

Habitat quality or quantity? Changes in niche marginality across 21 species of plant and animal suggest differential responses between highland and lowland species to past climatic changes

Raúl Araya-Donoso¹, Austin Biddy², Adrian Munguía-Vega³, Andrés Lira-Noriega⁴, and Greer Dolby²

¹Arizona State University

²The University of Alabama at Birmingham College of Arts and Sciences

³University of Arizona

⁴Instituto de Ecología AC

April 23, 2024

Abstract

Climatic changes can affect species distributions, population abundance, and evolution. Such organismal responses could be determined by the amount and quality of available habitats, which can vary independently. In this study, we assessed changes in habitat quantity and quality independently to generate explicit predictions of the species' responses since the Last Glacial Maximum (LGM) climatic changes. We built ecological niche models and distribution models for 21 reptile, mammal, and plant taxa from the Baja California peninsula inhabiting lowland or highland environments. Geological data suggests the CCSM global circulation model is a better representation of LGM climate for the Baja California peninsula. Significant niche divergence was detected for all clades within species, along with significant differences in niche breadth and area of distribution between northern and southern clades. Most clades showed a reduction in distribution area towards LGM. Further, niche marginality (used as a measure of habitat quality) was higher during LGM for most clades, except for northern highland species who experienced improvements in both. Our results suggest that changes in habitat quantity and quality can affect organismal response independently. This allows the prediction of genomic signatures associated with changes in effective population size and selection pressure that could be explicitly tested to support our models.

Habitat quality or quantity? Niche marginality across 21 plants and animals suggests differential responses between highland and lowland species to past climatic changes

Abstract

Climatic changes can affect species distributions, population abundance, and evolution. Such organismal responses could be determined by the amount and quality of available habitats, which can vary independently. In this study, we assessed changes in habitat quantity and quality independently to generate explicit predictions of the species' responses to climatic changes between Last Glacial Maximum (LGM) and present day. We built ecological niche models and distribution models for 21 reptile, mammal, and plant taxa from the Baja California peninsula inhabiting lowland or highland environments. Geological data suggests the CCSM global circulation model is a better representation of LGM climate for the Baja California peninsula. Significant niche divergence was detected for all clades within species, along with significant differences in the niche breadth and area of distribution between northern and southern clades. Most clades showed a reduction in distribution area towards LGM. Further, niche marginality (used as a measure of habitat quality) was higher during LGM for most clades, except for northern highland species. Our results suggest

that changes in habitat quantity and quality can affect organismal response independently. This allows the prediction of genomic signatures associated with changes in effective population size and selection pressure that could be explicitly tested to support our models.

Keywords:

Baja California peninsula, ecological niche modeling, effective population size, Last Glacial Maximum, niche centroid, selection pressure

Introduction

Understanding how taxa within a community respond to shared environmental variation is of particular relevance in the context of climate change. Climatic changes can affect species distributions, population abundance, and evolution due to impacts on genetic drift, structuring of genetic variation, gene flow, and selection (Foden et al., 2019; Román-Palacios & Wiens, 2020; Aguirre-Liguori et al., 2021). Species' responses depend on their ecological niche, defined as all the variables that influence organismal fitness (Hutchinson, 1957; Blonder, 2018). A species niche will determine the amount and quality of habitat available to populations, which can change independently. Habitat quantity has been commonly used as a metric of population abundance as predicted by metapopulation and island biogeography theory (Fahrig et al., 2013). However, the amount of habitat is not sufficient to describe all processes affecting a species and can be misleading, and evidence suggests that habitat quality should also be considered (Morletilli et al., 2010; Walting et al., 2020; Galán-Acedo et al., 2021; Regolín et al., 2021). Separately assessing how habitat availability and habitat quality changed over past climatic changes for a range of species offers an opportunity to understand the degree to which these patterns are coupled, and therefore offer more nuanced information about how organisms may respond to ongoing and future climate changes.

The ecological niche can be modeled in terms of the climate factors that determine the occurrence of species in space, or the "Grinnellian niche" (Soberón, 2007; Sillero et al. 2021). Most studies addressing the effect of climatic changes on species with a niche modeling approach focus on habitat quantity and distribution, and relatively fewer studies have focused on changes in habitat quality (But see Morente-López et al., 2022; Kebaïli et al., 2023). The ecological niche can be represented as an ellipsoid in multivariate space, consisting of the range of suitable conditions for a defined taxon based on a determined set of variables (Jiménez et al., 2019; Osorio-Olvera et al., 2020a). In this framework, the ellipsoid centroid (niche centroid) corresponds to high suitability conditions and high habitat quality, whereas positions in the multidimensional space near the ellipsoid borders correspond to more marginal conditions or lower habitat quality (Martínez-Meyer et al., 2012; Osorio-Olvera et al., 2020b). According to the center-marginal hypothesis (Eckert et al., 2008; Pironon et al., 2017), populations living under more suitable conditions present higher abundance and genetic diversity, whereas populations inhabiting more marginal conditions are expected to have lower abundance, lower genetic diversity, and higher drift (Lira-Noriega & Manthey, 2014; San Juan et al., 2021). Moreover, populations living at the limit of their tolerances often experience higher selection pressure and respond by adapting to those challenging environmental conditions (Aguirre-Liguori et al., 2017; Bontrager et al., 2020). Therefore, a population's distance to the ellipsoid centroid may be proportional to selection pressure.

As climatic conditions change, populations may track suitable environmental conditions geographically, assuming that niches do not evolve (i.e., niche conservatism; Wiens et al., 2010). This can result in changes in the species' distribution and leave a genomic signature of range expansion (Lenoir & Svenning, 2015; Tomiolo & Ward, 2018). It can also lead to founder effects and surfing of deleterious alleles at the margin of the expanding front ('allele surfing'; Escoffier et al., 2008; Gilbert et al., 2018). Further, climate changes can affect species abundance by the reduction or increase in the amount of suitable area (Fahrig et al., 2013). Regarding habitat quality, changes in climatic conditions can affect population fitness and selection pressure because the distribution of habitats closer to the niche centroid and marginal conditions could shift. For instance, a geographic location consisting of conditions matching the niche centroid at one time could shift to more marginal conditions at a different time, while still being suitable. Therefore, populations inhabiting this area would experience a population decline, and/or decrease in fitness and/or an increase in selection

pressure on traits related to variables that have become marginal at that location. This highlights that environmental changes can affect both habitat quantity and habitat quality independently and they yield different population genomic predictions.

The Baja California peninsula (BCP) is a good system to assess how different taxa respond to changes in habitat quantity and quality during different climatic conditions. It presents a wide variety of ecosystems ranging from desert scrub to high-altitude forests (Rebman & Roberts, 2012). It spans 10 degrees of latitude with stark differences in rainfall and temperature and since it is a peninsula, ecological and expansion-dispersal dynamics are constrained by its geography (Dolby et al., 2015). Native species have largely been co-distributed and isolated from the mainland since the Gulf of California finished flooding 6.3 Mya (Oskin & Stock, 2003; Darin et al., 2024). In particular, low and high amplitude glaciation cycles during the Pleistocene (~3 Mya) are expected to have had a large impact on redistributing climatic conditions and therefore the distribution and abundance of populations (Dolby et al., 2015). About 80 taxa show a diffuse north-south genetic co-divergence signal centered in the middle of the Peninsula (Dolby et al., 2015; Araya-Donoso et al., 2022) and show ecological niche divergence, suggesting potential adaptation to local environmental conditions (Cab-Sulub & Álvarez-Castañeda, 2021), which offers an opportunity to assess both species-level and clade-specific changes in habitat quantity and quality. It also allows us to test which organismal features determine responses to environmental change. For example, highland species that can resist cold may respond differently than species inhabiting lowland deserts adapted to low water availability, or taxonomic groups with different physiological requirements, such as mammals, plants, and reptiles, could also respond specifically.

Previous models and descriptions have detected contrasting patterns of species distribution to the Last Glacial Maximum (LGM) on the peninsula. Some taxa show range expansions during LGM (e.g. Graham et al., 2014; González-Trujillo et al., 2016; Harrington et al., 2017; Arteaga et al., 2020), whereas others show range contractions (Klimova et al., 2017; Valdivia-Carrillo et al., 2017). Cab-Sulub & Álvarez-Castañeda (2021) proposed that southern clades within species contracted their distribution ranges to LGM, whereas northern clades expanded. Furthermore, some studies have assessed species' past demography with genetic data showing signatures of population contraction towards LGM (Álvarez-Castañeda & Murphy, 2014; Ferguson et al., 2017; Phuong et al., 2017; Martínez-Nogues et al. 2020), which does not agree with the range expansion patterns proposed by some distribution models. Therefore, changes in population size could be determined by not just habitat quantity but also habitat quality.

Here, we used ecological niche modeling and species distribution modeling to compare intra-specific and inter-specific distribution patterns and niche marginality of 21 taxa from the Baja California peninsula including mammals, reptiles and plants that inhabit highland and lowland environments, and have different levels of genetic divergence along the peninsula. We aimed to assess changes in habitat quantity and quality between LGM and present day and determine if organismal characteristics affected these patterns. Then, we used our models to generate predictions about the effects of historical climate change on abundance and selection pressure on natural populations that can be tested in the future with genomic data.

Materials and Methods

Climatic data and characterization of the Baja California Peninsula

We characterized the current climatic conditions of the Baja California peninsula by using 19 bioclimatic variables (Supporting Information) with a spatial resolution of 1 km obtained from Worldclim (Fick & Hijmans, 2017). Additionally, we obtained data from two different global circulation models (CGMs): the Interdisciplinary Research on Climate (MIROC v3.2; Hasumi & Emori, 2004) and the Community Climate System Model (CCSM3; Collins et al., 2006), for characterizing the climate during the Last Glacial Maximum (LGM; ~ 21 kya).

We calculated the difference between present-day and LGM conditions for all temperature and precipitation variables for both GCMs. Since previous work showed discrepancies between GCM conditions on the BCP that affected SDMs (See Supporting Information for details), we compared the GCM differences to paleoprecipitation proxy data published for alluvial fan, pollen, lake core record, and midden data, across southern

California and the Baja peninsula to determine which GCM was more consistent with paleoclimate data at the LGM in this region.

Species georeferenced records

Our study focused on 21 taxa native to the BCP (Table 1), including eight mammals, four plants and nine reptiles. We selected species for which their genetic structure on the peninsula was previously published. We aimed to represent species that inhabit different elevations (highland or lowland), which we hypothesized could respond differently to LGM conditions. We identified the number of genetic clades described in previous studies for each taxon and classified them according to their geographic location in southern (south of the Vizcaíno peninsula, $\sim 27^{\circ}\text{S}$), northern (north of $\sim 27^{\circ}\text{S}$ including the Vizcaíno peninsula) and clades without north-south genetic differentiation (unstructured). For each taxon we obtained georeferenced records from the Global Biodiversity Information Facility (<https://www.GBIF.org>). Occurrences were manually filtered to accurately represent each taxon distribution, and a minimum convex polygon of each clade's distribution was used to assign occurrences within a 10 km buffer to their corresponding genetic clade. The values for the 19 bioclimatic variables (Table S1) were obtained from each occurrence point.

Table 1. List of species selected for this study indicating their corresponding taxonomic group (M: mammal; P: plant; R: reptile) and elevation (H: highland; L: lowland). We also indicate the reference (Ref) describing the species' genetic structure, along with the number and location (N: north; S: south; -: unstructured) of described genetic clades, and the type of genetic data (mit: mitochondrial; plastid; nuclear; or RADseq) used to determine the genetic structure. Finally, we show the number of occurrence records, the AUC value and the selected variables to build the ecological niche model for each genetic clade.

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
1	<i>Otospermophilus becheeyi</i>	M	H	1	mit	1	N	5734	0.924
2						2	S	121	0.984
3	<i>Sorex ornatus</i>	M	H	2	mit	1	-	476	0.926
4	<i>Spilogale gracilis</i>	M	H	3	mit	1	-	160	0.964
5	<i>Chaetodipus arenarius</i>	M	L	4	mit	1	N	1887	0.935
6						2	S	1569	0.986
7	<i>Chaetodipus spinatus</i>	M	L	5	mit	1	N	3833	0.898

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
8						2	S	850	0.982
9	<i>Dipodomys merriami</i>	M	L	6	mit	1	N	61	0.971
10						2	N	40	0.991
11						3	S	43	0.969
12	<i>Neotoma bryantii</i>	M	L	7	nuclear/mit	1	N	305	0.930
13						2	S	138	0.942
14	<i>Peromyscus maniculatus</i>	M	L	8	mit	1	-	5118	0.839
15	<i>Fouquieria columnaris</i>	P	H	9	plastid	1	N	608	0.967
16						2	S	41	0.951
17	<i>Pinus cem-broides</i> section	P	H	10	nuclear/ plastid	1	N	1940	0.970
18						2	S	344	0.999
19	<i>Encelia fari-nosa</i>	P	L	11	nuclear/ plastid	1	S	77	0.981
20						2	N	992	0.983

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
21	<i>Stenocereus gum-mosus</i>	P	L	12	nuclear	1	-	860	0.958
22	<i>Crotaphytus ves-tigium</i>	R	H	13	mit	1	N	194	0.934
23						2	S	53	0.993
24	<i>Elgaria multicarinata/velazquezi/paucicarinata</i>	R	H	14	nuclear/mit	1	N	3441	0.970
25						2	S	39	0.991
26						3	S	365	0.972
27	<i>Petrosaurus repens</i>	R	H	15	RADseq	1	N	25	0.996
28						2	S	88	0.991
29						3	S	52	0.999
30	<i>Plestiodon skiltonianus/lagunensis</i>	R	H	16	mit	1	N	1944	0.939
31						2	S	55	0.993
32	<i>Sceloporus orcutti</i>	R	H	15	RADseq	1	N	3785	0.886

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
33						2	S	613	0.988
34	<i>Callisaurus</i>	R	L	15	RADseq	1	N	2488	0.923
35	<i>dra-</i>					2	N	648	0.971
36	<i>conoides</i>					3	S	862	0.983
37						4	S	677	0.984
38						5	S	1534	0.997
39	<i>Sceloporus</i>	R	L	15	RADseq	1	N	420	0.977
40	<i>zos-</i>					2	S	398	0.982
41	<i>tero-</i>								
42	<i>mus</i>								
41	<i>Urosaurus</i>	R	L	15	RADseq	1	N	725	0.951
42	<i>nigri-</i>					2	S	1337	0.931
43	<i>caudus</i>					3	S	65	0.997
44						4	S	2149	0.993

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
45	<i>Uta stans- buri- ana</i>	R	L	17	mit	1	N	10596	0.860
46						2	S	3269	0.976

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	1: Phuong et al. 2017; 2: Mal- donado et al., 2001; 3: Fer- guson et al., 2017; 4: Álvarez- Castañeda & Ríos, 2011; 5: Álvarez- Castañeda & Mur- phy, 2014; 6: Álvarez- Castañeda et al., 2009; 7: Patton et al., 2007; 8: Kalk- vik et al., 2012; 9: Martínez- Noguez et al., 2020; 10: Montes et al., 2022; 11: Fehl- berg & Fehl- berg, 2017; 12: Lo- zano, 2013; 13: Mc- Guire et al., 2007;	

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	N° Occ.	AUC
---	---------	-----	-----	-----	-------------------------------	------------------	-----	------------	-----

Ecological niche models

The ecological niche of each clade was modeled by estimating the niche ellipsoid with the “ntbox” package (Osorio-Olvera et al., 2020a) in R 4.1.2 (R Core Team, 2021). Niche ellipsoids are a useful approximation to the fundamental niche of a species and hence, allow for a functional interpretation of the suitability values across clades (Osorio-Olvera et al., 2019; Osorio-Olvera et al., 2020b). The niche ellipsoid represented the 95% confidence ellipsoid used by the clade in the multivariate space built with bioclimatic data (Osorio-Olvera et al., 2020a). We used the occurrence points from each genetic group, retaining 30% of the data as a testing set. We determined the best model to describe the distribution of the genetic clades considering a subset of 3 or 4 variables from the bioclimatic variables after randomly removing one of each pair with a correlation higher than 0.95. The best model was selected based on the area under the receiver operating characteristic curve (AUC).

Niche differentiation between clades

To assess climatic niche differentiation between clades, we calculated the niche overlap based on niche ellipsoids with the “ellipsenm” package (Cobos et al., 2020) in R. The niche overlap corresponds to a value between 0 and 1, where 1 represents complete overlap and 0 represents no overlap. Niche overlap was calculated with the first three principal components obtained from a principal component analysis (PCA) of all scaled bioclimatic variables (See Supporting Information for details). We compared all clade pairs within taxa, and significance was obtained from 1,000 bootstrap replicates.

Niche breadth

Niche breadth was calculated for each clade in the multivariate space built from the PCA of all bioclimatic variables of current climatic conditions. For this, the area of the minimum convex polygon from occurrence points for each genetic clade within the first two dimensions of the multivariate climatic space (67.05% of variance) was calculated with the “adehabitatHR” (Calenge, 2023) and “sp” (Pevesma & Bivand, 2005) packages in R. Significant difference of niche breadth was tested among clade location within taxa (north, south, or unstructured), taxonomic group (mammal, plant, or reptile) and between elevation (highland or lowland), using a generalized linear mixed model (GLMM) in R with the “lme4” package (Bates et al., 2015) with a “gamma” distribution and an “inverse” link function, and including each taxon as a random variable.

Projection to present-day and LGM climates

The niche ellipsoid of each genetic clade, corresponding to the model with the highest AUC value, was projected onto the present-day geography to obtain each clade’s predicted distribution. Distribution models were binarized between suitable and non-suitable conditions by using a 10% of omission criterion. Then, we projected the niche ellipsoid to LGM climate using MIROC and CCSM GCMs. The amount of geographic area corresponding to suitable conditions for each clade was calculated for present-day and LGM climate in R with the “landscapemetrics” package (Hesselbarth et al., 2019). Further, we calculated the proportional change in area for each clade by dividing the LGM-predicted area by the present-day predicted area. Significant differences in the proportional change in area were tested among clade location (north, south, or unstructured), taxonomic groups (mammal, plant, or reptile), and elevation (highland or lowland), using a single GLMM in R with “lme4” using a “gamma” distribution and “inverse” link function, including each taxon as a random variable.

Niche marginality

As a measure of habitat quality, we used two approaches for assessing niche marginality for each genetic clade as well as changes in niche marginality from LGM to present. First, we calculated the present-day marginality as the Mahalanobis distance between the centroid of the niche ellipsoid from each clade to the centroid of the available multivariate space in the PCA of current climatic conditions with the “philentropy” package (Drost, 2018) in R. We also calculated the LGM marginality as the Mahalanobis distance between the clade’s niche centroid and the centroid of LGM available conditions in this same multivariate space. We then compared the niche marginality (i.e. Mahalanobis distances) between LGM and present by constructing a GLMM that included time period (LGM vs present), clade location (north, south, or unstructured), taxonomic group (mammal, plant, or reptile) and elevation (highland or lowland) as factors, including taxon as a random variable, and using a “gamma” distribution and “inverse” link function.

For the second measurement of marginality, for each genetic clade we obtained the suitability values for each cell from the raster projections of the niche models onto geographic space with the “raster” package (Hijmans, 2023) in R. We retained only values from cells with suitability above the 10% omission rate threshold. Then, each value was converted to niche marginality between 0 and 1, defined as the inverse of suitability with the formula:

$$1 - ((s - \min(s)) / (\max(s) - \min(s)))$$

Where “ s ” corresponds to the suitability values obtained from the raster projections, and “ $\min(s)$ ” and “ $\max(s)$ ” correspond to the minimum and maximum suitability values from the model, respectively. Then, we calculated the kernel density distribution of marginality within the suitable conditions with the “density” function in R, which represents the relative amount of area of different marginality values within suitable conditions. The calculation of the density distribution of marginality was done for the present-day and LGM distribution models. Then, we calculated the change in the marginality distribution between LGM and present by subtracting the kernel density curves from both time periods. Finally, to identify clusters of taxa that showed similar changes in their marginality density distribution between LGM and present, the density curves were hierarchically clustered with the “dad” package (Boumaza et al. 2021) in R by calculating the Hellinger’s distance between density curve pairs.

Results

Past climatic conditions on the Baja California peninsula and choice of GCM

We consulted geological literature to determine which GCM was best supported by paleoprecipitation proxies, which included alluvial fan, pollen, lake core record, and midden data across southern California and the BCP (Supporting Information). Unlike global climate, literature indicates that the BCP was generally wetter than present at the LGM (Lora, 2018; Lyle et al., 2012), culminating with an El Niño-like wettest period during the Late Pleistocene-Holocene transition ~14.5-10 ka (Antinao & McDonald, 2013). This was driven by strengthening East Pacific (westerly) precipitation that affected mainly southern California and the northern BCP in the form of winter rain and less seasonality (Antinao & McDonald, 2013; Antinao et al., 2016). On the other hand, while the south would have been drier overall after LGM, there is evidence from alluvial fan deposits and offshore cores that despite less precipitation, the precipitation came as stronger, and possibly more frequent, tropical cyclones reaching the southern BCP (Antinao et al., 2016). The Pacific High weakened ~17-11 kya and allowed warm tropical waters to move northward, partially strengthening the North American Monsoon (NAM) and leading to increasingly wetter conditions in the south comparable to what is observed today (Antinao et al., 2016). After that, the southerly NAM was stable but weaker, contributing less precipitation at least in part due to cooler Gulf of California sea surface temperatures 11-8 ka and a limited northward progression of those storms due to presence of the Pacific High.

Considering total annual precipitation (bio12), CCSM shows drying in the southern peninsula and increased wetness in the north (Figure 1b), which is in agreement with the paleoprecipitation data, whereas MIROC shows substantially wetter conditions throughout the peninsula (Supporting Information). Furthermore, the precipitation of the wettest month (bio13) shows a drying in the CCSM models in the south and slightly increased precipitation in the north, but the MIROC model shows wetter conditions throughout (also evident

in bio18). CCSM shows a slight strengthening of seasonality (bio15), while MIROC shows patchy decrease of moderate magnitude, the latter of which is more in line with the paleoprecipitation proxy data. Despite this last observation, we chose the CCSM GCM as the overall best model for our analyses because it appears to be more consistent with paleoprecipitation data particularly as it relates to the increased precipitation in the north and decreased effect of NAM precipitation and tropical storms in the south.

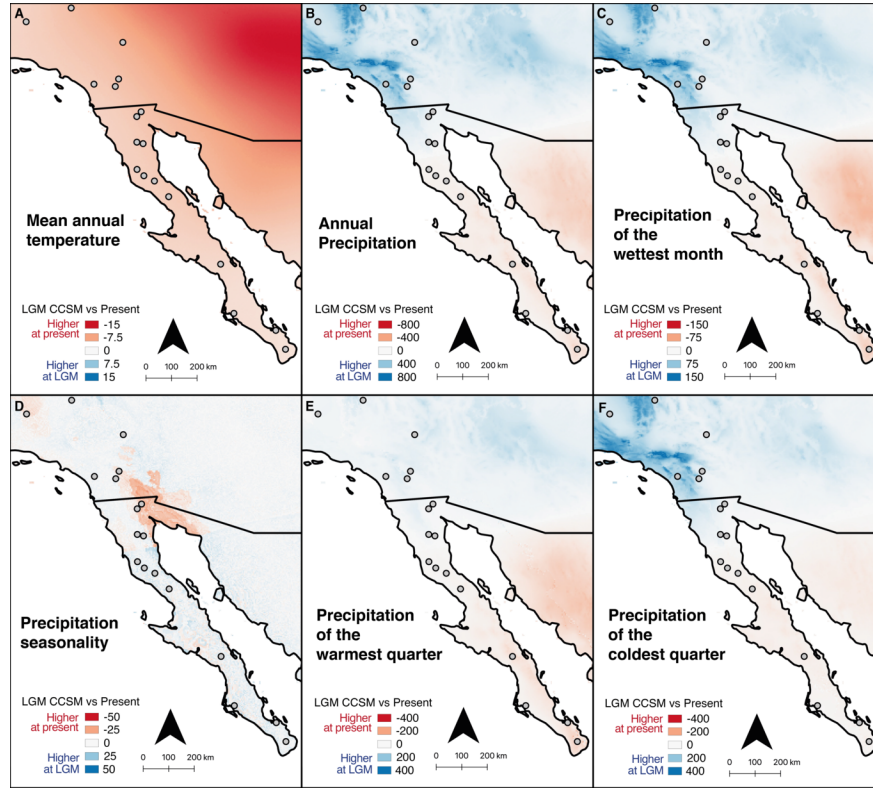


Figure 1. Change in climatic conditions on the Baja California peninsula between LGM and present day, considering the CCSM GCM. Circles represent georeferenced sites from the literature of paleoprecipitation proxy data that were used to evaluate regional accuracy of CCSM vs MIROC GCMs (Supporting Information).

Ecological niche models

We modeled the ecological niche of 47 clades from 21 taxa (Table 1). After filtering, our final dataset included a total of 65,373 georeferenced records representative of the known distribution of the studied species (range per clade 25-10,596). One out of four *Dipodomys merriami* clades presented only 7 occurrence records, therefore this clade was not included in further analyses. AUC values for the niche models were on average 0.961 (median: 0.972; range 0.839-0.999; Supporting Information includes other model evaluation metrics). The three most common variables selected to build the models were mean annual temperature (bio1), temperature seasonality (bio4) and precipitation seasonality (bio15, Table 1).

Between clades niche divergence

We used the first three dimensions of a PCA of current climatic conditions (84.97% of variance; see Supporting Information for details) to calculate niche overlap between populations. Between-clade climatic niche divergence was detected as overlap values were significantly lower than expected by chance for all clade pairs within species (Figure 2a). Overlap values ranged from 0.000 to 0.302 (Supporting Information). In general,

northern clades were located towards positive values of PC1 and PC2 (i.e. inhabit cooler environments with higher winter precipitation), whereas southern clades were mostly on negative values of PC1 and PC2 (i.e. warmer environments with higher summer precipitation). Significant differences were detected for the niche breadth between southern, northern and unstructured clades (Supporting Information). In general, northern and unstructured clades presented wider niches than southern clades (Figure 2b).

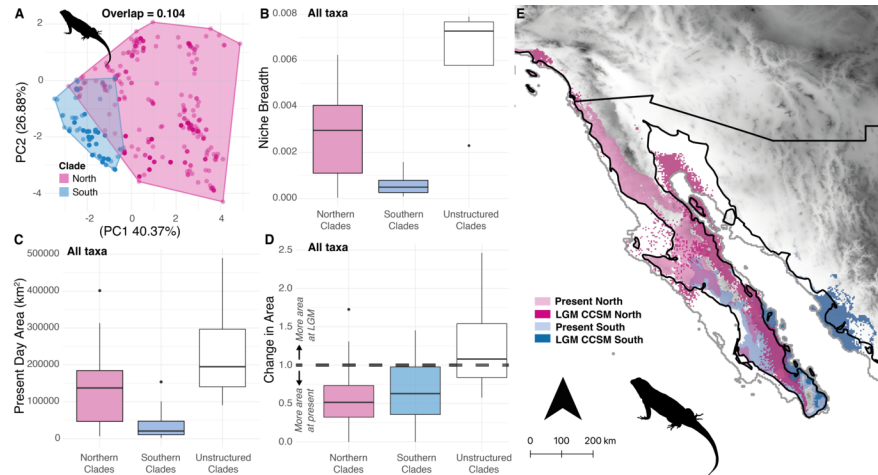


Figure 2. Ecological niche and distribution analyses. **A.** Niche overlap between northern and southern clades for *Sceloporus zosteromus*. **B.** Niche breadth for all genetic clades. **C.** Present day distribution area for all clades. **D.** Change in distribution area from LGM to present for all clades. **E.** Example of distribution model for *S. zosteromus* for present day and LGM CCSM climatic conditions, shows a contraction of the distribution for the northern and southern clades. The gray outline indicates the sea-level boundary for LGM conditions.

Contraction of the distribution area to LGM for most clades

When we projected the ecological niche onto geographic space (Figure 2e) and quantified the area occupied by each clade we detected a significant effect of clade location on the present-day area (Supporting Information), where northern and unstructured clades distribute over larger areas (Figure 2c) than southern clades. When projecting the models to LGM – CCSM conditions (Figure 2e), we detected that several clades showed a reduction in their geographic area (Figure 2d; Supporting Information shows projections to LGM using the MIROC GCM). The species *F. columnaris* did not present suitable area during LGM conditions for the CCSM GCM. No significant effect of clade was detected on the proportional change in area (Supporting Information). Most unstructured clades showed an increase in their distribution area during LGM (Figure 2d).

Increased niche marginality during LGM for most taxa except for highland northern clades

When assessing the change in centroid-based niche marginality between LGM and present, a significant effect was detected for the interaction between time and clade location (Supporting Information). In general, a decrease in marginality towards present day was detected for most highland and lowland clades (Figure 3), and three highland southern clade outliers (*Pinus cembroides*, *Elgariapauciarinata* and *Plestiodon lagunensis*) showed a strong decrease (Supporting Information). Five highland northern and two lowland southern clades showed an increase in centroid niche marginality to present day (black labels, Figure 3).

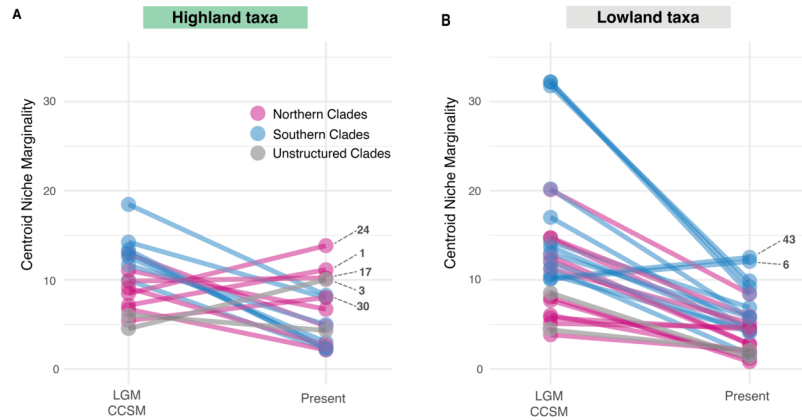


Figure 3. Centroid niche marginality at LGM and present for each genetic clade for highland (A) and lowland (B) taxa. A decrease in niche marginality is observed for most clades, except for five highland northern clades and two lowland southern that show an increase in marginality for present day climate, indicated with their numeric identifier according to Table 1. Figure not showing 3 highland outliers (see Supporting Information for graphs with the outliers).

As a second measure of niche marginality, we evaluated the change in the proportion of different marginality values within the suitable area for each clade for present day climate and LGM, and clustered the different clades based on the similarity of their change in normalized area of different marginality values (Figure 4a). The species *F. columnaris* was not included in this analysis since it did not present suitable areas for LGM GCM climatic conditions. The best supported number of clusters was five (Figure 4b) that can be qualitatively described as taxa with: i) much more marginal area at LGM, ii) much more marginal area at present, iii) slightly more marginal area at LGM, iv) slightly more marginal area at present, and v) similar marginality at present and LGM. Most highland species clustered in the more marginal area at present (group ii; Figure 4). There was no clear grouping by taxonomic group (plant, mammal or reptile) or location of the genetic clade.

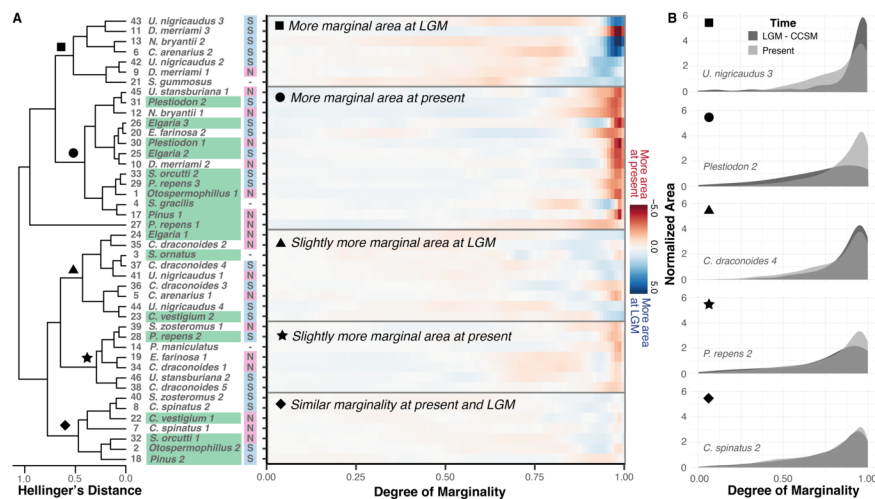


Figure 4. Change in the proportion of marginal conditions within suitable area for each clade. A. Cluster analysis showing five groups according to their changes in the normalized marginality area between LGM

and present (i: More marginal area at LGM, ii: more marginal area at present, iii: slightly more marginal area at LGM, iv: slightly more marginal area at present, and v: similar marginality at present and LGM). Highland taxa are highlighted in green. Pink (N) and blue (S) indicate location of genetic clade; “-” indicates unstructured clades. In the heatmap, red represents more area of a determined marginality value at LGM. **B.** Normalized area distribution of each marginality values for LGM CCSM and present-day climate for some example clades from each cluster.

Discussion

Environmental changes can affect the distribution, abundance, and allele frequency distributions of natural populations (Foden et al., 2019; Román-Palacios & Wiens, 2020; Aguirre-Liguori et al., 2021) by modulating the quantity and quality of available habitats. Organismal response will depend on intrinsic characteristics, which determine whether species persist in a location, shift their distribution and track suitable conditions, or evolve to expand their niches. In this study, we assessed how different taxa on a climatically heterogeneous landscape, the Baja California peninsula, have responded to environmental changes between LGM and present day with the aim of generating predictions about the effects of past climatic changes on population abundance and selection pressure.

The CCSM GCM better described LGM climate on the Baja California peninsula

Previous SDM studies on the Baja California peninsula have shown differences in their results based on the GCM used (Guevara et al., 2019). Using a GCM that adequately represents the climatic patterns in the study area is crucial for generating accurate niche models. Overall, we chose CCSM for hindcasting our SDMs because it shows higher consistency with multiproxy paleoprecipitation data provided by different sources (Antinao & McDonald, 2013; Antinao et al., 2016), particularly related to the increased precipitation in the north and decreased effect of NAM precipitation in the south. Both models (CCSM and MIROC) could not consistently capture the decrease in seasonality, though MIROC performed slightly better, and indicates that for species with strong circannual rhythms MIROC may be the better model. The northern peninsula may have been wetter at the LGM than CCSM predicts, suggesting that hindcasted SDMs for northern clades may slightly misrepresent habitat availability. In general, in a region that lies at the interface of several weather/climate systems whose components change in both interrelated and independent ways based on oceanic, land, and atmospheric features, it might be expected that GCMs perform differently here while they perform well globally. It is possible that the very narrow aspect of the peninsula, its high topography that traps some moisture sources (i.e. fog), and the stark oceanographic differences between the Pacific Ocean and Gulf of California on either side make paleoclimate predictions in this region challenging. On the other hand, the same diversity and complexity of microclimates seem to have played a role in the diversification of niches and accumulation of genetic divergence within species.

Niche patterns on the Baja Peninsula

Genetically divergent groups on the peninsula presented ecological niche divergence for all between-clade comparisons (Supporting Information). This agrees with previous studies including some of the same taxa (Cab-Sulub & Álvarez-Castañeda, 2021), and expands the niche divergence pattern further than just North-South of the Vizcaino region, but also between clades within a same region of the peninsula. This suggests that some species could have adapted to the high diversity of available environmental conditions, and could explain the high variation in the location of genetic breaks previously documented (Dolby et al., 2015; Araya-Donoso et al., 2022).

Niche breadth differed between clades located in the north and south of the peninsula (Figure 2), whereas elevation and taxonomic group showed no effect on niche breadth. The niche breadth was wider in northern clades than in southern clades, which could shape how populations responded to glacial oscillations (Carscadden et al., 2020). This is associated with a generally wider heterogeneity of available climatic conditions in the north than in the south. However, after standardizing by geographic area, the niche breadth in the north and south are similar (Supporting Information). It is important to note however that the niche utilization at the scale of the organism can differ greatly from predictions on a macroenvironmental scale (Ficetola et

al., 2018). Therefore, there may be less niche divergence than predicted by these models if organisms are experiencing microclimates that are less apparent at a macro scale.

Decreased habitat area for most taxa

We projected each clade distribution onto geographic space for present day and LGM climate. Consistent with the niche breadth results, northern clades distributed over wider areas for present day climate than southern clades (Figure 2). Most clades showed a reduction in their distribution area towards the eastern coast of the southern half of the peninsula (BCS) when projecting our models to LGM (Supporting Information). During LGM the peninsula was colder, drier in the south and wetter in the north (Figure 1, Antinao & McDonald, 2013; Antinao et al., 2016), conditions that could have been more challenging for desert-adapted species and therefore constrained their distributions. In general, organisms inhabiting arid sub-tropical regions have been described to show heterogeneous responses to Pleistocene climatic variation compared to organisms from temperate regions, since their response is highly dependent on local precipitation patterns (e.g. Anadón et al., 2015). The population contraction and subsequent isolation during Pleistocene glaciations could have produced and/or strengthened the divergence between genetic groups (Dolby et al., 2015; Araya-Donoso et al., 2022; Dolby et al., 2022).

Previous distribution modeling studies in this area have detected different patterns of LGM distribution. Some studies have detected population expansion towards LGM (Graham et al. 2014; González-Trujillo et al. 2016; Harrington et al. 2017; Arteaga et al. 2020), whereas others have detected range reductions (Valdivia-Carrillo et al. 2017; Klimova et al. 2017). Moreover, Cab-Sulub & Álvarez-Castañeda (2021) detected different patterns depending on the genetic clade within each taxon, in which southern clades showed area reduction and northern clades showed expansion. The differences between those studies and ours could be due to the modeling algorithm since all those studies implemented Maxent and we used minimum volume ellipsoids (See Supporting Information for further discussion).

Different patterns of niche marginality during LGM for highland and lowland species

We incorporated two measures of niche marginality in our analyses to assess habitat quality within our models, which allowed us to infer changes in population fitness and putative selection pressure from LGM to present. We detected higher centroid niche marginality during LGM for most clades, particularly southern highland clades (Figure 3a). Moreover, within suitable areas some clades presented a higher proportion of more marginal conditions during LGM (Figure 4). Both approaches showed consistent results, however the full distribution of marginal areas provided a more detailed description of how habitat quality changed through time. Despite a general reduction in the amount of habitat for all clades and species during LGM, changes in habitat quality between LGM and present day differed among desert-adapted lowland taxa and cold-adapted highland taxa. For lowland desert-adapted species, available environmental conditions were in general more challenging during LGM (Figure 3, Figure 4), and in the desert regions from the southern peninsula habitat quality improved more LGM to present relative to the north (Figure 3, Figure 4). In contrast, for most highland species habitat quality seems to have declined since LGM, but particularly in the Northern part of the Peninsula (Figure 3, Figure 4). Highland species generally present adaptations to cold environments, such as sustained activity during suboptimal temperatures in the lizard *Elgaria multicarinata* (Kingsbury, 1994) or the structure of needles in *Pinus* species (Jankowski et al. 2019). Highland species being favored during LGM conditions is consistent with studies from other regions such as the Afrotropical forests range expansions in the Horn of Africa (Casas-Gallego et al., 2023), or *Polyepis* woodlands on the Andes Mountains (Zutta & Rundel, 2017).

Model predictions that can be tested with genetic data

Integrating ENMs and SDMs with genomic data can be used to test whether our inferences about species responses to climate change are accurate and relevant and hence, make better predictions of potential responses to future climate change. The independent assessment of habitat quality in ecological niche models constitutes an improvement since, in addition to the inferences about changes in the species' distribution ranges, by analyzing changes in niche marginality between LGM and present day we can infer changes in

population fitness and selection pressure within a species' distribution (Figure 5a).

An example is the northern clade of *Plestiodon* (i.e. *Plestiodon skiltonianus*, highland species) which shows a contraction of its distribution from LGM to present (Figure 5b, Figure 5c), in addition to a decrease in habitat quality (i.e. increased marginality) at its northernmost distribution. Populations of this species at these locations should show signatures of a bottleneck along with increased selection pressure associated with higher temperatures and lower precipitation in present day climate (Figure 1, Figure 5d). This could be evidenced by adaptations in thermoregulation or water physiology, and positive selection should be focused to genes associated with these processes such as aquaporins (e.g. Araya-Donoso et al., 2021) or heat shock proteins (Chen et al., 2018). An example of a lowland desert adapted taxon is the southern clade of the packrat *Neotoma bryanti* (Figure 5e), which exhibits a geographical expansion towards the north from LGM to present (Figure 5f), associated with increased habitat quality (i.e. decreased marginality) in the central populations (Figure 5g). Stable populations between LGM and present for this species should reflect an increase in effective population size, and could show signatures of natural selection associated with LGM climate (Figure 5f, Figure 5g) while the northern part of the range may be expected to have lower diversity as a consequence of range expansion as well as surfing of deleterious alleles (Escoffier et al., 2008; Gilbert et al., 2018).

These predictions can be tested with genomic data, evaluating if the patterns of genetic variation reflect the expected changes in effective population size and signatures of selection predicted by our models. According to published genetic data, the mammals *Chaetodipus spinatus* (Álvarez-Castañeda & Murphy, 2014), *Spilogale gracilis* (Ferguson et al., 2017), and *Otospermophilus becheeyi* (Phuong et al., 2017) show population size reduction during LGM, which is in agreement with our prediction of reduced suitable area or increased marginality in the LGM distribution models (except for *C. spinatus*). Whole genome sequencing data from populations across the peninsula would be required to evaluate the selection pressure predictions from this study. An example of this approach is Farleigh et al. (2021), who used genomic data to infer changes in population size and potential genes under selection for the lizard *Phrynosoma platyrhinos* across the North American deserts, formally testing previous hypotheses about demographic changes and adaptation to different climates (Jezkova et al., 2016).

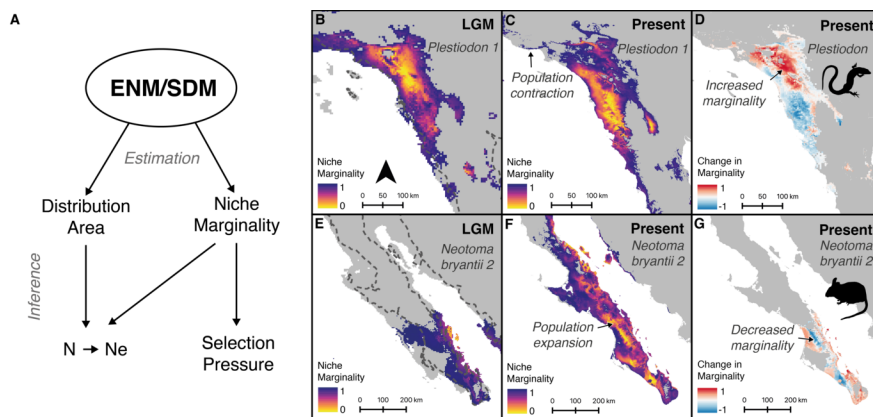


Figure 5. A. Diagram representing that ENMs and SDMs can be applied to infer changes in Ne and selection pressure for natural populations. B-D. Inference of population contraction (D) and increased marginality (E) areas between LGM and present within the distribution for the northern clade of *Plestiodon*. E-G. Inference of areas with population expansion (F) and decreased marginality (G) for the southern clade of *Neotoma bryanti* between LGM and present.

Conclusions

Assessing changes in quantity and quality of available habitats allows the generation of more detailed inter-

pretations of population dynamics in response to past climate changes, and predictions of future changes in climatic conditions. SDMs are useful to infer changes in distribution of organisms, and here we show how niche marginality can be used as a proxy to predict species' abundance and selection pressure. Results showed that species on the Baja California peninsula responded to changes in climatic conditions based on their ecological niche characteristics. Some highland clades were favored during LGM climatic conditions, since besides a decrease in the area of suitable conditions they may have presented increased fitness within those available habitats due to those habitats having lower niche marginality. This demonstrates the decoupling between habitat quality and quantity relevant to the evolution of populations. On the other hand, lowland desert clades seem to have better habitat conditions under present climates in terms of habitat quantity and quality. Overall, we were able to generate explicit predictions about population history that can be tested with genomic data to generate a better understanding of population dynamics driven by climatic changes in habitat quantity and quality.

References

- Aguirre-Liguori, J. A., Tenaillon, M. I., Vázquez-Lobo, A., Gaut, B. S., Jaramillo-Correa, J. P., Montes-Hernandez, S., Souza, V., & Eguiarte, L. E. (2017). Connecting genomic patterns of local adaptation and niche suitability in teosintes. *Mol. Ecol.*, 26(16), 4226-4240. <https://doi.org/10.1111/mec.14203>
- Aguirre-Liguori, J. A., Ramirez-Barahona, S., & Gaut, B. S. (2021). The evolutionary genomics of species' responses to climate change. *Nat. Ecol. Evol.*, 5(10), 1350-1360. <https://doi.org/10.1038/s41559-021-01526-9>
- Alvarez-Castaneda, S. T., Lidicker Jr, W. Z., & Rios, E. (2009). Revision of the *Dipodomys merriami* complex in the Baja California Peninsula, Mexico. *J. Mammal.*, 90(4), 992-1008. <https://doi.org/10.1644/07-MAMM-A-398.1>
- Alvarez-Castaneda, S. T., & Rios, E. (2011). Revision of *Chaetodipus arenarius* (Rodentia: Heteromyidae). *Zool. J. Linn. Soc.*, 161(1), 213-228. <https://doi.org/10.1111/j.1096-3642.2009.00630.x>
- Alvarez-Castaneda, S. T., & Murphy, R. W. (2014). The endemic insular and peninsular species *Chaetodipus spinatus* (Mammalia, Heteromyidae) breaks patterns for Baja California. *PLoS One*, 9(12), e116146. <https://doi.org/10.1371/journal.pone.0116146>
- Anadon, J. D., Gracia, E., Botella, F., Gimenez, A., Fahd, S., & Fritz, U. (2015). Individualistic response to past climate changes: niche differentiation promotes diverging Quaternary range dynamics in the subspecies of *Testudo graeca*. *Ecography*, 38(9), 956-966. <https://doi.org/10.1111/ecog.01163>
- Antinao, J. L., & McDonald, E. (2013). An enhanced role for the Tropical Pacific on the humid Pleistocene-Holocene transition in southwestern North America. *Quat. Sci. Rev.*, 78, 319-341. <https://doi.org/10.1016/j.quascirev.2013.03.019>
- Antinao, J. L., McDonald, E., Rhodes, E. J., Brown, N., Barrera, W., Gosse, J. C., & Zimmermann, S. (2016). Late Pleistocene-Holocene alluvial stratigraphy of southern Baja California, Mexico. *Quat. Sci. Rev.*, 146, 161-181. <https://doi.org/10.1016/j.quascirev.2016.06.008>
- Araya-Donoso, R., San Juan, E., Tamburrino, I., Lam-borot, M., Veloso, C., & Veliz, D. (2021). Integrating genetics, physiology and morphology to study desert adaptation in a lizard species. *J. Anim. Ecol.*, 91(6), 1148-1162. <https://doi.org/10.1111/1365-2656.13546>
- Araya-Donoso, R., Baty, S. M., Alonso-Alonso, P., Sanin, M. J., Wilder, B. T., Munguia-Vega, A., & Dolby, G. A. (2022). Implications of barrier ephemerality in geogenomic research. *J. Biogeogr.*, 49(11), 2050-2063. <https://doi.org/10.1111/jbi.14487>
- Arteaga, M. C., Bello-Bedoy, R., & Gasca-Pineda, J. (2020). Hybridization between yuccas from Baja California: Genomic and environmental patterns. *Front. Plant Sci.*, 11, 685. <https://doi.org/10.3389/fpls.2020.00685>
- Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*, 67(1), 1-48. <https://doi.org/10.18637/jss.v067.i01>
- Blonder, B. (2018). Hypervolume concepts in niche-and trait-based ecology. *Ecography*, 41(9), 1441-1455. <https://doi.org/10.1111/ecog.03187>
- Bontrager, M., Usui, T., Lee-Yaw, J. A., Anstett, D. N., Branch, H. A., Hargreaves, A. L., Muir, C. D., & Angert, A. L. (2021). Adaptation across geographic ranges is consistent with strong selection in marginal climates and legacies of range expansion. *Evolution*, 75(6), 1316-1333. <https://doi.org/10.1111/evo.14231>
- Boumaza, R., Santagostini, P., Yousfi, S., & Demotes-Mainard, S. (2021). dad: an R Package for Visualisation, Classification and Discrimination of Multivariate Groups Modelled by their Densities. *R J.*, Di Cook, Monash University, Australia, In press, 13 (2), pp.179-207. [hal-03344822](https://doi.org/10.3344822)
- Cab-Sulub, L., & Alvarez-Castaneda, S. T. (2021). Climatic dissimilarity associated with phylogenetic breaks. *J. Mammal.*, 102(6), 1592-1604.

<https://doi.org/10.1093/jmammal/gyab108> Calenge, C. (2023). Home range estimation in R: the adehabitatHR package – <https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf>

Carscadden, K. A., Emery, N. C., Arnillas, C. A., Cadotte, M. W., Afkhami, M. E., Gravel, D., Livingstone, S. W., & Wiens, J. J. (2020). Niche breadth: causes and consequences for ecology, evolution, and conservation. *Q. Rev. Biol.*, 95(3), 179-214. <https://doi.org/10.1086/710388>

Casas-Gallego, M., Hahn, K., Neumann, K., Demissew, S., Schmidt, M., Bodin, S. C., & Bruch, A. A. (2023). Cooling-induced expansions of Afromontane forests in the Horn of Africa since the Last Glacial Maximum. *Sci. Rep.*, 13(1), 10323. <https://doi.org/10.1038/s41598-023-37135-8>

Chen, B., Feder, M. E., & Kang, L. (2018). Evolution of heat-shock protein expression underlying adaptive responses to environmental stress. *Mol. Ecol.*, 27(15), 3040-3054. <https://doi.org/10.1111/mec.14769>

Cobos, M. E., Osorio-Olvera, L., Soberon, J., Peterson, A. T., Barve, V., & Barve, N. (2020). ellipsenm: Ecological niche's characterizations using ellipsoids. R package – <https://github.com/marloncobos/ellipsenm>

Collins, W. D., Bitz, C. M., Blackmon, M. L., Bonan, G. B., Bretherton, C. S., Carton, J. A., Chang, P., Doney, S. C., Hack, J. J., Henderson, T. B., Kiehl, J. T., Large, W. G., McKenna, D. S., Santer, B. D., & Smith, R. D. (2006). The community climate system model version 3 (CCSM3). *J. Clim.*, 19(11), 2122-2143. <https://doi.org/10.1175/JCLI3761.1>

Darin, M.H., Dorsey, R.J., Niemi, T.M., Salgado Munoz, V.O., Henry, M.W., & Pecha, M.E. (2024). Revised age of the Boleo Formation and marine flooding in the Central Gulf of California rift, Santa Rosalia basin, Baja California, Sur, Mexico. *Geol. Soc. Am. Spec. Pap.*(in revision).

Dolby, G. A., Bennett, S. E., Lira-Noriega, A., Wilder, B. T., & Munguia-Vega, A. (2015). Assessing the geological and climatic forcing of biodiversity and evolution surrounding the Gulf of California. *J. Southwest*, 391-455. <https://doi.org/10.1353/jsw.2015.0005>

Dolby, G. A., Bennett, S. E., Dorsey, R. J., Stokes, M. F., Riddle, B. R., Lira-Noriega, A., Munguia-Vega, A., & Wilder, B. T. (2022). Integrating Earth-life systems: A geogenomic approach. *Trends Ecol. Evol.*, 37(4), 371-384.

Drost, H. G. (2018). Philentropy: Information Theory and Distance Quantification with R. *J. Open Source Softw.*, 3(26), 765. <https://doi.org/10.21105/joss.00765>

Eckert, C. G., Samis, K. E., & Loughheed, S. C. (2008). Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.*, 17, 1170-1188. <https://doi.org/10.1111/j.1365-294X.2007.03659.x>

Excoffier L, Ray N. 2008 Surfing during population expansions promotes genetic revolutions and structuration. *Trends Ecol. Evol.* 23, 347 – 351. <https://doi.org/10.1016/j.tree.2008.04.004>

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.*, 40(9), 1649-1663. <https://doi.org/10.1111/jbi.12130>

Fehlberg, S. D., & Fehlberg, K. M. (2017). Spatial genetic structure in brittlebush (*Encelia farinosa*, Asteraceae) in the southwestern deserts of North America: a comparison of nuclear and chloroplast DNA sequences. *Plant Syst. Evol.*, 303, 1367-1382. <https://doi.org/10.1007/s00606-017-1463-2>

Farleigh, K., Vladimirova, S. A., Blair, C., Bracken, J. T., Koochekian, N., Schield, D. R., Card, D. C., Finger, N., Jenault, J., Leache, A. D., Castoe, T. A., & Jezkova, T. (2021). The effects of climate and demographic history in shaping genomic variation across populations of the Desert Horned Lizard (*Phrynosoma platyrhinos*). *Mol. Ecol.*, 30(18), 4481-4496. <https://doi.org/10.1111/mec.16070>

Ferguson, A. W., McDonough, M. M., Guerra, G. I., Rheude, M., Dragoo, J. W., Ammerman, L. K., & Dowler, R. C. (2017). Phylogeography of a widespread small carnivore, the western spotted skunk (*Spilogale gracilis*) reveals temporally variable signatures of isolation across western North America. *Ecol. Evol.*, 7(12), 4229-4240. <https://doi.org/10.1002/ece3.2931>

Ficetola, G. F., Lunghi, E., Canedoli, C., Padoa-Schioppa, E., Pennati, R., & Manenti, R. (2018). Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. *Sci. Rep.*, 8(1), 10575. <https://doi.org/10.1038/s41598-018-28796-x>

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37(12), 4302-4315. <https://doi.org/10.1002/joc.5086>

Foden, W. B., Young, B. E., Akcakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M. & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdiscip. Rev. Clim. Change*, 10(1), e551. <https://doi.org/10.1002/wcc.551>

Galan-Acedo, C., Arroyo-Rodriguez, V., & Chapman, C. A. (2021). Beyond patch size: The impact of regional context and habitat quality on three endangered primates. *Perspect. Ecol. Conserv.*, 19(2), 207-215. <https://doi.org/10.1016/j.pecon.2021.02.004>

Gilbert KJ, Peischl S, Excoffier L (2018). Mutation load dynamics during environmentally- driven range shifts.

PLoS Genet. 14(9): e1007450. <https://doi.org/10.1371/journal.pgen.1007450> Gonzalez-Trujillo, R., Correa-Ramirez, M. M., Ruiz-Sanchez, E., Salinas, E. M., Jimenez, M. L., & Garcia-De Leon, F. J. (2016). Pleistocene refugia and their effects on the phylogeography and genetic structure of the wolf spider *Pardosa sierra* (Araneae: Lycosidae) on the Baja California Peninsula. *J. Arachnol.*, 367-379. <https://doi.org/10.1636/R15-84.1> Gottscho, A. D. (2015). Lineage diversification of lizards (Phrynosomatidae) in southwestern North America: integrating genomics and geology – PhD thesis, University of California Riverside, US. Graham, M. R., Bryson Jr, R. W., & Riddle, B. R. (2014). Late Pleistocene to Holocene distributional stasis in scorpions along the Baja California peninsula. *Biol. J. Linn. Soc.*, 111(2), 450-461. <https://doi.org/10.1111/bij.12216> Guevara, L., Morrone, J. J., & Leon-Paniagua, L. (2019). Spatial variability in species' potential distributions during the Last Glacial Maximum under different Global Circulation Models: Relevance in evolutionary biology. *J. Zool. Syst. Evol. Res.*, 57(1), 113-126. <https://doi.org/10.1111/jzs.12238> Harrington, S. M., Hollingsworth, B. D., Higham, T. E., & Reeder, T. W. (2018). Pleistocene climatic fluctuations drive isolation and secondary contact in the red diamond rattlesnake (*Crotalus ruber*) in Baja California. *J. Biogeogr.*, 45(1), 64-75. <https://doi.org/10.1111/jbi.13114> Hasumi, H., & Emori, S., (2004). K-1 coupled GCM (MIROC) description. Technical Report 1, Center for Climate System Research, University of Tokyo, Tokyo, Japan. Hesselbarth, M. H., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42(10), 1648-1657. <https://doi.org/10.1111/ecog.04617> Hijmans (2023). raster: Geographic Data Analysis and Modeling – <https://cran.r-project.org/web/packages/raster/raster.pdf> Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427 <https://doi.org/10.1101/SQB.1957.022.01.039> Jankowski, A., Wyka, T. P., Żytkowiak, R., Danusevičius, D., & Oleksyn, J. (2019). Does climate-related in situ variability of Scots pine (*Pinus sylvestris* L.) needles have a genetic basis? Evidence from common garden experiments. *Tree Physiol.*, 39(4), 573-589. <https://doi.org/10.1093/treephys/tpy145> Jezkova, T., Jaeger, J. R., Oláh-Hemmings, V., Jones, K. B., Lara-Resendiz, R. A., Mulcahy, D. G., & Riddle, B. R. (2016). Range and niche shifts in response to past climate change in the desert horned lizard *Phrynosoma platyrhinos*. *Ecography*, 39(5), 437-448. <https://doi.org/10.1111/ecog.01464> Jimenez, L., Soberon, J., Christen, J. A., & Soto, D. (2019). On the problem of modeling a fundamental niche from occurrence data. *Ecol. Model.*, 397, 74–83. <https://doi.org/10.1016/J.ECOLMODEL.2019.01.020> Kalkvik, H. M., Stout, I. J., Doonan, T. J., & Parkinson, C. L. (2012). Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. *Ecography*, 35(1), 54-64. <https://doi.org/10.1111/j.1600-0587.2011.06994.x> Kebaïli, C., Sherpa, S., Guéguen, M., Renaud, J., Rioux, D., & Després, L. (2023). Comparative genetic and demographic responses to climate change in three peatland butterflies in the Jura massif. *Biol. Conserv.*, 287, 110332. <https://doi.org/10.1016/j.biocon.2023.110332> Kingsbury, B. A. (1994). Thermal constraints and eurythermy in the lizard *Elgaria multicarinata*. *Herpetologica*, 266-273. <https://www.jstor.org/stable/3892699> Klimova, A., Hoffman, J. I., Gutierrez-Rivera, J. N., Leon de la Luz, J., & Ortega-Rubio, A. (2017). Molecular genetic analysis of two native desert palm genera, *Washingtonia* and *Brahea*, from the Baja California Peninsula and Guadalupe Island. *Ecol. Evol.*, 7(13), 4919-4935. <https://doi.org/10.1002/ece3.3036> Leavitt, D. H., Marion, A. B., Hollingsworth, B. D., & Reeder, T. W. (2017). Multilocus phylogeny of alligator lizards (*Elgaria*, Anguidae): testing mtDNA introgression as the source of discordant molecular phylogenetic hypotheses. *Mol. Phylogenet. Evol.*, 110, 104-121. <https://doi.org/10.1016/j.ympev.2017.02.010> Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography*, 38(1), 15-28. <https://doi.org/10.1111/ecog.00967> Lira-Noriega, A., & Manthey, J. D. (2014). Relationship of genetic diversity and niche centrality: a survey and analysis. *Evolution*, 68(4), 1082-1093. <https://doi.org/10.1111/evo.12343> Lora, J. M. (2018). Components and mechanisms of hydrologic cycle changes over North America at the Last Glacial Maximum. *J. Clim.*, 31(17), 7035-7051. <https://doi.org/10.1175/JCLI-D-17-0544.1> Lozano, O. A. (2013). Analisis de la estructura genetica poblacional de la pitaya agria (*Stenocereus gummosus*) en el Desierto Sonorense – Master tesis, CIBNOR, Mexico. Lyle, M., Heusser, L., Ravelo, C., Yamamoto, M., Barron, J., Dittenbach, N. S., Herbert, T., & Andreasen, D. (2012). Out of the tropics: the Pacific, Great Basin Lakes, and Late Pleistocene water cycle in the western United States. *Science*, 337(6102), 1629-1633. <https://doi.org/10.1126/science.1218390> Maldonado,

- J. E., Vila, C., & Wayne, R. K. (2001). Tripartite genetic subdivisions in the ornate shrew (*Sorex ornatus*). *Mol. Ecol.*, 10(1), 127-147. <https://doi.org/10.1046/j.1365-294X.2001.01178.x>
- Martinez-Noguez, J. J., Leon De la Luz, J. L., Delgadillo Rodriguez, J., & Garcia-De Leon, F. J. (2020). Phylogeography and genetic structure of an iconic tree of the Sonoran Desert, the Cirio (*Fouquieria columnaris*), based on chloroplast DNA. *Biol. J. Linn. Soc.*, 130(3), 433-446. <https://doi.org/10.1093/biolinnean/blaa065>
- McGuire, J. A., Linkem, C. W., Koo, M. S., Hutchison, D. W., Lappin, A. K., Orange, D. I., Lemos-Espinal, J., Riddle, B. R., & Jaeger, J. R. (2007). Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. *Evolution*, 61(12), 2879-2897. <https://doi.org/10.1111/j.1558-5646.2007.00239.x>
- Montes, J. R., Pelaez, P., Moreno-Letelier, A., & Gernandt, D. S. (2022). Coalescent-based species delimitation in North American pinyon pines using low-copy nuclear genes and plastomes. *Am. J. Bot.*, 109(5), 706-726. <https://doi.org/10.1002/ajb2.1847>
- Morente-Lopez, J., Kass, J. M., Lara-Romero, C., Serra-Diaz, J. M., Soto-Correa, J. C., Anderson, R. P., & Iriando, J. M. (2022). Linking ecological niche models and common garden experiments to predict phenotypic differentiation in stressful environments: Assessing the adaptive value of marginal populations in an alpine plant. *Glob. Chang. Biol.*, 28(13), 4143-4162. <https://doi.org/10.1111/gcb.16181>
- Mortelliti, A., Amori, G., & Boitani, L. (2010). The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, 163(2), 535-547. <https://doi.org/10.1007/s00442-010-1623-3>
- Oskin, M., & Stock, J. (2003). Marine incursion synchronous with plate-boundary localization in the Gulf of California. *Geology*, 31(1), 23-26. [https://doi.org/10.1130/0091-7613\(2003\)031<0023:MISWPB>2.0.CO;2](https://doi.org/10.1130/0091-7613(2003)031<0023:MISWPB>2.0.CO;2)
- Osorio-Olvera, L., Soberon, J., & Falconi, M. (2019). On population abundance and niche structure. *Ecography*, 42(8), 1415-1425. <https://doi.org/10.1111/ecog.04442>
- Osorio-Olvera, L., Lira-Noriega, A., Soberon, J., Peterson, A. T., Falconi, M., Contreras-Diaz, R. G., Martinez-Meyer, E., Barve V., & Barve, N. (2020a). ntbox: An r package with graphical user interface for modelling and evaluating multidimensional ecological niches. *Methods Ecol. Evol.*, 11(10), 1199-1206. <https://doi.org/10.1111/2041-210X.13452>
- Osorio-Olvera, L., Yanez-Arenas, C., Martinez-Meyer, E., & Peterson, A. T. (2020b). Relationships between population densities and niche-centroid distances in North American birds. *Ecol. Lett.*, 23(3), 555-564. <https://doi.org/10.1111/ele.13453>
- Patton, J. L., Huckaby, D. G., & Alvarez-Castaneda, S. T. (2007). The evolutionary history and a systematic revision of woodrats of the *Neotoma lepida* group (Vol. 135). University of California Press.
- Pebesma, E., & Bivand, R. S. (2005). S classes and methods for spatial data: the sp package. *R news*, 5(2), 9-13.
- Phuong, M. A., Bi, K., & Moritz, C. (2017). Range instability leads to cytonuclear discordance in a morphologically cryptic ground squirrel species complex. *Mol. Ecol.*, 26(18), 4743-4755. <https://doi.org/10.1111/mec.14238>
- Pironon, S., Papuga, G., Villellas, J., Angert, A. L., Garcia, M. B., & Thompson, J. D. (2017). Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biol. Rev.*, 92, 1877-1909. <https://doi.org/10.1111/brev.12313>
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. -<https://www.R-project.org/>.
- Rebman, J. and N. C. Roberts. (2012). Baja California Plant Field Guide. San Diego Natural History Museum.
- Regolin, A. L., Oliveira-Santos, L. G., Ribeiro, M. C., & Bailey, L. L. (2021). Habitat quality, not habitat amount, drives mammalian habitat use in the Brazilian Pantanal. *Landsc. Ecol.*, 36(9), 2519-2533. <https://doi.org/10.1007/s10980-021-01280-0>
- Richmond, J. Q., & Reeder, T. W. (2002). Evidence for parallel ecological speciation in scincid lizards of the *Eumeces skiltonianus* species group (Squamata: Scincidae). *Evolution*, 56(7), 1498-1513. <https://doi.org/10.1111/j.0014-3820.2002.tb01461.x>
- Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proc. Natl Acad. Sci. USA*, 117(8), 4211-4217. <https://doi.org/10.1073/pnas.1913007117>
- San Juan, E., Araya-Donoso, R., Veliz, D., Quiroga, N., & Botto-Mahan, C. (2021). Genetic diversity in a restricted-dispersal kissing bug: The centre-periphery hypothesis halfway. *Mol. Ecol.*, 30(19), 4660-4672. <https://doi.org/10.1111/mec.16093>
- Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C. G., Sousa-Guedes, D., Martinez-Freiria, F., Real, R., & Barbosa, A. M. (2021). Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecol. Model.*, 456, 109671. <https://doi.org/10.1016/j.ecolmodel.2021.109671>
- Soberon, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*, 10(12), 1115-1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Tomuolo, S., & Ward, D. (2018). Species migrations and range shifts: A synthesis of causes

and consequences. *Perspect. Plant Ecol. Evol. Syst.*, 33, 62-77. <https://doi.org/10.1016/j.ppees.2018.06.001>

Upton, D. E., & Murphy, R. W. (1997). Phylogeny of the side-blotched lizards (Phrynosomatidae: *Uta*) based on mtDNA sequences: support for a midpeninsular seaway in Baja California. *Mol. Phylogenet. Evol.*, 8(1), 104-113. <https://doi.org/10.1006/mpev.1996.0392>

Valdivia-Carrillo, T., Garcia-De Leon, F. J., Blazquez, M. C., Gutierrez-Flores, C., & Gonzalez Zamorano, P. (2017). Phylogeography and ecological niche modeling of the desert iguana (*Dipsosaurus dorsalis*, Baird & Girard 1852) in the Baja California Peninsula. *J. Hered.*, 108(6), 640-649. <https://doi.org/10.1093/jhered/esx064>

Watling, J. I., Arroyo-Rodriguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L. M., Fang, R., Hamel-Leigue, A. C., Lachat, T., Leal, I. R., Lens, L., Possingham, H. P., Raheem, D. C., Ribeiro, D. B., Slade, E. M., Urbina-Cardona, J. N., Wood, E. M., & Fahrig, L. (2020). Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecol. Lett.*, 23(4), 674-681. <https://doi.org/10.1111/ele.13471>

Wiens, J. J., Ackery, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.*, 13(10), 1310-1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>

Zutta, B. R., & Rundel, P. W. (2017). Modeled shifts in *Polylepis* species ranges in the Andes from the last glacial maximum to the present. *Forests*, 8(7), 232. <https://doi.org/10.3390/f8070232>