Modeling Past, Present and Future niches: Species-specific responses to climate changes in three shrub congeners from South American drylands

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Abstract

Context

Climate and land use change threat biodiversity and impact on natural and anthropogenic systems as well, in all continents. Although these effects are deepened in regions beholding highly adapted species to particular environmental conditions, like drylands in the Global South, surprises the scarcity of studies exploring the impact of climatic forces across time in these regions.

Objectives

Our aim is to assess the spatial distribution and niche overlap of three dominant native shrubs of the Monte Desert under present climate conditions, to retrodict their potential past distribution, and anticipate their predicted range under future climate scenarios, to complement traditional approaches of biodiversity conservation and sustainability. These species are *Larrea cuneifolia* (*LC*), *L. divaricata* (*LD*), and *L. nitida* (*LN*) that span between 15 and 45°S latitude. They are key elements of the largest temperate dryland of South America, and are alternative forage for livestock.

Methods

We used ecological niche modeling and niche overlap approaches, which we then projected to past (Last Glacial Maximum LGM and Mid Holocene) and future (2050 and 2070) under two scenarios of greenhouse gas emissions and consequent climate change: Representative Concentration Pathway (RCP) 4.5 and 8.5, representing medium-to-low and high emissions levels, respectively. We evaluated these scenarios according to different global circulation models (GCMs) (CCSM4 and MIROC-ESM), to allow detailed assessment of uncertainty in model predictions.

Results

All species showed high niche overlap in the present (67–89%), and when projecting the models, we observed that *LC* and *LD* would have reached maximum suitability in the Mid Holocene and would remain stable by 2050. However, *LC* would gain and *LD* would loss suitability by 2070. Meanwhile, *LN* would have reached the maximum suitability in the LGM, which decreased in the Holocene, increased in the present and projects a severe reduction in the future.

Conclusion

We found species-specific responses even among species with current overlapping niches such as *LC* and *LD*, highlighting the need to develop mitigation measures particularly for *LD* and *LN* in the face of

climate change and land use pressures. Global South deserts are being highly degraded and information on future potential ranges of endemic species can support the development of sustainable conservation and management plans.

Introduction

Current distributions of plant species have been shaped by past periods of climate change (Hewitt 2000, Kreyling et al. 2012). However, present rapid climate and land use changes threat biodiversity and impact natural and anthropogenic systems as well, in all continents (IPCC. PCC, 2019), leading to large-scale shifts in species' ranges (Bardou et al. 2020). This is particularly relevant in drylands that cover c. 40% of the land global surface which deliver significant ecosystem services. Drylands are considered one of the most sensitive areas prone to suffer the effects of climate and land cover changes due to increasing hydro-climatic variance that will characterize forecasted 21st century warming (Huang et al. 2015). Global expansion of drylands has occurred over the past 60 years (Feng and Fu 2013, Huang et al. 2017a) and it is projected to accelerate (Huang et al. 2016a). In addition, approximately one third of global population, more than 2 billion people, inhabit this environment (Safriel et al. 2005). Thus, the expanded drylands together with extensive land use may aggravate the risk of land degradation and ecosystem vulnerability (Huang et al. 2017b). Therefore, estimates on projected range shifts of drylands are crucial to avoid global desertification intensification (Reynolds 2011).

Drylands include hyper-arid, arid, semiarid, and dry sub humid areas (Feng and Fu 2013), where temperature and precipitation forecasts vary with latitude and geographic region. It has been shown that temperate drylands might be reduced by a third and converted to subtropical drylands (Schlaepfer et al. 2017). Also, major expansions of semiarid regions would occur over the north side of the Mediterranean, southern Africa, and North and South America (Feng and Fu 2013). Nonetheless, early temperature and precipitation projections based on 20th century data indicate that while warming characterized most dry regions, the increase rate is less than the average for global drylands in the Sahel at the Horn of Africa and Southern South America (Hulme 1996). In contrast to the majority of dryland regions of the world, where no significant wetting or drying was measured, the estimations predict an increase in precipitation of approximately 18% for southern South American drylands (Hulme 1996, CONAF- CONAMA 2006). Similarly, hydroclimatological conditions, for the region, using local climate models for two-time series 1961–1990 and 2071–2100 indicated that dry zones of Argentina yielded wetter trends associated to greater water availability and an aridity index decrease, particularly towards temperate regions (Zaninelli et al 2019). Thus, different responses might be expected, particularly for widespread dryland species spanning through tropical, subtropical, and temperate environments (Vidal R. et al 2022).

Under the rapidly increasing demand for food due to population growth, urbanization, and increasing incomes in developing countries, efforts are placed on production of livestock in arid rangelands not naturally suited for extensive agricultural practices (Delgado 2005, Tadey and Souto 2016). These detrimental effects are deepened in regions with high endemism rates beholding species highly adapted to specific climatic conditions (Olson et al. 2001, Sánchez-Azofeifa et al. 2005, Miles et al. 2006, Souto et

al. 2015). Developing evidence-based management strategies that support the adaptive capacity of species is crucial under predicted climate change, which is leading to increased warming and summer droughts (Inouye, 2000; Hartmann, 2011), with potentially large repercussions for ecosystems productivity (Ciais et al., 2005; Gazol et al., 2018). Here we focus on improving the understanding of how dryland species responded to past and will do so under projected future climatic conditions to have a hint of potential responses of dominant *Larrea* species inhabiting Monte Desert, the largest continuous arid region of South America.

Ecological niche models (ENM) consist of the projection of environmental niches in the landscape. They are used to describe environmental tolerances of species and allow projecting potential responses of their ranges to past and future climate scenarios, estimating the favorability of the habitat (Peterson and Soberon, 2012). Environmental niche models can also predict the suitability of habitats across a landscape, and are increasingly been used to design conservation and restoration plans (Soberon et al 2017). A growing number of studies compare predicted habitat suitability generated by ENMs from different species to test hypotheses on historical processes that might be responsible for current distributions and also to forecast evolutionary responses of species under predicted future climates (Soberon et al 2017). Species distribution models (SDMs) and ecological niche models are constructed by correlating observations of occurrence with data on environmental conditions at occupied sites (Bradie and Leung 2017). Increasingly, conservation biologists are using species distribution models (SDMs) to assess the environmental parameters that shape species' distributions today and project these species–environment relationships into past and future conditions (Phillips et al. 2006; Elith and Leathwick 2009). In this sense temperate deserts in the Global South are being highly degraded and information is needed on future responses of key taxa. Particularly, temperate and semi-arid regions of Southern South America are undergoing rapid habitat conversion as a result of several human activities (i.e. grazing, logging, agriculture). These arid ecosystems contain many endemic species and have played an important role in the evolution of South American biota (Ojeda et al 1998).

In arid systems, the majority of studies have focused on predicting the effects of climate change on native species of the northern hemisphere rather than such impacts or landscape change on South American ones (Vidal R et al 2021). Many of these species lack comprehensive occurrence data, and the abiotic and biotic limits to species distributions are poorly understood (Lomolino and Heaney 2004). This information gap on the geographical distribution of many taxa, known as Wallacean shortfall (Whittaker et al 2005), can be addressed using SDMs to develop range and habitat suitability maps, which can be generated with as few as 5–25 occurrence points without knowledge of absence points (Hernandez et al. 2006; Pearson et al. 2006). Thus, it is of interest to fill the knowledge of understudied regions, which might contain key taxa vulnerable to changes in climate. Given the forecasted climatic change it is useful to compare the current distributions of species to assess their ability to cope with changes in climate (Sheller and Leon 2016) such as under the Last Glacial Maximum (LGM) and the Holocene, when agriculture and pastoralism emerged and spread (Boivin et al., 2016; Hofman and Rick, 2018). Although manipulative field- and laboratory-based studies can identify factors that shape niches and ranges (Hargreaves et al. 2014, Lee-Yaw et al. 2016), for most species logistical difficulties preclude examining

large numbers of variables and studying range limits across broad geographic scales. So, alternatively, environmental limits can be inferred using models of species' geographic ranges and niches.

Monte Desert, is a subtropical and temperate arid region that covers approximately 467,000 km^2 (Oyarzabal, 2018). As other temperate drylands, it is an important biodiversity hotspot characterized by intermediate to high levels of species richness and endemism (Olson et al. 2001, Sánchez-Azofeifa et al. 2005, Miles et al. 2006), probably due to its particular climatic setting (Turchetto-Zolet et al. 2013, Camps et al. 2018). In late Miocene and Pliocene, the geology and climate of the region was modeled by earlier volcanic and tectonic events related with the elevation of the Andean mountain range (Ramos and Ghiglione 2008). Also, paleoclimatic records and model simulations of past climates suggest significant variations in the atmospheric circulation, temperature and precipitation patterns since the Last Glacial Maximum (LGM) (Labraga and Villalba 2009). Linked to the LGM, this region was affected by dry and cold climates that facilitated the advance of xerophytic vegetation of northwestern Argentina even northwards (Ab'Saber 2000, Iriondo, 2010). Nonetheless, the late Holocene was characterized by a less severe dry period (Argollo Bautista and Iriondo, 2008, Iriondo, 2010). Models of climate change for 2100 forecast contrasting seasons, with increasing summer rainfall, but almost no changes or small reductions in winter precipitations across temperate drylands and temperature increases, larger in summer than in winter (CONAF-CONAMA 2006, Labraga and Villalba 2008). Thus, ongoing climate change highlights the need to understand vegetation responses to climate oscillations particularly in regions with projected changes different from the increasing temperature-decreasing precipitation standard global pattern (IPCC. PCC, 2019).

Unfortunately, agricultural expansion and overgrazing exploitation of the region affects not only the dominant shrubs species highly consumed by livestock, such as *Larrea* sp. (Souto and Tadey, 2018). Also, have severe and accelerated consequences that might scale globally, as deepening South America`s most dramatic biodiversity decline, reducing global green surface and natural cover (Hansen et al. 2013, WWF 2014, Vallejos et al. 2015). Studying multiple species' populations, within and beyond current ranges, can help identify whether demographic responses to climate change exhibit directionality, indicative of range shifts, and whether responses are uniform across a suite of species.

Hereby, we modeled the suitability of three species of the genus *Larrea*, a closely related group of species dominant in arid South American native rangelands, threatened not only by climate but also by land use change. We deployed models for the present (1975–2016), and then projected them into two scenarios in the past (LGM and Mid Holocene) and eight future climatic scenarios (2050 and 2070, under two scenarios of greenhouse gas emissions and two different global circulation models); to track changes in distribution through time. We aim to estimate current habitat suitability using spatial distribution modelling to retrodict the effects of historical climatic changes that occurred during the Quaternary glaciations and Mid Holocene, when anthropogenic disturbance started, on the spatial distribution of *Larrea* sp., and to predict species' range suitability under future climates. We hypothesize increasing habitat suitability during glacial periods for more cold-tolerant *Larrea* species. Milder Mid Holocene temperatures favored suitability of all studied species, whereas increasing precipitation and temperature

seasonality would differentially affect *Larrea* species according to their climatic tolerances. Drylands are highly threatened, in unstable equilibrium ecosystems, which have turned into a matter of great concern due to growing land degradation and productivity-loss, lately combined with climate change (Huang et al 2017). Despite their known importance as alternative forage and prevalence in the largest desert of South America, *Larrea* species are not fully understood, particularly in their ecological niches and how their sustainability would change with projected climates. We fill this gap assessing the spatial distribution and niche overlap of three native *Larrea* species under present climate conditions to retrodict their potential distribution in the past and anticipate them under future climate scenarios, in the end assisting biodiversity conservation and sustainability.

Materials And Methods

Studied species and Monte Climate

Studied species belong to the Zygophyllaceae, a plant family of herbs, shrubs and trees growing in seasonally dry deserts in the tropics and subtropics of the Global South and North America. We focus our study in an endemic and phylogenetically related group of evergreen shrubs species members of the genus *Larrea*, which occur amphitropically disjunct in North American and South American deserts, being more speciose in the Monte Desert phytogeographic region in Argentina (Fig. 1). This biome extends from 24°35´S in Salta province to 44°20´S in Chubut province, lying in the inner basins of the Andes of Catamarca and La Rioja, in the Precordillera, the Sierras Pampeanas and the basins of San Juan, Mendoza and San Luis, in western La Pampa, eastern Neuquen, central Rio Negro and northeastern Chubut. It is bordered on the west by the Andes, on the south by the Patagonian semidesert, and on the east by the dry subtropical woodlands of Chaco and Espinal (Morello, 1958; Cabrera, 1976). The Monte Desert constitutes the most arid rangeland of Argentina (Fernandez and Busso, 1997), where intensive agriculture is confined to irrigation valleys, and where fruit, vegetables and forage crops are grown. This semiarid to arid climate has high evaporation, enhanced by windy conditions, especially in the south (Patagonian Monte).

Mean annual rainfall varies between < 100 and 450 mm, strongly conditioned by the surrounding topography. Mean annual temperature varies between < 10 and 18°C; lowest values are found towards the southern range, where isotherms are also clearly topography-dependent. Rainfall occurs overwhelmingly in the summer in most of the Monte (up to 70% of the total in the north). A tendency to a reverse seasonality appears southward of 40°S, where westerly circulation becomes dominant and summers yield less than 20% of the annual rainfall (Prohaska, 1976). Long rainless periods may extend over seven months in the northern Monte but very seldom occur in the south, because of the alternation of air mass origins (Paruelo et al. 1998a). The southern Monte stretches from 35°S to 44°S, and is a temperate region with a Mediterranean- like rainfall regime produced by the westerlies from the Pacific Ocean affected by the rain shadow effect of the Andes. Another classification of the natural areas in the Monte is represented by the high and low elevations. The high Monte is characterized by mountains and valley bottoms landforms that primarily occur in northern Monte, whereas the low Monte is characterized

by piedmonts, hilly landscapes, along with plains and landforms of major desert stream valleys (central and southern Monte). In spite of the massive area occupied by the Monte (approximately 467,000 km^2) and the consequent variability in soils and climate, the vegetation of this biome is rather uniform in terms of physiognomy and floristic composition. Shrub steppe with dominance of *Larrea* spp. (Zygophyllaceae) is the typical vegetation, although several species of *Prosopis* occur in open woodlands where groundwater is accessible (Morello 1958, Cabrera 1976), and winter temperatures, as well as diurnal ranges, clearly depict the continentality of the temperature regime, enhanced by topographic enclosure (Le Houerou 1999). The predominant wind direction changes according to latitudinal variations; westerly winds predominate all the year round in the southern Monte, whereas in the northern Monte winds from the south and east prevail (Rundel et al. 2007). The limits of the Monte Desert are given by the 200 mm isohyet, ranging 100–450 mm/year, and although precipitation is relatively constant in this biome, its distribution varies in a latitudinal fashion from monsoon type with seasonally summer rains in the north, to scarce but regular precipitations throughout the year towards the Atlantic coast, and peaks of higher winter precipitation nearby Patagonian Andes (Ezcurra et al. 1991, Vidal R. et al. 2021). Annual temperature in the Monte Desert, also has a north–south gradient from 18 to 12°C (Labraga and Villalba 2009). The potential evapotranspiration ranges between 0.05 and 0.5, indicating a marked water deficit for the whole area (Rundel et al. 2007). These environmental characteristics provide a good model for investigating climatic niches, which can shed more light on drylands in the Americas.

Out of the five *Larrea* species, we left out two members of the genus, *L. ameghinoi*, which is an extremely rare species and, *L. tridentata* DC endemic of North American deserts (Hunziker et al. 1972, Laport et al. 2013, Yang 1970), and we sampled the three South American widespread species throughout their respective ranges: *Larrea cuneifolia* Cav (*LC*), *L. divaricata* Cav (*LD*), and *L. nitida* Cav (*LN*) (Hunziker et al. 1972) (Fig. 1). These three wide-ranging species tend to segregate spatially, although they grow in the same large region and can hybridize under natural conditions (Hunziker et al. 1969). Thus, *L. cuneifolia* occupies the driest and hottest extremes, and *L. nitida* occurs at higher altitudes or low latitude sites where cold windy pockets are produced, and water tends to accumulate, while *L. divaricata* occur under intermediate conditions. It has been suggested that the architectural, foliar and physiological characteristics of the South American species of *Larrea* reflect the selective forces that prevailed during the Pleistocene glaciations during which the Monte suffered a reduction in its geographic distribution until it reached its current range (Ezcurra et al. 1991).

Species Occurrence Data Set

We compiled our field georeferenced observations (stored in BOLD: Barcode of Life Data Systems http://v4.boldsystems.org/) of focal species' with online available occurrence sources: GBIF repository (12,970 records, GBIF.org, Occurrence Download https://doi.org/10.15468/dl.wjr69h), and herbaria: Darwinion (http://www.darwin.edu.ar/proyectos/floraargentina/fa.htm), USA_MOBOT (https://www.missouribotanicalgarden.org/) USA_ARIZ (https://cals.arizona.edu/herbarium/node/1), USA_NYBG (https://www.nybg.org/), and USA_COLO (https://www.colorado.edu/cumuseum/research-collections/botany-section-university-herbarium-colo). We use these occurrence records across the range

of each species to develop suitability models in the present (1975–2016), and projected them into past (LGM: 21,000 BP; and Mid Holocene) and future (2050 and 2070) climatic scenarios. To correct for biases in clustered or oversampled locality data, we used a subsampling technique in which we conservatively removed presence points located within a 500 m radius of one another (Elith et al. 2010; Fourcade et al. 2014). We checked each datum before including it in our data set, and removed all duplicates and neighbors. After quality-control, our subsampled data set of occurrence points exceeded low sample number thresholds suggested by Pearson et al. (2006). The curated data set included 301 records (*LC* = 62, *LD* = 189, *LN* = 50), which represents registered GPS-locations for each occurring specie, including latitude, longitude and elevation (Supplementary Information S1).

Climate, climatic variables and ecological niche models

Due to the large latitudinal span of the genus *Larrea*, environmental selective pressures should differentially impact on species inhabiting different portions of the climatic range, so in order to define the fundamental niche of the three *Larrea* species, we extracted 19 bioclimatic variables from WorldClim 2.0's Community Climate System Model Version 4.0 (CCSM4) for the present day (Hijmans et al. 2005). We used two Global Climate Model projections (GCMs), CCSM4 (cc) and MIROCESM (mr). Models for LGM (~ 21 000 years BP; 2.5 arcmin), Mid Holocene (~ 6000 years BP; 2.5 arcmin), years 2050 and 2070 (2.5 arcmin) climatic scenarios, also available in the WorldClim website (IPCC 2013, Fick and Hijmans 2017; http://www.worldclim.org). We defined a background area (M zone) using Qgis v. 3.14.0.Pi (2019), covering the entire range and potential areas of colonization. The study area (Fig. 1) (calibration area or M zone) was defined following Oyarzabal et al. (2018) including phytogeographic regions of Monte, Espinal, Prepuna, Puna, Chaqueña, Altoandina (until 44°S), and the ecotone Monte-Patagonian steppe. Calibration area extends from 71.04999° to 60.85000° West longitude, and from 21.77500° to 44.19166 South latitude, with a spatial resolution of 1 Km, covering 1,213,389.168 km^2. Then, we performed suitability models using MaxEnt v3.4.0 (Phillips et al. 2017). To estimate bioclimatic variable's relevance in each model, we run a jackknife procedure. We cross validate each model with 10 replicates, 500 iterations, 10 percentile training presence, and regularization multiplier of 1. Once we obtained each species' general model in MaxEnt, we applied dimension-reduction techniques to minimize strong covariance among environmental variables and to avoid over fitted models that reduce accuracy (Synes and Bsborne 2011; Boria et al. 2014). We performed Pearson's correlations among 15 bioclimatic variables (BIO8, 9, 18 and 19 were excluded as they are considered mathematically artificial (Booth 2022). We then eliminated highly correlated variables using the function *cor* in the package stats in Rv3.5, with a threshold of $r \leq 0.70$. For each species, we tested several models and sets of variables considering (1) statistical significance, (2) predictive power, and (3) model complexity. We used jackknifing procedures in MaxEnt and bioclimatic variables correlation matrixes to build alternative models for each species selecting different sets of variables that contributed the most to each model. Then, we applied model calibration, which is a Bayesian procedure that finds the combination of parameters that best represents the phenomenon of interest fitting with the data. For each species, we compared alternative models using KuENM R-script (Cobos et al. 2019), that automates important calibration and evaluation steps in ENMs. Each comparison included different sets of variables, multipliers (0.1 to 1, with 0.1 steps,

and 1 to 5, with 1 steps) and features (lineal, quadratic, product, and their combinations). For each species, we tested all possible models until obtaining a statistically significant simplified ecological niche model (S3ENM) (Supplementary Information S1 for detailed models). Using a random 50 percent of data for bootstrapping for partial ROC calculation, 500 iterations, with a tolerance of < 5% omission rate and AICc (Akaike correction for small number of samples), kuenm_mod function creates and executes a batch file for generating MaxEnt models using parameters previously selected with the kuenm_ceval function. kuenm_ceval evaluates candidate models in terms of statistical significance (partial ROC, Peterson et al., 2008), prediction ability (omission rates), and model complexity (AICc). After evaluation, this function selects the best models based on user-defined criteria.

Then, we projected these models into past and future scenarios using (kuenm_mod), with clampling extrapolation (CE), free extrapolation (FE) and without extrapolation (NE). Ten Bootstrap replicas, and output cloglog, into the transference area (G). For 4 scenarios in the past: Last Glacial Maximum and Mid Holocene considering two Global Climate Models (GCMs): CCSM4 (cc) and MIROCESM (mr). And 8 future scenarios: years 2050 and 2070 considering GCM cc and mr for two Representative Concentration Pathways (RCP) 4.5 and 8.5. With a spatial resolution of 1 km^2 (30”), except for Last Glacial Maximum which is approximately 4,5 km^2 (2.5’) in native resolution and was resampled to 1 km^2. To measure uncertainty when projecting, we run MOP analysis using (kuenm_mmop). We tested all projected scenarios with clampling extrapolation (EC), with 10% sampling in the calibration area, and compute each: 500 pixels per nucleus. We also used the kuenm_mopagree function to evaluate the agreement among GCMs (without implying a different configuration). And the kuenm_projchanges function to analyze projections changes. We analyzed all scenarios with EC extrapolation using the statistical output raster from the function kuenm_modstats (median and range). Continuous and binary maps of changes in suitability for all projected models were obtained using the smallest suitability value from the species presence points as the threshold value, and we report average results of models for GCMs cc and mr. Then we vectorized binary maps in QGIS (Zurich, 3.18) to calculate percentage of suitability changes along periods, as (suitability of the period X - suitability in the present) *100/ suitability in the present. We also summarized key climatic variables in environmental suitability models for the three studied *Larrea* species combined and used Kruskal-Wallis one-way ANOVA on ranks to show how these climatic variables changed through scenarios: Annual mean temperature (BIO1), Min Temperature of Coldest Month (BIO6), Mean Temperature of Warmest Quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Annual Precipitation (BIO12), Precipitation Seasonality (BIO15), and Precipitation of Wettest Quarter (BIO16).

Niche overlap

We estimated present niche overlap, to test shared environmental constrains between pairs of species. For each pairwise comparison we run the function nicheOverlap in the package Dismo using R v3.5, including each particular set of bioclimatic variables selected in the reduced models, and both species occurrences were pooled and randomly split into two datasets, maintaining the number of occurrences as

in the original dataset. Then niche overlap similarity statistics Schoener's D and 'I' were calculated, which show values that range from 0 (no overlap) to 1 (complete overlap) (Schoener 1968).

Results

Competing suitability models of three *Larrea* species from the Monte Desert included different sets of bioclimatic variables (Supplementary information S2. Table 1), three of which were shared by the three species, and seem to regulate these species' environmental sustainability: BIO6 = Min Temperature of Coldest Month, BIO11 = Mean Temperature of Coldest Quarter, and BIO12 = Annual Precipitation. Additionally, a fourth variable was unique to each species' suitability model: BIO16 = Precipitation of Wettest Quarterfor *L. cuneifolia*; BIO10 = Mean Temperature of Warmest Quarter for *L. divaricata*, and BIO15 = Precipitation Seasonality (Coefficient of Variation) for *L. nitida*.

Table 1
Pairwise present niche overlap estimated with the package Dismo: function nicheOverlap, which estimates niche overlap from predictions of species distributions with 'I' (above diagonal) and 'D' (below diagonal) similarity statistics. *LC*: *Larrea cuneifolia*, *LD*: *Larrea divaricata*, *LN*; *Larrea nitida*

	LC	***LD***	***LN***
LC	-	0.989	0.906
LD	0.895	-	0.901
LN	0.699	0.671	-

Present models

We deployed models for the present (1975–2016) and after applying reduction model techniques (Supplementary information S2, Table 1); for *L. cuneifolia* the best model selected among 784 candidate ones included BIO6 and BIO16; 2 as regularization multiplier, and quadratic-product feature classes (Fig. 2a); for *L. divaricata* the model included BIO4, BIO6 and BIO12; 0.1 regularization multiplier, and quadratic feature classes selected among 392 candidate models and the first in a list of 11 best models (Fig. 2b); for *L. nitida* the model included BIO1, BIO12, and BIO15; 0.4 as regularization multiplier, and lineal-quadratic-product feature classes which was selected among 588 candidate models and the first in a list of 14 best models (Fig. 2c).

Considering all species' records together along the Monte Desert, habitat suitability is characterized by low Annual Mean Temperature (BIO1 = 14.78 ºC), low Temperature Seasonality (BIO4 = 537.74 (SD*100), low winter temperature by the Min. Temperature of Coldest Month (BIO6 = -0.34 ºC), low Annual

Precipitation (BIO12 = 301 mm), low Precipitation Seasonality (BIO15 (CV) = 56.93, and low Precipitation of the Wettest Quarter (BIO16 = 135.28 mm) (Supplementary information S1 and S3).

Current suitability for *L. cuneifolia* was best described by Min Temperature of Coldest Month ($BIO6_{Mean}$ = -0.09, ranging from − 5.7 to 4.9 ºC) and Precipitation of Wettest Quarter ($BIO16_{Mean}$ = 128.27, ranging from 42 to 280 mm). Current suitability for *L. divaricata* was best defined by Temperature Seasonality (SD*100) ($BIO4_{Mean}$ =536.52, ranging from 332.95 to 676.26, Min. Temperature of the Coldest Month $BIO6_{Mean}$ = 0.13, ranging from − 6 to 6.4 ºC, and Annual Precipitation ($BIO12_{Mean}$ = 323.52 ranging from 93 to 772 mm), the latest of which represented the highest values among the three species. Current suitability for *L. nitida* was described by Annual Mean Temperature ($BIO1_{Mean}$ = 11.93, ranging from 2.24 to 17.85 ºC), Annual Precipitation ($BIO12_{Mean}$ = 255, ranging from 94 to 638 mm), and Precipitation Seasonality (CV) $BIO15_{Mean}$ =39.37, ranging from 16.24 to 122.59, representing the lowest values among the studied species (See current and projected Bioclimatic variables, along with more detailed summary statistics in Supplementary information S1 and S3). Pairwise niche overlap, showed high 'I' and 'D' similarity statistics in the present for all species (67–89%), which attained the highest values (0.989 and 0.895, respectively) between *L. cuneifolia* and *L. divaricata* (Table 1).

Past models

Considering the three species together, past scenarios showed that during LGM, Annual Mean Temperature and Minimum Temperature of Coldest Month were lower than in current climatic models ($BIO1_{LGM}$ = 11.14 ºC; $BIO1_{Current}$ = 14.78 ºC; and $BIO6_{LGM}$ = -3.09; $BIO6_{Current}$ = -0.34 ºC, respectively). *L. cuneifolia* suitability for LGM was reduced compared with present suitability (Fig. 2a, LGM), probably due to extremely low winter temperature and precipitation (BIO6 = -2.58 ºC, and BIO16 = 98 mm, respectively). For *L. divaricata* models showed as much loss as gain in suitability (Fig. 2b, LGM), despite the low winter temperature and precipitation (BIO6 = -2.47 ºC, and BIO12 = 290.86 mm, respectively). Conversely, *L. nitida* increased habitat suitability (Fig. 2c, LGM), as climate for the LGM showed the lowest annual temperature for the trio (BIO1 = 8.32 ºC), and precipitation was lower than in the present (BIO12 = 228.73 mm), with reduced seasonality (CV = 38.56) (Supplementary information S1 and S3).

By Mid Holocene modeled mean annual temperature increased to 13.81 ºC, and temperature and precipitation seasonality increased (BIO4 (SD*100) LGM = 520.61 and Mid Holocene = 503.69; and BIO15 (CV) LGM = 57.36 and Mid Holocene = 53.36) along with a reduction in Precipitation of Wettest Quarter (BIO16 LGM = 126.24 and Mid Holocene = 109.66 mm) (Supplementary information S1 and S3). The three studied species reached maximum suitability in models for the Mid Holocene (Fig. 2a, 2b, and 2c, Mid Holocene). These maximum suitabilities matched the driest modeled climate (Annual Precipitation BIO12 = 253.64 mm), with the lowest winter precipitation for *L. cuneifolia* (BIO16 = 98), the lowest Temperature Seasonality for *L. divaricata* (BIO4 (SD*100) = 504.86), and the lowest Precipitation Seasonality for *L. nitida* (BIO15 (CV) = 37.53) (Supplementary information S1 and S3).

Future models

Projected scenarios for the future indicated increased Annual Mean Temperature (BIO1 = 17.32 ºC), and Min. Temperature of Coldest Month (BIO6 = 2.44 ºC) by 2070, along with decreasing Temperature Seasonality (SD*100) (BIO4 = 537.93). Although not as much as for Mid Holocene, Annual Precipitation is projected to decrease by 2070 (BIO12 = 276.12mm), with Precipitation Seasonality (BIO15 (CV) = 59.36), and Precipitation of the Wettest Quarter (BIO16 = 129.64 mm). *L. cuneifolia* and *L. divaricata* would remain stable by 2050. However, *L. cuneifolia* would gain suitability by 2070 if Min. Temperature of Coldest Month would reach its maximum value (BIO6 = 2.68 ºC), and Precipitation of Wettest Quarter would decrease (BIO16 = 117.89 mm). Conversely, *L. divaricata* and *L. nitida* would loss suitability by 2070, *LD* probably due to maximum values for the species in Temperature Seasonality (BIO4 = 537.88 SD*100), and Min. Temperature of Coldest Month (BIO6 = 2.79 ºC), and *LN* probably associated to projected maximum values of Annual Mean Temperature (BIO1 = 14.48 ºC), and the lowest Annual Precipitation (BIO12 = 220.68 mm) for the species (Supplementary S1 and S3).

Projected suitability area changes

When we compared present and projected past and future scenarios, *L. cuneifolia* showed 44% of suitability area loss for the LGM, 61% of area gains for Mid Holocene, and relatively as much area gains as losses for 2050 and 2070, resulting in a comparatively small percentage of suitability area net gain in the future (Table 2a, Fig. 3, also see binary and continuous projected changes maps in Supplementary information 2. Figure 2a and b, and suitability area loss and gain values in Supplementary information 2 Table 3a). Meanwhile, for *L. divaricata*, we observed relatively as much area gains as losses for LGM, resulting in a comparatively small percentage of suitability area loss (6%), high suitability gains for the Mid Holocene (48%), and area losses are projected for 2050 and 2070 (between 33% and 55%) (Table 2b, Fig. 3, also see binary and continuous projected changes maps in Supplementary information 2. Figure 2c and d, and suitability area loss and gain values in supplementary information 2 Table 3b). For *L. nitida*, suitability area comparisons yielded, high gains in the past (61% for LGM and 57% for Mid Holocene, respectively), and high suitability area losses for the future (between 50% and 56% depending on year and RCP) (Table 2c, Fig. 3, also see binary and continuous projected changes maps in Supplementary Information Fig. 2e, 2f, and suitability area loss and gain values in Supplementary information 2 Table 3c).

Table 2

Percentage of suitability area loss, stable, gain and net value, between present models and projected past and future scenarios for three *Larrea* species in Monte Desert. Percentages calculated from kuenm–projchanges's binary results, as (suitability of the period X - suitability in the present) *100/ suitability in the present.

Larrea cuneifolia	**Past**		**2050**		**2070**	
	LGM	**Mid Holocene**	**RCP 4.5**	**RCP 8.5**	**RCP 4.5**	**RCP 8.5**
Loss (%)	44.28	11.39	21.58	22.94	24.51	32.02
Stable (%)	34.48	27.64	42.32	37.80	35.93	28.51
Gain (%)	21.23	60.97	36.10	39.26	39.56	39.46
Net (%)	-23.05	49.58	14.51	16.32	15.05	7.44

Larrea divaricata	**Past**		**2050**		**2070**	
	LGM	**Mid Holocene**	**RCP 4.5**	**RCP 8.5**	**RCP 4.5**	**RCP 8.5**
Loss (%)	35.63	11.47	32.95	42.21	42.96	55.77
Stable (%)	34.66	40.36	41.62	32.60	32.07	19.52
Gain (%)	29.71	48.17	25.42	25.18	24.97	24.71
Net (%)	-5.92	36.69	-7.53	-17.03	-17.99	-31.07

Larrea nitida	Past		2050		2070	
	LGM	Mid Holocene	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Loss (%)	13.02	3.24	50.11	51.68	51.51	55.60
Stable (%)	25.83	39.80	40.19	39.13	38.71	32.81
Gain (%)	61.14	56.97	9.71	9.19	9.78	11.60
Net (%)	48.13	53.73	-40.40	-42.48	-41.73	-44.00

Discussion

We found that dominant shrubs of Monte Desert *L. cuneifolia* (*LC*), *L. divaricata* (*LD*), and *L. nitida* (*LN*) share a set of key driver climatic variables (winter temperatures and annual precipitation). Yet each of them is sensitive to species-specific climatic cues as further reductions in precipitation of the wettest quarter would affect *LC* habitat suitability, increasing temperature seasonality would affect *LD* suitability, and higher precipitation seasonality would impact *LN* suitability. Changes in such climatic envelope, i.e. precipitation, temperature and seasonality, define the vulnerability of a system to cope with the adverse effects of climate change (IPCC. PCC, 2019). Calling for species-specific conservation and restoration management decisions.

Past

Our deployed models for past scenarios suggested that Monte Desert´s LGM temperatures were lower than in current climatic models, and by Mid Holocene temperature increased along with less temperature and precipitation seasonality. Literature suggested that the temperate drylands of South America were much reduced in size during the cold and dry glacial periods (Labraga and Villalba 2009). However, our LGM models suggested that while *LC* reduced its suitability areas, *LD*, probably shifted its range, colonizing eastern areas, since suitability area gain was as much as its loss. Similarly, the columnar cactus *Echinopsis terscheckii*, shifted its range easterly under LGM climatic conditions in northern Argentina (Quipildor et al 2018). *LD* has the capacity to take over new areas, and did so in the past when colonized North American deserts (Lia et al. 2001, Vidal et al 2022). While, the more cold-tolerant *LN* increased habitat suitability during glacial periods, it decreased *in situ* suitability during milder periods. Such past regional range expansion coupled with the development of desert ecosystems during the last glacial age has been also shown for alpine plant species (Wang et al 2009; Jia et al 2011).

By Mid Holocene, our studied trio underwent suitability expansions, when the climate became dryer and warmer under all year-round homogeneous conditions, *LC* and *LD* would have reached maximum suitability. Towards the east, into the Dry Chaco, climate was unstable resulting in larger areas during the glacial periods than at present (Ab'Saber, 2000; Pennington et al., 2004; Speranza et al., 2007; Iriondo, 2010; Iriondo and Brunetto, 2016). As a result, *LC* and *LD*, along with other xerophytic vegetation of north-northwestern Argentina advanced northwards very deep into the interior basins of central South America (Ab'Saber, 2000). Expansion of woody elements including shrubs occurred as aridity increased since LGM in other cold deserts as in the Great Basin of North America (Nowak et al 2017).

Future

Climate change is forcing species across the world to either adapt to different environments *in situ* or shift their range to track moving climates. Two of our studied *Larrea* sps. are projected to face suitability loss in the future (*LD* and *LN*) and *LC* would have the opportunity to shift its range, as models predicted as much suitability loss as gain, with a small net gain (Table 2, Fig. 3). In accordance with most global models, future scenarios forecast temperature increases and precipitation decreases. Also, our models predict more variable and probably extreme climatic conditions throughout the year, changing water deficit and harshening water balance. Such signals of climate induced spatial displacement have been reported in the observed distribution of species across the globe (Parmesan and Yohe 2003, Lenoir et al. 2020). However, plants face a number of challenges to track rapid climate change, mainly due to limited seed set and viability or, particularly in arid lands where already some plant species´s shifts have been documented (Lenoir et al. 2008, Parmesan and Hanley 2015, Zu et al. 2021). So as climate changes, some plant distributions might shift as species expand in newly favorable areas and decline in increasingly hostile areas (Kelly and Goulden 2008). Our results suggested that temperature and precipitation seasonality would tend to homogenize in the future, leading to more constant conditions along the year. Such seasonal shifts might influence resource availability, consequently affecting species' niches (Dayton 2008). *LC* and *LD* individuals that had long persisted in seasonal environments, i.e. in northern Monte where rainfall occurs overwhelmingly in the summer, would be better suited to adapt to shifts in environmental conditions, and thus would be able to exploit a vacant niche in the south. Improving our understanding of how species' ranges will shift is critical to advice future conservation efforts and ecosystem management (Pecl et al. 2017). In arid systems, the majority of studies have focused on predicting the effects of climate change on native species of the Northern Hemisphere rather than the impacts of climate or landscape change on South American ones.

Drylands exemplify evolutionary challenges that changing climate can deepen to organisms and ecosystems. Here we contribute to the acknowledgment of Global south drylands, as highly degraded and little studied ecosystems, estimating the suitability of the habitat of their endemic species to support the development of conservation and management plans for sustainability.

Area changes

Predicting species' range shifts under future climate is a central goal of conservation ecology. Studying multiple species' current ranges can help identify whether community responses to climate change exhibit directionality, and whether responses are uniform across a suite of species. Moreover, given the forecasted climatic change, it is useful to compare the legacy of the Last Glacial Maximum (LGM), the Mid Holocene and the current distributions of species to assess their ability to cope with the projections of climate change (Sheller and Leon 2016) in 2050 and 2070. We hereby have complemented a former phylogenetic approach that compared the same thrree *Larrea* sister taxa (Lia et al 2001) that can grow in sympatry and/or parapatry with distinct climate niches. So, which climatic variables regulate species' environmental sustainability for our species trio that dominate the largest desert in Southern South America? When compared past and present scenarios, our results suggest that probably decreasing minimum temperature of the coldest month (BIO6), would have been responsible for *LC´*s higher suitability area losses for the LGM, and projected suitability gain for 2050, as harsher (below 0) winter temperatures might induce physiological damage (Hatfield and Prueger 2015). Higher suitability area gains during Mid Holocene might had been due to lower than present temperature and precipitation seasonality (i.e tendence to homogeneous climate across the year), both also might be responsible for the relatively stable suitability areas for 2050, and suitability area gains for 2070. Meanwhile, comparing present and projected scenarios for *LD*, as much suitability losses as gains observed for LGM, suggests range shift, probably attributable to lower than current annual mean temperature, minimum temperature of coldest month and annual precipitation. Conversely, suitability gains were observed for the Mid Holocene compared with the present, when temperature and precipitation seasonality were lower, pointing that climatic stability would had been responsible for such suitability area changes. Forecasted increases in the future of annual mean temperature and minimum temperature of coldest month (i.e. higher temperatures) would probably explain suitability area losses for 2050 and 2070. For *LN*, suitability area comparisons yielded, gains in the past, attributable to lower annual mean temperature, temperature seasonality, minimum temperature of coldest month, precipitation seasonality, and precipitation of the wettest quarter, which also seem to be responsible for suitability gains along LGM and Mid Holocene. Projected suitability losses for 2050 and 2070 might be attributable to higher annual mean temperature, temperature seasonality, min temperature of the coldest month, precipitation seasonality, and precipitation of the wettest quarter, than current climatic variables. Suggesting that this species would struggle to cope with changing water deficit. Species-specific climatic niches as well as future range reductions were measured in *Juniperus phoenicea* complex inhabiting Mediterranean and Macaronesian regions which have been impacted by human activity and thus are considered vulnerable to current and future climate change (Salvà-Catarineu et al. 2021). Thus, closely related taxa that may nowadays coexist in sympatry and/or parapatry at some locations which in turn have differentially respond to past climates could be similarly affected by forecasted climates. On the other hand, phylogenetically independent plant species that dominate drylands of the Junggar Basin in northwestern China differed in terms of the climatic variables that best explain their distribution ranges and thus potential responses to climate change (Xiao et al.2019). Present ranges of individual species as well as of species' assemblages under current climates may vary in the future which need to be considered by policymakers when designing sustainable management and conservation actions of drylands.

Sustainability recommendations

Developing evidence-based management strategies that support the adaptive capacity of species is crucial under predicted climate change, which is leading to increased warming and summer droughts. We urgently need to predict species responses to climate change to minimize future biodiversity loss and ensure we do not waste limited resources on ineffective conservation strategies (Nadeau and Urban 2019). Here we focus on improve the understanding of how dryland species might have responded to past and projected future climatic conditions to have a hint of under what climatic conditions such ecosystems' productivity might be sustainable. We found species-specific responses even among species with current overlapping niches such as *LC* and *LD*. Our results highlight the need to develop mitigation measures particularly for *LD* and *LN* whose ranges will most probably decrease in the face of future climates and increase land use pressures. Suggesting that restoration actions and restrictions on livestock practices would be recommendable preventing tools to reach carbon neutrality objectives and hack climate change. Our results suggest that acknowledging drivers of biodiversity degradation and loss, and climate change deceleration politics might halt and reverse some future projected losses observed trends. These measures might include designing sustainable agricultural practices as well as to increase public awareness on the value of drylands, and the creation of protected areas in such systems. Also, we suggest to reduce livestock ranching to the minimum, and advise landowners to protect large shrubs within their rangelands, which would act as nurse plants to facilitate natural revegetation (Pelliza et al. 2022). The literature calls for urgent adaptation and mitigation measures to slow down the on-going erosion of biodiversity, and species' range shifts induced by climate and land use change, that have already triggered changes in phenology and species' extinctions (Thuiller et al. 2008). Our study deployed accurate projections of species' responses to future environmental changes in an understudied region of the Global south, to aid the growing awareness of adopting scientifically supported proactive conservation planning measures using forecasted species' responses to future environmental changes. This study also enables developing reliable adaptation and mitigation strategies to halt biodiversity loss considering shifts in specie's suitability range calling for alternative conservation strategies in a changing world.

Declarations

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Conflicts of interest

Authors declare no conflicts of interest

Contributions

CPS and MT: field work, CPS and LPZ: developed the analyses performed, LPZ: Figures 1 and 2, CPS, MT and ACP: write the manuscript. All authors review the final version of the manuscript.

Supplementary material 1. Bioclimatic variables for current models and Scenarios, where: lgm = Last Glacial Maximum; mid = Mid Holocene; cc= Global Climate Model CCSM4;mr = Global Climate Model MIROC-ESM. Model projections to the past (lgm_cc; lgm_mr; mid_cc; mid_mr. Model projections to the future: rcp45_2050_cc; rcp45_2050_mr; rcp45_2070_cc; rcp45_2070_mr; rcp85_2050_cc; rcp85_2050_mr; rcp85_2070_cc; rcp85_2070_mr

Supplementary material 2. Table 1. Detailed parameterization of ecological niche models used to study environmental suitability for three members of the Zygophyllaceae family: *Larrea cuneifolia*, *Larrea divaricata* and *Larrea nitida*. Table 2. MaxEnt model and summary of KuENM simplified models for each species. Figure 1. To measure uncertainty when projecting we run MOP analysis using (kuenm_mmop). Fig. 1a. MOP *Larrea cuneifolia*; Fig. 1b. MOP *Larrea divaricata*; Fig. 1c. MOP *Larrea nítida.* Figure 2. Maps for projected changes continuous and binary for *Larrea cuneifolia* (Fig. 2a and 2b); for *Larrea divaricata* (Fig. 2c and 2d); and for *Larrea nítida* (Fig. 2e and 2f).

Appendix S3. Summary of climatic variables used to develop environmental suitability models for three members of the Zygophyllaceae family: *Larrea cuneifolia*, *Larrea divaricata* and *Larrea nitida*. **Box and whisker plot and Kruskal-Wallis One Way Analysis of Variance on Ranks for:** Annual mean temperature (BIO1), Temperature seasonality (BIO4), Minimum Temperature of the Coldest Month (BIO6), Annual precipitation (BIO12), Precipitation seasonality (BIO15) and Precipitation of the wettest quarter of the year (BIO16)

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Figures

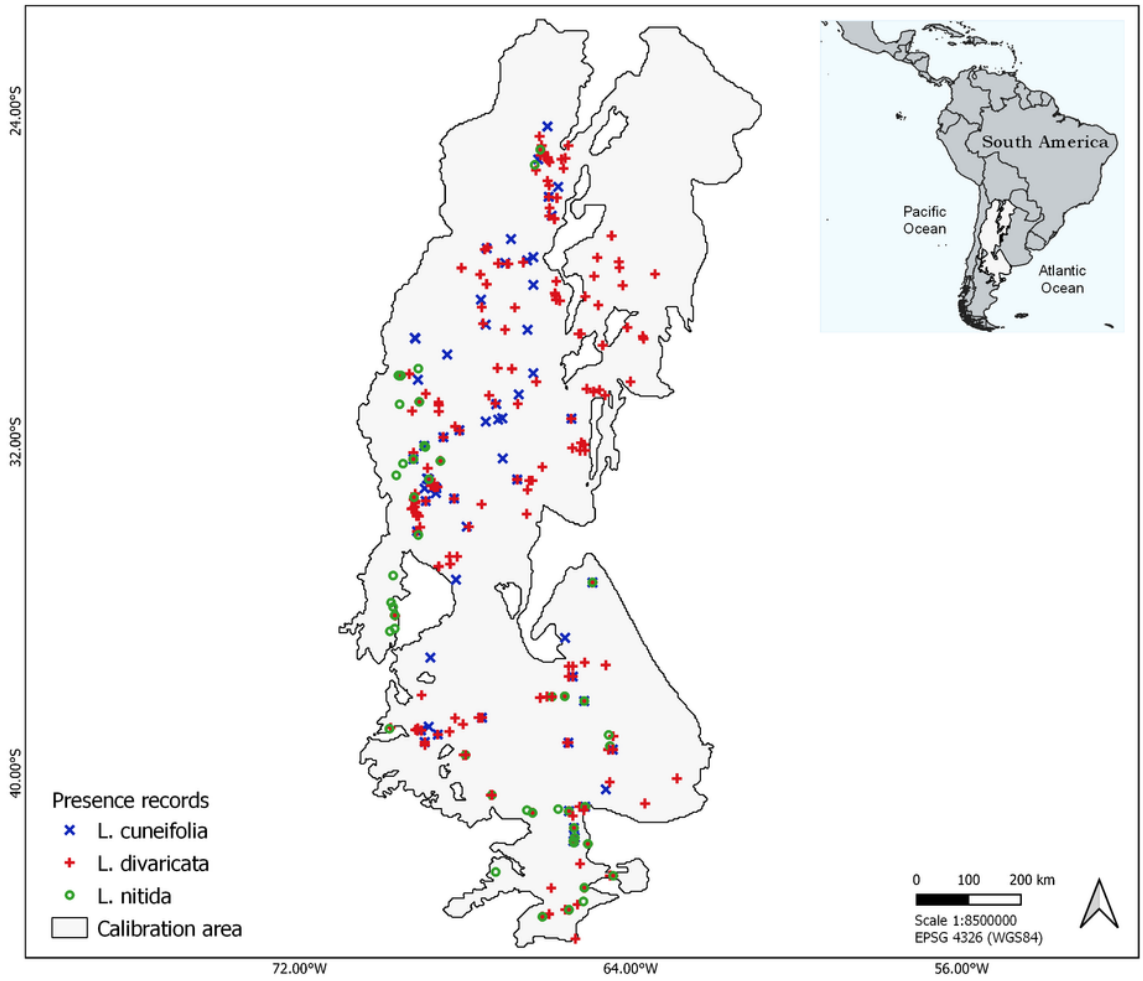
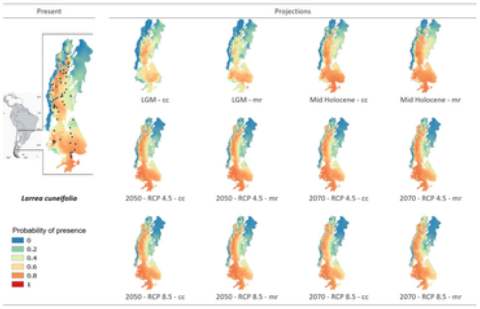


Figure 1

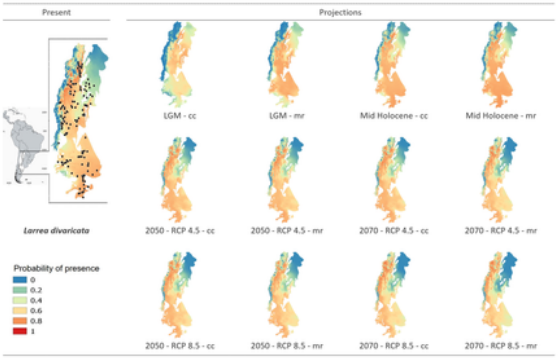
Presence records and calibration area for three *Larrea*species native of Monte Desert: *L. cuneifolia*, *L. divaricata* and *L. nitida*

Figure 2. Detailed model results for *Larrea* sp.: we test all possible models until obtaining a statistically significant simplified ecological niche model for the present (Present) and then projected alternative reduced models with KuENM to obtain combinations between climate during Last Glacial Maximum (LGM), Mid Holocene, 2050 and 2070 and two atmosphere-ocean general circulation models (GCM)cc and mr, considering RCP 4.5 and 8.5, for three members of the Zygophyllaceae family: *Larrea cuneifolia*, *Larrea divaricata* and *Larrea nitida*. Dots represent occurrence data.

a. For the present the model including BIO6 and 16; regularization multiplier = 2, and feature classes = quadratic-product was selected as the best model, among 784 candidate models for *Larrea cuneifolia*



b. For the present the model including BIO4, BIO6 and BIO12; regularization multiplier = 0.1 and feature classes = quadratic was selected among 392 candidate models, as the first in a list of 11 best models for *Larrea divaricata*



c. For the present the model including BIO1, BIO12 and BIO15; regularization multiplier = 0.4 and feature classes = lineal-quadratic-prodact, was selected among 588 candidate models, as the first in a list of 14 best models for *Larrea nitida*

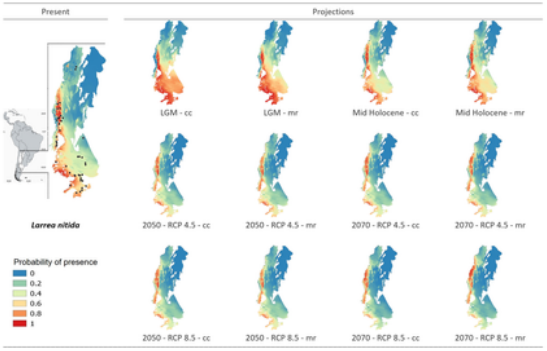


Figure 2

See image above for figure legend

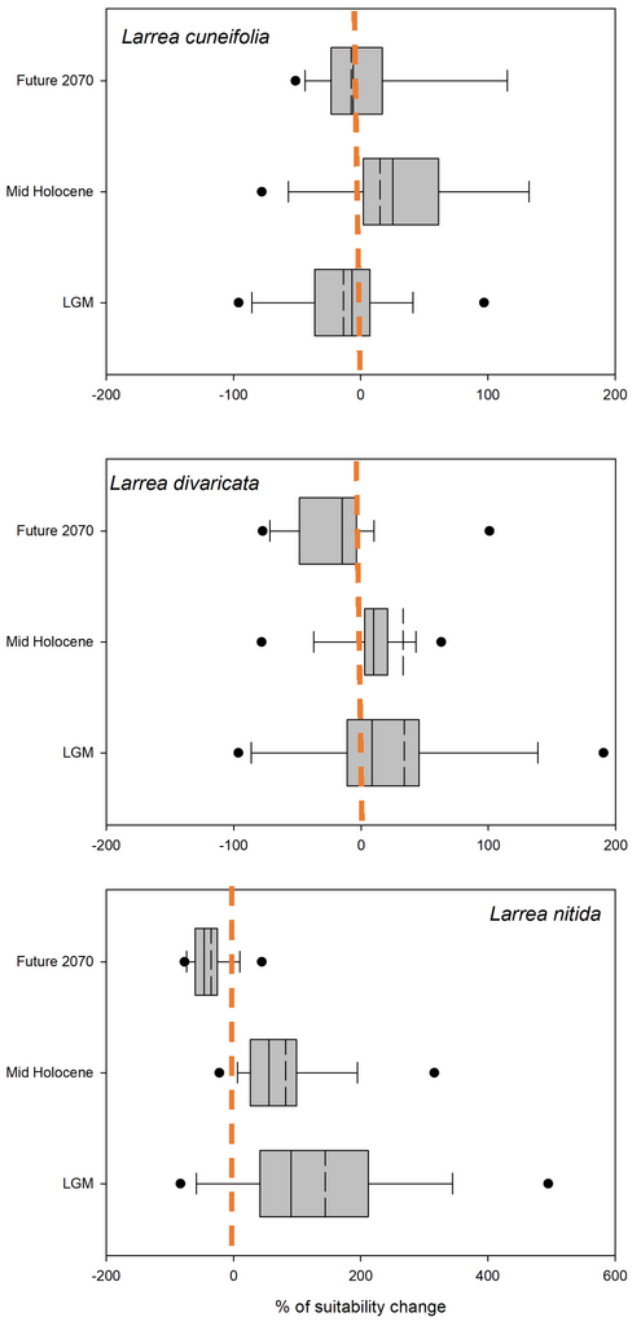


Figure 3

Box and whisker plots of percentage of suitability change based on (suitability of a period - current suitability) *100/ current suitability for LGM, Mid Holocene and year 2070, respectively in models for three members of the Zygophyllaceae family: *Larrea cuneifolia*, *Larrea divaricata* and *Larrea nitida*. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median values (long dot line represents mean values), and the boundary of the box farthest from zero indicates

the 75th percentile. Whiskers (error bars) above and below the box indicate the 95th and 5th percentiles. Dots indicate extreme outliers.

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