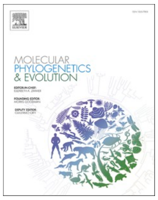
Molecular Phylogenetics and Evolution 180 (2023) 107701

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev



Phylogeography within the *Peromyscus maniculatus* species group: Understanding past distribution of genetic diversity and areas of refugia in western North America

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A R T I C L E I N F O

Keywords:
Deer mouse
Glacial cycles
Population structure
Phylogeography
Refugia

A B S T R A C T

The effects of anthropogenic climate change on biodiversity have been recognized on every continent, ocean, and across different taxonomic groups. Here, we study the range dynamics and demography of a cosmopolitan species: the deer mouse, *Peromyscus maniculatus*. We generated a multilocus SNP dataset using the ddRADseq protocol for 218 individuals across the geographic range within three western North American lineages of this species group. We evaluated population structure using several methods and explored the correlation between geographic and genetic distances. We modeled the demographic history using a site frequency spectrum approach and used a machine learning algorithm to infer current and past (Last Glacial Maximum; LGM) environmental suitability. Lastly, we explored the origin of population expansion for the identified lineages. The genome-wide SNP dataset was able to identify-three regionally distinct groups— 1) *P. m. gambelii* (southern California); 2) *P. keeni* (Pacific Northwest); 3) *P. m. sonoriensis* (a broad population spanning the Pacific Northwest through central California and across the Rocky Mountains into the Great Plains). Demographic analysis indicated the splits between the three populations occurred within the last 500 thousand years, with one very recent (late Holocene) split. Ecological niche models for each of these lineages predicted suitable environment present throughout their known ranges for current conditions, and a severe reduction of northern habitat in the past. The deer mouse has responded to past climate changes by expanding its range during interglacial periods and contracting its range during glacial periods leading to strong population differentiation. But lower magnitude climate change or other processes within the Holocene interglacial period led to population differentiation as well, which is likely still ongoing today given the substantial anthropogenic climate change and other landscape transformations caused by humans during the Anthropocene. By understanding the historical processes that led to the contemporary geographic distribution of biodiversity, we can determine the relative importance of different factors that shape biodiversity, now and into the future.

1. Introduction

The effects of anthropogenic climate change on biodiversity have been recognized on every continent, ocean, and across different taxonomic groups (see Parmesan, 2006 for a thorough review of this literature). Given the looming global biodiversity crisis due to climate change (Barnosky et al., 2011), understanding how species will respond is a central question in ecology and evolutionary biology (Dawson et al., 2011). Species will typically respond with one (or more) of three outcomes: adapt to changing conditions, track their climatic niche, or go extinct (Moritz and Potter, 2013; Parmesan, 2006). Because Earth system conditions are changing quickly today (Moritz and Agudo, 2013) and many species are unable to keep pace with these rates of change through either adaptation or dispersal (Warren et al., 2013), the risk of extinction is elevated (Sinervo et al., 2010). When a species goes extinct, not only do we lose the unique ecological roles played by a species but also all the genetic information uniquely contained in that species. Broadly distributed, cosmopolitan species are often overlooked in part because they have a lower risk of climate change-related extinction (Schwartz et al., 2006), but even for these species, population extirpation could lead to a reduction of genetic diversity and constrain the adaptive potential of the species (Sexton, 2019). It is thus important to

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https://doi.org/10.1016/j.ympev.2023.107701
Received 30 June 2022; Received in revised form 9 December 2022; Accepted 4 January 2023

understand how all species, even those with widespread distributions comprised of many populations, have responded to past climate change.

Populations within a species are the units distributed across space and time that are subject to different ecological and evolutionary constraints and opportunities (O'Neill et al., 2008). For example, the structure of genetic diversity within a species is fundamental to lineage divergence and speciation (Frankham et al., 2002; Yannic et al., 2014), adaptive evolution (Sexton, 2019), and to probability of extinction (Hughes et al., 1997; Urban, 2018). Climate change can influence the intraspecific distribution of genetic diversity through alterations to the ranges of historically significant lineages, alterations to phenotypic plasticity of individuals in different populations, and/or local adaptations to novel environmental conditions (Pauls et al., 2013). Changes in population structure usually reduce genetic diversity for species (Bálint et al., 2011; Pironon et al., 2017). Furthermore, the responses of populations to recent, human-induced climate change are taking place immediately following the loss of intraspecific genetic diversity due to climate change over the last 21,000 years and longer (Hewitt, 2000; Magyari et al., 2011; Miraldo et al., 2016), potentially leading to even more significant population-level diversity impacts. Past and contemporary climate change is also associated with substantial landscape transformation. For example, glacial-interglacial climate change was associated with widespread glaciers that covered large parts of the northern hemisphere (Dansgaard et al., 1993). To truly understand how intraspecific genetic diversity has been influenced by climate, we need to integrate our understanding of dynamic climate change through time with spatial landscape processes (Alvarado-Serrano and Knowles, 2014; Knowles and Alvarado-Serrano, 2010).

Climate refugia (termed refugia hereafter) are local areas with the appropriate environmental conditions to allow species to persist through time as climate and landscapes change (Keppel et al., 2012; Gavin et al., 2014); these regions should be particularly important for structuring intraspecific genetic variation. Refugial areas could harbor greater genetic diversity and influence the ability of a species to adapt to new environmental changes because adaptation potential is dependent on historical population structure (Dynesius and Jansson, 2000). Thus, identifying refugial regions for single species, and more importantly, refugia shared by multiple species, could be highly relevant to conservation efforts; such regions could indicate areas that are climatically stable through time and support higher genetic diversity even in unsampled species (Carnaval et al., 2009), and serve as reservoirs facilitating future adaptation with anthropogenic climate change (Gavin et al., 2014). By studying the dynamic climatic oscillations of the Pleistocene and Holocene and how species contracted into and expanded out of refugia as they responded to past climate changes, we can further our understanding of the processes that shape genetic diversity across the landscape.

The North American deer mouse, *Peromyscus maniculatus*, represents a good study system for addressing the impacts of climate-mediated historical population distribution and refugia on genetic diversity. *Peromyscus maniculatus* is indigenous to and distributed widely across North America (Shorter et al., 2012) and can be found in every terrestrial ecosystem (Dewey and Dawson, 2001); it thus is exposed to different environmental and climatic conditions across its geographic range. Based on mitochondrial DNA, *P. maniculatus* is likely a species complex, with six hypothesized monophyletic lineages (species names recognized by Bradley et al., [2019] are indicated in parentheses): 1) Northeastern USA and Eastern Canada (*P. maniculatus*); 2) Northeastern USA and Central Canada (*P. maniculatus*); 3) USA central plains (*P. sonoriensis*); 4) Southern California, USA (*P. gambelli*); 5) New Mexico, Arizona and Northern Mexico, USA (*P. sonoriensis*); 6) Western Canada and USA Pacific Northwest, California and as far east as Kansas, USA (*P. sonoriensis*) (Bradley et al., 2019; Dragoo et al., 2006; Greenbaum et al., 2019; Kalkvik et al., 2012). Additionally, there other several other recognized species that cluster phylogenetically within the *P. maniculatus* species complex: *P. keeni* (Rhoads, 1894; Zheng et al., 2003), *P. polionotus* (Hall, 1981; Osgood, 1909), *P. arcticus* (Bradley et al., 2019; Greenbaum et al., 2019; Lucid and Cook, 2007), and *P. melanotis* (Allen and Chapman 1897). *Peromyscus polionotus* occupies southeastern USA (the one region in North America *P. maniculatus* is not found), *P. melanotis* occurs throughout Mexico, and both *P. keeni* and *P. arcticus* occupy the North American Pacific Northwest. Recently, there has been a call to elevate some of the monophyletic lineages within the *P. maniculatus* species group to distinct species, in addition to those species already recognized, resulting in at least 9 species within the *P. maniculatus* species complex; however, this was based solely on mitochondrial DNA (Bradley et al., 2019; Greenbaum et al., 2019). Given the taxonomic complexity, especially related to the putative *P. sonoriensis* and *P. gambelii* [i.e., *P. sonoriensis* potentially includes multiple lineages (lineages 3, 5, and 6; Bradley et al., 2019) and *P. gambelii* was elevated to species in a recent study using only mitochondrial DNA (Greenbaum et al., 2017)], we consider these two taxa as subspecies throughout the rest of the manuscript.

Besides the suitability of *Peromyscus maniculatus* as a study system based on their broad range, it is important to understand the evolutionary history and population dynamics of *P. maniculatus* because they are reservoirs for several diseases, such as hantavirus and Lyme disease (Dragoo et al., 2006), and potentially SARS-CoV-2 (Fagre et al., 2020); different species of deer mice may serve different roles in disease transmission and effects, based on their genetic background or species interactions (Bedford and Hoekstra, 2015). But most relevant here, different populations of this species have already exhibited different responses to recent climate change, demonstrating potential for population-level variation to have long-term effects. A population of deer mice in Yosemite National Park has not shifted its elevational distribution in response to recent environmental change (over the last 100 years) (Moritz et al., 2008), though there may have been a cryptic geographic shift in genetic variation (Yang et al., 2011). In contrast, a population of *P. maniculatus* has shifted its distributional range over a recent ~ 30 year period in Michigan (moving northward; Myers et al., 2009), demonstrating that climate has likely influenced this population, and potentially the spatial population structure, in the recent past. Populations of *P. maniculatus* at different elevations exhibit different physiological performances and show different patterns of gene expression, which may be due to differences in local population structure and adaptation (Storz et al., 2019). Thus, changes to gene flow and population structure through time as a result of climate may have direct fitness consequences for different populations of deer mice.

Here, we focus on the ecological and evolutionary processes that have structured genetic diversity within several western North American lineages in the *P. maniculatus* species group (Fig. 1). We generated a multilocus SNP dataset on 218 individuals to answer two key questions: 1) Do we recover the distinct mtDNA lineages found in other studies (Bradley et al., 2019; Dragoo et al., 2006; Greenbaum et al., 2019, 2017; Kalkvik et al., 2012) using a genomic dataset? 2) What were the potential areas of refugia for each of these identified lineages throughout western North America, given the contemporary range of the *P. maniculatus* species group encompasses both previously glaciated and unglaciated regions? It has been suggested that lineages recognized as *P. maniculatus* only inhabited areas south of the continental ice sheets during the Last Glacial Maximums (Dragoo et al., 2006; Sawyer et al., 2017), and so we determine if genomic data provides evidence for refugia in Pacific Northwest coast or Beringia. We first detect the historical population structure found within these three lineages, and then use several different analyses to detect possible areas of refugia throughout North America.

2. Materials and Methods:

2.1. ddRAD library preparation and sequencing:

Genomic DNA was extracted from 218 individuals within the

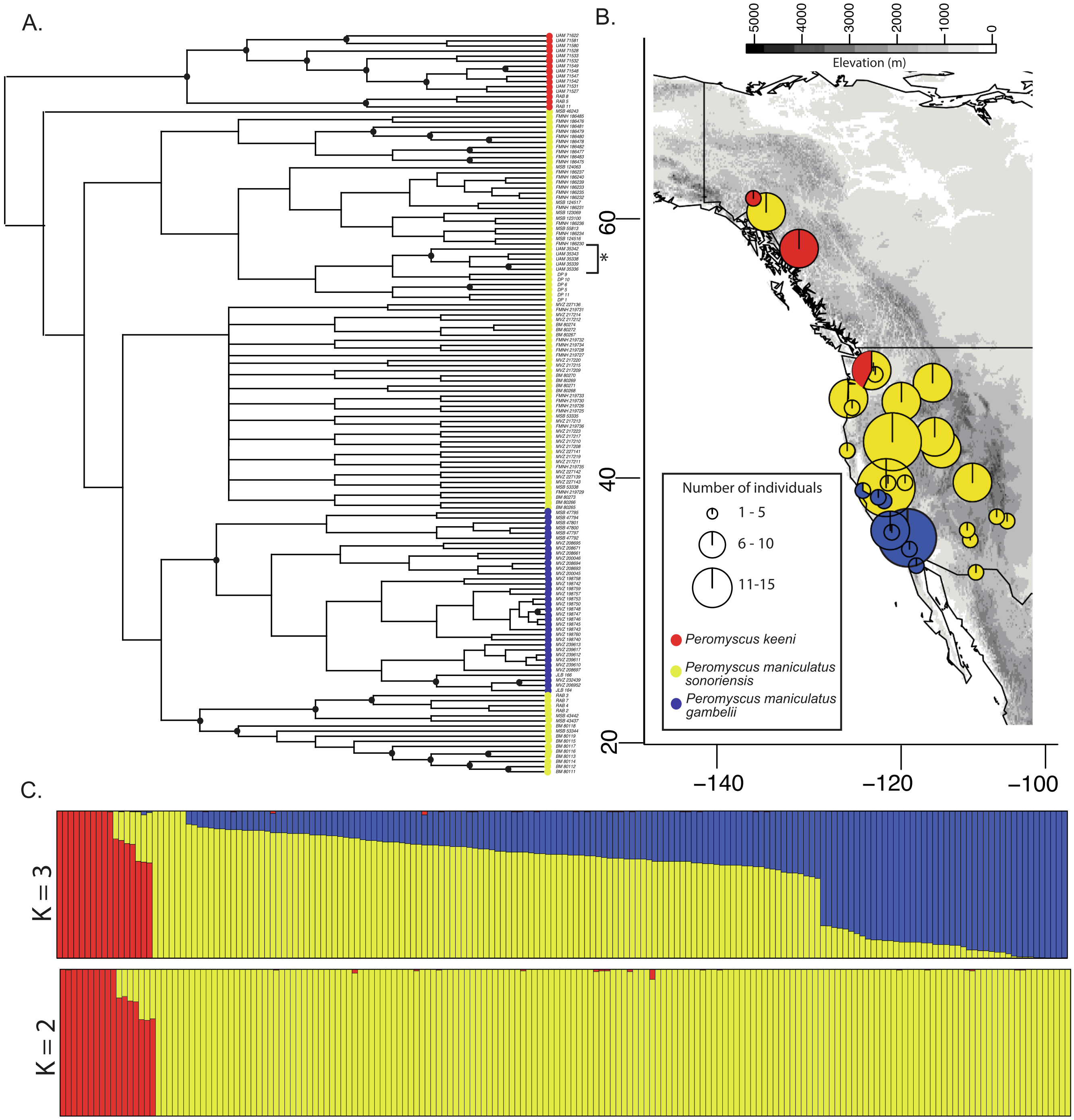

Fig. 1. The geographic structure of the *Peromyscus maniculatus* species complex across its range in western North America. A) phylogenetic relationships between individuals for the "highest quality" dataset, B) geographic position of the sampled localities, and C) STRUCTURE results showing $K = 2$ and $K = 3$. Colors on the branch tips correspond to the population assignment for STRUCTURE and DAPC for K = 3, and the size of the circles on the map indicate the number of individuals sampled per locality. The black circles at nodes indicate bootstrap support greater than 70. * is used to denote the Canadian locality found within *P. m. sonoriensis*.

Peromyscus maniculatus species group (and three individuals of *P. boylii* and *P. californicus* to serve as an outgroup) from 31 localities across the western North American range (Fig. 1; Supplementary Table 1) using a Qiagen extraction kit (Qiagen Inc.). Samples were obtained from fieldwork and several museum collections: Burke Museum ($n = 30$), Field Museum ($n = 33$), Museum of Southwestern Biology ($n = 29$), Museum of Vertebrate Zoology ($n = 75$), and University of Alaska Museum of the North ($n = 21$; Supplementary Table 1). Additionally, we received tissues from 10 individuals in Montana from Dr. Dean Pearson. We generated genomic SNP datasets using the ddRAD protocol (Peterson et al., 2012) and as detailed in Boria et al. (2020). Briefly, we digested 500 ng of genomic DNA with restriction enzymes *EcoR1* and the rare-cutting enzyme *MSP1*. We pooled and purified the tagged samples (12 individuals per pool) and used a Pippin Prep to size select for fragments between 300 and 500 bp long. Each pooled library was amplified via PCR with a second index primer to differentiate between all individuals. Finally, the libraries were sequenced at UC Berkeley on two lanes of an Illumina HiSeq 4000 to produce 50 bp single end reads (Supplementary

Table 2).

We cleaned and filtered the Illumina HiSeq raw reads using the iPyrad pipeline (v 0.9.65; Eaton and Overcast, 2020). Raw reads were aligned to a draft genome of *Peromyscus maniculatus* (NCBI: GCA 000500345.1). We used the iPyrad default settings, changing only to a 75 % threshold as the minimum number of individuals needed to retain a locus (we explored the effect of missing data using 50 %, 75 %, and 90 % thresholds and determined it had little influence on inference of population structure and the phylogenetic analyses). To increase the number of SNPs recovered by removing samples that did not sequence well, we excluded 19 individuals that had greater than 95 % missing data and reran the iPyrad pipeline (Cerca et al., 2021). Following the second iteration of iPyrad, we removed an additional 11 samples that had greater than 70 % missing data. Additionally, two individuals clustered with outgroup specimens in several preliminary analyses and were excluded from any downstream analyses because they may have been misidentified as *P. maniculatus* upon original collection. We retained 186 individuals for analyses: 180*P. maniculatus* species group, 3*P. californicus*, and 3*P. boylii*. Finally, we used vcftools to further filter the dataset to include only one biallelic SNPs and a thinning parameter of 50 bp (Danecek et al., 2011; see Supplementary Table 3 for which individuals are included in each analysis).

2.2. Population structure:

We used one model-based approach and one non-model-based approach to investigate population structure. Both methods attempt to determine the optimal number of populations present within the dataset. We used the non-model based method DAPC (Discriminate analysis of principal components) in the Adegenet package (Jombart, 2008; Jombart and Ahmed, 2011) in R (v. 3.5.1; R core team, 2020) to infer structure. For the DAPC analysis, we used Bayesian information criterion to determine the optimal number of populations. The model-based approach we ran was STRUCTURE (v 2.3.4; Pritchard et al., 2000), a Bayesian-clustering algorithm that identifies population structure. We ran it for 50,000 burn-in generations, 500,000 generations, $K = 1$–5 populations, for five iterations, and only used one SNP per loci. We only explored $K = 1$–5 populations based on previous *Peromyscus maniculatus* studies (Bradley et al., 2019; Dragoo et al., 2006; Greenbaum et al., 2019, 2017; Kalkvik et al., 2012). We used the Evanno method (Evanno et al., 2005) in Structure Harvester (v. 0.6.94; Earl and vonHoldt, 2012) to determine the optimal number of populations. To identify substructure, we re-ran STRUCTURE on the largest identified population for 50,000 burn-in generations, 250,000 generations, $K = 1$–5 populations, and for five iterations. Based on the population structure analyses, we assigned every individual to each lineage using previous research that included a subset of the specimens as anchors for the species or subspecific assignments. For example, some specimens used in this study had at least mitochondrial DNA previously sequenced (Dragoo et al., 2006, Sawyer et al., 2017, Bradley et al., 2019), so we considered the lineage assignments based these studies as anchor points and assigned newly sequenced individuals that clustered genetically or geographically with those anchor individuals to the same lineage name. Once we identified the optimal number of populations, we calculated pairwise Fst values between each population using the hierfstat R package (v. 0.1.17; Goudet, 2005).

We used a tree-based method to model the relationships between populations and admixture between sampling sites, Treemix (Pickrell and Pritchard, 2012). This method first builds a maximum likelihood tree, then adds potential migration paths and recalculates the likelihood scores. We consolidated four one-sample localities with nearby sampling sites (within 75 km) for a total of 27 populations (SFig. 1). We ran Treemix for 10 iterations for up to 10 migration vertices with 100 bootstrap replicates. We used the r package, OptM (Fitak, 2021), to determine the optimal number of migration vertices.

To determine if the patterns indicated by the population structure programs were caused by historical population structure and not isolation by distance (IBD), we ran a Mantel test on the genetic and geographic distances between individuals. We examined the Mantel test significance with 10,000 permutations in the Adegenet package (Jombart, 2008; Jombart and Ahmed, 2011). Further, we plotted the genetic and geographic distances among all individuals to determine if there was a distinct cline indicative of IBD or separate patches of individuals representative of distinct populations. Lastly, we assessed significance of IBD within each of the populations identified by the structure analyses.

2.3. Phylogenetic analyses:

We inferred phylogenetic relationships between individuals using two methods: 1) SVDquartets (Chifman and Kubatko, 2015); 2) a phylogenetic network analysis. We implemented SVDquartets using a multi-species coalescent model in PAUP* (v4.0a; Swoford, 2003), utilizing all quartets and 100 bootstrap replicates. We ran SVDquartets with two datasets: 1) a 'whole' dataset, which consisted of all 180 ingroup + 6 outgroup individuals; and 2) a 'highest-quality' dataset, in which we only used individuals that contained<30 % missing data (147 ingroup + 6 outgroup individuals) to reduce the amount of missing data and improve the phylogenetic resolution. Additionally, we used Splitstree (V 4.14.8; Huson and Bryant 2006) with only the *Peromyscus maniculatus* species group individuals to generate a phylogenetic network. We calculated distances between all ingroup individuals using the Jukes Cantor model (Jukes and Cantor 1969) and used the neighbornet method to build the network.

2.4. Demographic modeling:

We used a coalescent-based approach to model the demographic history, specifically with respect to isolation, population growth, and migration. We selected and parameterized the best-fit demographic model using fastsimcoal2 (FSC2, v2.5.2; Excoffier et al., 2013), which estimates demography from the site frequency spectrum (SFS). Users specify hypotheses with differing levels of complexity and fastsimcoal2 uses simulations to estimate the likelihood of competing hypothesis with different parameters. Individuals were assigned to populations using a 3-population model based on the population structure analyses (see above), with admixed individuals assigned to the majority population. We generated the observed joint SFS using code developed by Isaac Overcast (https://github.com/isaacovercast/easySFS).

We tested 17 different demographic scenarios (SFig. 2). Briefly, they describe variations of a 3-population model that have two divergence events with every possible topology and vary in the amounts of migration between populations and timing of population divergence. Additionally, we used a nuclear mutation rate of $5.4\text{x}10^{-9}$ mutations/site/generation based on estimates from germ line laboratory mice (Uchimura et al., 2015) and used an estimated 0.5 year generation time to convert to divergence times (Hager et al., 2022; Harris et al., 2016). For each model we ran 75 replicate fastsimcoal2 analyses, each using 250,000 coalescent simulations. We selected the best fit model by calculating AIC and ΔAIC scores to account for the differing number of parameters, following the guidelines of Excoffier et al. (2013). To ensure the simulations were not only sampling parameter estimates from a local maximum, we ran five replicates for each model starting with different initial conditions and chose the model with the highest likelihood score. Once the best model was obtained, we re-estimated parameter values by simulating 100 SFS from the maxL.par file and determining the mean parameter estimate and 95 % confidence intervals. We accounted for *P. maniculatus* being diploid by dividing the fastsimcoal2 estimates in half.

2.5. Effective genetic diversity and connectivity:

We visualized the spatial population structure and migration using the program EEMS (Estimated Effective Migration Surfaces; Petkova et al., 2016). This method requires no environmental data and uses SNP data at every sampling locality to calculate a pairwise dissimilarity matrix to identify regions where genetic similarity declines rapidly using an isolation-by-distance model. We conducted three independent runs using four different deme sizes (250, 500, 750, and 1,000), with a 1,000,000 burn-in period followed by a 21,000,000 MCMC run. The results across all runs were combined using the REEMSplots R package (Petkova et al., 2016). We assessed convergence across runs and plotted the effective genetic diversity and effective migration surfaces.

2.6. *Ecological niche modeling:*

We generated lineage-specific ecological niche models (ENMs) to predict areas of refugia. Occurrence localities were compiled from the fieldwork and museum specimens used in this study (see above, Supplementary Table 1). Additionally, we supplemented these data with localities that had associated genetic data from Kalkvik et al. (2012) and Sawyer et al. (2017) (Supplementary Table 4). To remove spatial biases, we spatially filtered the dataset to ensure no two localities were within 25 km of one another (Boria et al., 2014) using the R package spThin (Aiello-Lammens et al., 2015). For environmental data, we used Community Climate Simulation Model 3 (CCSM3; Liu et al., 2009). CCSM3 variables were downscaled to 50 × 50 km degree grid cells for North America from 21,000 years ago to the present day (Lorenz et al., 2016). To approximate modeling assumptions regarding dispersal and biotic interactions more closely, we delimited a custom study region by drawing a minimum convex polygon around the localities and adding a 5.0° buffer (Anderson and Raza, 2010; Barve et al., 2011). We used a machine learning algorithm, maxent (V3.4.1; Phillips et al., 2017; Phillips et al., 2006) to infer the ENMs. We calibrated and evaluated the models using a geographically structured 5 *k-fold* approach (Radosavljevic and Anderson, 2014) in the ENMeval package in R (Muscarella et al., 2014). To select species-specific model settings approximating optimal levels of complexity, we tuned model settings by varying different combinations of feature class and regularization multiplier (RM; Shcheglovitova and Anderson, 2013). To identify the optimal parameter settings, we evaluated model performance using sequential criteria (minimizing overfitting and then maximizing discriminatory ability; Shcheglovitova and Anderson, 2013; Muscarella et al., 2014). We used the optimal settings to project each of the ENMs into current climatic conditions and the LGM. We generated maps of stable regions through time for each lineage by thresholding each ENM and adding the time periods together.

2.7. *Range Expansion:*

We inferred areas of refugia by examining origins of recent range expansion within the three lineages: *Peromyscus maniculatus gambelii* (southern California); 2) *P. keeni* (the Pacific Northwest); 3) *P. m. sonoriensis* (a broadly distributed population spanning the Pacific Northwest through central California and across the Rocky Mountains into the Great Plains). For *P. m. sonoriensis*, we divided the range into three regions following the results from the EEMS analysis inferring migration (see above, section 2.5) and regions previously identified as areas of refugia for many tree species (Roberts and Hamann, 2015): 1) Pacific Northwest (PNW); 2) Rocky Mountains through the US Great Basin (GB); and 3) Southwestern US (SW [See SFig. 1]). We used the rangeExpansion package in R (Peter and Slatkin, 2013) to detect range expansion and infer the estimated location of the origin of expansion. The rangeExpansion package does this by calculating a directionality index (ψ), using SNP datasets and spatial coordinates, based on allele frequency clines found between multiple populations (Peter and Slatkin, 2013). Populations at the expanding edge will tend to have lower genetic diversity because of serial founder events and higher fixation rates (Peter and Slatkin, 2015). For this analysis, we only used SNPs that were present in at least 75 % of individuals within each lineage.

3. Results

3.1. *Sequence data*

We obtained 482,988,240 raw reads from the Illumina HiSeq 4000 runs across all individuals, and after removing individuals that did not sequence well and rerunning iPyrad, there were 786,528 prefiltered loci. After iPyrad quality filtering, 22,555 loci were retained with 178,389 SNPs across loci (Supplementary Table 5). Following filtering for one biallelic SNP per 50 bp, we retained 28,334 SNPs.

3.2. *Population structure and isolation by distance*

DAPC analysis identified $K = 3$ as the optimal number of populations (SFig. 3) and was consistent with the three major mtDNA-based lineages: 1) *Peromyscus maniculatus sonoriensis* (a broad “Northern” population spanning the Pacific Northwest through central California and across the Rocky Mountains into the Great Plains); 2) *P. m. gambelii* (San Francisco Bay through Baja); and 3) *P. keeni* (the Pacific Northwest); (SFig. 1A). Structure indicated a $K = 2$ (*P. m. sonoriensis* + *P. m. gambelii*; *P. keeni*) model best fit the data (SFig. 4), however, a $K = 3$ model provides the same population structure as DAPC. Both methods assigned the same individuals to the same population when using the $K = 3$ model: *P. m. sonoriensis* (119 individuals); 2) *P. m. gambelii* (44 individuals); 3) *P. keeni* (17 individuals). Further, Structure on the *P. m. sonoriensis* + *P. m. gambelii* groups identified $K = 2$ as the optimal model (SFig. 5). Pairwise F_{ST} showed strong differentiation between the *P. keeni* group and both the *P. m. sonoriensis* ($F_{ST} = 0.22$) and *P. m. gambelii* ($F_{ST} = 0.3$) groups and moderate differentiation between *P. m. sonoriensis* and *P. m. gambelii* ($F_{ST} = 0.06$; Supplementary Table 6). Given the similarity in population structure results among the model-based (Structure) and non-model-based (DAPC) approaches, we adjusted downstream analyses to reflect $K = 3$.

Treemix analyses produced a population graph that supported a phylogeographic division between *Peromyscus maniculatus* and *P. keeni*, and *P. m. gambelii* was nested within *P. m. sonoriensis* (SFig. 6). The optimal number of migration edges was $m = 2$ (SFig. 7). Both migrations edges involved *P. keeni*. One migration edge was from a *P. keeni* population in British Columbia to a population in Washington that contained three *P. keeni* individuals. The other migration edge was from a *P. m. sonoriensis* population in Arizona to a *P. keeni* population in British Columbia (SFig. 6),

The Mantel test showed significant isolation by distance for the overall dataset ($r = 0.61$, $p < 0.001$) with a distinct cline (SFig. 8A). We also discovered significant IBD within each lineage with distinct clines (SFig. 8B-D): *Peromyscus maniculatus sonoriensis*: $r = 0.427$ ($p < 0.001$); *P. m. gambelii*: $r = 0.222$ ($p < 0.001$); *P. keeni*: $r = 0.919$ ($p < 0.001$).

3.3. *Phylogenetic analyses*

Both the ‘whole’ and the ‘highest-quality’ SNP datasets produced weakly supported SVDquartets trees (Fig. 1; SFig. 9). For both datasets, there were two major monophyletic groupings: *Peromyscus maniculatus sonoriensis* + *P. m. gambelii* and *P. keeni*. Because the SVDquartets trees were similar, we continue with the ‘highest-quality’ dataset that incorporated the least amount of missing data. Although the tree was weakly supported, there were several well supported clusters of individuals. The *P. keeni* individuals formed a well-supported monophyletic group (red individuals in Fig. 1; SFig. 9). The *P. m. gambelii* individuals were nested within the *P. m. sonoriensis* group, and they clustered together in a strongly supported clade (and some relationships were well supported) (blue in Fig. 1) and its sister monophyletic group of *P. m. sonoriensis* individuals was also strongly supported; however, the overall group was weakly supported. Another group of individuals that was well supported were 7 individuals from the same locality in Canada, which were a part of the *P. m. sonoriensis* lineage (denoted by * in Fig. 1). The phylogenetic network analyses produced similar results: *P. m. gambelii* and *P. keeni* formed their own individual clusters and *P. m. sonoriensis* formed one large cluster with three individuals forming a cluster between *P. m. gambelii* and *P. keeni* (SFig. 10).

3.4. Demographic modeling

Using FSC2, the model that best fit the data according to AIC was scenario 14 (Table 1; Supplementary Table 7; Fig. 2). This model indicates the *P. maniculatus sonoriensis* and *P. m. gambelii* lineages coalesced most recently, with an older coalescent event between this cluster and *P. keeni* (Fig. 2; see Supplementary Table 8 for confidence intervals). This model also indicated there was no migration between the lineages. No other model had a reasonably close fit to the data (ΔAIC $<$ 5; Table 1).

Scenario 14 estimated the *P. maniculatus sonoriensis* and *P. m. gambelii* populations coalescing about 2,816 years ago (2,543 – 3,088) and the ancestral lineages coalescing with *P. keeni* about 468 kya (466,088 – 469,223; Fig. 2). All three lineages had large effective population sizes (greater than50 thousand individuals), though the model suggests the *P. m. gambelii* lineage experienced a population contraction event within the last 2,000 years, with effective population sizes decreasing from over one million to<100 thousand individuals.

3.5. Effective genetic diversity and connectivity

The EEMS analysis indicates there has been migration within the three lineages; however, there was minimal migration between them (Fig. 3A; orange indicates regions of lower-than-expected migration and blue shows regions of higher migration rates). Specifically, the core distributions of *Peromyscus keeni* (coastal western Canada) and *P. m. gambelii* (southern California) have strong migration barriers surrounding these regions. *Peromyscus m. sonoriensis* was the only lineage to have within-population migration barriers. Much of the range in western US has higher diversity than expected, except on the coast of the Pacific Northwest and southern California. Much of the range on the Canadian west coast has much lower genetic diversity than expected (Fig. 3B; orange displays regions of lower effective diversity and blue illustrates areas of higher effective diversity).

3.6. Ecological niche modeling

The *Peromyscus keeni* optimal Maxent settings were Linear, Quadratic, and Hinge features with a RM = 5.0 and had an AUC of 0.86 and an omission rate of 0.05 (Supplementary Table 9). The best settings for *P. m. gambelii* was the Hinge feature with a RM = 6.0 and had an AUC of 0.68 and an omission rate of 0. The optimal Maxent settings for *P. m. sonoriensis* was the Hinge feature with a RM = 2.0 (Supplementary Table 9). This model had an AUC of 0.71 and an omission rate of 0. For each lineage, the ENM inferred suitable environment present throughout the entire known range of these lineages for current conditions, and a reduction of potentially suitable areas during the LGM relative to the contemporary range (Fig. 4). Stable regions mainly occurred along the North American western coast for each lineage (SFig. 11).

Table 1
Top five demographic scenarios using fastsimcoal2 according to AIC scores for the *Peromyscus maniculatus* species complex across its range in western North America. Scenario 14 was clearly indicated as the model that best fit the data.

Scenarios	Parameters	AIC	ΔAIC	AIC$_W$
S14	10	338693.92	0	0.999
S5	13	340828.30	2134.38	<0.001
S14	13	340842.29	2148.37	<0.001
S7	15	340850.08	2156.16	<0.001
S6	13	340880.92	2186.99	<0.001

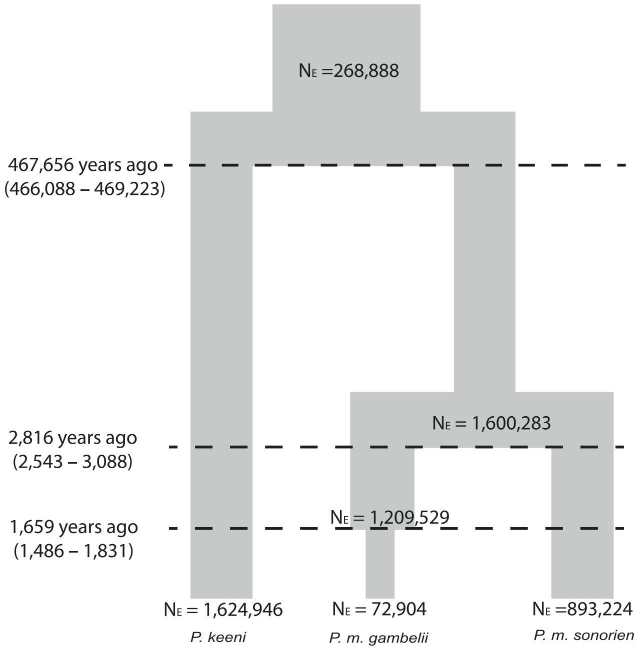

Fig. 2. The best fit scenario (S14) and parameter estimates of demographic history for the *Peromyscus maniculatus* species complex in western North America. The width of the gray bars indicates Ne (effective population size) and dashed lines indicate inferred timing (and confidence intervals) of different events such as population size contraction and lineage divergence.

3.7. Range expansion

For *Peromyscus keeni*, the range expansion analysis indicated the origin of expansion was in western British Columbia, Canada (near the southeastern Alaskan border; Fig. 4; Supplementary Table 10). The origin of expansion for the *P. m. gambelii* population was around the San Francisco Bay area. For *P. m. sonoriensis*, there were multiple potential areas of expansion. The PNW region had an origin of expansion in northwest British Columbia, Canada. The GB had an origin of expansion in northern Utah, and the SW region expanded from the US-Mexican border near New Mexico (Fig. 4).

4. Discussion

The spatial distributions of intraspecific genetic diversity and the role of climate refugia shapes the evolutionary and ecological processes of populations and possibly determines the potential for population and species persistence in the face of future climate change (Brown et al., 2016; Pauls et al., 2013; Yannic et al., 2014). By using a multilocus SNP dataset combined with ENMs and demographic modeling, we were able to determine the dynamic history of several lineages within the *Peromyscus maniculatus* species group across western North America. Here, we show how three lineages within the *P. maniculatus* species group have responded to past climatic shifts by contracting and expanding their ranges over the last 500,000 years, and the influence of those changes on overall genetic diversity across the species.

4.1. Taxonomic implications for Peromyscus maniculatus

Peromyscus maniculatus represents a likely species complex with several recognized species within the clade. There have been several recent attempts to break up the complex into several distinct species

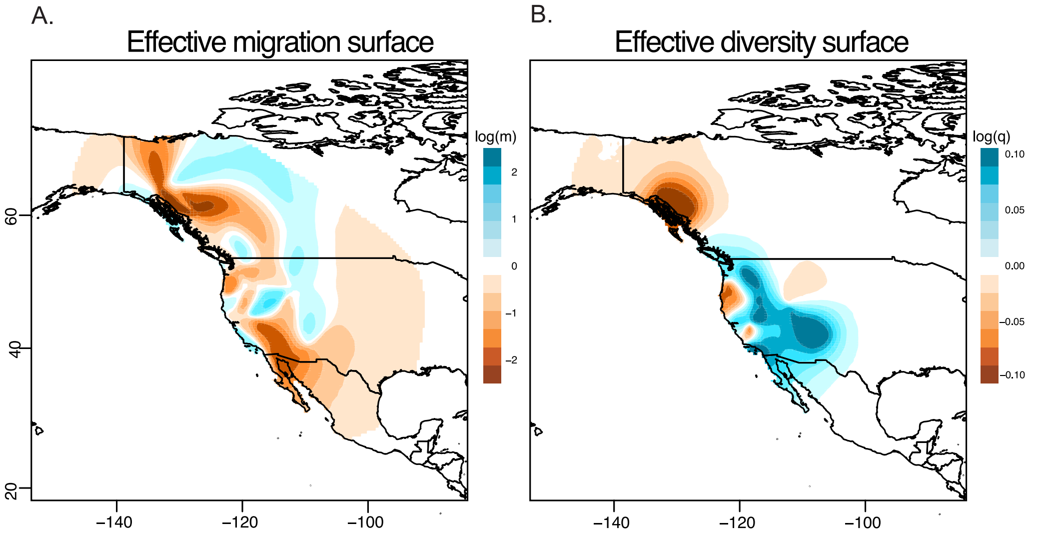

Fig. 3. Models of effective migration rates (A) and effective genetic diversity (B) as inferred by EEMS for the *Peromyscus maniculatus* species complex in western North America. For effective migration rates (A), orange indicates regions of lower than expected migration and blue shows regions of higher migration rates. For effective genetic diversity (B), orange displays regions of lower effective diversity and blue illustrates areas of higher effective diversity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Bradley et al., 2019; Greenbaum et al., 2019), in part because highly-supported mitochondrial DNA phylogenetic trees show six monophyletic lineages within *P. maniculatus* (see also Dragoo et al., 2006; Kalkvik et al., 2012). Focusing only on western North American lineages, we were able to recover three lineages within the species complex (Fig. 1). Both, *P. m. sonoriensis* and *P. m. gambelii* have been recommended or raised to the species level in recent taxonomic revisions (Bradley et al., 2019; Greenbaum et al., 2019, 2017). However, the current analyses, using 28,000 genome wide SNPs, show *P. m. sonoriensis* and *P. m. gambelii* are either very recently diverged or in the process of diversification and should not yet be raised to the distinct species. Given this active diversification and also our focus on sampling just in western North America, any further inferences regarding taxonomic status of *P. m. sonoriensis* and *P. m. gambelii* risk overinterpretation. Additional sampling across the full potential geographic distribution of *P. m. sonoriensis* may clarify lineage structure within this group and in relation to other lineages, but may also simply reinforce the very active diversification occurring within this lineage.

Another point of interest has been the placement of *P. keeni* within the species complex (Chirhart et al., 2005). Previous studies using mitochondrial markers or microsatellite data have found that *P. keeni* is more closely related to *P. m. gambelii* than the much geographically closer *P. m. sonoriensis* lineage (Bradley et al., 2019; Chirhart et al., 2005; Greenbaum et al., 2019, 2017; Kalkvik et al., 2012). However, Sawyer et al. (2017) used mitochondrial DNA and four nuclear loci with an emphasis on assessing the relationships among *Peromyscus* species in the Pacific Northwest. This study indicated a more recent common ancestor between the *P. m. gambelii* and *P. m. sonoriensis* lineages than either had with *P. keeni*. However, the tree lacked strong statistical support, similar to the results found here, likely due to incomplete lineage sorting (Sawyer et al., 2017). Here, using a multilocus dataset, we found support for the hypothesized relationships from Sawyer et al. (2017): population-level and demographic analyses both indicated *P. m. gambelii* and *P. m. sonoriensis* share a more recent common ancestor than either lineage does with *P. keeni* (Fig. 1; Fig. 2). Much more data (genomic and morphological data from across all geographic regions and not just western North America) is needed to fully resolve lineage relationships within *P. maniculatus* broadly, and more in-depth genomic sampling is needed to understand the dynamic, population-level processes in the Pacific Northwest in particular.

4.2. Impacts of glacial cycles on population structure

Pleistocene glacial-interglacial cycles have impacted the distribution of genetic diversity (Burbrink et al., 2016; Hewitt, 2004; Hope et al., 2015) and led to cycles of population fragmentation and merger in many North American species (e.g., Arbogast, 2007; Boria et al., 2020; Jezkova et al., 2016, 2015; Malaney et al., 2013; Massatti and Knowles, 2016; Reid et al., 2019; Sim et al., 2016). This appears to be particularly true for *Peromyscus maniculatus*: most of the diversification events within the *P. maniculatus* species complex likely occurred during the Pleistocene (Dragoo et al., 2006; Kalkvik et al., 2012). Our population structure analyses were able to identify-three major lineages within the western range of the *P. maniculatus* species group: 1) *P. m. sonoriensis* (a broadly distributed population spanning the Pacific Northwest through central California and across the Rocky Mountains into the Great Plains); 2) *P. m. gambelii* (southern California); and 3) *P. keeni* (the Pacific Northwest) (Fig. 1; SFig. 1). Although these lineages have been previously sequenced, previous work was based on only a few loci, overall population structure was based solely on phylogenetic trees (see §4.1, *Taxonomic implications for Peromyscus maniculatus* for further discussion on deer mouse phylogenetics; Dragoo et al., 2006; Kalkvik et al., 2012; Sawyer et al., 2017; Bradley et al., 2019; Greenbaum et al., 2019) and detailed population structure was unknown. Our dataset and analyses recovered the *P. m. sonoriensis, P. m. gambelii, and P. keeni* groups similar to monophyletic lineages found in previous studies (Bradley et al., 2019; Dragoo et al., 2006; Greenbaum et al., 2019, 2017; Kalkvik et al., 2012; Sawyer et al., 2017).

The demographic analysis based on the SFS indicates the divergence between the *Peromyscus keeni* population and the lineage leading to the *P. m. gambelii / P. m. sonoriensis* populations dates back to about 468 thousand years ago (Fig. 2), which is older than previous estimates (Sawyer et al. 2017). This timing coincides with the Marine Isotope Stage (MIS) 12 glacial period (Lisiecki and Raymo, 2005). The Laurentide and Cordilleran ice sheets likely were close to their maximal extent during this stage and covered much of northern North America with minimal separation between the two ice sheets (Batchelor et al., 2019), potentially restricting the *P. maniculatus* lineage to south of the ice sheets. Following the MIS 12 glacial stage, *P. maniculatus* likely expanded from a refugium in the southern part of North America as temperatures warmed during the MIS 11 interglacial (approximately 443 kya; Lisiecki and Raymo, 2005). The demographic model, EEMS and Treemix analyses indicate little to no migration between *P. keeni* and either of the other two populations (Table 1; Fig. 3; SFig. 5), and there is also high population differentiation between *P. keeni* and the other two lineages (Supplementary Table 6). Together, this is strong evidence that *P. keeni* remained isolated enough through the subsequent glacial and interglacial periods to maintain significant population differentiation.

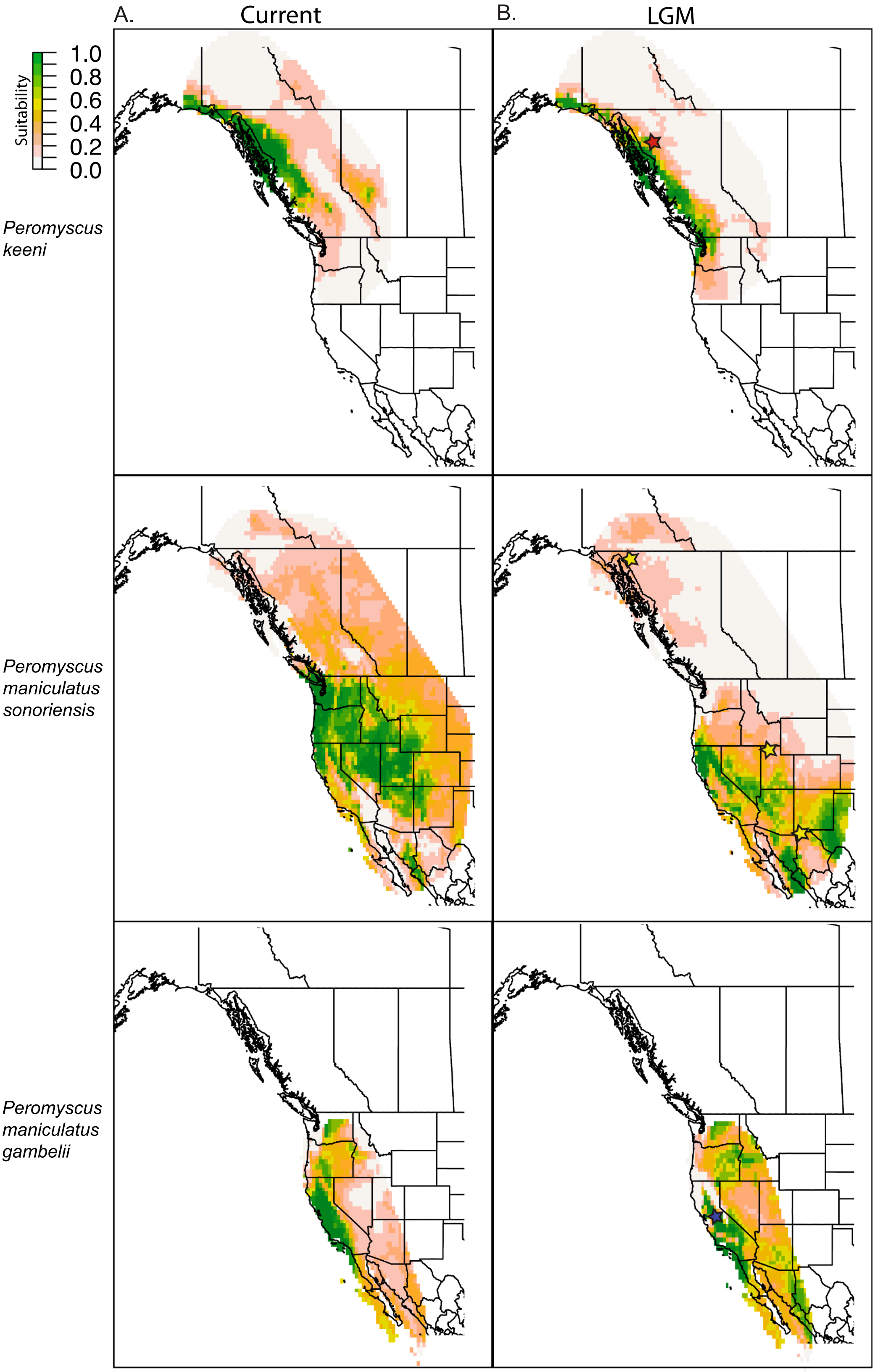

Fig. 4. Ecological niche models and range expansion analyses for each *Peromyscus maniculatus* lineage in western North America: A) inferred habitat suitability at the present; B) inferred habitat suitability during the Last Glacial Maximum. The yellow, blue, and red stars in panel B indicate the origin of expansion for *P. m. sonoriensis*, *P. m. gambelii*, and *P. keeni* lineages, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The *Peromyscus maniculatus gambelii / P. m. sonoriensis* populations diverged much more recently, about 3 kya during the Holocene (Fig. 2; Lisiecki and Raymo, 2005; Kawamura et al., 2007). This estimate is much younger than previous divergence estimates (Sawyer et al., 2017) and occurs during the generally climatically stable Holocene (Kaufman et al,. 2015). The recent split between these two populations is also indicated by much less differentiation (Supplementary Table 6). The phylogeographic break found across the San Francisco Bay Delta is a historically significant lineage diversification hotspot found in California; however, the timing of these diversification events is not concordant across species (Boria et al., 2020; Lavin et al., 2018; Phuong et al., 2014; Rissler et al., 2006). The San Francisco Bay area has remained an important lineage diversification hotspot through time and more work is needed to understand how this region shapes biodiversity.

4.3. Potential areas of refugia and expansion

During the glacial phases of the Pleistocene, colder climate and the physical formation of large ice sheets that covered most of northern North America (Batchelor et al., 2019; Dansgaard et al., 1993; Kleman et al., 2010) forced species to retreat to refugia, local areas where species were able to persist that are typically at least somewhat isolated from other refugial regions (Stewart et al., 2010). The exact nature of climate and landscape change was variable across regions, but within a refugial region species were broadly exposed to similar environmental conditions. Yet, evidence suggests many species responded individualistically to these environmental conditions (Burbrink et al., 2016; Hewitt, 2000). Typically in western North America, species persisted in refugia located in Beringia, the Pacific Northwest coast, or one of the many potential regions south of the continental ice sheets (see Waltari et al., 2007; Pielou, 1991; Fleming and Cook, 2002; Eddingsaas et al., 2004; Sawyer et al., 2017), with almost no mammal species occupying all three regions (for a possible exception see Dawson et al., 2014). Here, we provide evidence that western North American lineages within *Peromyscus maniculatus* responded to Pleistocene climate changes by expanding their ranges during interglacial periods and contracting its range during glacial periods (Fig. 4), occupying at least two of the main refugial areas in the western United States — the Pacific Northwest coast and likely multiple refugia south of the continental ice sheets.

Previously, *Peromyscus maniculatus* (the 6 monophyletic mitochondrial lineages) was thought to have only occupied regions south of the continental ice sheets during glacial periods and expanded north only during the interglacial periods (Dragoo et al., 2006), with other *Peromyscus* species inhabiting the Pacific Northwest coast (*P. keeni*; Lucid and Cook, 2004) and Beringia (*Peromyscus* sp; Sawyer et al., 2017) glacial refugia. However, previous studies only used mitochondrial DNA (e.g., Dragoo et al., 2006), or mitochondrial DNA with four nuclear loci (Sawyer et al., 2017). Here, we have assembled the largest multilocus SNP dataset to date for western North American lineages. We confirm previous results that showed *P. keeni* had a glacial refugium near the Pacific Northwest coast (Fig. 4; Sawyer et al., 2017). The ENMs indicated high suitability during the LGM in this region, and range expansion analysis that identifies the likely origin of expansion for the lineage as British Columbia, Canada (Fig. 4). However, the map of effective genetic diversity indicated this entire region has lower expected genetic diversity, which is contrary to expectations for a refugium. It is possible the demographic models used in this study were not able to adequately model the complex history of this species in this region and it could have experienced a recent population contraction. Additionally, only 17 individuals from our full dataset were identified genetically as *P. keeni*. More intensive sampling is needed in this region to explore this possible refugium.

The much larger *Peromyscus maniculatus sonoriensis* lineage likely had multiple refugia during glacial periods, including one potential Pacific Northwest refugium, contrary to expectations from previous work (Dragoo et al., 2006; Sawyer et al., 2017). During the LGM, there was a severe reduction in the suitability of northern regions south of the continental ice sheets, with moderate suitability in the Pacific Northwest and high suitability from northern California to areas further to the south (Fig. 4). The range expansion analysis for the PNW region reveals a possible origin of expansion in northwest British Columbia, Canada (near the southeast Alaska and Yukon borders), an area of potentially moderate suitability (Fig. 4). This location is similar to the “minor refugium” found in other species (e.g., Sim et al., 2016; reviewed by Shafer et al., 2010). Again, this region had less diversity than expected and more sampling is needed to determine whether this was indeed a refugium for *P. m. sonoriensis*. For the GB region, the origin of expansion was effectively the Utah-Idaho border near the Snake River Plain refugia found in Roberts et al (2015). This region also had higher genetic diversity than expected, consistent with a refugium. The SW area populations had an origin of expansion in Mexico (near the New Mexico-Mexico border) (Fig. 4). This region was predicted as highly suitable during the LGM and is a region with higher-than-expected genetic diversity (Fig. 3), consistent with a refugium (Carnaval et al 2009). We did not sample the entire distribution of *P. m. sonoriensis* and there are potentially more areas of refugia within this lineage, particularly east of the Rocky Mountains.

Much of the contemporary distribution of the *Peromyscus maniculatus gambelii* population was also highly suitable during the LGM (Fig. 4). The origin of expansion for this lineage was near the San Francisco Bay-Delta region, a known lineage diversity hotspot in California for reptiles, amphibians (Lavin et al., 2018; Rissler et al., 2006), and possibly mammals (Boria et al., 2020; Phuong et al., 2014). This region generally has higher than expected levels of genetic diversity (Fig. 3), bolstering support for the San Francisco Bay-Delta region as a refugium. There is also a hotspot of genetic diversity and high suitability during the LGM in Baja California, Mexico; however, greater sampling depth for the southern California population (specifically along the Baja peninsula) is needed to determine if this could have also been a refugium. Additionally, there is a region in California that has lower than expected genetic diversity (Fig. 3), roughly coincident with the Transverse Ranges and the inland transition to the southern Sierra Nevada mountains. This region is not clearly shown as a barrier to migration, but future analyses focused on *P. m.gambelii* may provide a different picture than the EEMS analyses combined across all three lineages. Demographic models indicated *P. m. gambelii* experienced a population contraction within the last 2,000 years (Fig. 2) that could contribute to the lack of genetic diversity in this region. To date, this is the first study to identify a possible population contraction event within this lineage. A deer mouse predator, the California spotted owl, has also seen a recent decline in this region (Tempel et al., 2022) which was attributed mostly to fire; however, it is possible that trophic level dynamics are contributing to population contractions as well.

As populations of deermice expanded out of refugia, there appears to have been little migration between the lineages (Fig. 2), although the *Peromyscus maniculatus sonoriensis* lineage has contact zones with the other two populations (Figs. 1, 4). The STRUCTURE plot indicates there is possible admixture between the two *P. maniculatus* populations (Fig. 1, SFig. 5B); however, different demographic histories can produce very similar graphs (Lawson et al., 2018). Treemix and phylogenetic network analyses indicate there is some migration between lineages (although one migration edge is from a *P. keeni* locality to a locality that contains *P. keeni* and *P. m. sonoriensis* individuals [SFig. 6 and 10], so it may not represent between-population migration). However, the demographic modeling and EEMs analyses indicate there is little to no migration between populations (Figs. 2 and 3), despite including multiple models with different levels and timing of migration in the original set of demographic hypotheses (SFig. 2). More data near potential population range edges is needed to establish the amount of migration occurring between lineages. Finally, although we find no evidence of reticulation in this current study, more work is needed to fully understand the evolutionary history of the deer mouse and if hybridization has played a key role.

4.4. Future directions and conclusions

Site frequency spectrum simulations are an extremely valuable tool, albeit one with some limitations (Hickerson, 2014). Specifically, although we choose a range of different models, we are only exploring a small sample of parameter space, and the demographic history of *P.*

maniculatus is probably much more complex. For example, EEMS analyses indicated there was a lack of genetic diversity in the North American Pacific Northwest (Fig. 3); however, the demographic model chosen here did not identity population contraction events in the lineages that occur in this area (Fig. 2). Additionally, the mutation rate assumed in these models are based on germline laboratory mice and could impact the inferences presented here. Lastly, all analyses presented here would be improved with greater sampling so that we could model the history for each individual population. Nonetheless, genome-wide datasets and the potential to exploit SFS patterns is a huge advance in the field of population genetics and these data and methods will continue to provide insight into complex biogeographic histories.

Determining how intraspecific genetic diversity is distributed across the landscape is crucial because the structure of this diversity is fundamental to the processes of lineage divergence and speciation (Yannic et al., 2014). Thus, to fully understand the impacts of climate change on biodiversity we need to determine how climate change will affect intraspecific variation. Furthermore, population responses to recent and ongoing human-induced climate change are taking place immediately following the longer-term loss of intraspecific genetic diversity due to climate change over the last 21,000 years and longer (Hewitt, 2000; Magyari et al., 2011; Miraldo et al., 2016). Here, we show that despite a wide geographic distribution, at least one lineage within *Peromyscus maniculatus* (*P. m. gambelii*) has experienced a severe decline in Southern California over the last 2,000 years. This is adding to evidence of ongoing, and divergent, recent population-level responses to climate change within *Peromyscus maniculatus* (Moritz et al., 2008; Myers et al., 2009; Yang et al., 2011). Although species with large geographic distributions are considered less at risk in the Anthropocene, important genetic lineages can be lost. By only focusing on species loss, we miss the intermediate yet critical step of population extirpation (Ceballos and Ehrlich, 2002; Yannic et al., 2014).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We thank Blois lab members, two anonymous reviewers, and the deputy editor for their helpful comments and discussion throughout this project. This research was primarily supported by a Ford Predoctoral Fellowship to R. Boria and a National Science Foundation (NSF) CAREER award to J. Blois (EAR-1750597); R. Boria was additionally supported by an NSF Postdoctoral Research Fellowship in Biology (NSF-2109652) and an NSG AGEP Fellowship (HRD-1820875 to UC Merced). The authors gratefully acknowledge computing time on the Multi-Environment Computer for Exploration and Discovery (MERCED) cluster at UC Merced, which was funded by National Science Foundation Grant No. ACI-1429783. We gratefully acknowledge the Burke Museum, Field Museum, Museum of Southwestern Biology, Museum of Vertebrate Zoology, and University of Alaska Museum of the North, and Dr. Dean Pearson for providing tissues used in this study. We also acknowledge the University of California Natural Reserve System and the UC Merced Vernal Pools and Grassland Reserve (DOI: 10.21973/N3FT0M) for access to new sampling localities.

Data archiving:

The DNA sequences used in this study are deposited at NCBI SRA (accession: PRJNA885878). All R code and data used to perform the analyses is available at https://github.com/bloispaleolab/Peromyscus_refugia.

Author contributions: R.A.B. and J.L.B. conceived the ideas;; R.A.B. performed the lab work and analyzed the data; both authors interpreted results; R.A.B. led the writing; and J.L.B. contributed to writing; both the authors contributed to and approved the final manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107701.

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