 2003; Parmesan, 2006). Range shift in response to an environmental change is expected when the species' ecological niche remains conserved (identical) through time (Fig. 1a), a property of a species referred to as 'niche conservatism' (Wiens & Graham, 2005; Warren *et al.*, 2008). Large-scale geographic range shifts have been documented during the late Pleistocene (ca. 126 000–10 000 BP), when the desert regions of the western United States (Fig. 2) experienced pronounced and repeated climate change (Spaulding, 1990a; Thompson, 1990). During the latest glacial period, lower temperatures and higher precipitation caused downward (latitudinal or elevational) shifts in plant assemblages, resulting in a general reduction of size and continuity of desert habitats (Thompson & Mead, 1982; Thompson & Anderson, 2000). This shift was most extreme during the last glacial maximum (LGM), about 21 000 years before present (Harrison, 2000). During this time, many kinds of desert organisms that are currently widespread throughout the western deserts were absent from the northern regions (i.e., the Great Basin Desert and adjacent Columbia Plateau) and persisted within southern refugia (located within the Mojave or Sonoran deserts) where environmental conditions remained suitable (e.g., Jones, 1995; Mulcahy, 2008). These taxa subsequently expanded into the northern regions only when desert habitats were re-established as climate warmed after the LGM (Jones, 1995; Britten & Rust, 1996; Hockett, 2000).

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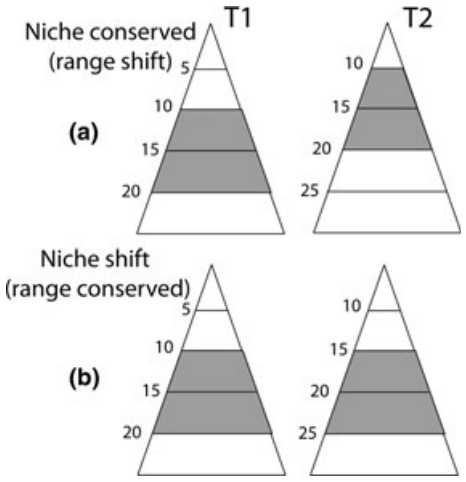

Fig. 1 Two types of species' responses to an environmental change represented by a hypothetical variable. The species' predicted distribution is represented by the gray trapezoid. In (a), the species' niche remains conserved from T1 to T2 and the species responds to an environmental change with a range shift. In (b), the species was able to shift its niche and remain in place despite the climatic change.

Populations of some desert species, however, persisted without substantial range shifts during major late Pleistocene environmental changes, perhaps because of an ability to shift their realized or fundamental niches (Fig. 1b) due to plasticity or evolutionary change, respectively. For example, several species of woodrats (*Neotoma* spp.) responded to cooling climate during glacial periods by increasing their body mass (Bergmann's Rule) instead of shifting their distributions to lower latitudes or altitudes as would be predicted if their climatic niches remained conserved (Smith & Betancourt, 2003). Consequently, one could ask, why are some taxa or populations capable of shifting their niches to novel conditions (Hadly, 1997; Smith & Betancourt, 2003) while others respond to an environmental change by tracking the conditions to which they are already adapted (Parmesan *et al*., 1999; Pounds *et al*., 1999)? Vrba (1992) proposed that taxa capable of utilizing alternative environments are most likely to persist through environmental changes. In general terms, a species would be able to shift its niche and maintain populations under changing climates if (1) it exhibits plasticity in relevant physiological, phenological, morphological, or behavioral traits that allows its realized niche to expand or shift – a process we call 'niche drifting'; or (2) its fundamental niche is modified via evolutionary change, which we call 'niche evolution'. Understanding which taxa or populations are capable of niche shifts (both 'niche drifting' and 'niche evolution') is critical to predicting their likely responses to ongoing and future climate change.

The chisel-toothed kangaroo rat (*Dipodomys microps*) inhabits four desert regions of western North America (Mojave Desert, Colorado Plateau, Great Basin Desert, and Columbia Plateau; Fig. 2) and exhibits two distinct ecotypes that differ in certain ecological, behavioral, and physiological traits (Csuti, 1979). Throughout most of its range, *D. microps* occupies low-elevation saltbush habitat (dominated by several species of *Atriplex* – *A. confertifolia*, *A. canescens*, *A. polycarpa*, or *A. spinifera*; herein referred to as *Atriplex* habitat) where it is mostly folivorous, with 80% of its diet consisting of *Atriplex* (Kenagy, 1973; Csuti, 1979). In the southern parts of its range, within the Mojave Desert, the species occupies mid-elevational blackbrush habitat (*Coleogyne ramosissima;* herein referred to as *Coleogyne* habitat), where it is generally granivorous and its diet comprises a variety of different plants (Csuti, 1979). Accordingly, we hypothesize that species such as *D. microps* that demonstrate discrete feeding preferences across two very distinct habitats might be capable of niche shifts that allow them to persist in place during major episodes of climate change.

We test the null hypothesis that the climatic niche of *D. microps* remained conserved through time and that this species responded to the changing climate of the late Pleistocene by tracking the climatic changes (represented by several climatic axes; see Materials and methods) to which it has been adapted (Fig. 1a). In particular, this hypothesis predicts that *D. microps* persisted in glacial refugia within the southern deserts during the LGM and expanded northward after the LGM, in concert with many other desert taxa (Jones, 1995; Britten & Rust, 1996; Hockett, 2000; Mulcahy, 2008). Alternatively, given its rather broad habitat preferences, the 'niche shift' hypothesis predicts that *D. microps* might have been able to persist within the Great Basin throughout the colder and wetter climates of the LGM (Fig. 1b).

To test our hypotheses, we first use climatic niche modeling to map the climatic niche of *D. microps* during the LGM under the assumption that it has remained conserved between the LGM and present time. From these models, we identify general areas that the species occupies today but would have been unsuitable during the LGM. We contrast these models with indices of genetic variation and diversity, assessed from mitochondrial DNA (mtDNA) sequences sampled across the current range of *D. microps*. We evaluate whether areas now occupied, but inferred by models as being unoccupied during the LGM, truly exhibit a genetic signal of a recent range expansion and whether those modeled as being geographically persistent exhibit a genetic signal of population stability. Mitochondrial DNA exhibits a relatively high mutation rate, which in combination with its small effective population size

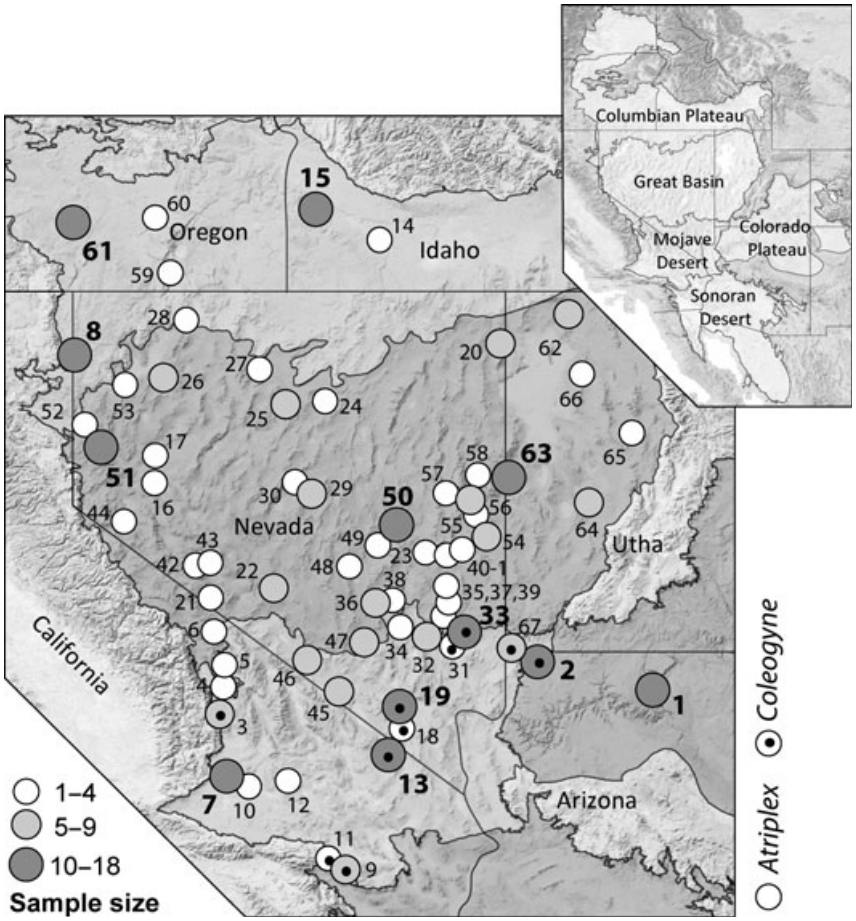

Fig. 2 Sampling localities for *Dipodomys microps*. The circle size and shading reflects the sample size, progressing from 1 to 18. Empty circles and circles with black dots represent populations occupying *Atriplex* and *Coleogyne* habitats, respectively. The lighter shading in the inset represents the extent of the four ecoregions where *D. microps* occurs (adapted from Olson *et al.*, 2001).

(four times smaller than nuclear DNA) allows tracking recent population histories, including demographic and geographic changes (Moore, 1995; Avise, 2000; Zink & Barrowclough, 2008). Our predictions are derived from the discipline of molecular phylogeography (Avise, 2000). A genetic signal of expanding populations is predicted by 'leading edge' colonization, which is a general model for a genetic structure that should be exhibited by populations that expanded into a particular geographic area relatively recently (Hewitt, 1996). Based on the 'leading edge' model, newly invaded areas are colonized by a subset of individuals (and therefore a subset of genotypes) from the colonization front that inhibits establishment by later migrants. This type of expansion results in a decrease of genetic (i.e., nucleotide and haplotype, see Materials and methods) diversity within newly established populations and a decrease in genetic variation among populations in the direction of the expansion (Fig. 3a). 'Leading edge' colonization is typical for rapid, large-scale geographic expansions exhibited by numerous taxa after the LGM (Hewitt, 1996, 2000; Austerlitz *et al.*, 1997; Excoffier *et al.*, 2009; Kerdelhue *et al.*, 2009). Conversely, populations that have remained geographically persistent in a given area should exhibit higher genetic diversity within populations due to the accumulation of mutations through time, as well as higher genetic variation among populations due to geographic structuring (Hewitt, 1996, 2000). Therefore, if populations of *D. microps* experienced a 'niche shift' and retained much of their current geographic range throughout the latest glacial-interglacial cycle (as proposed by our alternative hypothesis), the genetic signal of geographically persistent populations (high genetic diversity within and high variation among) would be detected throughout the species' range (Fig. 3b). We employ several phylogeographic and population genetic methods to evaluate the two predictions outlined above (Fig. 3a and b) with regards to the recent geographic and population history of *D. microps*.

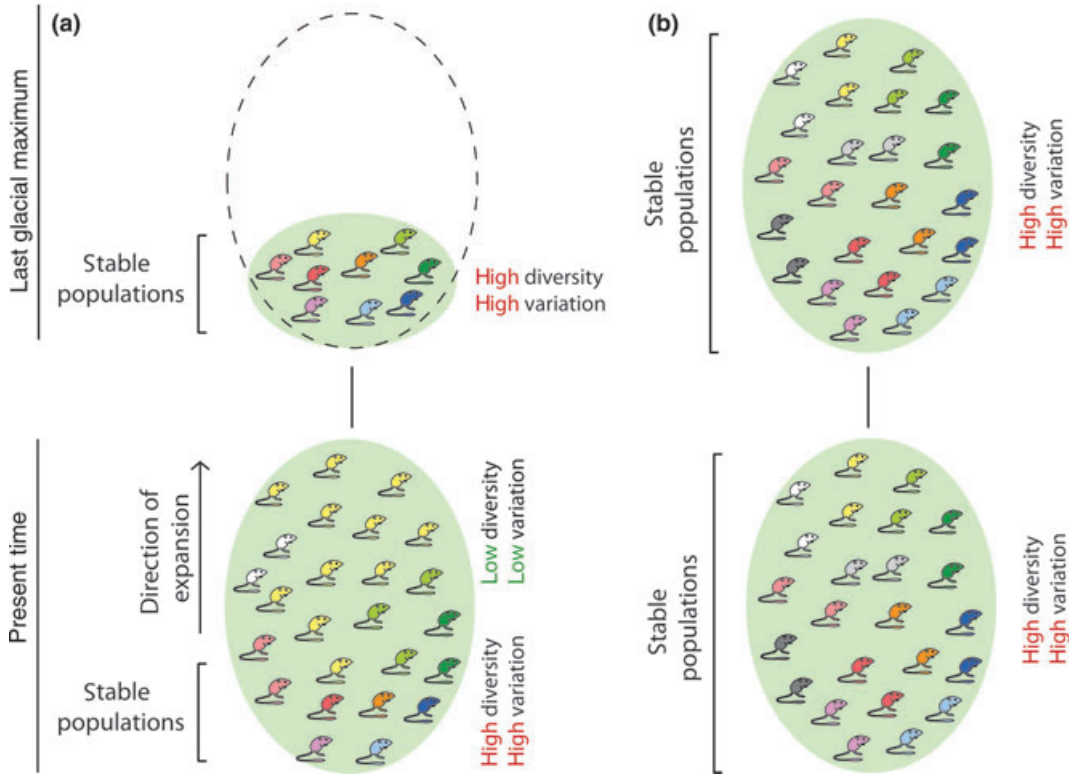

Fig. 3 The genetic consequences based on the two proposed hypotheses: (a) The null hypothesis of range shift where stable populations (top) harbor a large number of genotypes (represented by an array of different colors) generating high genetic diversity within and variation among populations. Under the 'leading edge' model of population expansion (bottom), the genotypes are gradually lost in the direction of the expansion which results in decrease of genetic diversity and variation. (b) The alternative hypothesis of 'niche shift' resulting in population persistence within the species' range despite climatic changes. Population persistence during the last glacial maximum generates high genetic diversity and variation (top) that are preserved and detected in present populations (bottom). In this generalized illustration, genetic diversity represents both nucleotide and haplotype diversity, and genetic distances represent both mismatch distances and frequency of private haplotypes but see Materials and methods and Discussion for more details about each genetic index.

Materials and methods

Taxon sampling

We acquired tissue samples from 364 individuals of *D. microps* from 83 unique localities; localities closer than 10 km without an obvious physical barrier were pooled together for a total of 67 general localities (Fig. 2; Table 1; Table S1 in Supporting Information). Most of the animals sampled specifically for this study (n = 340) were ear-clipped and released (n = 315), some (n = 25) were euthanized following methods approved by the American Society of Mammalogists (Gannon *et al.*, 2007) and the University of Nevada, Las Vegas Animal Care and Use Committee Protocol R 0709-244, and were deposited in the mammal collection at the New Mexico Museum of Natural History. We requested 14 tissue samples from the Museum of Texas Tech University and 10 samples from the Museum of Vertebrate Zoology, University of California (Table S1 in Supporting Information). These 10 samples (six of which were represented by skin clips) came from the two most southern localities at Joshua Tree National Park (locality 9) and Yucca Valley (locality 11) where *D. microps* might be currently extinct (Drost & Hart, 2008).

As different analyses require different sampling strategies, we used the following subsets and modifications of the original dataset. For climatic niche models, we used all unique sampling localities resulting in 83 presence records for *D. microps*. For genetic analyses, we used three different datasets. For calculating overall genetic indices and for phylogeographic analyses that do not require large sample size per a locality, we used all 364 individuals combined [Network, Bayesian skyline plot (BSP), overall mismatch distribution, and diversity indices] or with each assigned to one of the 67 general localities (pairwise genetic distances). We refer to this as the 'full dataset'. For population genetic analyses that require multiple individuals per locality (mismatch distributions and diversity indices for individual localities, and the R_2 test) we excluded all localities with sample size smaller than 10 which resulted in 12 sampling localities (165 samples), referred to as the '10+ dataset'. Finally, the nucleotide and haplotype diversity and frequency of private haplotypes used in the landscape interpolation assessment were

Table 1 General sampling localities for *Dipodomys microps* depicted in Fig. 2. The geographic coordinates represent an approximate location; the exact coordinates for each sample are listed in Table S1 (Supporting Information). *n* represents the sample size for each location

Locality number	State	County	Locality	Latitude	Longitude	*n*
1	Arizona	Coconino	House Rock Valley	36.49	−111.96	11
2	Arizona	Mohave	Wolf's Hole	36.89	−113.56	15
3	California	Inyo	Haiwee	36.15	−117.98	7
4	California	Inyo	Owens Valley	36.54	−117.93	1
5	California	Inyo	Saline Valley	36.84	−117.91	1
6	California	Inyo	Deep Spring Valley	37.30	−118.06	4
7	California	Kern	Koehl Lake	35.29	−117.88	12
8	California	Modoc	Eagleville	41.16	−119.99	13
9	California	Riverside	Joshua Tree NP	33.99	−116.23	8
10	California	San Bernardino	Boron	35.15	−117.57	1
11	California	San Bernardino	Yucca Valley	34.15	−116.47	2
12	California	San Bernardino	Superior Lake	35.23	−117.03	2
13	California	San Bernardino	Clark Mountain	35.56	−115.64	14
14	Idaho	Owyhee	Bruneau Canyon	42.76	−115.76	4
15	Idaho	Owyhee	Murphy	43.19	−116.64	10
16	Nevada	Churchill	Fallon	39.38	−118.88	2
17	Nevada	Churchill	Hot Springs Mountains	39.76	−118.87	3
18	Nevada	Clark	Cottonwood Valley	36.00	−115.45	2
19	Nevada	Clark	Kyle Canyon	36.26	−115.48	14
20	Nevada	Elko	Tecoma	41.32	−114.08	9
21	Nevada	Esmeralda	Fish Lake Valley	37.78	−118.10	1
22	Nevada	Esmeralda	Tonopah	37.91	−117.22	6
23	Nevada	Esmeralda	White River Valley	38.41	−115.12	3
24	Nevada	Eureka	Beowawe	40.52	−116.51	4
25	Nevada	Humboldt	Battle Mountain	40.48	−117.06	5
26	Nevada	Humboldt	Sulphur Landing	40.84	−118.76	7
27	Nevada	Humboldt	Golconda	40.96	−117.42	2
28	Nevada	Humboldt	30 mi S Denio	41.65	−118.44	2
29	Nevada	Lander	Monitor Valley	39.23	−116.70	6
30	Nevada	Lander	Big Smoky Valley	39.39	−116.93	1
31	Nevada	Lincoln	Coyote Spring	37.15	−114.72	3
32	Nevada	Lincoln	Pahranagat NWR	37.23	−115.10	8
33	Nevada	Lincoln	Kane Spring Valley	37.30	−114.58	18
34	Nevada	Lincoln	Tickaboo Valley	37.37	−115.47	4
35	Nevada	Lincoln	Delmar Valley	37.52	−114.87	2
36	Nevada	Lincoln	Rachel	37.71	−115.81	6
37	Nevada	Lincoln	Dry Lake Valley	37.71	−114.80	3
38	Nevada	Lincoln	Tempiute	37.74	−115.58	1
39	Nevada	Lincoln	Dry Lake Valley	37.94	−114.83	2
40	Nevada	Lincoln	Cave Valley	38.37	−114.82	3
41	Nevada	Lincoln	Lake Valley	38.45	−114.61	3
42	Nevada	Mineral	Marietta, Teels Marsh	38.23	−118.31	1
43	Nevada	Mineral	Tonapah Junction	38.27	−118.11	3
44	Nevada	Mineral	Smith Valley	38.84	−119.31	1
45	Nevada	Nye	Ash Meadows NWR	36.47	−116.32	6
46	Nevada	Nye	Beatty	36.91	−116.76	9
47	Nevada	Nye	Nevada Test Site	37.16	−115.97	5
48	Nevada	Nye	Hot Creek Valley	38.21	−116.18	2
49	Nevada	Nye	Railroad Valley	38.51	−115.79	3
50	Nevada	Nye	Currant	38.79	−115.53	12
51	Nevada	Washoe	Mullen Pass	39.87	−119.62	13
52	Nevada	Washoe	Flanigan	40.19	−119.85	3

Table 1 (continued)

Locality number	State	County	Locality	Latitude	Longitude	*n*
53	Nevada	Washoe	Gerlach	40.75	−119.29	1
54	Nevada	White Pine	Snake Valley	38.63	−114.27	7
55	Nevada	White Pine	Spring Valley	38.94	−114.42	2
56	Nevada	White Pine	Spring Valley	39.14	−114.50	7
57	Nevada	White Pine	Steptoe Valley	39.23	−114.84	1
58	Nevada	White Pine	Spring Valley	39.49	−114.39	1
59	Oregon	Harney	Fields	42.31	−118.66	4
60	Oregon	Harney	20 mi S Narrows	43.07	−118.87	4
61	Oregon	Lake	Alkali Lake	43.01	−120.01	10
62	Utah	Boxelder	Kelton	41.73	−113.14	9
63	Utah	Juab	Snake Valley	39.46	−113.96	13
64	Utah	Millard	White Sage Valley	39.10	−112.85	9
65	Utah	Tooele	Rush Valley	40.08	−112.26	1
66	Utah	Tooele	Puddle Valley	40.90	−112.95	4
67	Utah	Washington	Beaver Dam Mountains	37.08	−113.92	8

calculated for localities with sample size equal or larger than five, resulting in 29 sampling localities (277 samples) and referred to as the '5+ dataset'.

Climatic niche models

We modeled the climatic niche of *D. microps* to approximate the species' current distribution and distribution during the LGM under the assumptions that (1) climate is an important factor driving the species' distribution and (2) the climatic niche of *D. microps* remained conserved between the LGM and present time. The climatic niches were reconstructed using the methodology of ecological niche modeling, where environmental data are extracted from occurrence records and random points (represented by geographic coordinates) and habitat suitability is evaluated across the landscape using program-specific algorithms (Elith *et al.*, 2006). The current models were then projected on the climatic reconstructions of the LGM.

For occurrence records, we used our unique sampling localities. The current climate was represented by bioclimatic variables from the WorldClim dataset v. 1.4 (http://www.worldclim.org/; Hijmans *et al.*, 2005) that are derived from monthly temperature and precipitation data, and represent biologically meaningful aspects of local climate (Waltari *et al.*, 2007; Jezkova *et al.*, 2009). Because some of the 19 bioclimatic variables are correlated (Kozak & Wiens, 2006), we calculated pairwise correlations on values extracted from the occurrence records, and considered any two variables highly correlated when the correlation coefficient was ≥ 0.9. We excluded those variables that were highly correlated with more than one variable, and from pairs of highly correlated variables, we excluded monthly averages over quarterly averages. This assessment resulted in a total of 14 variables that we used for ecological niche modeling. For environmental layers representing the climatic conditions of the LGM, we used ocean–atmosphere simulations (Harrison, 2000) available through the Paleoclimatic Modelling Intercomparison Project (Braconnot *et al.*, 2007). These reconstructions of the LGM climate are based on simulated changes in concentration of greenhouse gases, ice sheet coverage, insulation, and topography (caused by lowering sea levels). We used two models that have been previously downscaled for the purpose of ecological niche modeling (Waltari *et al.*, 2007): Community Climate System Model v. 3 (CCSM; Otto-Bliesner *et al.*, 2006) and the Model for Interdisciplinary Research on Climate v. 3.2 (MIROC; Hasumi & Emori, 2004). The original climatic variables used in these models have been downscaled to the spatial resolution of 2.5 min under the assumption that changes in climate are relatively stable over space (high spatial autocorrelation) and were converted to bioclimatic variables (Peterson & Nyari, 2008).

Climatic niche models were built in the software package MAXENT v. 3.2.1 (Phillips *et al.*, 2006), a program that calculates relative probabilities of the species' presence in the defined geographic space, with high probabilities indicating suitable environmental conditions for the species (Phillips *et al.*, 2004). We used the default parameters in MAXENT (500 maximum iterations, convergence threshold of 0.00001, regularization multiplier of 1, and 10 000 background points) with the application of random seed and logistic probabilities for the output (Phillips & Dudik, 2008). We masked our models to the four regions where *D. microps* occurs (Mojave Desert, Great Basin, Columbia Plateau, and Colorado Plateau) because reducing the climatic variation being modeled to that which exists within a geographically realistic area improves model accuracy and reduces problems with extrapolation (Pearson *et al.*, 2002; Thuiller *et al.*, 2004; Randin *et al.*, 2006). We ran 50 replicates for each model, and an average model was presented using logistic probability classes of climatic niche suitability. The presence–absence map was determined using the 'minimum training presence threshold' where the omission error of all occurrence records is set to zero (i.e., locations of all occurrence records are predicted as 'suitable'). We used the receiver operating characteristic for its area under the curve (AUC) value to evaluate the model performance (Fielding & Bell, 1997; Raes &

ter Steege, 2007). AUC values range from 0.5 for a random prediction to 1 for perfect prediction (Winker *et al.*, 2007).

Laboratory methods

We isolated total genomic DNA from preserved heart, kidney, or ear tissue following the protocol for the DNeasy Extraction Kit (Qiagen Inc., Valencia, CA, USA). We amplified ca. 1000 base pairs (bp) of the mitochondrial control region using genus-specific primer L15926DIOR (GTATAAAAATTACTCAGGTCTTGT) and an universal primer H651 (Kocher *et al.*, 1989). Amplifications were accomplished in 12.5 μL reactions using Takara Ex Taq Polymerase Premix (Takara Mirus Bio Inc., Madison, WI, USA) followed by purification using ExoSap-IT (USB Corp., Cleveland, OH, USA). Thermal cycling was accomplished at a 56 °C annealing temperature in 40 cycles. We conducted double-stranded cycle sequencing using fluorescence-based chemistry (BigDye Terminator v. 3.1 Cycle Sequencing Kit; Qiagen Inc., Valencia, CA, USA) and the genus-specific primers L15926DIOR and H651Lpen (TAACTGCAGAAGGCTAGGAC). For the six museum skins of *D. microps*, the targeted region was amplified and sequenced using five overlapping genus-specific primer pairs about 250 bp each (the primer sequences can be provided upon request). The electrophoresis was conducted on an ABI Prism 3130 automated sequencer (Applied Biosystems Inc., Foster City, CA, USA). The sequences were aligned using SEQUENCHER v. 4.6 (Gene Codes Corp., Ann Arbor, MI, USA) and verified manually. The final DNA segment for all samples included 902 bp of control region sequence.

Genetic analyses

For the full dataset, we calculated the number of variable sites, parsimony informative sites, and a net uncorrected *p*-distance in MEGA v. 4 (Tamura *et al.*, 2007), and haplotype diversity (H_d) and nucleotide diversity (π_d) in ARLEQUIN v. 3.11 (Excoffier *et al.*, 2005). For the 10+ dataset, we calculated pairwise F_{ST} values indicative of population structuring in ARLEQUIN. Preliminary phylogenetic analyses of the mtDNA dataset showed that *D. microps* exhibits shallow structuring (Fig. S1 in Supporting Information). Accordingly, we used a median-joining network (Bandelt *et al.*, 1999) to reconstruct relationships among the unique mtDNA sequences (referred to as haplotypes) as networks represent an appropriate phylogeographic method when levels of genetic divergence are low, multifurcations occur, and ancestral haplotypes are still present in the populations (Crandall & Templeton, 1996). Network analysis was conducted for the full dataset in the program NETWORK v. 4.5.1.6 (website fluxus-engineering.com; Bandelt *et al.*, 1999) with transversions weighted twice as high as transitions, and with the maximum parsimony option employed to remove excessive links from the network (Polzin & Daneshmand, 2003).

We calculated four genetic indices that can elucidate species geographic and demographic processes, such as a potential recent northward expansion of *D. microps* from southern refugia. Two indices reflect genetic variation among populations (genetic distances and frequency of private haplotypes within populations) and two indices represent genetic diversity within populations (nucleotide and haplotypes diversity; Fig. 3). The genetic distances are represented by mismatch distances between sequences from neighboring sampling sites calculated in the program ALLELES IN SPACE (Miller, 2005) for the full dataset (67 locations). These pairwise genetic distances were assigned to mid-points between sampling sites using the Delaunay triangulation-based connectivity network (Miller *et al.*, 2006). We used residual genetic distances derived from the linear regression of genetic vs. geographical distance to account for correlation between these two distances (Manni *et al.*, 2004; Miller *et al.*, 2006). The residual genetic distances were interpolated across uniformly spaced 2.5 min grids (~5 km) using the inverse distance weighted interpolation procedure (Watson & Philip, 1985) in ARCGIS 9.2 (ESRI, Redlands, CA, USA). We restricted the interpolations to the geographic range of *D. microps*, approximated using the climatic niche model for current climatic conditions.

We calculated nucleotide diversity in ARLEQUIN as an average number of nucleotide differences per site among sequences in each sampling locality and haplotype diversity as a probability that two randomly chosen haplotypes in a population are different, regardless of genetic distance between them. These two indices of genetic diversity can reveal slightly different signals of population history (see Discussion). The private haplotype frequency was calculated by hand as a frequency of DNA sequences in a population that are unique (do not occur in any other population). Recently expanded populations should exhibit low frequency of private haplotypes as the same haplotypes expand across large geographic areas and consequently occur in multiple populations (Fig. 3a). We calculated nucleotide and haplotype diversity, and frequency of private haplotypes for the 5+ dataset. We used the Pearson's correlation coefficient (r) in SYSTAT v. 12 (Systat Software Inc., Chicago, IL, USA) (Hilbe, 2008) to confirm that the diversity indices are not positively correlated with sample size and to evaluate whether the diversity indices are negatively correlated with latitude, as would be expected under the model of northward expansion. The three diversity indices were imported into ARCGIS (ESRI) and interpolated across landscape as described above for genetic distances.

We analyzed past demographic changes of *D. microps* to detect any significant changes in population sizes through time. For example, if the species experienced a range expansion after the LGM, we would detect a significant increase in the overall effective population size dating to sometime after the LGM. We used the BSP coalescent model (Drummond *et al.*, 2005) implemented in the program BEAST v. 1.5.3 (Drummond & Rambaut, 2007) that generates plots of estimated posterior distribution of the effective population size through time (Drummond *et al.*, 2005). Following assessment in MRMODELTEST, we selected the substitution model GTR+I+Γ (a set of rules derived from the data under which one nucleotide is being substituted for another), along with a strict molecular clock (after assessing clock-like behavior), and a 1 year generation time (Thomas *et al.*, 1990; Gummer *et al.*, 1997). Since mutation rates for *D. microps* control region are unavailable from the literature, we applied a broad range of

rates of 1.5% and 6% lineage^{-1} million years^{-1} (Myr) that have been used for the same DNA region of other small mammals (Galbreath *et al*., 2009). We conducted several independent Markov Chain Monte Carlo (MCMC) runs of 80 million generations with a burn-in of 10% (percentage of MCMC generations discarded to ensure convergence). For final analysis, three adequate MCMC runs were combined using LOGCOMBINER (distributed with BEAST) and the median and 95% highest posterior density intervals were visualized using TRACER v. 1.5 (Rambaut & Drummond, 2007).

We further tested for demographic changes using mismatch distribution analyses under the sudden expansion model (Rogers & Harpending, 1992; Schneider & Excoffier, 1999) in ARLEQUIN for the full dataset and the 10+ dataset. Mismatch distribution analysis calculates the number of pairwise differences among sequences and identifies populations with star-like phylogeny, a structure typical for populations that experienced a sudden expansion (Excoffier, 2002; Excoffier *et al*., 2009). The star-like phylogeny will appear as unimodal distribution of pairwise differences with the peak corresponding to a lower number of pairwise differences in younger expansions and higher number in older expansions (Excoffier, 2002). This analysis results in a multimodal graph if a population is in demographic equilibrium, subdivided or in decline (Slatkin & Hudson, 1991; Rogers & Harpending, 1992). A significant sum of squared deviation (SSD, $P < 0.05$) and Harpending's raggedness index (r, $P < 0.05$) indicate the rejection of the null hypothesis of sudden expansion. If the sudden expansion model was not rejected, we calculated population expansion parameters τ (time since expansion), θ_0 (population size prior to expansion), and θ_1 (final population size). The parameter τ was used to calculate time in years since expansion (Rogers & Harpending, 1992) using the same mutation rates and generation time as above.

To further evaluate whether the species experienced an expansion, we used Ramos-Onsins and Rozas' R_2 test (Ramos-Onsins & Rozas, 2002) in DNASP v. 5.1 (Librado & Rozas, 2009) for the full dataset and the 10+ dataset. The R_2 test is based on the differences between the number of singleton mutations (mutations that occur in only one individual) and the average number of nucleotide differences (Ramos-Onsins & Rozas, 2002), and significantly low ($P \leq 0.02$) R_2 values indicate population growth.

Results

Ecological niche models

The mean AUC value for the current ecological niche model was 0.82. The model of current conditions (Fig. 4a) captures well the known distribution of *D. microps* but with some over-predictions of occurrence within the eastern part of the Colorado Plateau and on the Snake River Plain in southern Idaho. These areas, however, might currently be unoccupied by *D. microps* due to non climate-related factors, such as insufficient time for colonization and establishment of more widespread populations (these two areas exhibit signals of a recent expansion, see below), recent habitat destruction (especially on the Snake River Plain), or possibly competition with other species (e.g., congeneric Ord's kangaroo rat, *D. ordii*). The paleo-models (Fig. 4b and c) indicate absence of a suitable climatic niche in the Great Basin and on the Columbia Plateau during the LGM. A suitable climatic niche is predicted to have been available within the Mojave Desert, but it is modeled as being fragmented and more restricted in distribution compared to present.

Genetic analyses

Of the 902 bp of control region, 205 characters are variable and 160 are parsimony informative. The overall haplotype diversity (0.9957 ± 0.0008) and nucleotide diversity (0.0242 ± 0.0118) are high, and the net mean pairwise uncorrected p-distance is 2.4%. The pairwise F_{ST} values revealed significant population structuring within and between the *Atriplex* and *Coleogyne* habitat types (Table S2 in Supporting Information). The median-joining network (Fig. 5) collapsed the 364 sequences into 243 haplotypes. The number of mutations between haplotypes ranges from 1 to 14, and the number of sequences belonging to any given haplotype ranges from 1 to 10. Most haplotypes are restricted to a single locality and of the 13 haplotypes shared among localities (Fig. 5), three are shared between *Atriplex* and *Coleogyne* localities. The central parts of the network comprise missing (extinct or unsampled extant) or low frequency haplotypes from which a burst of haplotypes is separated by up to 40 mutational steps. Nucleotide diversity within populations ranges from 0.00056 to 0.02222 (Fig. 6a), and there is no significant correlation between sample size and nucleotide diversity ($r = -0.223$, $P = 0.244$; Fig. S2a in Supporting Information). The nucleotide diversity does not decrease in the northward direction, as would be expected under the 'leading edge' colonization model ($r = -0.148$, $P = 0.443$; Figs 3 and 6a, Fig. S2b in Supporting Information). Nucleotide diversity is relatively high throughout the entire species' range except the edge populations in the Colorado Plateau (northern Arizona), southern Mojave Desert (southern California), and northwestern Columbia Plateau (northeastern California, southern Oregon, and southwestern Idaho). Haplotype diversity (Fig. 6b) ranges from 0.46 to 1.00 (where 1.00 represents populations with no redundant haplotypes) and is not significantly correlated with sample size ($r = -0.260$, $P = 0.174$; Fig. S2d in Supporting Information) or latitude ($r = 0.229$, $P = 0.232$; Fig. S2e in Supporting Information). Haplotype diversity is highest within the

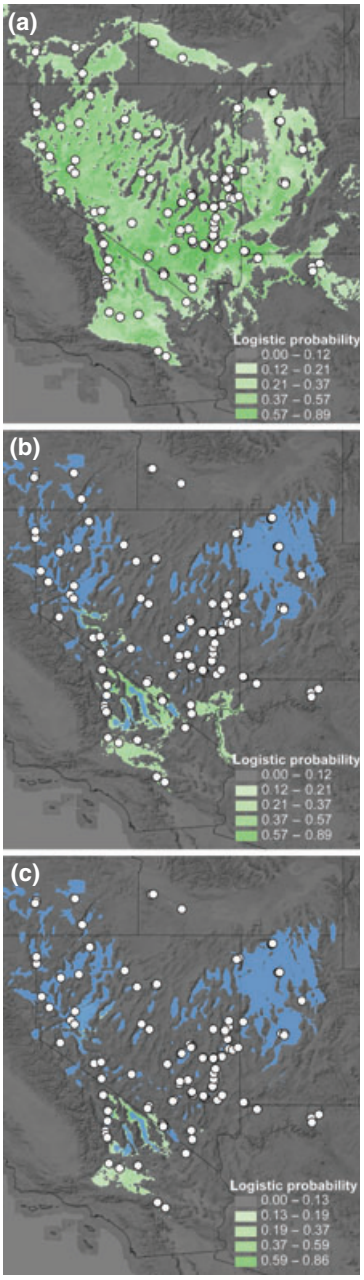

Fig. 4 Climatic niche models for *Dipodomys microps* based on 14 bioclimatic variables representing current climatic conditions (a), and projected on two reconstructions of climatic conditions at the last glacial maximum (LGM) – Community Climate System Model (b) and Model for Interdisciplinary Research on Climate (c). The green shading represents areas identified as suitable using the minimum presence threshold for logistic probabilities. Blue areas correspond to the extent of pluvial lakes during the LGM (Raines *et al.*, 1996). White dots represent occurrence records of *D. microps* used to build the models.

central parts of the species' range and lowest within northwestern, southeastern, and southern edge localities (Fig. 6b).

The residual genetic distances range from −0.0209 to +0.0127 (Fig. 6c). The negative values indicate that the genetic distance between populations is lower than the average, given the geographic distances between them. The genetic distances among populations are relatively high throughout the entire range of *D. microps*, indicating genetic structuring and limited gene flow, inconsistent with recent northward expansion (Fig. 3a). Low genetic distances are found within the peripheral areas and generally correspond with areas of low nucleotide and haplotype diversity (Fig. 6a and b). Sampling localities within the area covered with the pluvial Lake Bonneville during the LGM show intermediate genetic distances (Fig. 6c). The private haplotype frequency ranges from 0.41 to 1.00 (frequency of 1.00 represents populations where none of the haplotypes occurs in any other population), is high throughout most of the range (Fig. 6d), and is not correlated with sample size ($r = -0.273$, $P = 0.455$) or latitude ($r = 0.142$, $P = 1.000$; Fig. S2f in Supporting Information).

The BSPs (Fig. 7a) indicate an increase in genetic diversity, then a period of relatively stable genetic diversity, followed by a recent decline. This signal is consistent (but see Discussion for possible caveats) with an increase in effective population sizes during the middle to late Pleistocene (ca. 750 Kya at 1.5% mutation rate; ca. 200 Kya at 6% mutation rate), followed by constant population sizes (starting ca. 500 Kya at 1.5% mutation rate; ca. 125 Kya at 6% mutation rate), and declines during the late Pleistocene or early Holocene (ca. 20 Kya at 1.5% mutation rate; ca. 5 Kya at 6% mutation rate).

The mismatch distribution (Fig. 7b) for the full dataset shows a unimodal distribution of pairwise sequence differences consistent with a rapid population expansion. This expansion, however, was likely not recent as the median of the distribution corresponds to 27 pairwise differences. The SSD and Harpending's raggedness index are not significantly different from a model of rapid population expansion (SSD = 0.003, $P > 0.05$; $r = 0.001$, $P > 0.05$; Table 2). This expansion was further supported by the values of θ, as $\theta_1 > \theta_0$ ($\theta_1 = 105.045$, 95% CI = 75.418–71515.045; $\theta_0 = 0.004$, 95% CI = 0.00–4.642). The beginning of population expansion based on the value of τ ($\tau = 25.127$, 95% CI = 18.389–28.549) and the two mutation rates applied roughly correspond to 928 570 (95% CI = 679 564–1 055 026) and 232 140 (95% CI = 169 891–263 756) years ago. Out of the 12 evaluated populations (Table 2; Fig. S3 in Supporting Information), five (localities 8, 15, 50, 61, 63) show a unimodal mismatch distribution. Localities 8, 15, and 61 have likely experienced a relatively recent population expansion while localities 50

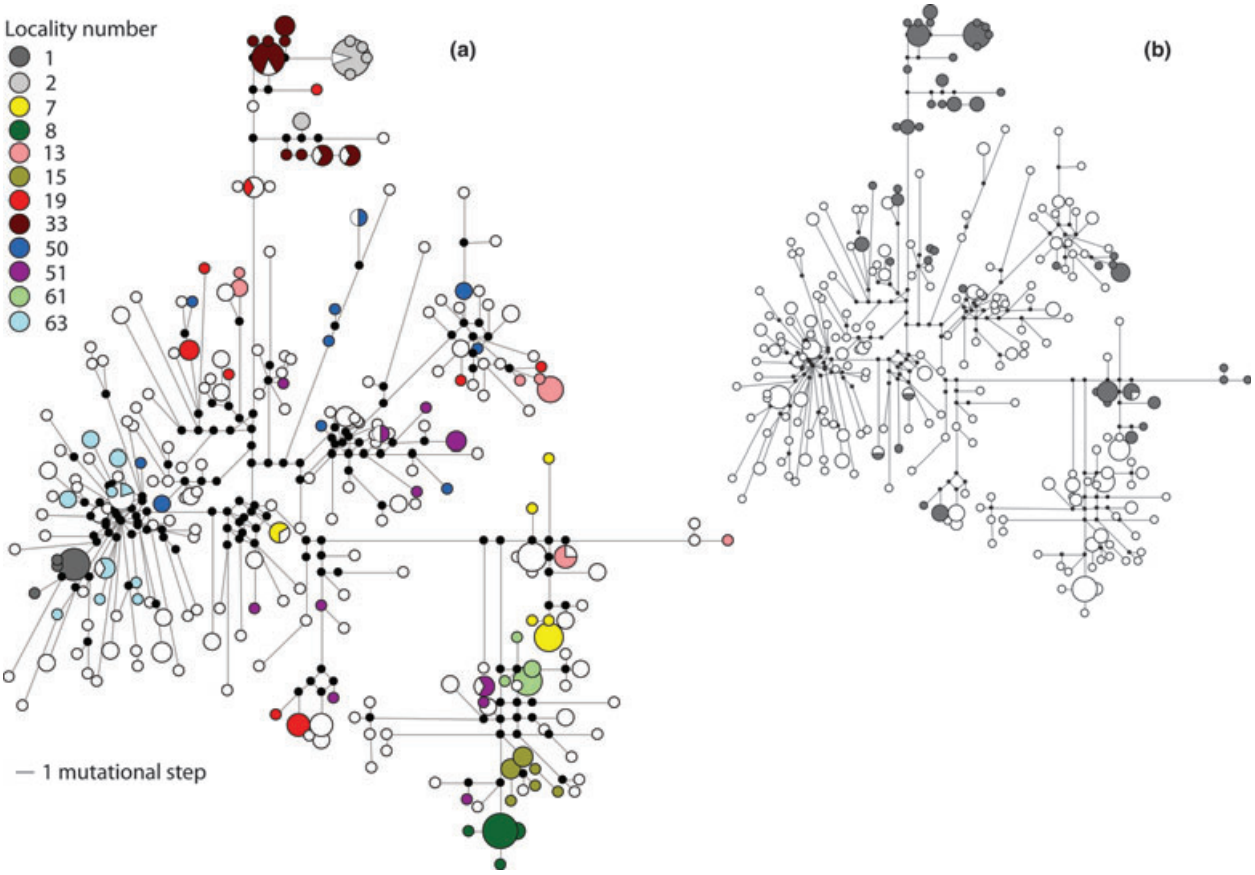

Fig. 5 Median-joining network of control region sequences for 364 samples of *Dipodomys microps*. Circle size reflects the number of individuals exhibiting a haplotype (smallest = 1, largest = 10). The length of connection lines between haplotypes is proportional to the number of mutational changes. In (a), the colored circles represent haplotypes present in the 12 sampling localities with sample size equal or larger than 10. In (b), the white and dark gray circles represent haplotypes found in *Atriplex* and *Coleogyne* populations, respectively.

and 63 probably experienced population growth long before the LGM. Recent population expansion is not supported by the R_2 test for the full dataset and for none of the localities with the exception of locality 63 (Table 2). The sensitivity of the R_2 test decreases with the time since the expansion, and this decrease is even more rapid when sample size is small (Ramos-Onsins & Rozas, 2002) which could explain why the middle-late Pleistocene expansion (indicated by the BSP and mismatch distribution graph) was not detected by this test.

Discussion

Discordance between climatic niche models, genetic data, and the fossil record

In this study, we evaluated whether *D. microps* shifted its range in response to climate changes after the LGM, or alternatively, whether the species retained most of its range and shifted its niche to cope with the changing environment. The ecological niche models, built under the assumption that the climatic niche of *D. microps* has remained conserved between the LGM and present day, indicate that the climatic conditions within the Great Basin and Columbia Plateau would have been unsuitable to the species during the LGM and suitable habitats within the Mojave Desert would have been reduced and fragmented (Fig. 4). These results imply that if the climatic niche of the species was conserved, *D. microps* would have persisted only within the Mojave Desert during the LGM and experienced a substantial expansion northwards after the LGM. Our climatic models, however, were built under the assumption that the bioclimatic variables, based solely on temperature and precipitation data, define the species' niche. Although climate undeniably plays an important role in shaping the species' niche, other factors are strongly advised to be considered when possible (Pearson & Dawson, 2003). Therefore, we independently evaluated

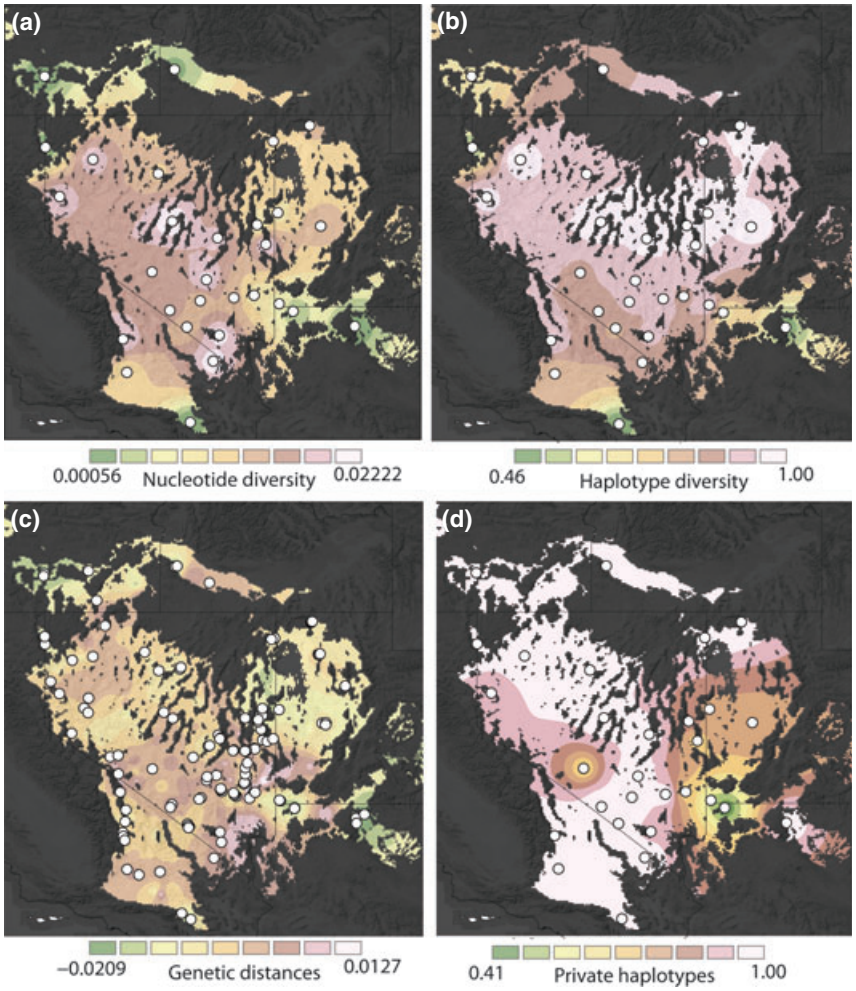

Fig. 6 Interpolated nucleotide diversity (a), haplotype diversity (b), pairwise genetic distances (c), and frequency of private haplotypes (d) across landscape for *Dipodomys microps* restricted to the current climatic niche model of the species. The shading gradation progresses from green (lowest values), yellow, brown to white (highest values). The white circles indicate sampling localities used in each analysis (see Materials and methods for details).

our models using available information on the LGM environment reconstructed from packrat midden and pollen records (Spaulding *et al*., 1983; Spaulding, 1990b; Thompson, 1990). These reconstructions are in agreement with our climatic niche models as they indicate that during the LGM, the low-elevation *Atriplex* habitats within the Great Basin and Columbia Plateau, that currently represent the prime habitat for *D. microps*, were covered with large pluvial lakes (Grayson, 1993; Reheis, 1999) or replaced by an assemblage of plants currently found in higher elevations (Spaulding *et al*., 1983; Spaulding, 1990a,b; Thompson, 1990; Grayson, 1993), such as *Artemisia* (sage), *Chrysothamnus* (rabbitbrush), and various woodland species (e.g., Utah juniper, *Juniperus osteosperma*; Single-leaf Pinyon, *Pinus monophylla*). At the habitat scale sampled by the pollen and packrat midden records, *Atriplex*-dominated communities were not established until the end of Pleistocene or even the beginning of Holocene, when the climate warmed, plant communities shifted upwards and northwards, and the large pluvial lakes desiccated (Spaulding, 1990b; Thompson, 1990). One caveat, however, is that both packrat midden and pollen records are known to be biased in several ways. For example, packrats will only sample vegetation in the vicinity of habitats suitable to midden construction such as rocky outcrops and cliffs while pollen record generally represents a larger, regional picture of the palaeo-vegetation but with less detail (Thompson, 1990). As such, we cannot rule out the possibility that small patches of *Atriplex* habitat persisted, e.g., along lakeshores. Nevertheless, recorded vegetation shifts imply that environmental conditions during the LGM within the northern parts of the current range of

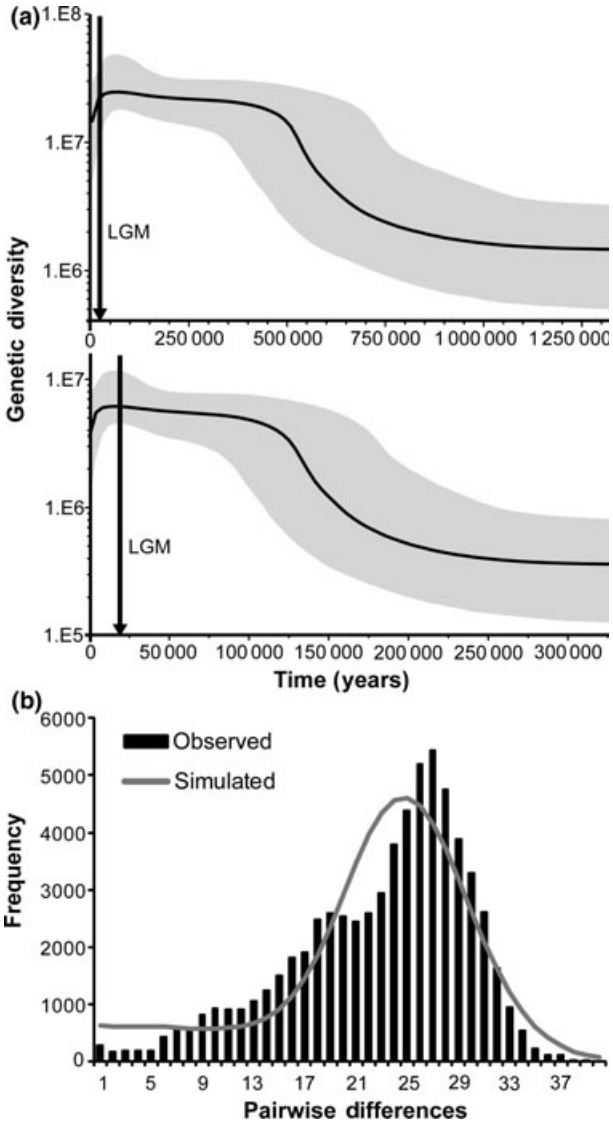

Fig. 7 (a) Bayesian skyline plots derived from control region sequences for 364 samples of *Dipodomys microps* at 1.5% and 6% mutation rates, respectively. The *x*-axis shows the time progressing from right (oldest) to left (present). The *y*-axis shows an index of effective population size assuming a 1-year generation time. The black line is the median, and the gray area shows the 95% upper and lower highest posterior density limits. The arrows point to the timing of the last glacial maximum (~21 Kya). (b) Mismatch distribution analysis under the sudden expansion model.

D. microps were quite different from those that the species experiences today. The response of *Coleogyne* to the latest climate changes is less well understood (Summers *et al*., 2009), but it is believed that *Coleogyne* could have persisted mostly *in situ* (Wells, 1983) and therefore could have maintained suitable niche for *D. microps* within the Mojave Desert and adjacent southern regions, in agreement with our climatic models.

Despite these environmental changes, none of the genetic analyses supported post-LGM range expansion from the Mojave Desert into the Great Basin and onto the Colombia Plateau. We did not detect the decrease in nucleotide or haplotype diversity in a northward direction (Fig. 6a and b; Fig. S2b and e in Supporting Information) that would be predicted under the 'leading edge' model of post-LGM range expansion (Fig. 3a). High nucleotide and haplotype diversity is usually a result of population stability as mutations are accumulated over time, but can also be maintained under a 'phalanx' model of population expansion (Hewitt, 1996). Under this model, new populations at the expansion front are formed from a more even mixture of ancestral populations, resulting in only marginal decrease in local genetic diversity. Although genetic diversity within populations remains higher under this model, genetic variation among expanding populations would be low as in the 'leading edge' model (see below), because the expanding populations will consist of similar groups of genotypes. The 'phalanx' model of colonization has been documented in populations expanding slowly, with high population densities, high gene flow, and wide colonization front; therefore, it is not typically observed for rapid expansions after the LGM (Hewitt, 1996; Schmitt *et al*., 2005). Relatively high nucleotide diversity can also be observed within expanding areas when previously isolated (and therefore quite divergent) populations come to secondary contact, for instance after expansion from multiple refugia (Hewitt, 1999). In such cases, however, we would observe lower levels of haplotype diversity within the areas of secondary contact in comparison to the stable areas, because of the reduced number of individual haplotypes coming from each of the colonization fronts.

We detected high genetic distances among populations (Fig. 6c) and a high frequency of private haplotypes within populations (Fig. 6d), suggesting geographic structuring typical for long-term population persistence with limited gene flow (Kerdelhue *et al*., 2009). Such signal contradicts the 'leading edge' as well as the 'phalanx' models of population expansion, where certain genotypes expand across large areas in the direction of the expansion and result in decrease of genetic distances and frequency of private haplotypes (Excoffier *et al*., 2009; Kerdelhue *et al*., 2009). Low genetic distances were only detected within the extreme edges in the northern, southern, and southeastern parts of the species' range (localities 2, 8, 9, 15, 61), in localities that also exhibit low haplotype and nucleotide diversity. These areas could indeed be recently colonized or might represent pockets of isolated populations that exhibit a signal of a population bottleneck consistent with macroecological predictions of

Table 2 Full dataset and localities identified by number, sample size (n), haplotype diversity (H_d), nucleotide diversity (π_d), R_2 test, and mismatch distribution

Locality number	n	H_d	π_d	R_2	SSD	r	Distribution curve
1	11	0.49	0.0010	0.178	0.262**	0.151	Bimodal
2	15	0.65	0.0025	0.100	0.06	0.125	Bimodal
7	12	0.76	0.0101	0.143	0.088	0.145	Multimodal
8	13	0.53	0.0010	0.147	0.009	0.093	Unimodal
13	14	0.85	0.0220	0.189	0.070**	0.079**	Multimodal
15	10	0.87	0.0023	0.132	0.004	0.04	Unimodal
19	14	0.90	0.0215	0.136	0.049**	0.092**	Multimodal
33	18	0.87	0.0081	0.155	0.053	0.076	Multimodal
50	12	0.97	0.0183	0.139	0.014	0.031	Unimodal
51	13	0.96	0.0192	0.133	0.023	0.038	Multimodal
61	10	0.64	0.0012	0.156	0.126	0.424	Unimodal
63	13	0.96	0.0089	0.099*	0.013	0.048	Unimodal
Full dataset	364	0.99	0.0242	0.051	0.003	0.001	Unimodal

The mismatch distribution curves are evaluated as unimodal, bimodal, or multimodal.
*R_2 indicates significant population growth at $P \leq 0.02$.
**Unimodal curves are evaluated for departure from the expansion model at $P \leq 0.05$ using sum of squared deviation (SSD) and Harpending's raggedness index (r).

'core-to-edge' patterns of genetic diversity (Avise, 2000).

The demographic analyses (BSP and mismatch distributions) did not imply significant post-LGM increase in effective population sizes that would be expected if the species experienced a range expansion (Fig. 7a and b). The estimate of effective population size, however, is confounded with genetic structuring (Drummond *et al.*, 2005) which means that highly structured populations with low gene flow will exhibit larger genetic diversity (and therefore seemingly higher effective population size) than panmictic populations (random mating of individuals). Since *D. microps* exhibits pronounced geographic structuring in mtDNA (as apparent from the patterns of genetic diversity; Fig. 6c), the assumption of panmixia might have been violated in both demographic analyses. Accordingly, we also performed mismatch distributions for the 12 sampling locations that had adequate sample size. Samples were collected for each of these localities from a small geographic area (less than 10 km) with no obvious barriers and should approximate a panmictic population. The resulting graphs (Fig. S3 in Supporting Information) further support our conclusions that most populations throughout the species' range did not experience a recent expansion. In summary, we believe that our genetic analyses support the hypothesis that *D. microps* has not experienced a post-LGM northward expansion, but rather was able to retain most of its range despite pronounced climatic and environmental changes since the LGM to present (Fig. 3b). We limit our interpretation of the observed genetic patterns to this general conclusion that is likely robust despite the use of a single mtDNA marker. We avoid overreaching interpretation of geographic structuring and intraspecific divergences as mtDNA can sort quite rapidly and stochastically due to maternal inheritance and a small effective population size (four times smaller than that of nuclear genes), and can even be under a strong selection pressure (Ploetner *et al.*, 2008).

There is no fossil record for *D. microps* dating back to the LGM that would corroborate our interpretation of the genetic data that the species persisted throughout the northern parts of its current range. However, an abundant fossil record spanning the last 11 300 years (end of Pleistocene and Holocene) is available from the Homestead Cave in Northeastern Utah (Grayson, 2000). This fossil record documented fluctuations in numbers of *D. microps* coinciding with climate oscillations throughout the Holocene (Grayson, 2000). At this locality, the species fossil record was quite rare at the end of the Pleistocene and beginning of the Holocene, with a subsequent increase and peak in relative abundance during the middle Holocene, presumably reflecting the warming climate that promoted the increase of *Atriplex* in the area. As the warm middle Holocene ended, fossils of *D. microps* declined in relative abundance again (Grayson, 2000). Our BSPs (Fig. 7a) could indeed be consistent with a decrease in effective population sizes during the late Holocene but our general conclusions do not support the increase in abundance during the early and middle Holocene. We speculate that apparent low numbers of *D. microps* recovered from the oldest strata might result from the geographic position of the

cave. Homestead Cave is situated in the middle of the pluvial Lake Bonneville (near our locality 66) and therefore might not have been colonized until after the water level receded. *Dipodomys microps* might therefore have been only locally but not regionally rare within the Great Basin at the beginning of the Holocene.

'Niche drift' or 'niche evolution'?

Empirical and experimental studies show that species often respond individualistically to environmental change (Graham *et al*., 1996; Parmesan, 2006 and citations within; Colautti *et al*., 2010; Rowe *et al*., 2010). The geographic distributions of many taxa expand and retract their ranges in response to an oscillating climate, as implied from the fossil record (Grayson, 2000; Hockett, 2000) as well as from direct observations of range shifts caused by recent human-induced climate changes (Parmesan *et al*., 1999; Moritz *et al*., 2008). Some taxa have showed plastic responses in morphological, phenological, or physiological characters that allow them to meet the challenge of changing environment *in situ* and thus retain large portions of their current geographic distributions (Post *et al*., 1999; Menzel, 2000; Gibbs & Breisch, 2001; Huppop & Huppop, 2003; Smith & Betancourt, 2003). Such niche responses resulting from an alteration of the realized niche (Jackson & Overpeck, 2000; Rodder & Lotters, 2009) do not require evolutionary adaptation. As such, here we defined a change in realized niche space as 'niche drifting' to differentiate it from 'niche evolution', a change in the fundamental niche of a species. 'Niche evolution' incorporates a shifting or broadening of the niche to meet new environmental conditions through evolutionary adaptation (Davis & Shaw, 2001; Reale *et al*., 2003; Davis *et al*., 2005; Urban *et al*., 2007). Above, we inferred that the climatic niche of *D. microps* has not been conserved between the LGM and present time, but we have not yet addressed the possible mechanisms that may have allowed the species to cope with the changing climate. Thus, we ask the question, has the niche of *D. microps* drifted or evolved?

In a previous study, Csuti (1979) demonstrated that *D. microps* currently exhibits a generalized genotype that allows differential exploitation of food resources between *Atriplex* and *Coleogyne* habitats. In the lab, animals from one habitat were able to adjust behaviorally and physiologically to exploit food resources from the other habitat. Despite this general plasticity, however, the descendants of the *Atriplex* population were still more efficient in shaving the *Atriplex* leaves than the descendants of the *Coleogyne* population, which suggests a certain level of evolutionary adaptation. The idea of a generalized genotype and therefore 'niche drift' seems to be a favored mechanism that allowed the species to persist within the newly developing *Atriplex*-dominated community after the last glacial period. Frequent glacial-interglacial fluctuations of the Pleistocene likely favored the retention of a generalized genotype and prevented fixation of a specialized genotype for any particular habitat. Without the unpredictability conferred by climatic fluctuations, it is possible that differential selective pressure in *Atriplex* and *Coleogyne* habitats would induce genetic differences among populations and promote diversification and specialization.

Interestingly, Kenagy (1973) suggested that it was adaptation to *Atriplex* that allowed *D. microps* to diverge from granivorous congeners in the Pliocene or beginning of the Pleistocene. This adaptation is apparent from set of morphological and physiological traits that confer a potential for *D. microps* to process and metabolize *Atriplex* leaves that is unique among species of kangaroo rats (*Dipodomys* spp.; Kenagy, 1973; Haysen, 1991). These traits are conserved even in *Coleogyne* populations where *Atriplex* consumption is low or where *Atriplex* is not consumed at all. But why would a species specialize to a plant community typical of only short interglacial periods? Although *Atriplex*-dominated communities are likely prevalent only during interglacials (Spaulding *et al*., 1983), *Atriplex* itself was present throughout the entire Pleistocene. In particular, *A. confertifolia* was recorded in non-analogous plant communities within the Mojave Desert and the Great Basin during the last glacial period, mixed with plants currently found in higher altitudes (Spaulding *et al*., 1983). It is currently not clear whether *Atriplex* represented a dominant food source for *D. microps* during glacial periods or whether the species utilized a wider variety of plant material as it currently does in the *Coleogyne* habitat. It is possible, however, that the permanent presence of *Atriplex* facilitated persistence of *D. microps* throughout much of its current range during the profound climate transition following the LGM.

Relevance for future predictions

In the face of ongoing and projected future warming trends, research has increasingly focused on predicting how species respond to climatic and environmental changes. These predictions are often accomplished under the assumptions of a species' niche being conserved through time. However, if the species' niche does not remain conserved but instead shifts through time, the species might not respond to climatic changes in a predictable fashion. Therefore, it is important to identify what taxa are capable of shifting their niches in response to the changing environment. 'Niche shift' vs. 'niche conservatism' can be studied by direct observa-

tions of species' responses to ongoing and simulated climatic changes (Chapin *et al*., 1995; Rowe *et al*., 2010). Alternatively, we show that reconstructions of species' responses to past climatic changes can also be useful in revealing whether a niche of a species is likely to shift or remain conserved through time. We compare the LGM and present time, two time periods that are ideal for studying species' responses to climate change as they represent two extremes of global climate: the LGM is one of the coldest periods of the late Pleistocene in contrast to the current interglacial warm climate (Hewitt, 1999). Species that shifted their ranges in response to environmental change between the LGM and present time to maintain their niche are more likely to do so in the future. On the other hand, species that persisted in place throughout the climatic fluctuation of the late Pleistocene (such as *D. microps*) might respond differently to future climate changes as they might be capable of tolerating conditions beyond their current limits through either 'niche drifting' or 'niche evolution'. Future research should focus on identification of factors and mechanisms that determine whether and to what extent taxa are able to cope with the changing environment.

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Supporting Information

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

Table S1. Samples of *Dipodomys microps* sorted by locality identification number. Ear-clips are identified by a tissue number (LVT – Las Vegas Tissues); vouchers are identified by a tissue and voucher number (MVZ – Museum of Vertebrate Zoology, TTU – Texas Technical University, NMMNH – New Mexico Museum of Natural History). Latitude and longitude are in decimal degrees and WGS 84 datum.

Table S2. Population pairwise F_{ST} values calculated from pairwise differences in ARLEQUIN among 12 populations of *Dipodomys microps* with sample size equal or larger than 10. 'C' and 'A' after the locality number correspond to *Coleogyne* and *Atriplex* populations, respectively. The color shadings delineate values within and between the two habitat types. All values are significant at $P \leq 0.05$.

Figure S1. A phylogenetic tree reconstructed in the program MRBAYES (version 3.1.1) for unique haplotypes of *Dipodomys microps* and relevant outgroups using the following parameters: GTR+I+Γ model, 8 000 000 generations, 25% burn-in, and heating decreased to 0.02.

Figure S2. Scatterplot between nucleotide diversity and sample size (a), nucleotide diversity and latitude (b), genetic distance among populations and latitude (c), haplotype diversity and sample size (d), haplotype diversity and latitude (e), and frequency of private haplotypes and latitude (f) based on control region sequences of *Dipodomys microps*.

Figure S3a. Mismatch distributions for 12 sampling localities with sample size greater than or equal to 10 (graphs 1–6).

Figure S3b. Mismatch distributions for 12 sampling localities with sample size greater than or equal to 10 (graphs 7–12).

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