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

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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 for genetic groups within 21 reptile, mammal, and plant taxa from the Baja California peninsula inhabiting lowland or highland environments. 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. We quantified habitat quantity from the distribution models, and 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 responses independently. This allows the prediction of genomic signatures associated with changes in effective population size and selection pressure that could be explicitly tested from our models.

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

Introduction

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 and Wiens 2020, Aguirre-Liguori et al.

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2021). Species' responses depend on the quantity and quality of habitat available to populations, which are expressions of their ecological niche (i.e. all variables that determine organismal fitness; Hutchinson 1957, Blonder 2018) that can change independently. While habitat quantity can be understood as the amount of habitat that is suitable to a species, habitat quality is a measurement of how well the environment can provide conditions that allow population persistence (Mortelliti et al. 2010), and hence is related to population fitness.

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). One approach is to represent the ecological niche as an ellipsoid in multivariate space, consisting of the range of suitable conditions for a taxon based on a 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. 2013, 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 and 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. 2021). 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 and Svenning 2015, Tomiolo and Ward 2018). It can also lead to founder effects and surfing of deleterious alleles at the margin of the expanding front ('allele surfing'; Excoffier and Ray 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.

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 (Morente-López et al. 2022, Kebaïli et al. 2023). 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 (Mortelliti et al. 2010, Watling et al. 2020, Galán-Acedo et al. 2021, Regolín et al. 2021). Separately assessing how habitat quantity and quality changed over past climatic changes for a group of species offers an opportunity to understand the degree to which these patterns are coupled, offering more nuanced information about how organisms may respond to ongoing and future climate changes. It also allows us to test whether some organismal traits shape their responses to environmental change. For example, highland species that can resist cold may respond differently than species inhabiting deserts adapted to low water availability, or taxonomic groups with different physiological requirements, such as mammals, plants and reptiles, could also respond specifically.

Here, we used ecological niche modeling to compare intra-specific and inter-specific changes in habitat quality and quantity of 21 taxa from the Baja California peninsula (BCP). The BCP is a good system to assess these questions because native species have largely been co-distributed and isolated from the mainland since the Gulf of California finished flooding 6.3 Mya (million years ago) (Oskin and Stock 2003, Darin et al. 2024). About 80 taxa show a diffuse north-south genetic co-divergence signal centered in the middle of the Peninsula concordant with ecological niche divergence, suggesting potential adaptation to local environmental conditions (Dolby et al. 2015, Cab-Sulub and Álvarez-Castañeda 2021, Araya-Donoso et al. 2022). Low and high amplitude glaciation cycles during the Pleistocene (2.6–0.01 Mya) are expected to have had a large impact on redistributing climatic conditions particularly due to the complex topography of the peninsula and therefore the distribution and abundance of populations (Dolby et al. 2015). Previous studies have detected contrasting patterns of species distributions to the Last Glacial Maximum (LGM) on the peninsula. Some taxa show range expansions during LGM, whereas others show range contractions (Graham et al. 2014, González-Trujillo et al. 2016, Harrington et al. 2018, Klimova et al. 2017, Valdivia-Carrillo et al. 2017, Arteaga et al. 2020, Cab-Sulub and Álvarez-Castañeda 2021). Furthermore, some studies have assessed species' past demography with genetic data showing signatures of population contraction towards LGM (Álvarez-Castañeda and Murphy 2014, Ferguson et al. 2017, Phuong et al. 2017, Martínez-Noguez et al. 2020), which do not agree with the range expansion patterns proposed by some distribution models. Therefore, these discrepancies and changes in population size could be determined by not just habitat quantity but also habitat quality.

We performed ecological niche models to assess changes in habitat quantity and quality between LGM and present-day climatic conditions. Niche models predicted species distributions onto the geography to measure the amount of available habitat, and we measured niche marginality to assess the quality of such habitats. We compared mammals, reptiles and plants that inhabit highland (> 500 m) and lowland environments and that have different levels of genetic divergence along the peninsula to determine if organismal characteristics affected the patterns of change in habitat quantity or quality. Finally, 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.

Material and methods

Climatic data and characterization of the Baja California Peninsula

We characterized the current climatic conditions of the BCP using 19 bioclimatic variables (Supporting information) with a spatial resolution of 1 km obtained from Worldclim ver. 2 (Fick and Hijmans 2017). Additionally, we obtained data from two different global circulation models (CGMs): the Interdisciplinary Research on Climate (MIROC ver. 3.2; Hasumi and 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). Since previous work showed discrepancies between GCM conditions on the BCP that affected SDMs (Guevara et al. 2019, Supporting information), we compared the GCM differences to paleoprecipitation proxies to determine the best model. Literature indicates that the northern BCP was generally wetter than present at the LGM, whereas the south would have been drier overall after the LGM (Lyle et al. 2012, Antinao and McDonald 2013, Antinao et al. 2016, Lora 2018). We selected the CCSM GCM as the best climatic model for our analyses because it appears to be more consistent with paleoprecipitation data (Fig. 1, Supporting information).

Species georeferenced records

Our study focused on 21 taxa native to the BCP (Table 1), including eight mammals, four plants and nine reptiles. We analyzed some species for which their genetic structure on the peninsula was previously assessed with mitochondrial, plastid, or nuclear genetic markers. We aimed to represent species that inhabit different elevations (highland or lowland; Fig. 1c). While topographic complexity can be highly relevant to determining the changes in the amount and quality of habitats, we focused on the elevation range because it relates to the organism's physiology and we hypothesized that organisms inhabiting similar elevations could respond similarly to climatic changes. For each taxon, the number of genetic clades was identified following Dolby et al. (2015): at least 0.8 bootstrap support or Bayesian posterior probability in a phylogenetic analysis for reciprocally monophyletic clades, appreciable genetic divergence ($F_{ST} \geq 0.2$), or statistical support in a Bayesian structure analysis. We classified clades according to their geographic location in the south (south of the Vizcaíno peninsula, ~ 27°S, Fig. 1c), north (north of

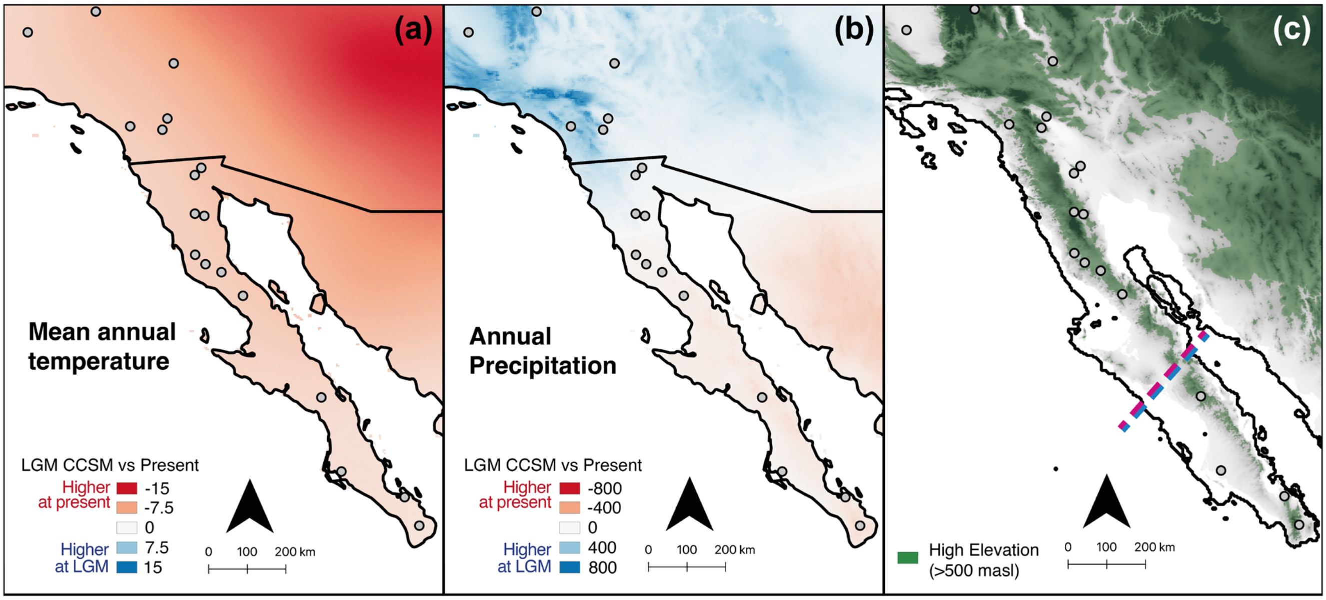

Figure 1. Change in climatic conditions on the Baja California peninsula between LGM and present day, considering the CCSM GCM. Circles represent georeferenced sites from the literature of paleoprecipitation proxy data that were used to evaluate regional accuracy of CCSM versus MIROC GCMs (Supporting information). (a) Mean annual temperature, (b) annual precipitation, (c)elevation threshold for lowland and highland taxa at 500 m. a.s.l., black outline indicates the sea-level boundary for LGM conditions, and the dotted line indicates the area corresponding to the previously described north–south codivergence signal (Dolby et al. 2015).

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	No. occurences	AUC	Variables
1	*Otospermophilus becheeyi*	M	H	1	mit	1	N	5734	0.924	bio2, bio3, bio15
2						2	S	121	0.984	bio1, bio9, bio15
3	*Sorex ornatus*	M	H	2	mit	1	-	476	0.926	bio7, bio14, bio17
4	*Spilogale gracilis*	M	H	3	mit	1	-	160	0.964	bio1, bio5, bio6, bio10
5	*Chaetodipus arenarius*	M	L	4	mit	1	N	1887	0.935	bio4, bio6, bio8
6						2	S	1569	0.986	bio1, bio5, bio11, bio12
7	*Chaetodipus spinatus*	M	L	5	mit	1	N	3833	0.898	bio4, bio15, bio18
8						2	S	850	0.982	bio4, bio7, bio14, bio19
9	*Dipodomys merriami*	M	L	6	mit	1	N	61	0.971	bio8, bio9, bio11, bio18
10						2	N	40	0.991	bio1, bio3, bio11, bio13
11						3	S	43	0.969	bio2, bio4, bio7, bio15
12	*Neotoma bryantii*	M	L	7	nuclear/mit	1	N	305	0.930	bio1, bio10, bio14
13						2	S	138	0.942	bio1, bio6, bio9, bio17
14	*Peromiscus maniculatus*	M	L	8	mit	1	-	5118	0.839	bio2, bio7, bio15
15	*Fouquieria columnaris*	P	H	9	plastid	1	N	608	0.967	bio6, bio8, bio11, bio13
16						2	S	41	0.951	bio1, bio13, bio19
17	*Pinus cembroides* section	P	H	10	nuclear/plastid	1	N	1940	0.970	bio3, bio12, bio14
18						2	S	344	0.999	bio1, bio4, bio15
19	*Encelia farinosa*	P	L	11	nuclear/plastid	1	S	77	0.981	bio8, bio9, bio11
20						2	N	992	0.983	bio6, bio8, bio11, bio13
21	*Stenocereus gummosus*	P	L	12	nuclear	1	-	860	0.958	bio4, bio5, bio12
22	*Crotaphytus vestigium*	R	H	13	mit	1	N	194	0.934	bio1, bio9, bio14
23						2	S	53	0.993	bio3, bio4, bio12, bio17
24	*Elgaria multicarinata/velazquezi/ paucicarinata*	R	H	14	nuclear/mit	1	N	3441	0.970	bio10, bio12, bio14
25						2	S	39	0.991	bio1, bio14, bio13, bio19
26						3	S	365	0.972	bio1, bio4, bio7, bio13
27	*Petrosaurus repens*	R	H	15	RADseq	1	N	25	0.996	bio1, bio6, bio13
28						2	S	88	0.991	bio4, bio5, bio12, bio17
29						3	S	52	0.999	bio2, bio9, bio10, bio12
30	*Plestiodon skiltonianus/ lagunensis*	R	H	16	mit	1	N	1944	0.939	bio4, bio7, bio15
31						2	S	55	0.993	bio4, bio6, bio7, bio12
32	*Sceloporus orcutti*	R	H	15	RADseq	1	N	3785	0.886	bio5, bio12, bio15
33						2	S	613	0.988	bio8, bio9, bio15, bio17
34	*Callisaurus draconoides*	R	L	15	RADseq	1	N	2488	0.923	bio1, bio7, bio9, bio14
35						2	N	648	0.971	bio11, bio13, bio16, bio18
36						3	S	862	0.983	bio2, bio6, bio11
37						4	S	677	0.984	bio5, bio9, bio15, bio17
38						5	S	1534	0.997	bio2, bio7, bio12, bio15
39	*Sceloporus zosteromus*	R	L	15	RADseq	1	N	420	0.977	bio1, bio4, bio9, bio10
40						2	S	398	0.982	bio1, bio4, bio10, bio14

(Continued)

Table 1. Continued.

N	Species	Tax	Elv	Ref	Type of genetic data	Genetic clade	Loc	No. occurences	AUC	Variables
41	*Urosaurus nigricaudus*	R	L	15	RADseq	1	N	725	0.951	bio3, bio15, bio18
42						2	S	1337	0.931	bio2, bio5, bio8
43						3	S	65	0.997	bio1, bio2, bio11, bio12
44						4	S	2149	0.993	bio2, bio3, bio4, bio15
45	*Uta stansburiana*	R	L	17	mit	1	N	10596	0.860	bio2, bio10, bio14
46						2	S	3269	0.976	bio4, bio7, bio17

1: Phuong et al. 2017, 2: Maldonado et al. 2001, 3: Ferguson et al. 2017, 4: Álvarez-Castañeda and Ríos 2011, 5: Álvarez-Castañeda and Murphy 2014, 6: Álvarez-Castañeda et al. 2009, 7: Patton et al. 2007, 8: Kalkvik et al. 2012, 9: Martínez-Noguez et al. 2020, 10: Montes et al. 2022, 11: Fehlberg and Fehlberg 2017, 12: Lozano 2013, 13: McGuire et al. 2007, 14: Leavitt et al. 2017, 15: Gottscho 2015, 16: Richmond and Reeder 2002, 17: Upton and Murphy 1997

~27°S including the Vizcaíno peninsula, Fig. 1c) and clades without geographical genetic differentiation (unstructured). For each taxon we obtained georeferenced records from the Global Biodiversity Information Facility (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 (Supporting information) were obtained from each occurrence point.

Principal component analysis of current climatic conditions

To compare niche properties among the studied taxa (i.e. niche overlap, niche breadth and centroid based niche marginality) we performed a principal component analysis (PCA) of the available environmental space with all scaled bioclimatic variables. For this, we used a set of 5000 random points to sample the current climatic conditions in R ver. 4.1.2 (www.r-project.org). In the analysis, PC1 (40.37% of variance) was positively associated with annual precipitation (bio12), and precipitation of the driest (bio17) and coldest (bio19) quarters; and negatively associated with mean annual temperature (bio1), and mean temperature of the coldest (bio10) and warmest (bio11) quarters. PC2 (26.68%) was positively associated with isothermality (bio3), temperature seasonality (bio4) and temperature annual range (bio7), and negatively associated with precipitation seasonality (bio15). PC3 (17.92%) was associated with precipitation of the warmest quarter (bio18).

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. Briefly, a set of environmental background points were tested to be positioned within any or both ellipsoids representing the niche of two taxa in the multivariate space (Nuñez-Penichet et al. 2021). The niche overlap corresponds to a value between 0 and 1, where 1 represents complete overlap (i.e. all background points occurring in the intersection of both ellipsoids) and 0 represents no overlap (i.e. background points occurring in each ellipsoid separately). Significance is then obtained from 1000 bootstrap replicates. Niche overlap was tested for all clade pairs within taxa using the first three principal components obtained from the PCA of all scaled bioclimatic variables (84.97% of variance). Significantly low niche overlap was considered as evidence for niche divergence.

Niche breadth

Niche breadth was calculated for each clade in the PCA of all bioclimatic variables of current climatic conditions as the area of the minimum convex polygon from occurrence points within the first two dimensions of the multivariate climatic space (67.05% of variance). The minimum convex polygon was calculated with the ‘adehabitatHR’ (Calenge 2023) and ‘sp’ (Pebesma and Bivand 2005) packages in R. Differences of niche breadth were 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.

Ecological niche models and projection to present-day and LGM climates

The ecological niche of each clade was modeled by estimating the niche ellipsoid with the ‘ntbox’ package (Osorio-Olvera et al. 2020a) in R. We used minimum volume ellipsoids instead of other modeling algorithms because this approach assumes that the niche has a convex shape as predicted by ecological niche theory (Jiménez et al. 2019), and an ellipsoidal shape has been proposed as a good descriptor of the relationship between fitness and distance from the niche centroid (Osorio-Olvera et al. 2019, 2020b). Hence, ellipsoids are a useful approximation to the potential niche of a species and allow for a functional interpretation of the suitability values across clades, which was important for this study. ‘ntbox’ computes an n-dimensional ellipsoid in the multivariate space covering a determined proportion of the occurrence points in the training set. We represented the 95% confidence ellipsoid used by the clade in the multivariate space of bioclimatic data (Osorio-Olvera et al. 2020a), and we used the occurrence points from each genetic group retaining 30% of the data as a testing set. For this analysis, we used raw variables instead of principal components because previous studies have shown that models using minimum volume ellipsoids and raw variables with a low omission rate have a better predictive power of population abundance (Osorio-Olvera et al. 2020b). Highly correlated variables were removed by randomly removing one of each pair with a correlation higher than 0.95. Then, ‘ntbox’ uses an exhaustive method to assess different combinations of three or four from the retained variables to determine the best model to describe the distribution of the genetic clades. The best model was selected based on the partial receiver operating characteristic area under the curve (AUC), omission rates and model complexity (Cobos et al. 2019, Osorio-Olvera et al. 2020a).

The niche ellipsoid of each genetic clade was projected onto the present-day geography to obtain each clade’s predicted distribution. Habitat suitability was estimated with ‘ntbox’ using the Mahalanobis distance between the species niche centroid and each cell in the geographic conditions’ raster (Osorio-Olvera et al. 2020a). To determine the potential distribution for each taxa, the niche models were binarized between suitable and non-suitable conditions by using a 10% omission criterion. Then, we projected the niche ellipsoid to LGM climate using MIROC and CCSM GCMs with ‘ntbox’. 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

We used two approaches to assess niche marginality as a measure of habitat quality using Mahalanobis distances, which are described to be a good descriptor of organismal fitness as a function of distance from the niche centroid (Soberón 2018, Santini et al. 2019, Osorio-Olvera et al. 2020b). First, we quantified niche marginality as the distance between the species niche centroid and the centroid of available environmental conditions in the multivariate space. For this, we calculated the Mahalanobis distance between the centroid of the niche ellipsoid from each clade and the centroid of the available multivariate space in the PCA of present-day or LGM climatic conditions with the ‘philentropy’ package (Drost 2018) in R. We then compared the niche marginality (i.e. Mahalonobis distances) between LGM and present by constructing a GLMM that included time period (LGM versus 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.

We further implemented a second measurement of marginality based on the distribution models generated with ‘ntbox’. Given that in ellipsoid-based ecological niche models the suitability is calculated from the Mahalanobis distance to the ellipse centroid (Osorio-Olvera et al. 2020a), niche marginality was measured as the inverse of suitability. Thus, we used the ‘raster’ package (Hijmans 2023) in R to obtain the suitability values for each cell from the raster of the geographically projected niche models for each genetic clade. We measured niche marginality only within the predicted species’ distribution. Thus, we retained only values from cells with suitability above the 10% omission rate threshold. Each value was converted to niche marginality between 0 and 1, defined as the inverse of suitability and normalized by the predicted distribution range with the formula:

$$1-\left(s-\min_s\right)/\left(\max_s-\min_s\right)$$

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 (www.r-project.org), which represents the relative amount of area of different marginality values within the distribution. 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 between LGM and present by subtracting the kernel density curve of the present from the density curve of the LGM. Finally, to assess whether the changes in the marginality density distribution between LGM and present were similar among organisms with shared features (taxa, elevation or location), 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

Occurrence records

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 contained only 7 occurrence records, therefore this clade was not included in further analyses.

Between clades niche divergence

Between-clade climatic niche divergence was detected with overlap values significantly lower than expected by chance for all clade pairs within species (Fig. 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 clades had niches ~four times larger than southern clades (Fig. 2b), whereas unstructured clades' niche breadth was over six times larger than southern clades.

Contraction of the distribution area to LGM for most clades

The constructed niche models had an average AUC value of 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). When we projected the ecological niche onto geographic space (Fig. 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 areas at least twice as large than southern clades (Fig. 2c). When projecting the models to LGM – CCSM conditions (Fig. 2e), we detected that several clades showed a reduction in their geographic area (Fig. 2d; Supporting information shows projections to LGM using the MIROC GCM). The species *F. columnaris* did not have suitable area during LGM conditions for the CCSM GCM. While no significant effect of clade was detected on the proportional change in area (Supporting information), northern clades showed a mean reduction to 56.7% of their present-day area, southern clades' available habitat was reduced to 67%, and unstructured clades showed an average 30% increase in their distribution area during LGM (Fig. 2d, 5).

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 (reduced by 60%) and lowland clades (reduced by 70%; Fig. 3, 5), and three highland southern clade outliers (*Pinus cembroides*, *Elgaria pauciarinata* 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, Fig. 3).

As a second measure of niche marginality, we evaluated the change in the proportion of marginality values within the suitable area for each clade for present day climate and LGM. Then, we clustered the clades based on similarity of the kernal density plots representing marginality distributions from LGM to present to evaluate if organisms with similar features (taxonomic group, elevation or location) presented similar responses between LGM and present day (Fig. 4a). The species *F. columnaris* was not included in this analysis since it did not have suitable areas for LGM GCM climatic conditions. The best supported number of clusters was five (Fig. 4b) which can be qualitatively described as taxa with: 1) much more marginal area at LGM, 2) much more marginal area at present, 3) slightly more marginal area at LGM, 4) slightly more marginal area at present, and 5) similar marginality at present and LGM. Most highland species clustered in the more marginal area at present (group ii; Fig. 4). There was no clear grouping by taxonomic group (plant, mammal or reptile) or location of the genetic clade.

Discussion

Climatic changes can affect the distribution, abundance, and allele frequency distributions of natural populations (Foden et al. 2019, Román-Palacios and Wiens 2020, Aguirre-Liguori et al. 2021) by modulating the quantity and quality of available habitats. In this study, we assessed changes in habitat quantity and quality between LGM and present day for different taxa on a climatically heterogeneous landscape, the Baja California peninsula. We evaluated whether organisms with different characteristics showed differential responses to climate change, and we generated predictions about the effects of past climatic changes on population demography and selection pressure. Most clades showed a reduction in distribution area towards LGM, in particular northern clades (Fig. 5). Further, niche marginality (used as a measure of habitat quality) was in general higher during LGM for most clades, except for some northern highland clades (Fig. 5). Thus, some northern highland species may have been favored during LGM in terms of habitat quality. Under this framework, the independent assessment of habitat quantity and quality enables the generation of explicit predictions about species' response to climate change.

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 and Álvarez-Castañeda 2021), and expands the niche divergence pattern further than simply north versus south, but also between clades within those geographic designations. This suggests that niche differentiation is stronger than previously considered; some species may have differentially adapted to the diversity of available environmental conditions and could therefore explain the high number and geographic variation of genetic breaks previously documented on the peninsula (Dolby et al. 2015, Araya-Donoso et al. 2022).

Niche breadth differed strongly between clades located in the north versus south of the peninsula (Fig. 2) while 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 at the macroenvironmental scale (Ficetola et al. 2018). Therefore, there may be less niche divergence than predicted by these models if organisms experience or choose microclimates that are not reflected at a macro scale.

Decreased LGM 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 (Fig. 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

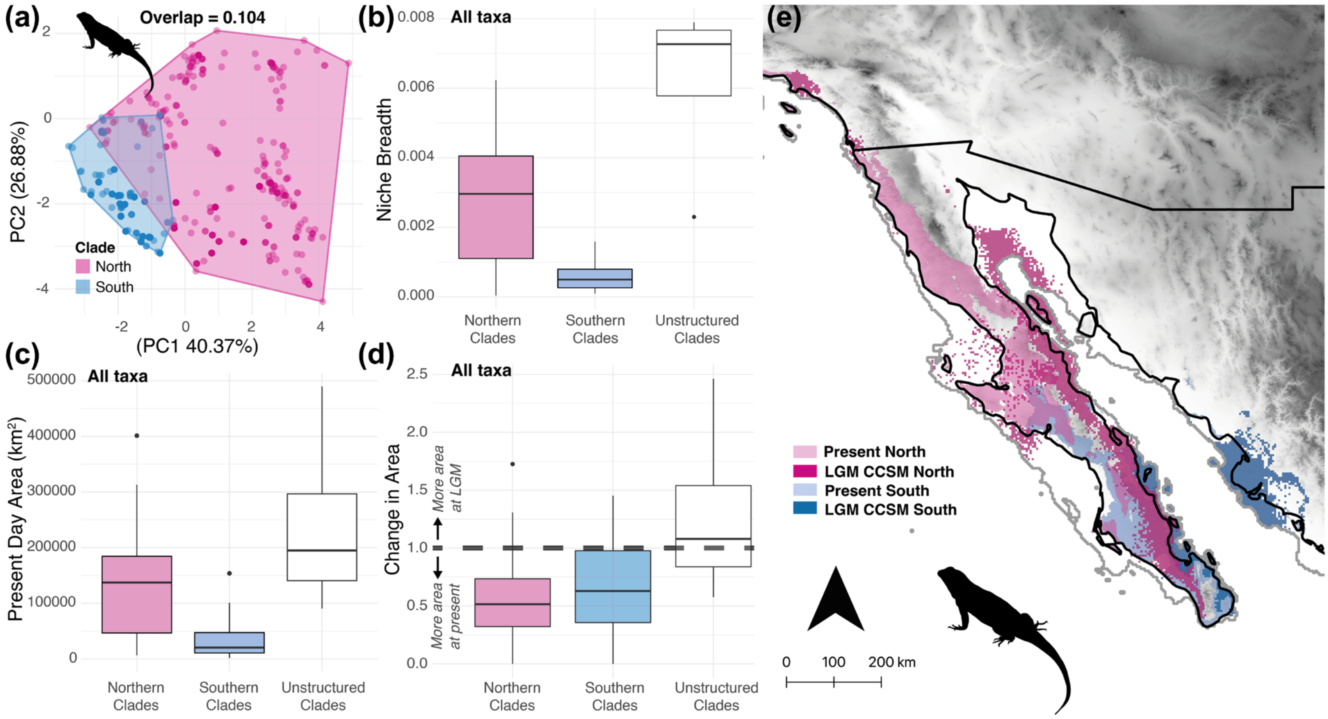

Figure 2. Ecological niche and distribution analyses. (a) Niche overlap between northern and southern clades for *Sceloporus zosteromus*. (b) Niche breadth for all genetic clades. (c) Present day distribution area for all clades. (d) Change in distribution area from LGM to present for all clades. (e) 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.

the north (Fig. 1, Antinao and 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 as showing heterogeneous responses to Pleistocene climatic variation compared to organisms from temperate regions, since their response is highly dependent on local precipitation patterns (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, 2022, Araya-Donoso 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. 2018, Arteaga et al. 2020), whereas others have detected range reductions (Valdivia-Carrillo et al. 2017, Klimova et al. 2017). Moreover, Cab-Sulub and 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. Many factors can affect the performance of ecological niche models, including the modeling algorithm, how the global circulation models (GCM) used to build the environmental layers perform regionally, variable selection, the quality and quantity of occurrence records, and the size of the study area (Soberón 2007, Sillero et al. 2021). Discrepancies in SDMs have been observed in models built with CCSM and MIROC GCMs (Graham et al. 2014, Guevara et al. 2019, Cab-Sulub and Álvarez-Castañeda 2021). For this reason we compared the climatic patterns of those GCMs against paleoprecipitation data, and determined that the CCSM GCM was a better descriptor of LGM climate for the Baja California Peninsula (Supporting information). Any difference between other studies and ours could be due to the modeling algorithm since all those studies implemented Maxent and we used minimum volume ellipsoids. To evaluate this hypothesis, we ran Maxent on the same data and variables used for our SDMs. The results from Maxent were different from those generated by niche ellipsoids, particularly when projecting to LGM (Supplementary information). This shows results are dependent on the modeling approach and it is unclear which one is more accurate. Since we aimed to interpret our models functionally and to estimate selection pressure, we chose ellipsoids because this methodology represents the fundamental niche of the species and therefore the suitability values are better predictors of fitness (Osorio-Olvera et al. 2019, 2020b, Lee-Yaw et al. 2022). We suggest that caution should be taken when selecting the modeling approach that will be used for studies addressing the ecological niche and distribution of organisms, based on the specific aims of each study and the advantages/disadvantages of the different modeling approaches.

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 (Fig. 3a). Moreover, within suitable areas some clades also presented a higher proportion of more marginal conditions during LGM (Fig. 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, and could be used in conjunction with historical demographic modeling from genetic data (e.g. SMC ++ Terhorst et al. 2017). 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

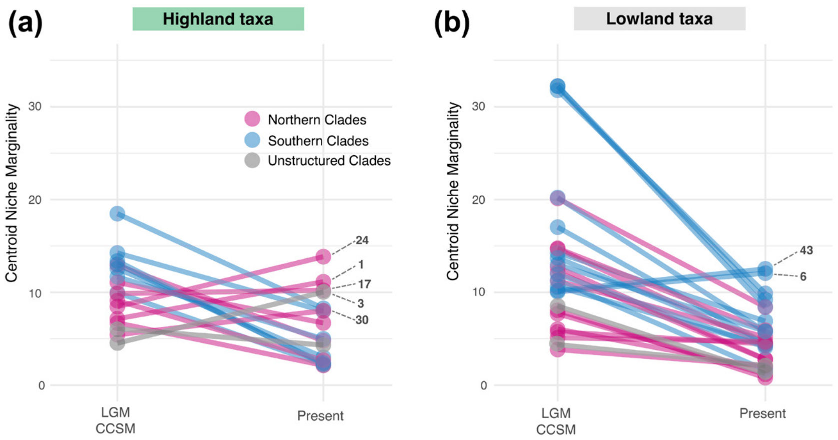

Figure 3. Centroid niche marginality at LGM and present for each genetic clade for highland (a) and lowland (b) taxa. A decrease in niche marginality is observed for most clades, except for five highland northern clades and two lowland southern that show an increase in marginality for present day climate,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

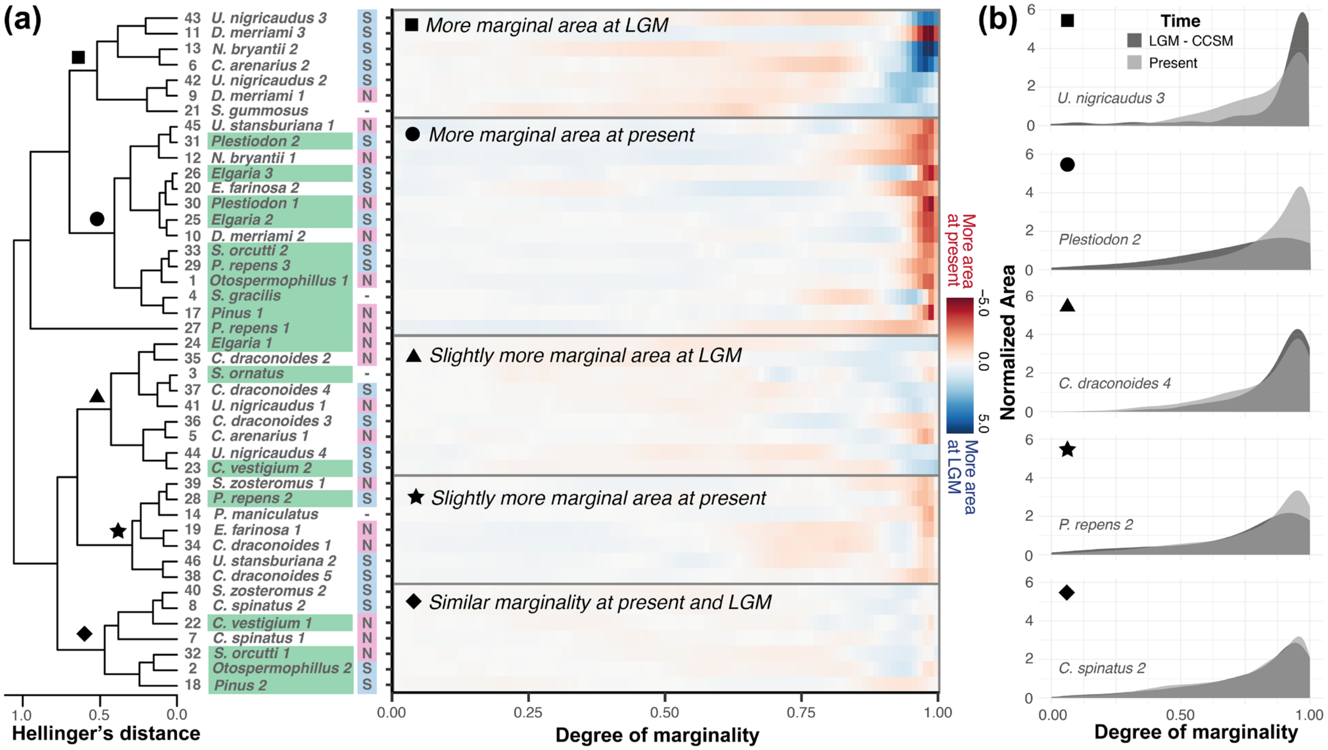

Figure 4. Change in the proportion of marginal conditions within suitable area for each clade. (a) Cluster analysis showing five groups according to their changes in the normalized marginality area between LGM and present (i: more marginal area at LGM, ii: more marginal area at present, iii: slightly 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.

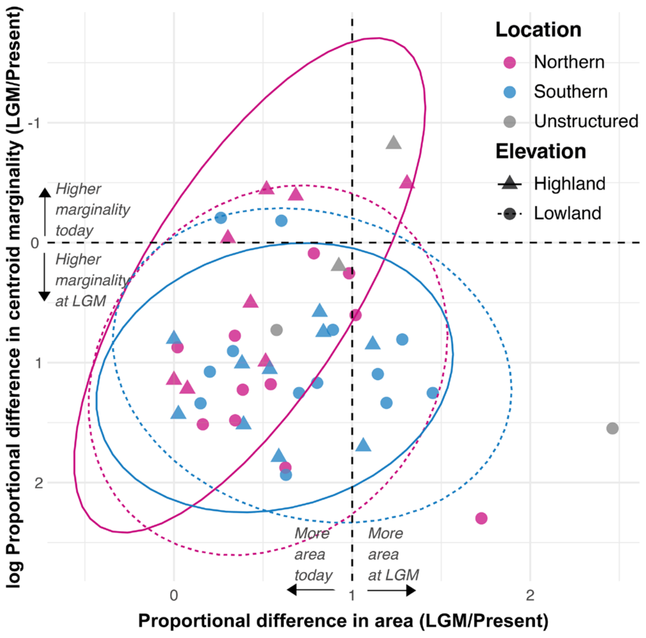

Figure 5. Proportional change in area versus the log converted proportional change in centroid-based niche marginality for all studied taxa. In particular, northern highland clades seem to have higher niche marginality values today than at LGM.

warm-adapted lowland taxa and cold-adapted highland taxa. For lowland desert-adapted species, available environmental conditions were in general more challenging during LGM (Fig. 3, 4), and in the desert regions from the southern peninsula habitat quality improved more LGM to present relative to the north (Fig. 3, 4). In contrast, for most highland species habitat quality declined towards present-day, particularly in the northern Peninsula (Fig. 3, 4). Highland species 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 Afromontane forests range expansions in the Horn of Africa (Casas-Gallego et al. 2023), or *Polyepsis* woodlands on the Andes Mountains (Zutta and Rundel 2017). We would expect different historical selection pressures and effective population sizes for these species relative to lowland species.

Model predictions that can be tested with genomic data

Integrating ENMs and SDMs with genomic data can be used to test whether our inferences about species responses

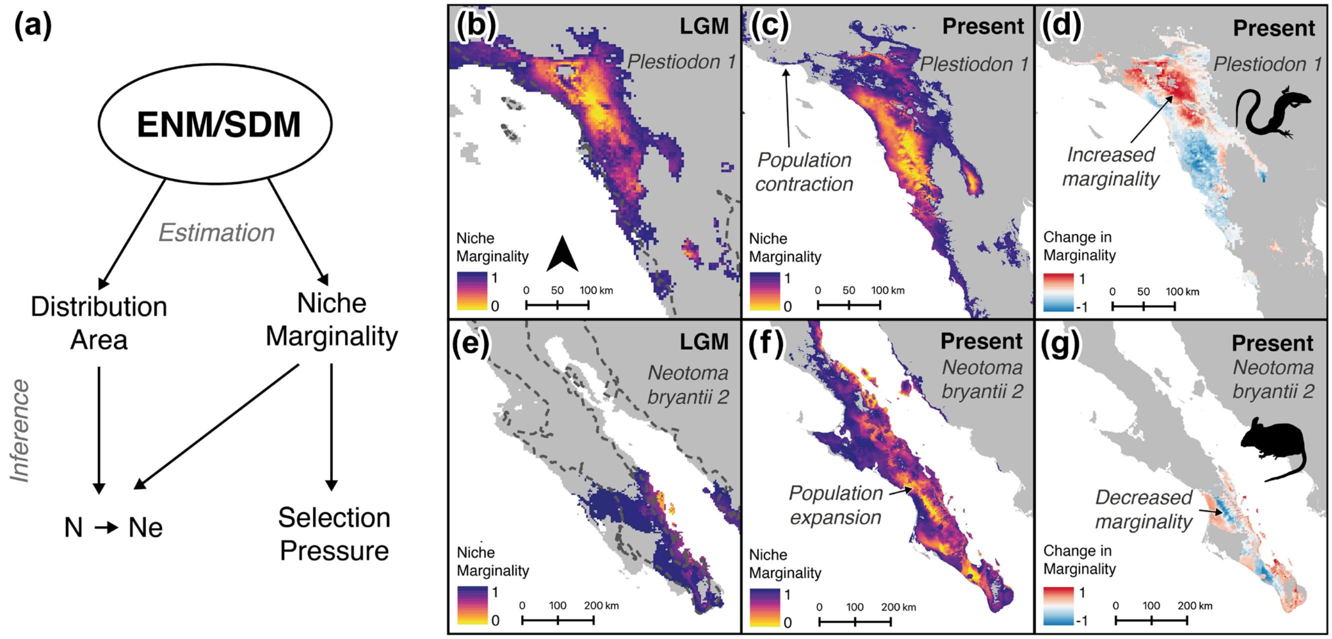

Figure 6. (a) Diagram representing that ENMs and SDMs can be applied to infer changes in Ne and selection pressure for natural populations. (b–d) Inference of population contraction (d) and increased marginality (e) areas between LGM and present within the distribution for the northern clade of *Plestiodon*. (e–g) Inference of areas with population expansion (f) and decreased marginality (g) for the southern clade of *Neotoma bryantii* between LGM and present.

to climate change are accurate and relevant and therefore 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 (Fig. 6a).

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 (Fig. 6b, c), 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 (Fig. 1, 6d). This could be evidenced by adaptations in thermoregulation or water physiology, and positive selection should be found in genes associated with these processes such as aquaporins (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* (Fig. 6e), which exhibits a geographical expansion towards the north from LGM to present (Fig. 6f), associated with increased habitat quality (i.e. decreased marginality) in central populations (Fig. 6g). Stable populations between LGM and present for this species should reflect a stable effective population size, and could show older signatures of natural selection associated with LGM climate (Fig. 6f, g) while the northern part of the range may be expected to have lower diversity as a consequence of range expansion as well as a higher proportion of deleterious alleles (Excoffier and Ray 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 and Murphy 2014), *Spilogale gracilis* (Ferguson et al. 2017), and *Otospermophilus becheeyi* (Phuong et al. 2017) show population size reduction during LGM, which agrees 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).

Conclusions

Assessing changes in quantity and quality of available habitats allows the generation of more detailed interpretations 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, so while there was a decrease in the area of suitable conditions many may have had increased fitness within those available habitats due to those habitats having lower niche marginality (higher suitability). 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 show the importance of decoupling habitat quantity from quality and in doing so were able to generate explicit predictions about population history that can be tested with genomic data to generate a better understanding of population dynamics due to climate driven habitat changes.

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Author contributions

Raúl Araya-Donoso: Data curation (lead), Formal analysis (lead), Investigation (equal), Methodology (equal), Validation (lead), Visualization (lead), Writing – original draft (lead). **Austin Biddy**: Formal analysis (equal), Investigation (equal), Methodology (supporting). **Adrian Munguía-Vega**: Conceptualization (equal), Funding acquisition (equal), Investigation (supporting), Methodology (supporting), Project administration (equal), Resources (equal), Supervision (equal), Writing – review and editing (supporting). **Andrés Lira-Noriega**: Conceptualization (equal), Investigation (supporting), Methodology (lead), Project administration (supporting), Software (equal), Supervision (equal), Validation (equal), Writing – review and editing (supporting). **Greer Dolby**: Conceptualization (equal), Funding acquisition (lead), Investigation (equal), Project administration (lead), Resources (lead), Supervision (lead), Visualization (supporting), Writing – review and editing (lead)

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The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/ecog.07391.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bk3j9kdkr (Araya-Donoso et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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