UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
BIOLOGÍA EVOLUTIVA

(**PROYECTO**)

DEMOGRAFÍA HISTÓRICA DE *POLIOPTILA CALIFORNICA* (AVES: POLIOPTILIDAE) UN AVE

ENDÉMICA DE BAJA CALIFORNIA

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

SYNCHRONOUS DEMOGRAPHIC AND DISTRIBUTION SHIFTS THROUGH TIME IN AN ENDANGERED

DESERT SPECIALIST

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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CIUDAD UNIVERSITARIA, CD. MX., OCTUBRE 2023.

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M. en C Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **31 de julio de 2023** se aprobó el siguiente jurado para el examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **BIOLOGÍA EVOLUTIVA** de la alumna **MARTÍNEZ AVILA CAMILA** con número de cuenta **314280350** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Synchronous demographic and distribution shifts through time in an endangered desert specialist",** que es producto del proyecto realizado en la maestría que lleva por título: **"Demografía histórica de *Polioptila californica* (Aves: Polioptilidae) un ave endémica de Baja California",** ambos realizados bajo la dirección del **DR. HERNÁN VÁZQUEZ MIRANDA,** quedando integrado de la siguiente manera:

Presidente:	DR. ADOLFO GERARDO NAVARRO SIGÜENZA
Vocal:	DR. LUIS ANTONIO SÁNCHEZ GONZÁLEZ
Vocal:	DR. SANTIAGO ALEJANDRO RAMÍREZ BARAHONA
Vocal:	DRA. CLAUDIA PATRICIA ORNELAS GARCÍA
Secretaria:	DRA. CAROLINA GRANADOS MENDOZA

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 27 de septiembre de 2023

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

c. c. p. Expediente del alumno

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Índice

Resumen

Las oscilaciones climáticas que ocurrieron durante el periodo Cuaternario modificaron la distribución de los ecosistemas alrededor del mundo, especialmente en las zonas cercanas a los polos. Estos cambios ambientales afectaron a las especies que habitaban estas regiones, de modo que dichas especies presentan firmas genómicas y demográficas particulares que nos brindan información sobre los fenómenos y procesos que han experimentado.

El objetivo de este estudio fue evaluar algunos de los procesos históricos ambientales que moldearon genómica y espacialmente a la perlita de California, *Polioptila california*, un ave pequeña que habita principalmente en los matorrales costeros de las zonas áridas de la península de Baja California. Para evaluar de manera más integral la historia evolutiva de la especie empleamos dos herramientas analíticas distintas: los modelos de demografía histórica y los modelos de distribución de especies.

Los resultados mostraron que las poblaciones de la perlita de California pasaron por un severo cuello de botella al finalizar el Último Máximo Glacial (UMG), cuando el hábitat disponible para la especie estaba restringido a la porción más sureña de la península. Este declive poblacional produjo una pérdida significativa de diversidad genética de la cual *P. california* no ha logrado recuperarse. No encontramos evidencia de estructura genética en la perlita de California, de manera que nuestros resultados no apoyan ninguna de las hipótesis de subespecies planteadas previamente por otros autores.

A pesar de que es bien reconocido el rol fundamental de los factores ambientales en la determinación de las tendencias evolutivas de las poblaciones naturales, en algunos casos aún no sabemos de manera precisa cuáles son los procesos que incidieron en las poblaciones ni cómo influyen en propiedades biológicas como el tamaño o la estructura poblacional. Aquí encontramos que los cambios en la distribución geográfica probablemente jugaron un papel clave en los procesos demográficos de un ave peninsular. Este estudio presenta un ejemplo de cómo variaciones ambientales naturales de gran magnitud han influido en la evolución de las especies.

Abstract

The climatic oscillations that took place during the Quaternary period modified the ecosystems' distributions around the world, especially near the poles. These environmental changes affected the species inhabiting these regions, so that those species have particular genomic and demographic signatures that give us information about the phenomena and processes that these species have experienced.

The objective of this study was to evaluate some of the historical environmental processes that modelled genomically and spatially the California gnatcatcher, *Polioptila californica*, a small avian species that lives primarily on the coastal scrubs from the arid lands on the Baja California Peninsula. To assess more integrally the species' evolutionary history, we used two different analytical tools: the historical demography models and the species' distribution models.

The results showed that the California gnatcatcher's populations went through a severe bottleneck after the end of the Last Glacial Maximum (LGM), when the available habitat for the species was restricted to the southern part of the peninsula. This population decline produced a significant loss of genetic diversity from where *P. californica* has not been able to recover yet. We did not find evidence of genetic structure in the California gnatcatcher; thus, our results do not support any of the subspecies' hypotheses proposed by other authors.

Even though the fundamental role of the environmental factors on the determination of populations' evolutionary tendencies is well known, in some cases we still do not know what precise processes affected the populations nor how these mechanisms influence on biological properties such as population size or structure. Here we found that the geographic distributional changes likely played a central role in the demographic processes of a peninsular bird. This study presents an example of how major environmental changes have influenced species' evolution.

Introducción

Elucidar los procesos que promueven la divergencia de linajes es una pregunta central en biología evolutiva. Múltiples hipótesis se han planteado para explicar el origen de nuevas especies a partir de las poblaciones preexistentes. Probablemente el mecanismo más frecuentemente propuesto en grupos animales es la especiación alopátrida, la cual plantea que el surgimiento de barreras físicas en la distribución geográfica de una especie puede promover la separación de la población original en dos o más grupos de individuos. Eventualmente, los grupos derivados de la separación comienzan a divergir por acción de la deriva génica o las presiones de selección (Hoskin et al., 2005). Comúnmente, se piensa en barreras físicas como ríos o montañas que evitan la dispersión (i.e., flujo génico); sin embargo, la baja disponibilidad de sitios ecológicamente óptimos para las especies también puede representar una barrera al flujo génico. De este modo, cuando las especies no encuentran las condiciones para sobrevivir, los individuos pueden quedar geográficamente aislados de otros. Así, las barreras al flujo génico dadas por cambios en la distribución de las especies y pérdida de la conectividad del paisaje pueden derivar en la divergencia de linajes (Klinga et al., 2019; Pyron y Burbrink, 2010).

Por lo anterior, regiones geográficas que recientemente han sufrido eventos tectónicos u orográficos son buenos modelos para el estudio de la divergencia de linajes y la especiación. Un ejemplo de ello es la península de Baja California, la cual ha sido llamada un laboratorio natural (Álvarez-Castañeda y Murphy, 2014; Brown, 1987) debido a su historia geológica (Sedlock, 2003) y su alta diversidad de biomas, lo que ha provocado que las poblaciones que allí habitan tengan historias biogeográficas particulares y contrastantes entre sí. Por ejemplo, Riddle et al. (2000) revisó los análisis filogeográficos previos de 12 especies que se distribuyen en la península y encontró cuatro patrones geográficos diferentes que reflejaban la historia biogeográfica de los grupos genéticos en estas especies. Dichos autores hacen hincapié en la independencia de la biota de la península y la del desierto sonorense. También existen estudios que proponen que un único evento tectónico u orogénico no sería suficiente para crear los complicados patrones filogeográficos que encontramos en las especies peninsulares. Tal es el caso de un estudio hecho con seis mamíferos y seis reptiles en donde se sugirió que los efectos combinados de las incursiones marinas y el vulcanismo son los que explican de mejor manera la complejidad de estas historias (Leaché et al., 2007).

Se ha reportado que distintos eventos geológicos y climáticos que ocurrieron en la península, o cerca de la región peninsular, han inducido procesos de especiación, endemismo y fragmentación de las áreas de distribución (Klimova et al., 2017). Tres ejemplos de estos grandes eventos geológicos son la formación de un canal marino en la porción media de la península durante el Pleistoceno, la

transgresión hacia el norte del mar de Cortés durante el Plioceno tardío, y la formación de un canal marino en el Plioceno que atravesaba el istmo de La Paz (Riddle et al., 2000). Es importante recalcar que la península está situada sobre múltiples placas tectónicas que se comportan de manera diferente. La parte occidental se encuentra sobre una falla transformante, mientras que la porción oriental concuerda con un límite divergente. Recientemente, se definieron ocho unidades biogeográficas dentro de la península de Baja California con base en la geología y las comunidades biológicas que habitan en el área, cada una representando una biota distinta. Las ocho unidades son: Desierto Central, Costa Central del Golfo, Isla de Guadalupe, Desierto del Vizcaíno, Sierra de la Giganta, Llanuras de Magdalena, Cabo y Sierra de la Laguna (Morrone, 2021).

Además de las particularidades de la península de Baja California, los eventos de magnitud global que ocurrieron durante las glaciaciones, como los cambios en el nivel del mar, la temperatura global y la precipitación (Hewitt, 2004), deben ser tomados en cuenta cuando buscamos inferir la historia evolutiva de una especie. El periodo Cuaternario (2.5 millones de años-actualidad) se ha caracterizado por presentar numerosos periodos glaciales e interglaciales (Bennett, 1990; Mantooth et al., 2013). Sin embargo, en los últimos 245,000 años han ocurrido múltiples glaciaciones de magnitudes variantes. La última glaciación comenzó hace aproximadamente 110,000 años, pero no fue hasta hace 20,000 años cuando la glaciación alcanzó su pico, iniciando así uno de los eventos climáticos más importantes del Pleistoceno: el Último Máximo Glacial, en el cual los glaciales de todo el mundo alcanzaron su tamaño máximo. Este evento tuvo mayor impacto en las regiones cerca de los polos donde la radiación solar es menor, lo que provocó que las zonas adyacentes sufrieran bajas considerables en la temperatura ambiental, favoreciendo la expansión de los glaciales. De este modo, las zonas templadas del hemisferio Norte fueron empujadas hacia el Ecuador reduciendo drásticamente el área de los ecosistemas templados (Williams et al., 2004). Un caso especial fue el de los desiertos del oeste de Norteamérica. La extensión de estos ecosistemas se redujo significativamente durante el periodo glacial del Pleistoceno, y no fue sino hasta que finalizó el periodo glacial (hace aproximadamente 10,000 años) que los desiertos recuperaron territorio, alcanzando su distribución máxima durante el Óptimo Climático del Holoceno (hace aproximadamente 8,000 años) (Mantooth et al., 2013; Riddle y Hafner, 2006).

Así como los biomas se redujeron, durante el UMG muchas poblaciones de regiones tropicales y áridas sufrieron cuellos de botella y fragmentación poblacional debido a la contracción de sus hábitats (Hewitt, 2000, 2004; Ony et al., 2021). Contrario a esto, con el establecimiento del periodo interglaciar y la regresión de los glaciales, las poblaciones del Hemisferio Norte pasaron por una explosión demográfica y una expansión en la distribución geográfica hacia el norte del continente (Nason et al., 2002). Por eso se ha propuesto que particularmente las especies de zonas áridas de

Norteamérica presentan firmas genéticas de divergencia y posterior diversificación que concuerdan con los cambios climáticos y geográficos de la región durante el Cuaternario. Específicamente, en los genomas de especies asociadas a ambientes áridos existe evidencia de aislamiento poblacional. Esto se ha asociado con grupos de individuos que quedaron aislados en refugios pleistocénicos y, tras el fin del UMG, cuando las condiciones climáticas fueron más adecuadas y se recuperó la vegetación, recobraron la conectividad y el flujo génico con el resto de la población (Graham et al., 2020; Sánchez-del Pino et al., 2020; Wilson y Pitts, 2012).

El uso combinado de herramientas genómicas y de modelos de distribución de especies (SDM, por sus siglas en inglés) permiten evaluar preguntas biológicas desde distintas perspectivas, de manera que, si los resultados de ambos enfoques concuerdan, las conclusiones que obtenemos adquieren mayor robustez (Aguirre-Liguori et al., 2021). Por un lado, los métodos de estimación de tamaño efectivo a partir de datos genómicos han ganado mucha popularidad en distintas áreas como la biología evolutiva, la ecología o la genómica de la conservación. Saber cómo han reaccionado las poblaciones en el pasado ante eventos específicos puede brindarnos información para inferir cómo podrían actuar en el futuro bajo escenarios particulares como la pérdida o fragmentación del hábitat, el calentamiento global y la disponibilidad de agua (Prates et al., 2016). Por otro lado, los SDM nos permiten visualizar los cambios que han ocurrido en el espacio geográfico con respecto a las condiciones climáticas y los recursos ambientales necesarios para la supervivencia de las especies, siempre asociado con el nicho ecológico particular de cada especie (Miller, 2010). De este modo, estudios que evalúan a la par los cambios distribucionales y la demografía poblacional pueden ayudarnos a comprender de mejor manera cómo los cambios climáticos de gran escala han moldeado las poblaciones actuales.

En este estudio buscamos evaluar si los cambios climáticos que ocurrieron durante el UMG redujeron la extensión de las zonas áridas de la península de Baja California y si esto provocó que las especies que habitan estos desiertos pasaran por cuellos de botella poblacionales asociados con la reducción de su hábitat. Para ello usamos como especie modelo a la perlita de California, *Polioptila californica*, una pequeña ave paseriforme endémica de la península de Baja California. Esta ave se encuentra asociada particularmente con regiones áridas y semiáridas desde el sur de California, EE.UU., hasta la punta sur de Baja California Sur. Estudios previos han encontrado evidencia limitada de una reciente expansión poblacional que concuerda temporalmente con la conclusión del UMG (Zink et al., 2013), así como falta de estructura genética y aislamiento geográfico a lo largo de la península (Vázquez-Miranda et al., 2022; Zink et al., 2016). Lo anterior sugiere que la especie no ha sufrido fragmentación, que el tiempo de aislamiento no fue suficiente para inducir divergencia, o

bien, que posterior a la divergencia el flujo génico fue tal que permitió la homogenización genética de las poblaciones.

Actualmente existe un debate sobre la clasificación infraespecífica de *Polioptila californica,* dado que se han planteado múltiples hipótesis de subespecies (algunas de ellas resumidas por Zink et al. 2000). Particularmente, se ha propuesto que las poblaciones que habitan en los matorrales costeros de EE.UU. pertenecen a una entidad taxonómica distinta clasificada como la subespecie *P. californica californica* (McCormack y Maley, 2015). Esta hipótesis está basada en la cantidad de color blanco en las plumas de la cola, vocalizaciones ligeramente más agudas y diferencias en la preferencia de hábitat con respecto a las aves del resto de la península. Esta subespecie se encuentra listada en el Acta de Especies (ESA, por sus siglas en inglés) de EE.UU. (ESA; 16 USC 1531 et seq; U.S. Fish and Wildlife Services 1995) y ha sido usada como especie bandera para la conservación de los matorrales de costa. Los estudios mencionados anteriormente fueron realizados con unos pocos genes mitocondriales y nucleares, por lo que realizar un estudio usando un mayor número de genes nucleares no ligados (independientes) puede permitir inferir con mayor solidez la historia evolutiva de la especie. Todo lo anterior hace a la perlita de California un modelo ideal para estudiar el efecto de los cambios climáticos en la estructura genética, la demografía y la distribución geográfica de las especies peninsulares.

1 **TITLE**

2 Synchronous demographic and distribution shifts through time in an endangered desert specialist.

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ABSTRACT

The climatic oscillations that took place during the Quaternary period altered the ecosystems distributions around the world. Different biomes contracted and expanded as temperature and precipitation fluctuated over time yielding characteristic demographic signatures in the genome of species associated to changing habitats. Here, using coalescent-based historical demography and species distribution models, we assessed the demographic processes experienced by an arid-land bird species from the Baja California Peninsula. We evaluated how the climatic and environmental changes that occurred during and after the last glaciation affected the population of the California gnatcatcher (*Polioptila californica*). We found that the gnatcatcher's population went through an extreme genetic bottleneck around the end of the Last Glacial Maximum, when its suitable habitat was almost entirely restricted to the south of the Peninsula. Population decline led to a significant loss of genetic diversity from which the species has not yet recovered. We did not find evidence for subpopulation structure. Our study is an example of the effects of historic climatic changes on species with arid-like habitat preferences and mid-low dispersal ability.

Keywords: distributional shifts, genomics, historical demography, Pleistocene, *Polioptila californica*.

SIGNIFICANCE STATEMENT

Our study formally tests the role of environmental factors in modelling the evolution of biological populations. Specifically, we test which genomic and demographic processes affect biological properties like demography, genetic levels and subpopulation structure. Here we provide evidence in favor that changes in the geographic range play a major role in the population size of a peninsular avian species adapted to arid environments. Our study highlights the profound impact that drastic historical environmental variations can have on a species' population genetic diversity.

INTRODUCTION

Determining the processes promoting lineage divergence is a central question in evolutionary biology. Several hypotheses have been proposed to explain the origin of new species from preexisting populations. Probably the most commonly proposed mechanism in animals is the allopatric speciation which states that the emergence of geographic barriers in an otherwise continuous distribution of a species splits the original population in two or more groups. As time goes by, these populations start diverging due to the action of genetic drift or selective pressures (Hoskin et al., 2005). Normally, we think of these barriers as rivers or mountains that restrain dispersal and gene flow of individuals from both sides of the barrier. Nevertheless, the absence of available and suitable habitat can also act as a barrier. Consequently, species that do not have the conditions to thrive in these unsuitable places, can become isolated in geographically distinct spaces. Therefore, changes in species distribution and landscape connectivity constitute barriers to gene flow that can drive divergence (Klinga et al., 2019; Pyron & Burbrink, 2010).

Geographic regions that have recently experienced tectonic or orographic events are excellent model systems for studying speciation. This is the case of the Baja California Peninsula, which has been called a natural laboratory (Álvarez-Castañeda & Murphy, 2014; Brown, 1987) due to its intricate geologic history (Sedlock, 2003) and high biome diversity, yielding populations with rather particular and varied biogeographic histories. For example, Riddle et al. (2000) evaluated phylogeographic analyses from 12 species distributed on the Baja California peninsula and found four different geographic patterns related with the location of genetically distinct groups. In this study, the authors highlight the independency of the peninsular biotas from those of the Sonoran Desert. There are also studies proposing that a single event is not sufficient to create the complex phylogeographical patterns of the peninsular biota. This is the case of a study made with six mammals and six reptiles suggest that the combined effect of water incursions and volcanism may be a better explanation for the complexity of these patterns (Leaché et al., 2007).

Furthermore, distinct geologic and climatic events that took place in or near the peninsula have powered speciation, endemism, and separating distribution areas (Klimova et al., 2017). Three of these major geological events are the formation of a midpeninsular seaway during middle Pleistocene, a northward expansion of the Sea of Cortéz and the formation of a seaway across the southern peninsular Isthmus of La Paz in the Pliocene (Riddle et al., 2000). Moreover, Baja California has a complex tectonic history: the western portion is located on a transform fault, while the eastern part rests divergent boundary. Based on its geology and the biological communities inhabiting it, eight biogeographic units were recently proposed within the peninsula, each one representing a unique biotic assemblage: Central Desert, Gulf Central Coast, Guadalupe Island, Vizcaíno Desert, Sierra de la Giganta, Magdalena Plains, Cape and Sierra de la Laguna (Morrone, 2021).

Additionally, global events that took place during glaciations, such as changes in sea level, global temperature, and precipitation (Hewitt, 2004) must be considered when inferring the evolutionary history of the species. The Quaternary was a period characterized by multiple glacial and interglacial cycles (Bennett, 1990; Mantooth et al., 2013). One of the most important events occurred approximately 20,000 years ago during the Pleistocene: The Last Glacial Maximum (LGM), where glaciers around the world reached their maximum size. LGM the most impact near the poles, where solar radiation is lowest, and regions experienced significant temperature decreases that led to the expansion of glaciers. Temperate zones in the Northern hemisphere expanded southwards towards the Equator, greatly shrinking tropical and template biomes (Williams et al., 2004). A particular case was that of the Western North American deserts. These ecosystems experienced a reduction in extension during the Pleistocene glacial period, and it was not until after the Wisconsin glaciation that the deserts reestablished completely, reaching its maximum range during the Holocene Climatic Optimum (Mantooth et al., 2013; Riddle & Hafner, 2006).

In the same way as biomes, during the LGM many tropical and arid-related populations went through demographic bottlenecks and fragmentations due to their habitats' reductions (Hewitt, 2000; Hewitt, 2004; Ony et al., 2021). In contrast, the interglacial period and the retraction of the glaciers, those populations on the North hemisphere experienced a demographic growth and geographic range expansion northwards (Nason et al., 2002). Species' genetic signatures of divergence and subsequent diversification are concordant with the climatic and geographic transformation of the region during the Quaternary in North America. Specifically, in species associated with arid environments, there is evidence in their genomes of population differentiation and isolation. This has been associated with populations distributed along Pleistocene refugia, which later dispersed southwards after the LGM, expanding their distribution ranges, connectivity and gene flow, as climatic conditions became more suitable and the vegetation recovered lost ground (Graham et al., 2020; Sánchez-del Pino et al., 2020; Wilson & Pitts, 2012).

The combined use of genomic tools and species distribution models (SDM) allows us to formally address biological questions from different perspectives, thus if both approaches agree, the conclusions drawn gain more robustness (Aguirre-Liguori et al., 2021). Methods for estimating effective population size from genomic data have had a big boom in diverse areas such as evolutionary biology, ecology, and conservation genomics. Knowing genetic and demographic patterns of populations in the past, might help predicting the population's behavior under future scenarios like habitat loss or fragmentation, global warming, water scarcity, among others (Prates et al., 2016). On the other hand, SDM enable to visualize changes in geographic space with respect to climate conditions and environmental resources necessary for the survival of species, associated with their specific ecological niches (Miller, 2010). Thus, the joint study of distributional changes and population demography can help understand more in-deep how global climatic changes have shaped the populations we see today.

125   In this study we our aim was to model the effect of the climate changes that took place

126   during the LGM on the expansion of arid regions along the Baja California Peninsula, and to

127   determine if and how such habitat changes impacted the demography and genetic patterns of the

128   California gnatcatcher, *Polioptila californica* (Aves: Polioptilidae). *P. californica* is a small

129   perching bird endemic to the Baja California Peninsula, distributed in the arid and semi-arid regions

130   of southern California to the southernmost tip of Baja California Sur in Mexico. Previous studies

131   have shown a lack of genetic and geographic structure of this species along the peninsula as well as

132   first insights of a recent population expansion in concert with that matches the time following the

133   LGM (Vázquez-Miranda et al., 2022; Zink et al., 2013; Zink et al., 2016). These results suggest that

134   population maintained a continuous distribution or that the time elapsed since the genetic and

135   geographic isolation has not been enough for the subpopulations to diverge.

136   The infraspecific classification of the species is still in debate since multiple subspecies

137   hypothesis have been proposed (see Zink et al. 2000). Particularly, it has been suggested that the

138   populations inhabiting the coastal shrublands in south-eastern USA belong to a distinct taxonomic

139   entity, classified as the subspecies *P. californica californica* (McCormack & Maley, 2015). This

140   proposal is based on the amount of white color in the tail feathers, slightly sharper vocalizations and

141   habitat preferences (Atwood, 1988). This subspecies is listed in the Endangered Species Act (ESA;

142   16 USC 1531 et seq; U.S. Fish and Wildlife Services 1995) and is a flagship species for the

143   conservation of the coastal shrublands that inhabits. Those previous studies used a few

144   mitochondrial and nuclear genes. Therefore, assessing the evolutionary history of this species will

145   benefit from the analysis of multiple nuclear, unlinked loci. The lack of more comprehensive studies

146   makes the California gnatcatcher an ideal model to study the effect of climatic changes on the

147   genetic and geographic structure, demography, and distribution of peninsular species.

148

149

RESULTS

Genetic diversity and population structure

Here we present the GBS-derived data for the estimation of genetic diversity and assessment of population structure. From the VCF file we identified a total of 96,208 SNPs which was thinned to keep only one SNP per locus resulting in 50,505 SNPs. After applying all the filters, the number of SNPs was 9,233 for the whole date set, and 4,720 SNPs for the thinned one. Two individuals from the original sampling belonging to Cataviña population were removed from further analyses since the preliminary analyses showed that the genetic differences between these two individuals and the remaining sampled individuals were greater than the differences to the sister species *P. melanura*.

The estimated genetic diversity in *P. californica* was overall low. The mean observed heterozygosity (H_o) among the five locations was 0.0661, while gene diversity was 0.0872. The total inbreeding coefficient (F_{IS}) was 0.2411, although F_{IS} for any given location never exceeded 0.167. Similarly, the paired F_{ST} values were relatively low and never exceeded 0.072 indicating low genetic differentiation between the sampled locations.

The low diversity and almost no differentiation was supported by the results obtained for genetic structure shown (Figure 1). The California gnatcatcher individuals clustered in a single group. ADMIXTURE results found $k=1$ as the best model (for all 10 independent runs), based on the smallest cross-validation error. Likewise, fastSTRUCTURE indicated that the most probable number of populations ranged from one to two, which also suggests clustering of all the *P. californica* individuals as one genetic group. Similarly, DAPC results (Figure 1), showed differences among groups are minor, with overlap between locations. Interestingly, only gnatcatchers from Riverside and Santa Rosalillita have high assignment probabilities to their nominal localities. The other samples have mixed probabilities that suggest lack of genetic structure. The gene flow events also support the lack of structure (Figure 2), where the TreeMix

175   results showed that there was at least one migration event from El Cien in Baja California Sur to

176   Cataviña, Baja California. Even though the migration weight (i.e., the fraction of alleles in the target

177   population that came from the parental population) is low, it shows that gene flow did occur

178   between locations.
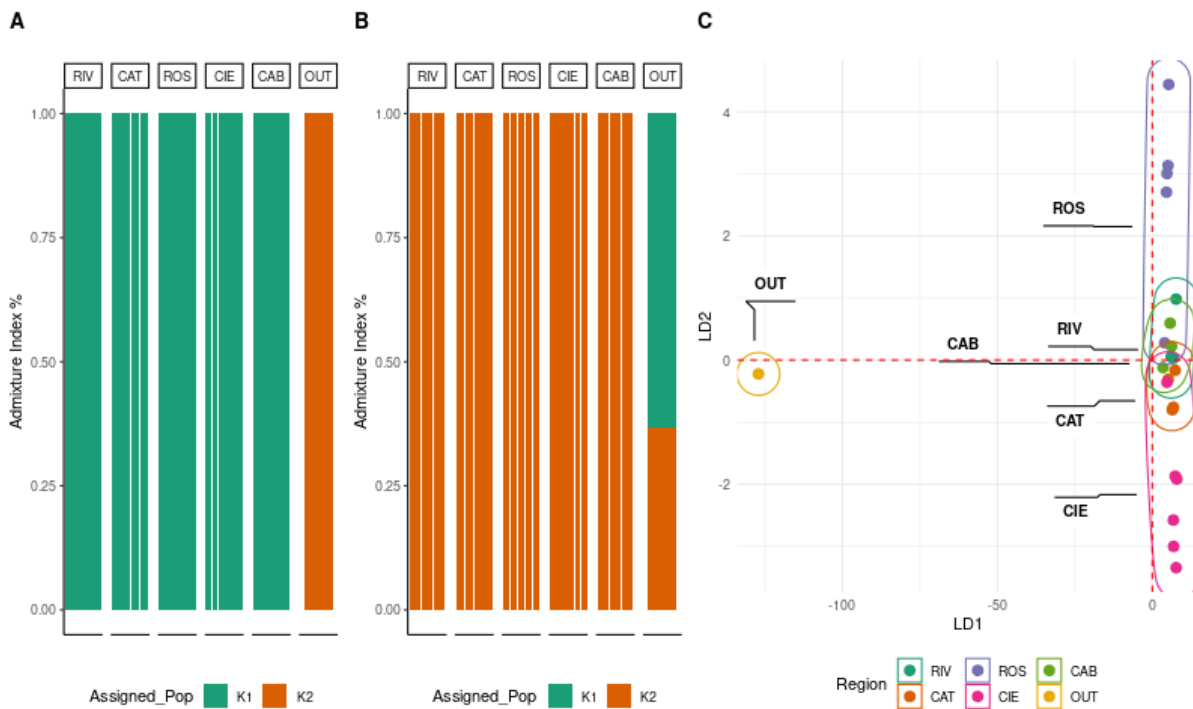
179

180   **Fig. 1. Population genetic structure in the California gnatcatcher on GBS genomic data**

181   **inferred by different methods. A** corresponds to the structure inferred with *ADMIXTURE* and **B**

182   with *fastSTRUCTURE*. The labels on top indicate the individuals' location. The color represents the

183   genetic cluster each individual was assigned to. **C** depicts the genetic clusters identified with the

184   first two linear discriminants (LD1 and LD2). The colors specify the location of each individual as

185   indicated in the bottom legend. RIV; Riverside, CAT; Cataviña, ROS; Santa Rosalillita, CIE; El

186   Cien, CAB; Cabo Pulmo, OUT; outgroup (*P. melanura*).

187

188   There is no clear clustering of the individuals based on the geographic location they were

189   collected from, except for the birds from Riverside and almost all the individuals from Santa

190   Rosalillita (Figure 3). The SVDquartets analysis revealed that birds from these two localities were

14

191 genetically closer to individuals from their same locality in comparison with the rest of the sampled

192 locations.
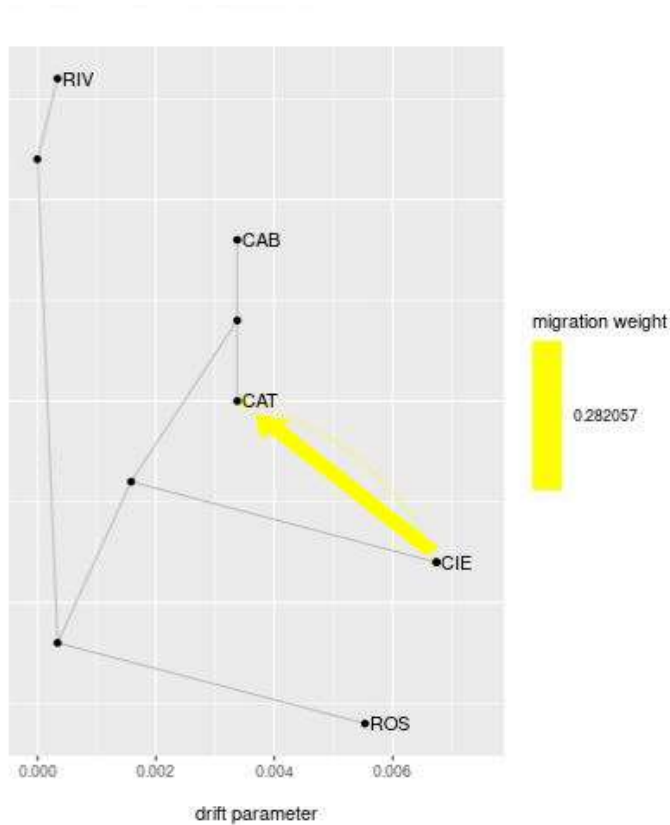
193

194 **Fig. 2. Estimation of gene flow among *P. californica* populations with *TreeMix* with GBS data.**

195 The yellow arrow represents an interchange of genetic alleles from the populations in El Cien to

196 those in Cataviña. The x-axis indicates the amount of genetic drift experienced by each population,

197 while the bar at the right illustrates the magnitude of the genetic flow. In this case only one event

198 was inferred.

199

200   Interestingly, results obtained with RAD-Seq data (Supplementary Material) indicate a

201 somewhat different story. First, gene diversity was much higher and the F_{IS} lower, with values of

202 0.27 and 0.0857, respectively. Also, the estimated paired F_{ST} was lower, meaning genetic

203 differences between sampled locations were lower in comparison with the GBS data. The lack of

204 genetic differentiation was confirmed by the population assignment methods, which showed all

205 sampling locations formed a single genetic cluster. Nonetheless, they also showed that the *P.*

206 *melanura* individual belongs to the same genetic cluster as the focus species. The sister species was

207 placed at the center of all the *P. californica* individuals in the DAPC.
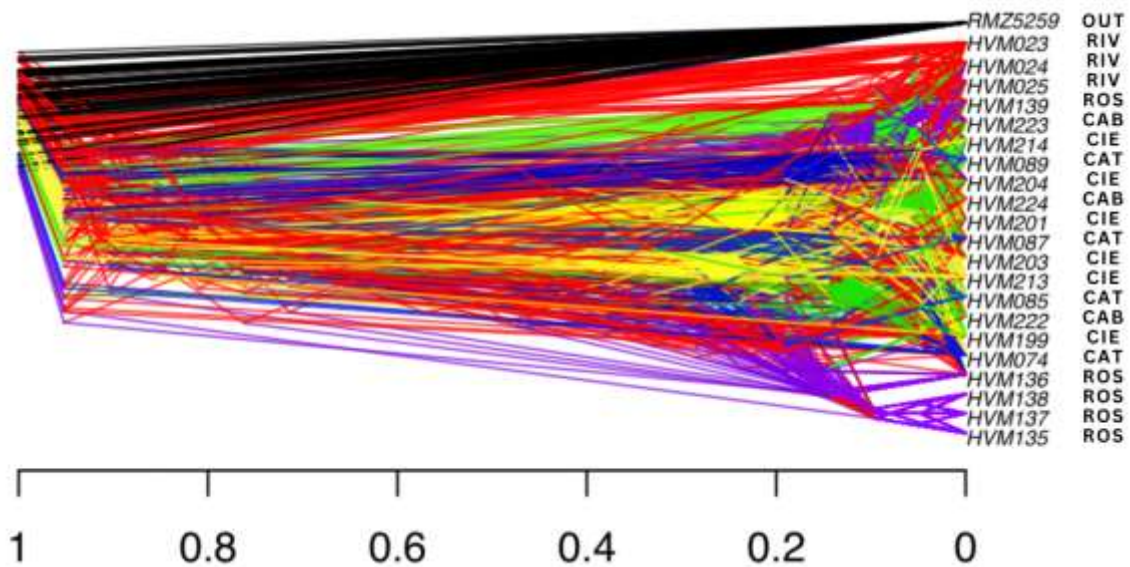
208
209 **Fig. 3. Geographic structure of *P. californica* populations inferred with *SVDquartets* with GBS**

210 **data.** In the right the code names for the sampled birds, whilst the colors denote the population each

211 individual belongs to. From top to bottom: black - OUT (outgroup), red - RIV (Riverside), purple -

212 ROS (Santa Rosalillita), green - CAB (Cabo Pulmo), yellow - CIE (El Cien), and blue - CAT

213 (Cataviña).

214

215 **Historical demography**

216   As runs reproduced the same demographic patterns independently of the number of free

217 parameters (i.e., coalescent rates) indicated, we only describe the results from the runs with the

218 lowest number of free parameters and, therefore, less associated error. The demographic shifts

219 indicated by the red dark line in Figure 4 resume the MSMC2 results on RAD-Seq data using 18

220 free parameters (remaining runs on Supplementary Material). These revealed that *P. californica* had

221 a high population size as far back as 100,000 years ago, with an estimated stable population size of

222 up to a million effective birds. Around 18,000 years ago, *ca.* the end of the LGM (at the left of the

223 dark blue block in Figure 4), the population size declined. The bottleneck was so strong that the

224 population effective size reached the tens of thousands.

225   The population decline continued reaching a thousand effective individuals, until about a

226 hundred years ago that population size increased again reaching almost the same effective size as

227 before the glacial period. These results suggest that the population has currently a stable size of

228 hundreds of thousands. Although results were more consistent (bootstrap values) along the more

229 recent times (Figure 4) they concurrently show that: (1) it was after the LGM peak that the

230 population suffered the bottleneck, and (2) approximately 10,000 years ago the population

231 expanded during the interglacial period.
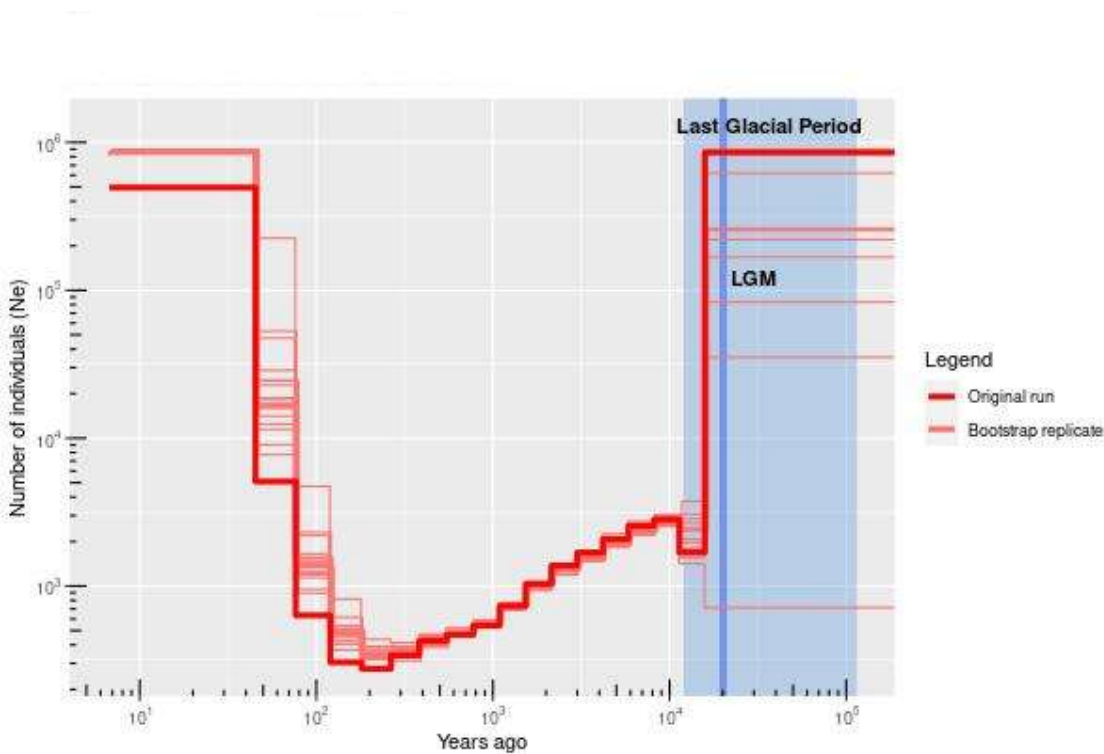
232

233 **Fig. 4. Historical demographic changes in the California gnatcatcher estimated from**

234 **autosomal RAD-Seq data.** The dark red line depicts the results from the *MSCM2* run with the

235 original data, the translucent lines correspond to each one of the 20 runs made with bootstrap data.

236 The light blue rectangle indicates the time span of the Last Glacial Period, while the dark blue line

237 represents the time span for the LGM. Both axes are in log scale. LGM; Last Glacial Maximum,

238 Ne; population effective size.

240   Results for the sex Z chromosome using four parameters (Supplementary Material) showed

241   that, even though the population size declined after the end of the glacial period, it was a gradual

242   change (along about 10,000 years) in contrast with the autosomal analysis (Figure 5). Moreover, the

243   main run and the replicates did not show the same patterns, although most of them exhibited a high

244   population size. In addition, all bootstraps showed that the current population size is lower than that

245   indicated by the main run. Nevertheless, all of them revealed markedly lower than the trend

246   observed for autosomal SNPs, which may indicate that there is sex bias.
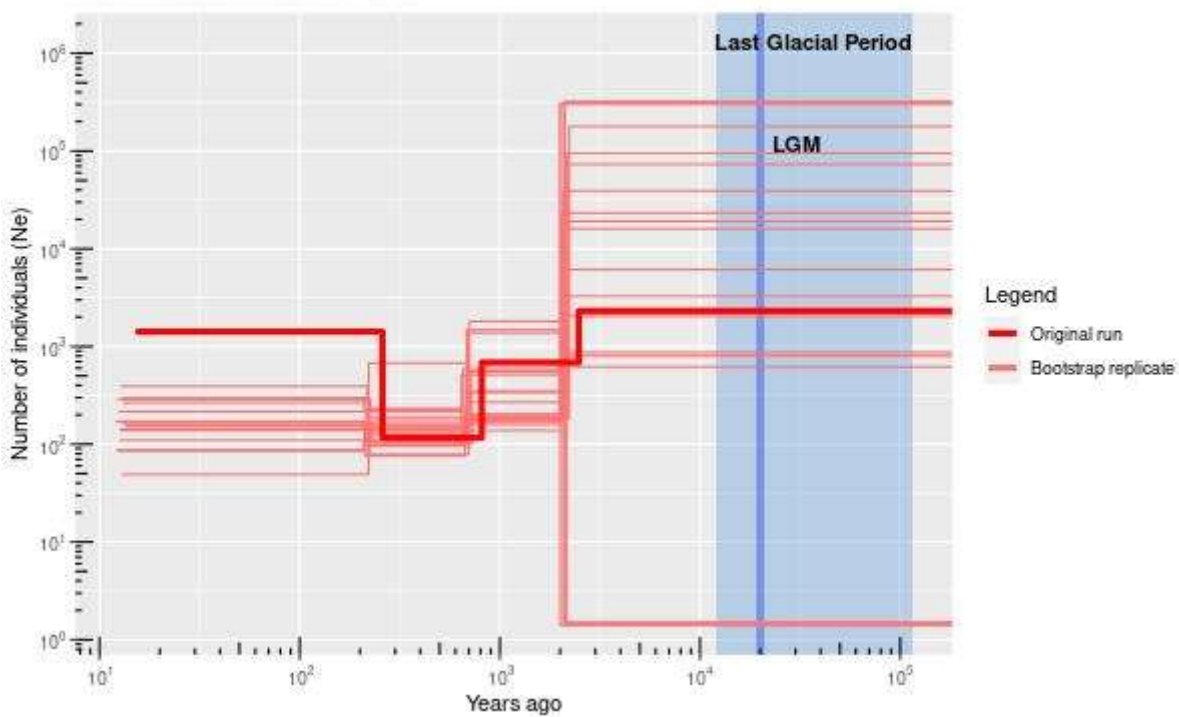
Fig. 5. Historical demographic changes in the sex Z chromosome of the California gnatcatcher estimated from RAD-Seq data. The dark red line depicts the results from the *MSCM2* run with the original data, the translucent lines correspond to each one of the 20 runs made with bootstrap data. The light blue rectangle indicates the time span of the Last Glacial Period, while the dark blue line represents the time span for the LGM. Both axis are in log scale. LGM; Last Glacial Maximum, Ne; population effective size.

254

255   We also evaluated the demographic history on the GBS data (Supplementary Material),

256 which showed almost the same demographic trends as the RAD-Seq data, with the difference that in

257 the former the population decline was not as fast. With these data population decline started about

258 10,000 years after the LGM ended, but less than five thousand years since the beginning of the

259 interglacial period. This trend continued until almost 100 years ago when the population increased.

260 Regarding sex chromosomes, results indicated a lack of agreement between the original run and the

261 bootstraps. Bootstraps indicated a high population size during the glacial period and a large part of

262 the interglacial period, where the sex Z chromosome did not decrease in size until 1,000 years ago,

263 far from the LGM ending. This date is only a few thousand years after the date estimated with GBS

264 data.

265   Overall, both data show the same demographic patterns, differing only in the time where the

266 bottleneck began, with a signal of higher population size before the LGM, while after the glacial

267 period ended populations went through a strong bottleneck. The estimated effective size for the sex

268 Z chromosome was lower compared with the autosomal chromosomes, with a longer time for the

269 sex chromosome to decline independently of the genomic data it was derived from.

270 **Geographic distribution modelling**

271   From a total of 1,065 occurrences (1,022 from GBIF, 38 from Waltari et al. 2007 and five

272 from our own records), cleaned occurrences resulted in only 269 samples. The collinearity test

273 resulted in 10 non-correlated variables, including bio1 (annual mean temperature), bio2 (mean

274 diurnal range), bio4 (temperature seasonality), bio5 (max temperature of warmest month), bio8

275 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio14

276 (precipitation of driest month), bio15 (precipitation seasonality), bio18 (precipitation of the warmest

277 quarter) and bio19 (precipitation of coldest quarter).

278   Results of the potential distribution model for the present, showed an AUC value of 0.965.

279 The predicted potential distribution for the California gnatcatcher included practically all the Baja

280 California Peninsula and the southern part of California (Figure 6). Despite the extent of the

281 distribution is high, the presence probability of the predicted area ranges from about 0.4 to 1, where

282 the coasts had higher probability. This can be associated with the fact that the Peninsula is

283 characterized by a high abundance of xeric scrubs and other arid ecosystems, which are the

284 preferred habitats of the species.
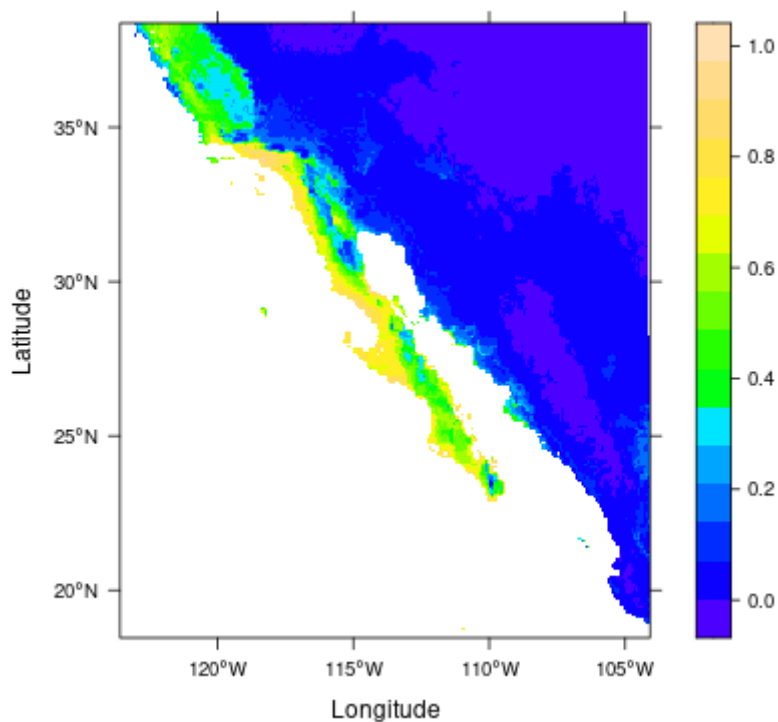
285

286 **Fig. 6. Potential current distribution for *P. californica* inferred with *MaxEnt*.** The color band at

287 the right indicates the probability of occurrence of the species in the evaluated area. Warmer colors

288 suggest higher probability. The size of each pixel is 2.5".

289

290   In contrast with the results for the present, both LGM models showed that the predicted

291 extent of habitable area for *P. californica* was lower. However, the probability for the entire inferred

292 areas was higher, ranging from 0.6 to 1. The latter suggest that in the LGM, there were more

suitable places for the California gnatcatcher compared to those in the present (Figure 7). The LGM

distribution showed that the species could not have lived in the northern region of the Peninsula

neither in the south of California, where occurrence probability was almost zero. Thus, the habitable

area in the LGM was restricted to mainly two regions: one to the southern Baja California

Peninsula, again, particularly closer to the coast, and along the area joining the peninsula with the

rest of the continent; a region that today is mostly below the sea.
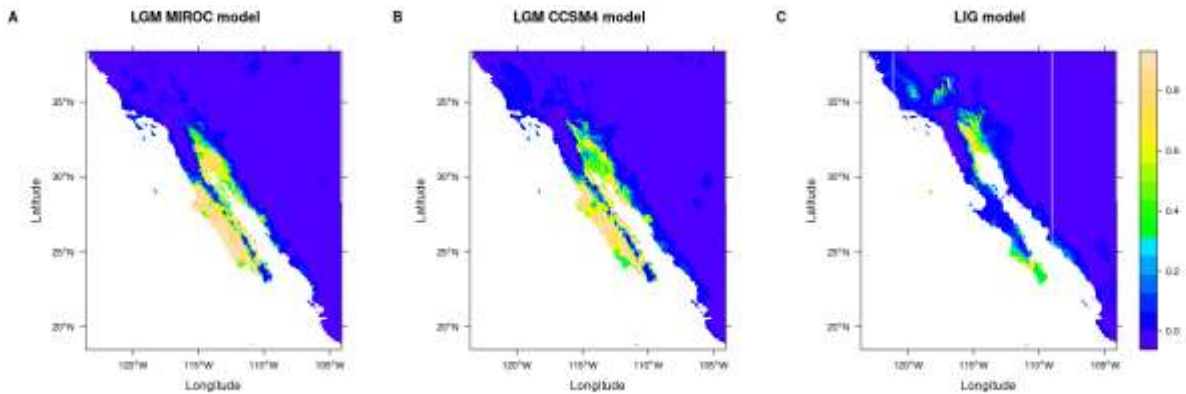
Fig. 7. Potential distribution for *P. californica* for different historic times inferred with

***MaxEnt*. A-B** are the estimated potential distributions of the species during the LGM. **A** is based on

the MIROC general circulation model and **B** is based on the CCSM4 one. **C** is the potential

distribution during the LIG inferred with the only available global bioclimatic variables for this

period. The color band at the right indicates the probability of occurrence of the species in the

evaluated area. Warmer colors suggest higher probability. The size of each pixel is 2.5". LGM; Last

Glacial Maximum, LIG; Last Interglacial.

        Regarding the potential distribution during the LIG (Last Interglacial), results showed that

the predicted areas were located in the same region as in the LGM models (Figure 7). Nevertheless,

the extent of both areas is smaller and the probability of occurrence is very low (ca. 40% presence).

This indicates that the species distribution during the Interglacial was more restricted and climate

conditions were not ideal.

DISCUSSION

Low genetic diversity is often seen in populations that have passed through a recent bottleneck. In this scenario, the reduced population size would have increased the effect of genetic drift leading to loss of random alleles, which in turn decreases genetic diversity. Additionally, population size declining is linked with higher probabilities of inbreeding (Keller & Waller, 2002; Palstra & Ruzzante, 2008; White & Searle, 2007). That seems to be the case for the California gnatcatcher, which showed markedly low genetic variability. Zink et al. (2000) and Zink et al. (2013) reported low genetic diversity for this species, particularly for populations distributed in the north of the peninsula. We found lower values, which are the only ones based on multiple nuclear loci. Furthermore, the overall inbreeding coefficients we observed are indicative of inbreeding within the *P. californica* populations we studied.

Population bottlenecks and isolation have been associated with population structure, as shown by different species during the climatic oscillations of the Pleistocene (Burg et al., 2006; McDonough et al., 2022; Menezes et al., 2021). However, our results consistently showed no evidence of genetic population structure *(F_{ST}* and three population assignment methods). Only the SVDquartets analysis suggested some potential grouping of individuals from Santa Rosalillita and Riverside. However, it is important to note that, because populations of this species from coastal California are listed in the Endangered Species Act, we could not sample individuals and the three ones used in this study came from a single nest with evidence of predation. Thus, it is not unexpected that samples from Riverside are closely grouped.

Nonetheless, this was not the case for the Santa Rosalillita's samples, which given that it is located in the middle of the species range, it is unlikely this population diverged without the northern and southern populations diverging, particularly considering that there are no barriers isolating these individuals from the rest of the peninsula. The fact that we identified gene flow, suggesting that at least one event of genetic interchange between distant populations occurred,

338 makes it likely that gene flow happened between other populations. We acknowledge that we

339 needed a larger sample size to corroborate if this population is differentiated or if it was only an

340 artifact of our analysis. Nonetheless, our overall results support the hypothesis that *P. californica* is

341 not genetically structured, thus the proposed subspecies scheme is not adequate for this species.

342 Similar patterns have been observed for other bird species with comparable ecological

343 characteristics. Brown et al. (2013) found that the mallee emu-wren (*Stipiturus mallee*), an

344 Australian bird with low dispersal ability that inhabits semi-arid and fire-prone regions, has low

345 genetic diversity. This is due in part to the spatial and temporal changing patterns of its habitat, and

346 because of the effects caused by fires that triggered local extinction and recolonization processes,

347 which in turn cause loss of genetic diversity and lack of genetic structure.

348 The historical demography and distribution patterns shown by the California gnatcatcher are

349 concordant with the above. The strong effect of the LGM climate changes is demonstrated by the

350 drastic population size decrement happening right after the end of the LGM. Moreover, the

351 suggested potential distribution of *P. californica* during this period is restricted to the south. This

352 agrees with the south Pleistocene refugia hypothesis for species from the north hemisphere (Hewitt,

353 2001; Stewart et al., 2009). In fact, Waltari et al. (2007) found evidence indicating the existence of a

354 *P. californica* refugium at the south of the peninsula. It has also been proposed as one of the main

355 phenomena that drove the distribution of other species, especially those with low dispersal

356 capability (Drovetski et al., 2018). Thus, the loss of suitable habitat in southern USA that took place

357 during the LGM could have driven the decline of the *P. californica* populations.

358 When the glacial period ended, about 10,000 years ago, the range of the arid lands of North

359 America expanded, enabling these ecosystems to reach distribution areas very similar to their

360 present extent (Herzschuh, 2020; Moncrieff et al., 2015). Currently, the California gnatcatcher can

361 be found as far as southern California and all along the Baja California Peninsula, supporting that

362 the species' distribution could and did expand. However, although the availability of habitat

increased, it presumably took many generations for the species to recover. Two likely reasons for the stable low effective sizes observed would be high genetic load and low genetic diversity. It is not until the high inbreeding leads to the expression of deleterious mutations and natural selection erases these mutations that populations can begin to grow and recover from the bottleneck (Jackson et al., 2022).

Interestingly, our demographic and distribution models for the LIG (about 110,000 years ago) are inconsistent. Namely, demographic results suggested there were millions of individuals, whereas the SDM showed very low habitat suitability and availability. This conflicts with our hypothesis, as we would expect low effective sizes associated with low habitat inferred area. Nonetheless, it must be taken into account that the SDM models assume that ecological niches do not evolve, meaning that if the populations from which *P. californica* originated had a different niche, it will not reflect the real biogeographic history of the species since the environmental preferences considered were those of today's populations (Owens et al., 2013; Svenning et al., 2011). In addition, inference errors increase, and resolution power is lost as analysis pretend to model distributions deeper into the past (Feng et al., 2019). Although the demographic method used could also influence these results, we used MSMC2 that is a robust method when working with a higher number of haplotypes (Schiffels & Wang, 2020).

Despite the differences between the results obtained with GBS and with RAD-Seq data, the overall historical demographic and genetic structure patterns are consistent. Both agree in terms of the reduction of *P. californica* population size after the end of the LGM, only differing in the exact time to reach the bottleneck (by less than 10,000 years). They also concur in the lower effective size estimated for sex chromosomes with respect of the autosomes, which might indicate there were more females than males in the population, because in birds females are the heterogametic sex (ZW) (Ellegren & Fridolfsson, 1997). This sex-ratio bias may influence genetic diversity and population stability (Eberhart-Phillips et al., 2017). They also agree regarding the lack of genetic

388 structuring in *P. californica*. It should be mentioned that the grouping of *P. melanura* within a *P.*

389 *californica* cluster is not due to a misidentification of the individual. This bird was collected from a

390 locality in Sonora, Mexico, which is not part of the California gnatcatcher natural distribution.

391 Thus, it could be the result of errors during the genomic library or the sequencing process.

392   We can conclude that our findings demonstrate that the geographic distribution and genetic

393 patterns in the California gnatcatcher are tightly linked to the climatic and environmental changes

394 during the Quaternary. Furthermore, the fact that *P. californica* responds in such tune with this

395 habitat changes is of high concern under a scenario of global climatic change. It is still unknown if

396 bird species with arid-like preferences will be favored by the contemporary desertification

397 worldwide, but the rapid population's response shown in our study should be taken as a warning

398 signal to target conservation efforts for this and other species with similar ecological niches.

399

400 **MATERIALS AND METHODS**

401 **Sampling and genotyping**

402   We used genomic data from Vazquez-Miranda et al. (2022; NCBI SRA BioProject

403 PRJNA719408). Briefly, those data consist of 23 individuals of *P. californica* obtained from five

404 localities along the natural distribution of the species (Figure 1, Supplementary Material). DNA

405 extraction followed a phenol-chloroform-isoamyl protocol and two types of reduced-representation

406 sequencing (RRS) genomic libraries were created: one for single-end GBS (Genotyping By

407 Sequencing) and one for paired-end RAD-Seq (Restriction site Associated DNA Sequencing) data

408 following Gamble et al. (2015). For the GBS library, genomic DNA was digested with the *PstI*

409 enzyme, whereas for the RAD-Seq the *SbfI* enzyme library was used. Sequencing of both type of

410 libraries was carried out in independent lanes of the Illumina HiSeq 2000 platform at the University

411 of Minnesota. The individuals sequenced with RAD-Seq represent a subset of the individuals

412 sequenced with GBS. There were 23 California gnatcatcher samples for GBS data and 15 for RAD-

413   Seq. Additionally, in the sequencing one individual from the sister species, *P. melanura* (Zink &

414   Blackwell, 1998) was included, to enable structure comparisons and for rooting phylogenetic

415   analysis.

416   **Bioinformatics**

417   Raw reads were demultiplexed using Cutadapt (Martin, 2011) for the GBS data and *PyRAD*

418   (Eaton, 2014) for the RAD-Seq data. Then, adapters were removed with Cutadapt and reads were

419   trimmed with Trimommatic (Bolger et al., 2014). We evaluated the quality of the remaining reads

420   with FASTQC (Andrews, 2010) and created global reports with MultiQC (Ewels et al., 2016).

421   Additionally, we merged the R1 and R2 reads from RAD-Seq paired-end reads with PEAR (Zhang

422   et al., 2014). The cleaned reads were used as input for the BWA-MEM (Li, 2013) algorithm

423   implemented in Galaxy (Afgan et al., 2018) to map against the nuclear genome of *Taeniopygia*

424   *guttata* (RefSeq GCF_003957565.2_bTaeGut1.4.pri). Next, we filtered the sequences that were not

425   a primary alignment or had a quality below 30 with BAMTools (Barnett et al., 2011).

426   We used the *ref_map.pl* module from Stacks (Catchen et al., 2013) to identify the SNPs

427   based on the *T. guttata* nuclear genome. VCF files were generated using the *populations* module of

428   *Stacks*. For each genotyping method we had two VCF files: one with all the identified SNPs and

429   one with only one SNP per locus, the latter obtained by adding the argument *write-single-snp* from

430   *Stacks*. The final files were filtered with VCFTools (Danecek et al., 2011) so that we only recovered

431   biallelic loci, with a minimum allele count (MAC) of three or more, and up to 20% of missing data.

432   The software Plink (Purcell et al., 2007) was used to generate *bed*, *bim* and *treemix* files.

433   **Genetic diversity and population structure**

434   To estimate the genetic diversity, we used the VCF file that had all the SNPs, along with the

435   R (R Core Team, 2022) *adegenet* (Jombart, 2008) and *hierfstat* (Goudet, 2005) packages. We

436   estimated heterozygosity and gene diversity, as well as the paired fixation index (F_{ST}) following

437   Weir & Cockerham (1984) among the sampled localities of the California gnatcatcher. Also, to

438   evaluate genetic structure we applied three methods: ADMIXTURE (Alexander et al., 2009),

439   fastSTRUCTURE (Raj et al., 2014), and DAPC (Jombart et al., 2010), with which we evaluated

440   from k=2 (considering *P. californica* and *P. melanura* as two completely different genetic clusters)

441   to k=6 (deeming the individuals of each sampled locality as a distinct genetic group). Although the

442   three methods look for the number of clusters that best explain the genetic variation in the data,

443   each one follows a slightly different approach. ADMIXTURE is based on maximum likelihood,

444   fastSTRUCTURE works with Bayesian inference, and DAPC is a multivariate approach which does

445   not consider the nominal populations nor the identity of the individuals (Stift et al., 2019). We ran

446   10 repetitions on each k on each approach.

447   To determine the geographic structure of the California Gnatcatcher, we inferred an

448   individual-level phylogeny. We achieved this with SVDquartets (Chifman & Kubatko, 2014)

449   implemented in PAUP* (Swofford, 2003). Since this program requires a NEXUS file, we first used

450   the Python script *vcf2fasta.py* (https://github.com/santiagosnchez/vcf2fasta) to obtain a fasta file

451   from the VCF file that accounts for linkage disequilibrium. Then, we transformed the fasta file into

452   NEXUS using ALTER (Glez-Peña et al., 2010). Finally, we ran *SVDquartets* and calculated the

453   bootstrap value for each branch. These results were plotted on a densitree using *ape* (Paradis &

454   Schliep, 2019) and *phangorn* (Schliep, 2011).

455   Also, we estimated gene flow with TreeMix (Pickrell & Pritchard, 2012), which works with

456   a maximum likelihood approximation. For this we tried up to eight migration events (M) and ran

457   each M 10 independent times. To determine the number of migratory events that maximizes the

458   likelihood of the model we used OptM (Fitak, 2021) and *popcorn*

459   (https://github.com/andrewparkermorgan/popcorn) to plot the resulting graph.

460   **Historical demography**

461   To evaluate changes in effective population size we first used clean and trimmed reads from

462   one individual from each sampled location to reduce the computational time. From these reads we

463   removed every read that mapped against the mitochondrial genome of *T. guttata* (RefSeq

464   NC_007897.1), and then mapped to the nuclear genome of the Zebra Finch. These reads were then

465   passed through *MarkDuplicates* in Picard (http://broadinstitute.github.io/picard/) implemented in

466   GATK (van der Auwera & O'Connor, 2020) to remove sequence duplicates.

467   After this, we followed the instructions indicated by the authors of MSMC (Schiffels &

468   Durbin, 2014) and called the SNPs in a chromosome-based fashion with the tool *mpileup* from

469   SAMTools. Then, by combining the data from all the individuals, we generated the *multihetsep* files

470   with the '*generate_multihetsep.py*' tool (https://github.com/stschiff/msmc-tools). These files have

471   four columns: one with the number of the chromosome, one with the particular position on that

472   chromosome, one with the total number of homozygous sites since the last segregation site, and the

473   last one with the called alleles fort the heterozygous sites, in order of appearance, of the evaluated

474   haplotypes. We did not phase the SNPs nor did we used a mask file, since we used MSMC2, rather

475   than MSMC, as we only wanted to estimate the effective size changes and not the divergence time

476   (Schiffels & Wang, 2020). Two analyses with different sets of *multihetsep* files were ran: one with

477   all the autosomal chromosomes and one for the Z chromosome only.

478   With this *multihetsep* files we ran the program *msmc2* (https://github.com/stschiff/msmc-

479   tools) and evaluated up to three different segmentation patterns using 18, 20, and 28 free parameters

480   for the autosomal chromosomes, and four, four, six, and seven parameters for the sexual

481   chromosome Z. Additionally, the program was forced to run only on specified pairs. This assumes

482   that each indicated pair of haplotypes belongs to a different population. Lastly, we used the

483   '*multihetsep_bootstrap.py*' to create 20 sets of multihetsep files with random regions of missing

484   data to evaluate the robustness of the analysis. In each of these sets we re-ran *msmc2* under the

485   same parameters. The bootstrap was only estimated for the 18- and the four-parameters runs.

486   To scale the data to individuals per year, we used the mutational rate per year in

487   Passeriformes (Smeds et al., 2016), which is 2.3 x 10^{-9}, as well as the generation time which in *P.*

488   *caerulea* is estimated to be of one year (Smith et al., 2018).

489   **Geographic distribution modelling**

490   First, we downloaded the occurrence data of *P. californica* from GBIF, using *rgbif*

491   (Chamberlain et al., 2017). To reduce potential errors, we only used those records based on

492   preserved specimens that have associated coordinates. The occurrences were filtered with

493   *CoordinateCleaner* (Zizka et al., 2019) and *spThin* (Aiello-Lammens et al., 2015) to remove

494   duplicated data and to thin the registers using a distance buffer of 2 km, respectively. Also, we

495   added five occurrence records that correspond to the five locations we sampled to obtain the

496   genomic data and the 39 occurrences used by Waltari et al. (2007) to identify Pleistocene refugia for

497   the California gnatcatcher.

498   To select the environmental data for our model, we used the 19 bioclimatic variables of

499   WordlClim2 (Fick & Hijmans, 2017) from 1970-2000 at a resolution of 2.5 minutes. These files

500   were cropped in QGIS (QGIS.org, 2022) using a squared *shape* file so that the entire actual extent

501   of the Baja California Peninsula was included. Additionally, we downloaded and cropped the 19

502   bioclimatic variables for the LGM of two different General Circulation Models (CGM): CCSM4 y

503   MIROC-ESM (Fick & Hijmans, 2017), and the ones for the Last Interglacial. All at the same

504   resolution of 2.5 minutes.

505   To create the model, we tested for collinearity among the current variables with the function

506   *vifcor* from the R package *usdm* (Naimi et al., 2014) with a threshold value of 0.8. The variables

507   with the highest VIF were excluded. Using the remaining variables and the final occurrence

508   database, we created a model of the potential geographic distribution using the MaxEnt algorithm

509   (Phillips et al., 2006) implemented in *dismo* (Hijmans et al., 2015). To build the potential

510   distribution model for the present, we randomly kept 20% of the total occurrences to evaluate the

511   model. We used the linear, quadratic and product functions in MaxEnt considering that the shape of

512   an ecological niche is ellipsoidal and other functions add unnecessary complexity and reduce the

513   performance of the algorithm (Warren & Seifert, 2011). We then projected this model to the three

514   past scenarios: the LGM model CCSM4, the LGM MIROC-ESM one, and the LIG (Last

515   Interglacial). Finally, to evaluate the differences among the created models, we used *ENMTools*

516   (Warren et al., 2021) to calculate the area of overlap between the contemporary and the past models.

517

518   **DATA ACCESSIBILITY**

519   The datasets supporting this article, as well as the scripts used for the analyses, were

520   deposited in https://figshare.com/s/d8842f8a34e7d486bcdc.

521

532

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Discusión y conclusiones

En poblaciones que recientemente han experimentado cuellos de botella se suele observar una disminución del tamaño poblacional, así como una baja diversidad genética (Forsdick et al., 2017; Hu et al., 2020). La reducción del tamaño poblacional resultado del cuello de botella incrementa el efecto de la deriva génica, con consecuente pérdida aleatoria de alelos y disminución de la diversidad genética. Además, se ha demostrado que la reducción poblacional se relaciona con una mayor probabilidad de apareamientos no aleatorios, aumentando la consanguinidad (Keller y Waller, 2002; Palstra y Ruzzante, 2008; White y Searle, 2007). Este parece ser el caso de la perlita de California, sobre la cual Zink et al. (2000) y Zink et al. (2013) reportaron baja diversidad genética, particularmente para las poblaciones del norte de la península. Aquí, usando múltiples loci nucleares, encontramos valores de diversidad genética más bajos a los reportados en estudios previos. Asimismo, los valores de endogamia que observamos indican consanguinidad moderada en la población estudiada.

Los cuellos de botella y el aislamiento poblacional se han relacionado con la estructura poblacional, como se ha visto previamente con otras especies durante las oscilaciones climáticas del Pleistoceno (Burg et al., 2006; McDonough et al., 2022; Menezes et al., 2021). En el caso de la perlita de California, los resultados mostraron de manera consistente que no existe evidencia de estructura genética (F_{ST} y tres métodos de asignación poblacional). Solamente el análisis con SVDquartets sugirió un potencial agrupamiento de los individuos de Santa Rosalillita y los de Riverside; sin embargo, es necesario mencionar que, ya que las poblaciones de esta ave que habitan en la costa de California forman parte del Acta de Especies en Peligro de Extinción de EE.UU., no fue posible muestrear individuos en California. De hecho, las tres muestras de Riverside que empleamos en este estudio provienen de un único nido encontrado en campo, mismo que tenía indicios de depredación. Por ello, no resulta extraño que los individuos de dicha localidad formen un clúster genético.

Este no fue el caso de las muestras de Santa Rosalillita donde, debido a que la localidad se encuentra en la parte media del área de distribución de la especie, es poco probable que estos individuos hubieran divergido sin que, de igual forma, lo hicieran las poblaciones del norte y el sur; especialmente considerando que no existen barreras que aíslen a esta localidad del resto de la península. El hecho de que los resultados indicaran la presencia de flujo génico, donde encontramos soporte para al menos un evento de intercambio genético entre localidades distantes, sugiere que puede existir flujo génico entre otras localidades. Estudios futuros podrían ampliar el muestreo para comprobar este resultado y determinar si en realidad los individuos de esta localidad se separaron

genéticamente del resto o es un artefacto del diseño de nuestro estudio. No obstante, en general, los resultados aquí obtenidos apoyan la hipótesis de que *P. californica* no presenta estructura genética, por lo que cualquier esquema de clasificación infraespecífico resulta inadecuado para la historia evolutiva de la especie.

De manera importante, se han reportado resultados similares en otra especie con características ecológicas similares. Brown et al. (2013) encontraron que el maluro de mallee (*Stipiturus mallee*), un ave australiana con baja capacidad de dispersión que habita en ambientes semiáridos propensos a incendios presenta baja diversidad genética. Esto es en parte debido a los patrones espaciotemporales cambiantes de su hábitat, pero también debido a procesos de extinción y recolonización locales dados por los incendios. Mismos que, a su vez, provocan la pérdida de diversidad y estructura genética.

Estos patrones genéticos concuerdan con los resultados de demografía histórica y distribución geográfica. En primer lugar, que la especie experimente un declive demográfico hacia finales del Último Glacial Máximo (UMG) muestra algunos de los potenciales efectos de los cambios ambientales sobre la especie. Además, la distribución potencial inferida con los SDM para la perlita de California durante este periodo indica que la especie se encontraba restringida al sur de la península, región que ya había sido propuesta como un refugio pleistocénico para otras especies del Hemisferio Norte (Hewitt, 2001; Stewart et al., 2009). De hecho, Waltari et al. (2007) encontraron evidencias de poblaciones aisladas de *P. californica* en la porción sur de la península. Asimismo, se ha propuesto que la recolonización desde refugios pleistocénicos es uno de los principales fenómenos determinantes asociados con la distribución actual de muchas especies, especialmente para aquellas con baja capacidad de dispersión (Drovetski et al., 2018). Así, la reducción en el tamaño efectivo de las poblaciones de *P. californica* se relaciona directamente con la pérdida de hábitat adecuado al sur de EE.UU. que ocurrió durante el UMG.

Al término del periodo glacial, hace aproximadamente 10,000 años, la temperatura global ascendió y las tierras áridas de Norteamérica pudieron extenderse hacia el norte, permitiendo que los ecosistemas alcanzaran una distribución muy similar a la actual (Herzschuh, 2020; Moncrieff et al., 2015). Actualmente, la perlita de California se distribuye en toda la península de Baja California, desde el sur de California en EE.UU. hasta la punta sur de Baja California Sur en México. Dada la diferencia entre la distribución durante el UMG y la distribución actual, inferimos que la distribución de la especie efectivamente se incrementó. Sin embargo, a pesar de una mayor disponibilidad de hábitat, tuvieron que transcurrir múltiples generaciones para que la especie pudiera recuperarse en términos demográficos. Dos posibles explicaciones para la estabilidad del reducido tamaño efectivo de la especie son la alta carga genética y la baja diversidad genética, donde es necesario que existan

altos niveles de consanguinidad en una especie para inducir la expresión de mutaciones deletéreas. Es entonces cuando la selección natural pudiera actuar eliminando dichas mutaciones, permitiendo que la población crezca y salga del cuello de botella (Jackson et al., 2022).

De la misma forma, cerca del Último Interglacial (UIG), hace aproximadamente 110,000 años, existe una contradicción entre los resultados de los análisis demográficos y los geográficos. Por una parte, la demografía indica que en el periodo interglacial la población alcanzaba un tamaño efectivo que rondaba los millones de individuos, mientras que los análisis geográficos demuestran que la idoneidad y disponibilidad del ambiente eran bajas. Esto último está en contraposición con nuestra hipótesis, ya que esperaríamos que la inferencia de áreas habitables reducidas se asocie con tamaños efectivos reducidos. Sin embargo, es importante tomar en cuenta que los modelos SDM asumen que el nicho ecológico de las especies no cambia, es decir, que el nicho no evoluciona. Lo que implica que si la población que dio origen a *P. californica* tenía preferencias ambientales diferentes a las de la población actual entonces el modelo no reflejaría de manera certera la distribución de la población durante el UIG (Owens et al., 2013; Svenning et al., 2011). Debemos considerar que este tipo de modelos pierden resolución conforme nos alejamos demasiado en el tiempo, ya que el error de inferencia incrementa en tiempos más antiguos (Feng et al., 2019). Esta falta de concordancia también puede deberse al modelo demográfico empleado, sin embargo, en este estudio usamos el programa MSMC2, el cual es más robusto a tiempos antiguos incluso cuando se emplea con un número de haplotipos relativamente alto (Schiffels y Wang, 2020).

A pesar de las diferencias observadas entre los resultados obtenidos con GBS (Genotipado por secuenciación) y con RAD-Seq (Secuenciación de DNA asociada a sitios de restricción), los patrones generales de demografía histórica son consistentes. Ambos concuerdan en la reducción del tamaño efectivo de *P. californica* al término del UMG, aunque difieren (por menos de 10,000 años) en el tiempo exacto en el cual la especie entró en el cuello de botella. También concuerdan en el bajo tamaño efectivo estimado para los cromosomas sexuales con respecto al estimado para los autosomas, lo cual podría indicar que en la población había menos machos que hembras. Esto porque, en las aves, las hembras son el sexo heterogamético (cromosomas sexuales ZZ en machos y ZW en hembras; Ellegren y Fridolfsson, 1997). Esta desviación en la proporción sexual puede haber influido en la diversidad genética de la especie, así como en la estabilidad poblacional de la misma (Eberhart-Phillips et al., 2017). Por último, ambos métodos sugieren que no existe estructura genética en *P. californica*. Es importante mencionar que, si bien los resultados obtenidos a partir de RAD-Seq sugieren que *P. melanura* y *P. californica* pertenecen a un mismo clúster genético, ello no es resultado de una mala identificación de los especímenes muestreados. El individuo de la especie hermana, la perlita del desierto, fue colectado fuera del área de distribución natural de la perlita de California. Así,

la falta de divergencia genética entre ambas especies en esta prueba pudo deberse a un error durante la preparación de la genoteca o el proceso de secuenciación.

Si bien este estudio nos brinda una idea más clara sobre el estado de las poblaciones de *P. california* y el impacto que han tenido los cambios climáticos globales en la demografía de las especies de zonas áridas del noroeste de América, reconocemos las limitaciones de este estudio. Por lo tanto, creemos que un muestreo exhaustivo que incluya tanto un mayor número de individuos como una mayor cantidad de localidades podría resolvernos dudas sobre la estructura genética de la especie. Asimismo, un genoma de mayor cobertura daría mayor resolución a los análisis de demografía histórica al incluir un mayor número de loci. Sin embargo, los resultados de este trabajo muestran que la distribución geográfica y los patrones genéticos de la perlita de California están asociados a los cambios climáticos y ambientales que tuvieron lugar en el periodo Cuaternario. Más aún, el hecho de que los patrones demográficos observados para *P. californica* se asociaran a los cambios del UMG y el UIG es alarmante bajo un escenario de cambio climático como el que vivimos actualmente.

Aún desconocemos si la desertificación global que enfrentamos hoy en día presentará un escenario favorable para aquellas aves con preferencias por ambientes áridos, pero los patrones y la escala temporal que mostró la perlita de California deben ser considerados como una señal de alerta para tomar urgentemente medidas de conservación mejor informadas para ésta y otras especies con nichos ecológicos similares. Una de las principales amenazas para la especie son los recurrentes incendios en la zona de la península, por lo que crear planes de control que mantengan la cantidad y magnitud de los incendios en temporada de sequía al mínimo podría beneficiar a la especie al reducir el posible aislamiento entre poblaciones debido a la falta de matorrales.

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Apéndices

Supplementary Material

TITLE

Synchronous demographic and distribution shifts through time in an endangered desert specialist

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Supplementary Tables

Table S1. Sampled individuals, locations and sequencing method

Sample ID	Location	GBS	RAD-Seq	Voucher location
JK99-023	Riverside, California, USA	X	X	Bell Museum, University of Minnesota
JK99-024	Riverside, California, USA	X		Bell Museum, University of Minnesota
JK99-025	Riverside, California, USA	X	X	Bell Museum, University of Minnesota
BCHVM-064	Cataviña, Baja California, México		X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-070	Cataviña, Baja California, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-085	Cataviña, Baja California, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-087	Cataviña, Baja California, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-089	Cataviña, Baja California, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-118	Cataviña, Baja California, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-135	Santa Rosalillita, Baja California,	X		Museo de Zoología, Facultad de Ciencias, UNAM, México

	México			
BCHVM-136	Santa Rosalillita, Baja California, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-137	Santa Rosalillita, Baja California, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-138	Santa Rosalillita, Baja California, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-139	Santa Rosalillita, Baja California, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-199	El Cien, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-201	El Cien, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-203	El Cien, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-204	El Cien, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-213	El Cien, Baja California Sur,	X		Museo de Zoología, Facultad de Ciencias, UNAM, México

	México			
BCHVM-214	El Cien, Baja California Sur, México	X		Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-222	Cabo Pulmo, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-223	Cabo Pulmo, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
BCHVM-224	Cabo Pulmo, Baja California Sur, México	X	X	Museo de Zoología, Facultad de Ciencias, UNAM, México
RMZ5259	Sonora, México	X	X	Bell Museum, University of Minnesota
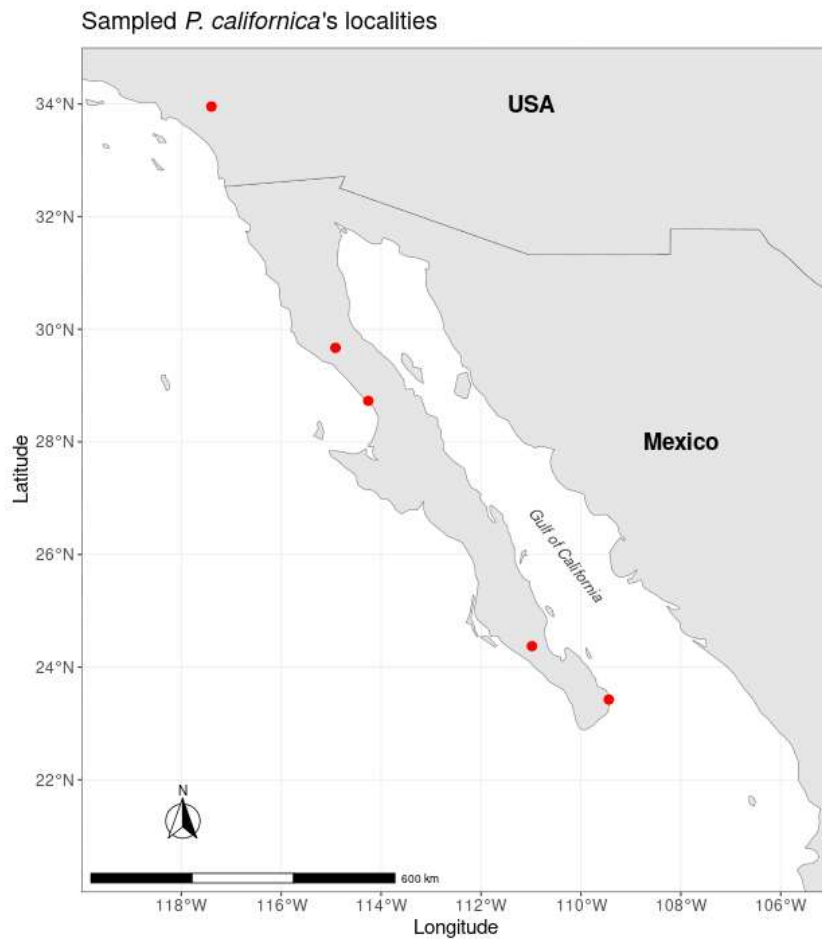
Fig. S1. Sampled localities of the California gnatcatcher. The individuals sequenced in this study came from the five localities indicated by the red dots. From North to South the locations are: Riverside, California, EE.UU.; Cataviña, Baja California; Santa Rosalillita, Baja California; El Cien, Baja California Sur; and Cabo Pulmo, Baja California Sur.
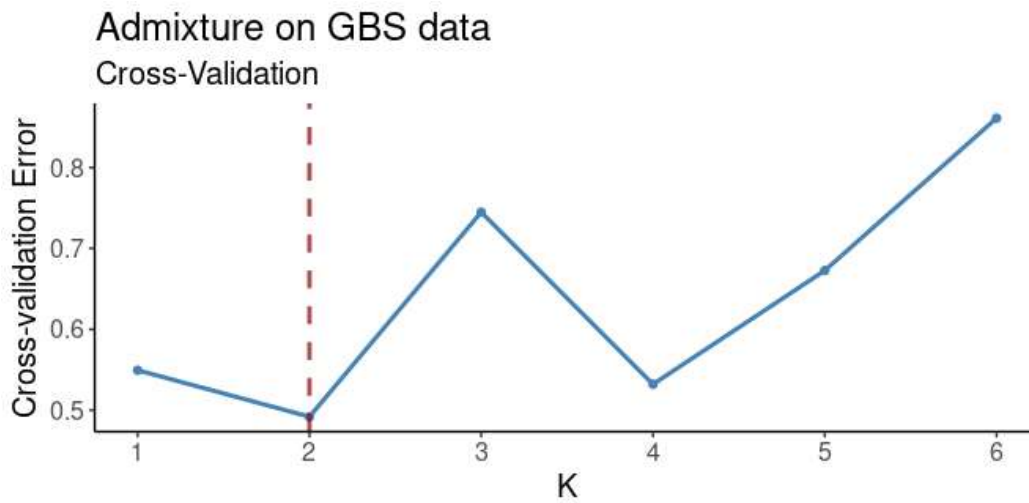
Fig. S2. Cross-validation error for the different number of evaluated clusters (*k*). For the GBS

data we evaluated *k* values from 1 to 6 on *ADMIXTURE*. The red dotted line indicates that *k*=2 is

the number of clusters that has the highest probability of explaining the data.
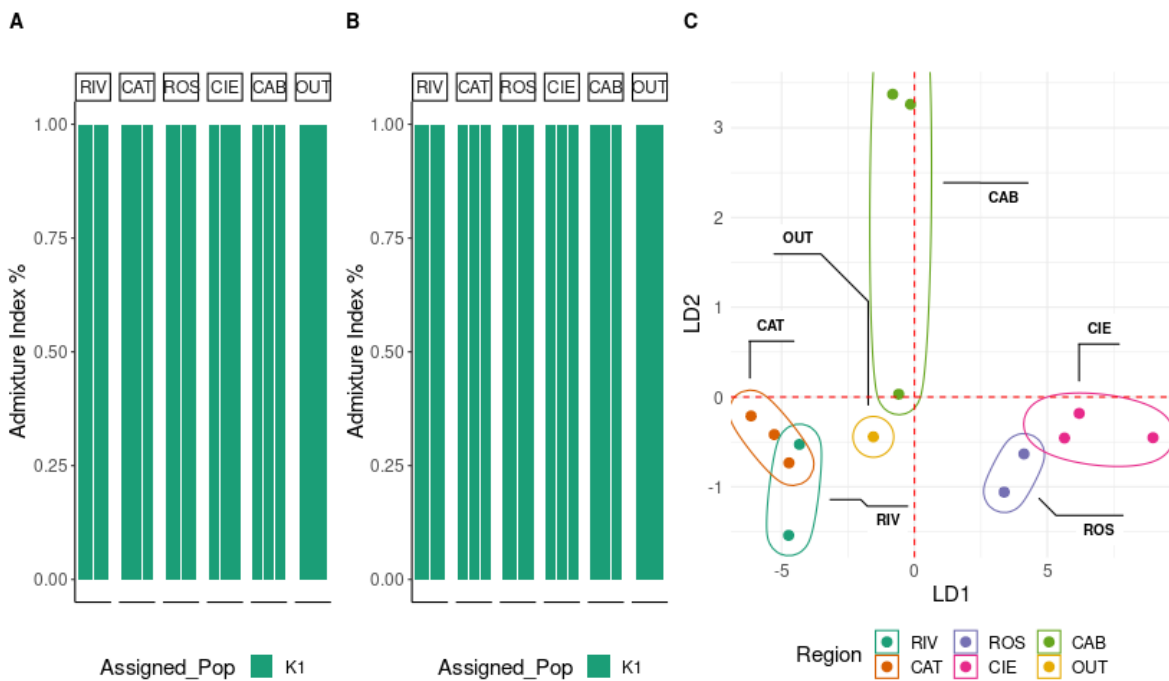
Fig. S3. Population structure for *P. californica* based on RAD-Seq data. The figures depict to which genetic group the sampled individuals belong showing that all the smaples grouped in a single cluster. A and B illustrate the results obtained with *ADMIXTURE* and *fastSTRUCTURE*, respectively. While C shows the genetic coordinates of the samples based on a DAPC analysis. LD: linear discriminant.
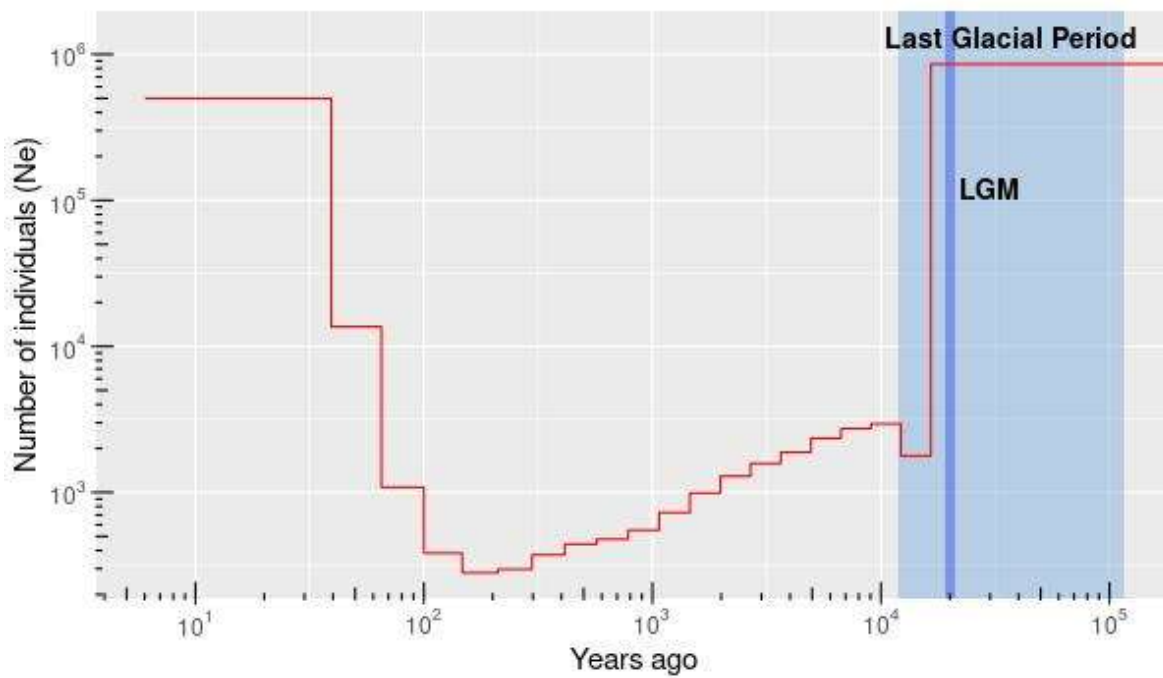
Fig. S4. Historical demography of *P. californica*'s autosomes based on RAD-Seq data with 20 free parameters. The red line shows the demographic trend of the California gnatcatcher sampled locations. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.
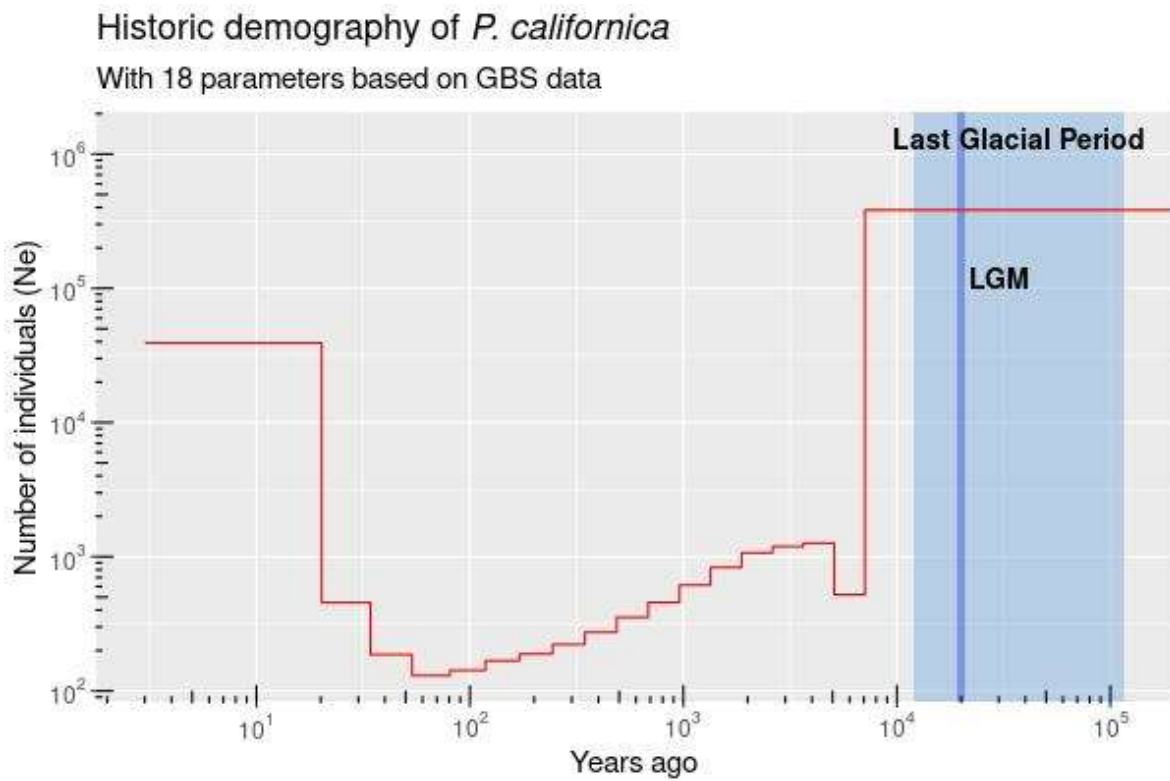
Fig. S5. Historical demography of *P. californica*'s autosomes based on RAD-Seq data with 28 free parameters. The red line shows the demographic trend of the California gnatcatcher sampled locations. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.
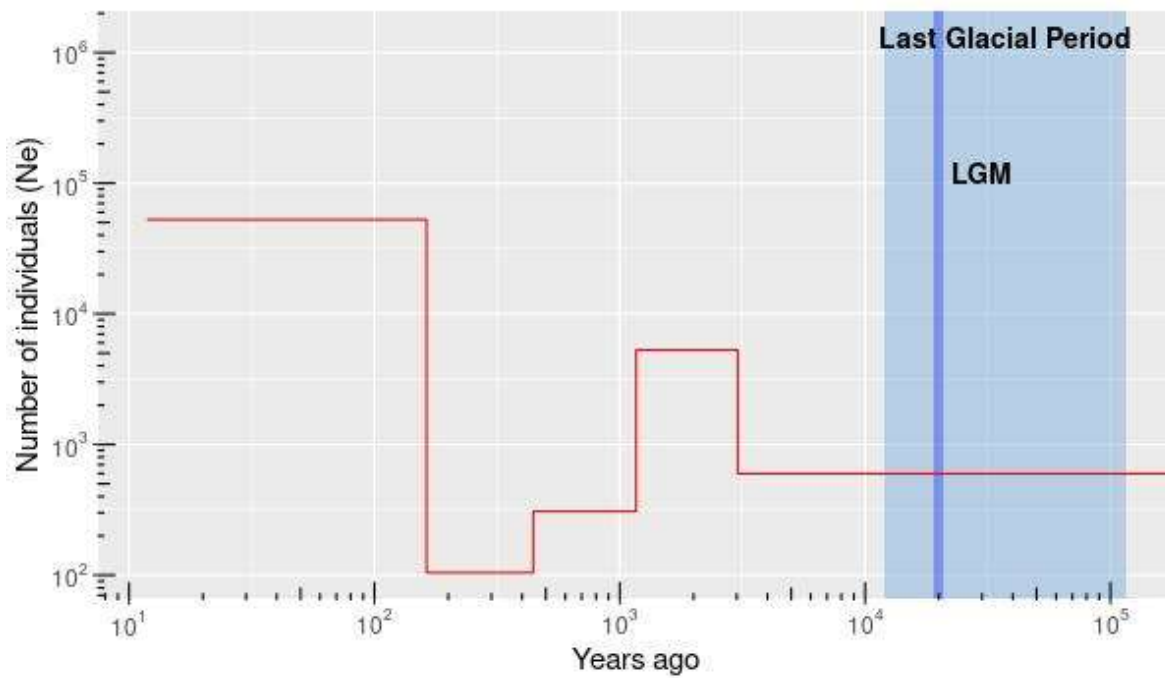
Fig. S6. Historical demography of *P. californica*'s autosomes based on GBS data with 18 free parameters. The red dark line shows the demographic trend of the California gnatcatcher sampled locations and the light red lines are bootstrap replicates of the original run. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.
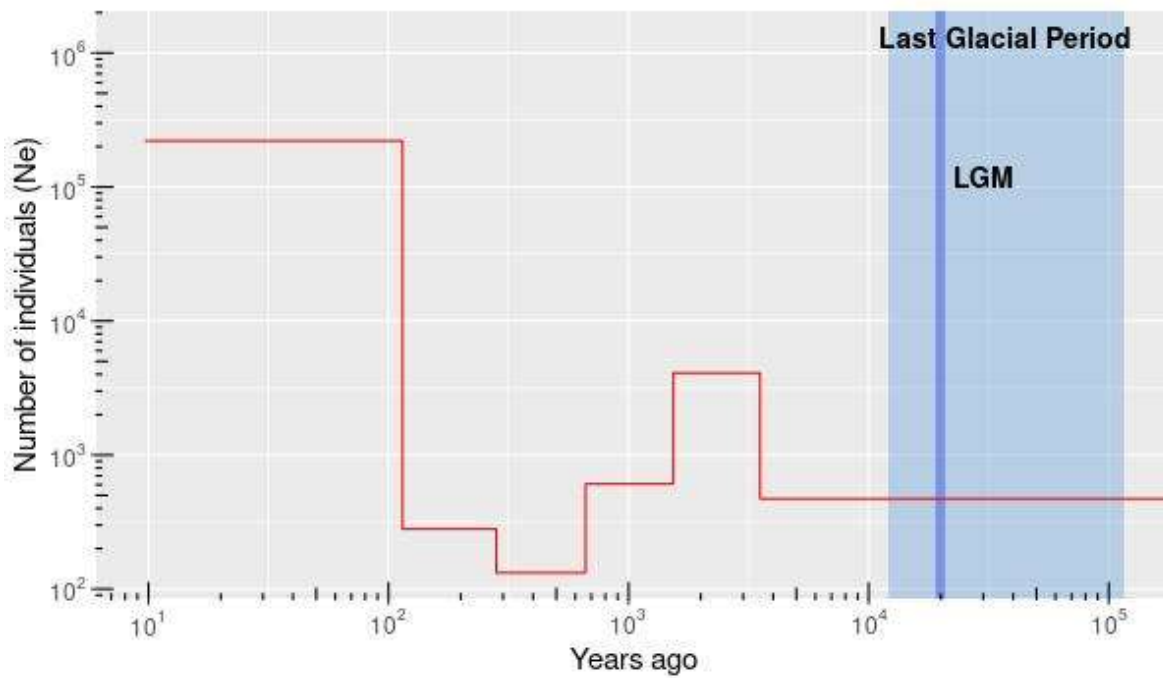
Fig. S7. Historical demography of *P. californica* for the sex Z chromosome based on RAD-Seq data with 6 free parameters. The red line shows the demographic trend of the California gnatcatcher sampled locations. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.

Fig. S8. Historical demography of *P. californica* for the sex Z chromosome based on RAD-Seq data with 7 free parameters. The red line shows the demographic trend of the California gnatcatcher sampled locations. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.

Historic demography of *P. californica*
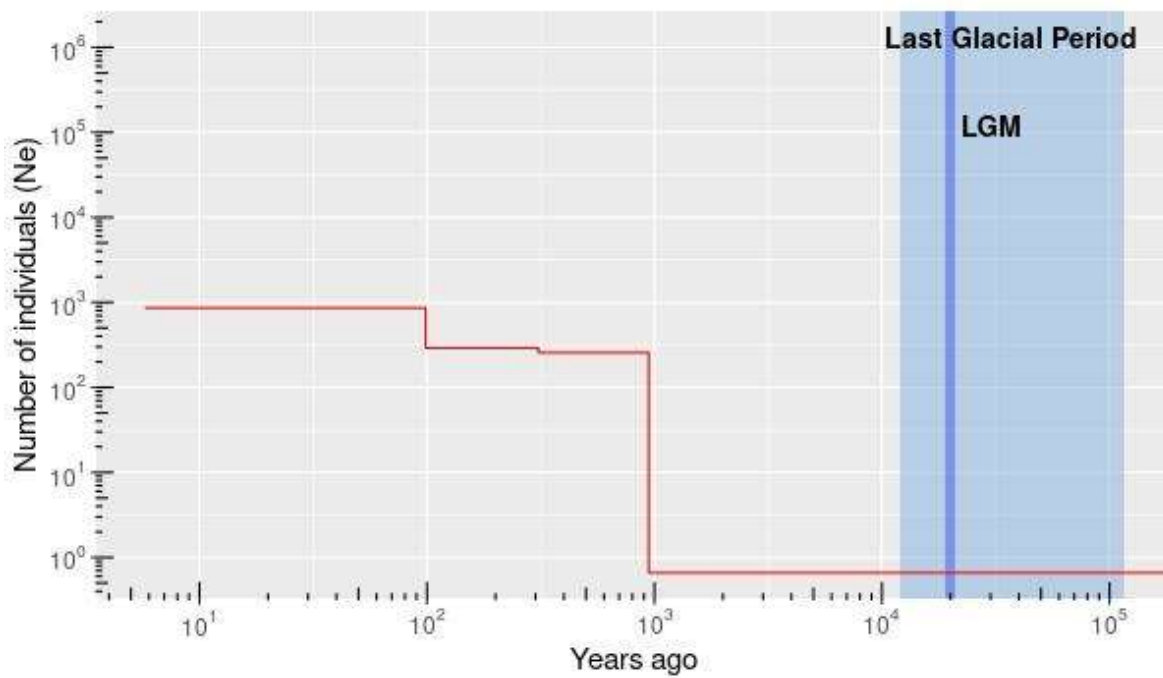
Sex Chromosome Z with 4 parameters based on GBS data

Fig. S9. Historical demography of *P. californica* for the sex Z chromosome based on GBS data with 6 free parameters. The red line shows the demographic trend of the California gnatcatcher sampled locations and the light red lines are bootstrap replicates of the original run. The light blue rectangle indicates the extent of the Last Glacial Period, while the dark blue line represents the duration of the Last Glacial Maximum.
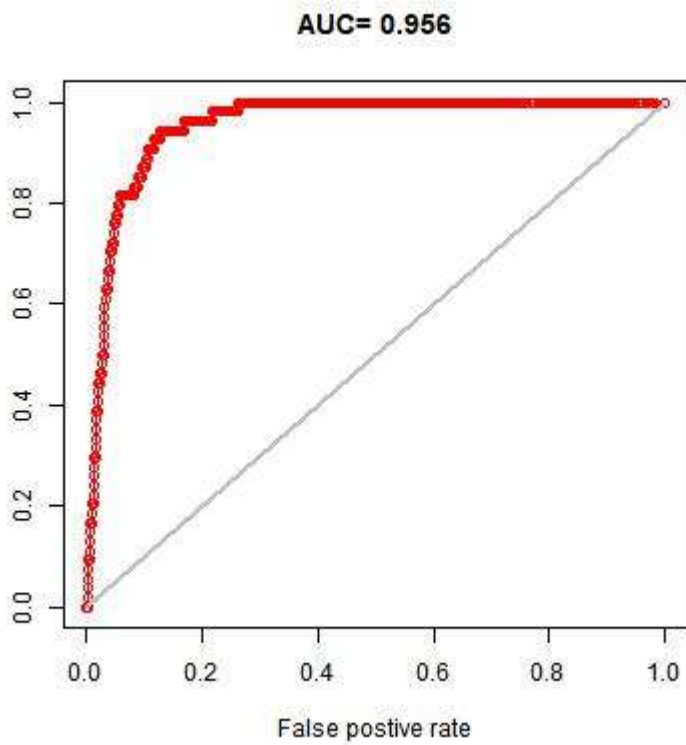
Fig. S10. ROC curve for the *MaxEnt* model based on the current bioclimatic variables. The red line depicts the cumulative increase between the specificity (false positive rate) in the *x* axis and the sensibility (true positive rate) in the *y* axis. The Area Under the Curve (AUC) value was 0.956.