



Winners and losers in the predicted impact of climate change on cacti species in Baja California

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Abstract The Cactaceae is considered one of the most threatened taxa in the world. However, the extent to which climate change could compromise the conservation status of this group has rarely been investigated. The present study advances this issue under three specific aims: (1) to assess the impact of climate change on the distribution of endemic cacti species in the Baja California Peninsula ($n = 40$), (2) to study how the impact of climate change is distributed in this group according to the species' conservation status, and (3) to analyze how these impacts are organized from a biogeographical and functional perspective. We addressed these objectives under three socioeconomic emission pathways (RCP 2.6, 4.5, and 8.5), and using two extreme migration

scenarios: full climate change tracking and no migration. Altogether, all socioeconomic emission pathways under the two extreme migration scenarios show consistency regarding the identity of the species most vulnerable to climate change, and depict a discrepant future scenario that has, on one hand, species with large potential habitat gains/stability (winners); and on the other, species with large habitat reductions (losers). Our work indicates that winner species have a tropical affinity, globose growth, and includes most of the currently threatened species, whereas loser ones are in arid and Mediterranean systems and are mostly non-threatened. Thus, current and future threat factors do not overlap in the biogeographic and taxonomic space. That reveals a worrisome horizon at supraspecific levels in the study area, since the total number of threatened species in the future might largely increase.

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Introduction

The Cactaceae family, probably the most representative group of plants of the arid and semiarid systems of the Americas, is the fifth most globally threatened taxon assessed to date (Santos-Díaz et al. 2010; Goettsch et al. 2015). Up to 31% of the 1478 evaluated species in this group are threatened, mostly due to land conversion to agriculture and aquaculture, collection as biological resources, and residential or commercial development (Goettsch et al. 2015). In addition, the future impacts of climate change on cacti species have begun to be explored in relatively recent terms; so far, the existing works in this regard have shown positive (Dávila et al. 2013, Carrillo-Angeles et al. 2016), negative (Téllez-Valdés and Vila-Aranda 2003; Butler et al. 2012), or mixed (Cortes et al. 2014) outcomes.

Given the threatened status of numerous species within this family, a relevant conservation issue is to what extent the impact of climate change (i.e. positive or negative in terms of range size) will be correlated with the conservation status of the species (e.g. threatened or non-threatened). It should be noted that current literature on this and other taxa indicates that analyzing the effects of climate change from a multi-species approach with a wide variety of ecological preferences may lead to a discordant scenario, with species showing large increases in their suitable climatic areas (i.e. winner species), whereas other species are expected to show significant reductions (i.e. loser species) in them (Araújo et al. 2011; Cortes et al. 2014). Accordingly, three outcomes are possible. Under the null hypothesis, the impact of climate change could be randomly distributed across threat status. The alternative hypothesis offers two opposite outcomes. In the first, climate change could reduce the climatically suitable area for threatened species significantly more than for the non-threatened; under this scenario, climate change could exacerbate current conservation threats at the species level. In the second, non-threatened species will be negatively impacted, showing a reduction in their suitable climatic conditions, whereas threatened species would maintain or even increase their suitable areas under climate change; this would indicate an enhanced vulnerability at the supraspecific level.

Predictions on changes in the extent of climatic suitable areas cannot be considered realistic unless refined dispersal or movement processes are included

into the models. Thus, it is crucial to address the ability of the target species to track changing conditions (Dawson et al. 2011; Corlett and Westcott 2013). However, the characterization of migration constraints needs to be based on species-specific data, which require a large amount of knowledge and data to be calibrated, usually not available when analyzing large sets of species (Morin and Thuiller 2009). In order to overcome this issue, in the present work, we model the impact of climate change on the distribution of cacti species under two migration scenarios: one assuming no dispersal constraints (i.e. full climate tracking) and other considering no migration (e.g. Thuiller et al. 2005, 2006). From a broader perspective, our interest is to avoid over or underestimations of the species' movements, which could lead to suboptimal information for the conservation of this highly vulnerable family. Hence, we aim to analyze to what extent the predictions of both extremes of the migration spectrum coincide, and based on these results, identify the limitations of the method and its applications to develop conservation measures for the target taxa. Matching patterns between both migration scenarios indicate that conservation measures can be planned and developed even in the absence of fine migration data. On the contrary, mismatching patterns between migration scenarios indicate high uncertainty in the predictions, and therefore dispersal processes should be included to accurately evaluate species vulnerability (Morin and Thuiller 2009; Franklin 2010).

Finally, in order to deepen our ecological understanding of how the impacts of climate change are organized across different species of the Cactaceae, we analyzed how the predicted impacts of climate change on species' distribution are correlated with species' traits. Understanding the relationship between species traits and climate change effects is a highly active area of research in global change studies (e.g., Williams et al. 2008; Buckley and Kingsolver 2012; Estrada et al. 2015). Specifically, we selected five traits that have been described as correlated to differential sensitivity to climate change in other case studies (Table 1). Analyzing the results of these relationships are relevant, as this contributes to identifying climate-sensitive biogeographical and functional groups of species.

Under the general aim of assessing the future impact of climate change on the distribution of cacti species in Baja California, Mexico, our specific

Table 1 Traits related with species sensitivity to climate change

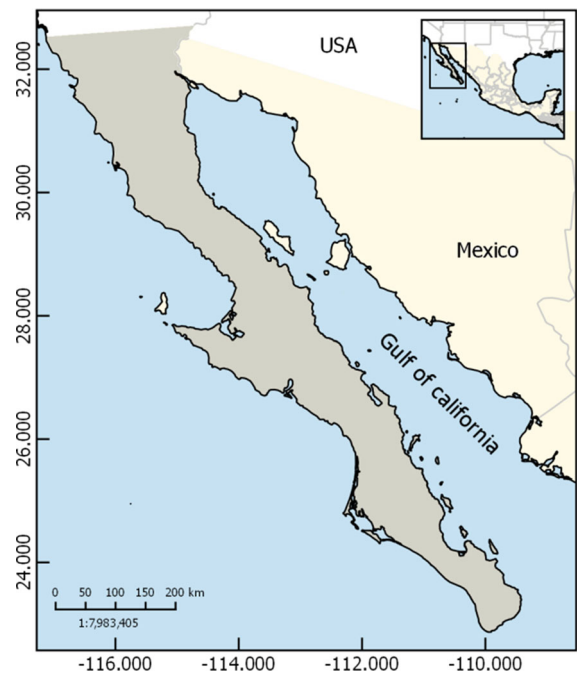
Trait	Pattern observed	Author
Range size	Species with more restricted ranges are more sensitive to climate change	Johnson (1998), Thuiller et al. (2005)
Niche breadth	Generalist species, which by definition can tolerate a broad range of conditions, can cope better with climate change than specialist ones	Brown (1995), Thuiller et al. (2005), Pöyry et al. (2009), Carrillo-Angeles et al. (2016) (for Cactaceae)
Growth form	The growth form of cacti species is related to differential habitat requirements. Globose cacti have shown higher habitat specificity, opuntoid cacti are a more cosmopolitan group, and columnar cacti appears to be limited by low temperatures	Mourelle and Ezcurra (1997)
Main climatic distribution driver (temperature vs precipitation)	Succulent plants display a clear relationship between their morphological traits and climatic conditions Due to the more idiosyncratic nature of changes in precipitation induced by climate change, it has been proposed that the impact of climate change on those species controlled mostly by precipitation are more variable and species-specific than those in species mostly controlled by temperature	Parra and Monahan (2008), Anadón et al. (2015)
Chorotype	Relating species chorotypes to their percentage of habitat range expansion or contraction, enables the identification of biogeographical patterns of species response to climate change, as well as future trends and directions of the ecosystem	Thuiller et al. (2005)

objectives are: (1) To assess how climate change will affect the distribution of the species by the year 2070 under two different migration scenarios, one considering no-migration and another considering full climate change tracking, (2) To test how these impacts differ between currently threatened and non-threatened species, and (3) To test how these impacts are correlated with species traits, including range size, chorotype, growth form, niche breadth, and main climatic distribution driver.

Methods

Study area

Our study area comprises the Baja California Peninsula (Mexico) with an area of 143,396 km² and an approx. length of 1250 km (Fig. 1). Three major ecoregions are recognized in the peninsula based on the attributes and organization of plant communities (Shreve and Wiggins 1964; Wiggins 1980; González-Abraham et al. 2010): (1) Temperate-Mediterranean in

**Fig. 1** Location of the study area

the northwest, with temperate and moderately wet winters alternating with dry and hot summers, (2) Tropical and subtropical conditions in the southern end, and (3) a central vast arid region with minimal precipitation and summer temperatures reaching up to 50 °C, distributed from the center of the peninsula with a transitional area between both ends. The Baja California Peninsula contains approximately 10% of cacti diversity in Mexico, of which about 76% are endemic (“Results” section). Overall, it is one of the most cacti species-rich regions of the Americas, although it is not considered one of the main diversification centers (Barthlott et al. 2015).

Occurrence data

We first compiled a list of endemic cacti species of Baja California Peninsula by means of a comprehensive literature review, and consultation of herbaria records worldwide, which were obtained through REMIB database (*Red Mundial de Información sobre Biodiversidad*, CONABIO 2015), regional herbaria (Online Resource 1, collections consulted), the Global Biodiversity Information Facility database (GBIF 2019), and from National Forest and Soils Inventory of Mexico 2009–2014 (CONAFOR 2014). In addition, these data were curated based on the observations of a Baja California Cactaceae specialist (J. Rebman), with extensive fieldwork experience in the study area. We excluded from the assessment strictly insular endemic species. Subsequently, presence-only data of the 42 endemic species identified were derived from the previously obtained herbaria records. Occurrence data were checked for errors. In particular, we checked that occurrence data were compatible with the known distribution range of the species as described by existing literature. In many instances, errors were due to taxonomic misidentification at the species level, since the occurrence matched up at genus level, but at specific level the known distribution range was located hundreds of kilometers away, and/or in different ecogeographic regions.

Distribution modeling

Species distribution models for each species were developed using MaxEnt v3.3.3 (Phillips et al. 2006), a modeling approach that performs well in a comparison of species distribution modeling methods (Elith

et al. 2011). Default Maxent settings regarding feature classes and regularization multipliers were used for all species. Since we consider only endemic species, our models capture the full realized niche of the species and thus minimize bias associated with incomplete realized niche sampling (Broennimann et al. 2006). To reduce the effects of data clustering and spatial sampling bias that can result in an over-representation of environmental conditions associated with regions of higher sampling; we removed clusters of localities using the R package ‘*spThin*’ (version 0.1.0; Aiello-Lammens et al. 2015). Since our species pool contains a wide variety of distribution range sizes, from species distributed in most of the study area to highly restricted micro endemism, instead of establishing a single separation distance filter between two record locations (Galante et al. 2018), we selected two different filtering approaches based on range size, as estimated by the minimum convex polygon (MCP) around all the occurrence points of each species. Thus, the two groups were differentiated as: (1) widely distributed endemics, whose MCP values were higher than 60 km², and to which a thinning distance of 5 km was applied; (2) micro endemic species, whose MCP values were lower than 60 km², and to whom a thinning distance of 1 km was applied. Ideally, all species should have a large number of occurrence data (e.g., > 30, Wisz et al. 2008), but in the case of micro endemics, the entire range was covered only by a few cells. Modeling the distribution of species with an extremely limited number of occurrence data is acceptable as long as the occurrence localities adequately cover the environmental conditions where the species is present (Pearson et al. 2007). Concurrently, in our study, micro endemics met that condition; as an additional precautionary measure only those species with > 10 georeferenced locations were considered for modeling, since Maxent still shows a good performance with this sample size (Wisz et al. 2008).

The extent of the modeling (training) area in species’ distribution models may have a large effect on model predictions (Anderson and Raza 2010; Barve et al. 2011). We selected training areas using a limited geographical extent approach; this method involves the selection of pseudo-absence points within a geographic area, whose delimitation is based on a buffer of fixed distance encompassing species’ presence points. The ideal buffer distance (radius) was chosen based on model performance; we tested

varying radii around known presence points, resulting in a 200 km radius (Barbet-Massin et al. 2012; Senay et al. 2013). This led to a better representation of the true range of environmental conditions that the species experiences (Barve et al. 2011).

Maxent models were trained in present conditions using the bioclimatic variables obtained from the dataset WorldClim (Hijmans et al. 2005) at a spatial resolution of 30 arc-seconds (~ 1 km). Variables with high multi-collinearity were removed until all remaining variables had a variance inflation factor (VIF) of < 5 (Abdelal et al. 2019) using the ‘*sdm*’ package in the R-environment. Remaining variables for model training include mean diurnal range (bio2), isothermality (bio3), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), precipitation of driest month (bio14), precipitation seasonality (bio15), and precipitation of coldest quarter (bio19). Models were obtained by an average of 50 repeated subsampled models in which the presence points were repeatedly split into two subsets: one for training (80%) and another for model validation (20%). Predicted distributions for the future were obtained by means of projecting the present models using the same predictor variables of the 14 Global Circulation Models (GCM) available for the study area (online resource 2), based on three Representative Concentration Pathways (RCP) 2.6, 4.5, and 8.5, as obtained from WorldClim (Hijmans et al. 2005). This represents a spectrum of climatic scenarios based on mitigation policies that include an “optimistic scenario” where anthropogenic emissions start declining by 2020 and reach zero by 2100 (RCP2.6), an “intermediate scenario” where anthropogenic emissions reach their peak by 2040 and thereafter start to decline (RCP 4.5), and a “business-as-usual” or “worst-case” scenario (RCP 8.5), which assumes increasing and continuous global anthropogenic emissions of greenhouse gases after the end of this century and does not include any specific climate mitigation target (Riahi et al. 2011; IPCC 2013). Year 2070 was the selected timespan to detect more substantial changes in species distributions for future depictions. Non-analog climate issues (i.e. the projection of the model in climatic conditions not included in the training area) were handled by means of the “clamping” feature in Maxent, which constraint the data by setting out-of-the range variables to the minimum or maximum trained value. We applied fading by clamping

(removal of suitability patches where clamping occurred).

For further analysis, Maxent continuous suitability maps were transformed into binary maps by means of a threshold suitability value. Here we selected maximum training sensitivity plus specificity area as the threshold since this approach has demonstrated high accuracy with presence-only data (Liu et al. 2013). An inspection of the resulting maps showed that binary maps consistently overrepresented the predicted distribution range for micro endemic species opposed to widely distributed endemic species (as defined above). To address this issue, suitable patches with no current occurrence data and without connectivity to other occupied suitable patches were not considered as part of the distributional range of micro endemic species (Anadón et al. 2015). Thus, we assume that although the climate of the patch might be suitable for the presence of the species, it is absent due to limited dispersal or other historical constraints.

Sensitivity to climate change and migration scenarios

To assess the impacts of climate change on each species, we made comparisons of its present distribution and the model ensemble of all GCMs available in the WorldClim database for the study area ($n = 14$) across the three selected RCPs. This consensus method produces solid predictions and reduces uncertainty (Marmion et al. 2009), as it gives the same weight to all available GCMs. In the comparison we quantified the range area that is lost, gained or that remain stable (i.e. suitable in the present and in the future; Online Resource 3) using the ‘*raster*’ package in the R-environment.

Based on the average values of suitable climatic area lost, gained or stable, we assessed the impacts of climate change for each species under two different migration scenarios. The first assumes unlimited migration (i.e., all the suitable areas in the future are considered part of its future distribution range). The impact under this full climate change tracking scenario was described by the net difference in area between the current and the future projected distributions (i.e., stable + gain-loss areas). The second scenario assumes no migration (i.e., only those cells that are occupied in the present can be occupied in the future). The impact under this scenario was described by the

area of current range that remains suitable under the projected climate change scenarios (i.e. stable areas). It should be noted that the unlimited migration scenario allows for both positive and negative responses (either increases or decreases of the distribution range), whereas the more conservative no-migration scenario only allows for negative responses to climate change (decreases in distributional range). A Kruskal–Wallis test was performed to evaluate differences in species responses to climate change across RCPs under the two migration scenarios.

Conservation status and role of species' traits

We studied the relationship between the amount of change in the species' range and species conservation status and five life traits: growth form, chorotype, niche breadth, present range size and main distribution driver (precipitation vs temperature) (Table 1). Conservation status was described as a binary variable with two levels: Threatened (including *Endangered* and *Vulnerable* status) and Non-threatened (*Least concern* status), following IUCN classification (IUCN 2019). Species currently classified as *Data deficient* or *Not Evaluated* were not included in this analysis.

Growth form characterization was based on the classification proposed by Mourelle and Ezcurra (1997) that recognizes three types: columnar/barrel, globose and opuntoid. Assignment of chorotypes was made following regionalization proposed by Shreve and Wiggins (1964), Wiggins (1980) and González-Abraham et al. (2010) that resulted in seven chorotypes: Central Desert, Magdalena, Mediterranean, Transition Mediterranean-central desert, Tropical, Tropical Transition, and Peninsular (Online Resource 4). This last type was assigned to those species that were present in five or more of the proposed regions (i.e., distributed along the entire peninsula). Niche breadth was defined as the area of minimum convex polygon of the occurrence points projected in a bi-dimensional environmental space of the study area, determined by the two first axes of a principal component analyses of the five bioclimatic variables used to calibrate the models. Main climatic distribution driver (variable Tem/Pre) was described by a continuous variable defined as the summed importance of precipitation variables (as opposed to temperature variables) as quantified by Maxent.

Relationship between species' range change due to climate change and IUCN conservation status and life traits was assessed by means of linear models. For species traits, in a first step we performed simple linear models to describe the relationship between the response variables (range change under full tracking and no migration scenarios, respectively) and each life trait. On a second step, for each response variable we built multiple regression models to assess to what extent the explanatory power of single life traits was due to correlation among explanatory variables, using AIC as variable selection criteria (Burnham and Anderson 1998).

It should be noted that because of the nature of our modeling approach our work does not address how life history traits determine differences in the impact of climate change on distributions (e.g. Angert et al. 2011; Auer and King 2014), but it tests how the magnitude of the impact of climate change on species' ranges, based on niche climatic projections, is distributed along different life history traits (e.g. Thuiller et al. 2005; Broennimann et al. 2006; García et al. 2014).

Results

Species distribution models

42 species were identified as endemic cacti in the Baja Peninsula (Table 2). Number of occurrence data per species ranged from 10 to 360 (mean = 57). Overall, Maxent models exhibited a good discrimination capacity. Average AUC values across all species was 0.86 (range = 0.75–0.98). Two species (*Cylindropuntia lindsayi* and *C. waltoniorum*) were removed from subsequent analysis due to low AUC value (0.6270 and 0.557, respectively) yielding a final subset of 40 species (Table 2). Predicted distribution area for the remaining species for the present time ranged from 1613 km² (*Echinocereus mombergerianus*) to 98,968 km² (*Pachycereus pringlei*).

Species sensitivity to climate change

A Kruskal–Wallis test showed that species sensitivity to climate change is not significantly different across RCP's, under both unlimited migration ($p = 0.45$) and the no migration scenarios ($p = 0.98$). Overall, the

Table 2 Species distribution models and sensitivity results for the endemic species of Cactaceae in the Baja California under RCP4.5

Species	N	AUC	Area (km ²)	Range change (%)		Chorotype	Growth	Status
				Unlimited migration	No migration			
<i>Cochemiea poselgeri</i>	84/51	0.8382	24,266	91.61	13.32	TROPTR	G	NONTHR
<i>Cochemiea setispina</i>	26/11	0.8635	19,619	– 64.82	66.18	CD	G	NONTHR
<i>Cylindropuntia alcahes</i>	149/ 112	0.749	83,781	21.00	18.22	PEN	O	NONTHR
<i>Cylindropuntia calmalliana</i>	20/13	0.8285	8837	144.75	1.59	DES	O	NONTHR
<i>Cylindropuntia cholla</i>	233/ 178	0.7894	62,478	28.10	12.67	PEN	O	NONTHR
<i>Cylindropuntia molesta</i>	57/39	0.8272	37,496	30.34	33.02	M/D	O	NONTHR
<i>Cylindropuntia sanfelipensis</i>	22/17	0.9271	7090	15.56	4.80	DES	O	NONTHR
<i>Cylindropuntia tesajo</i>	108/51	0.7762	43,605	– 11.43	31.05	M/D	O	NONTHR
<i>Echinocereus brandegeei</i>	98/60	0.8088	30,035	158.56	15.68	TROPTR	G	NONTHR
<i>Echinocereus ferreirianus</i>	30/11	0.7719	70,317	– 27.12	31.40	DES	G	NONTHR
<i>Echinocereus maritimus</i>	83/55	0.9075	26,496	15.42	25.52	M/D	G	THR
<i>Echinocereus mombergerianus</i>	10/10	0.9349	1613	– 20.56	25.13	MED	G	–
<i>Echinocereus pacificus</i>	10/9	0.8564	9344	– 45.11	54.56	MED	G	NONTHR
<i>Echinocereus pensilis</i>	13/11	0.8753	2311	– 65.34	71.07	TROP	G	NONTHR
<i>Echinocereus sciurus</i>	10/9	0.8011	3447	4.37	7.78	TROP	G	THR
<i>Ferocactus fordii</i>	29/23	0.9139	16,513	91.98	28.41	M/D	CB	THR
<i>Ferocactus gracilis</i>	56/38	0.8381	36,064	– 56.02	65.17	M/D	CB	NONTHR
<i>Ferocactus peninsulæ</i>	114/83	0.7447	32,878	– 1.86	40.34	TROPTR	CB	NONTHR
<i>Ferocactus rectispinus</i>	40/23	0.9031	20,011	– 36.10	50.57	PEN	CB	–
<i>Grusonia invicta</i>	32/22	0.8461	33,556	117.08	11.64	TROPTR	O	–
<i>Lophocereus gatesii</i>	11/10	0.8255	18,983	92.46	3.40	TROPTR	CB	THR
<i>Mammillaria albicans</i>	28/19	0.7889	9571	421.46	0.49	TROPTR	G	NONTHR
<i>Mammillaria armillata</i>	25/20	0.926	7321	353.21	1.23	TROPTR	G	THR
<i>Mammillaria brandegeei</i>	30/24	0.8349	28,643	67.69	17.66	MD	G	NONTHR
<i>Mammillaria capensis</i>	12/11	0.9399	8461	250.95	0.33	TROP	G	THR
<i>Mammillaria evermanniana</i>	15/12	0.8025	10,975	45.49	3.90	–	G	NONTHR
<i>Mammillaria fraileana</i>	10/9	0.961	6490	191.40	6.46	TROP	G	NONTHR
<i>Mammillaria hutchinsoniana</i>	31/25	0.8443	23,598	85.59	24.23	TROP	G	NONTHR
<i>Mammillaria peninsularis</i>	13/9	0.9646	1980	163.15	1.65	–	G	THR
<i>Mammillaria petrophila</i>	20/19	0.8908	7496	324.04	7.19	TROP	G	THR
<i>Mammillaria phitauiana</i>	10/9	0.9032	2481	200.30	13.47	TROP	G	NONTHR
<i>Mammillaria schumannii</i>	24/20	0.8779	5780	477.97	0.92	TROP	G	THR
<i>Myrtillocactus cochal</i>	81/46	0.9116	23,075	0.03	36.50	PEN	CB	NONTHR
<i>Opuntia bravoana</i>	11/10	0.8269	6237	162.92	11.84	–	O	NONTHR
<i>Opuntia pycnantha</i>	27/25	0.8269	1630	– 96.88	97.13	MAG	O	NONTHR
<i>Opuntia tapona</i>	82/47	0.9833	20,454	124.55	7.22	TROPTR	O	–
<i>Pachycereus pringlei</i>	360/ 229	0.8527	98,968	7.38	14.93	PEN	CB	NONTHR
<i>Peniocereus johnstonii</i>	22/15	0.8064	14,537	77.24	26.96	PEN	CB	NONTHR

Table 2 continued

Species	N	AUC	Area (km ²)	Range change (%)		Chorotype	Growth	Status
				Unlimited migration	No migration			
<i>Stenocereus eruca</i>	52/26	0.8255	8391	– 65.07	72.97	MAG	CB	NONTHR
<i>Stenocereus gummosus</i>	254/ 172	0.8813	70,371	42.31	3.83	PEN	CB	NONTHR

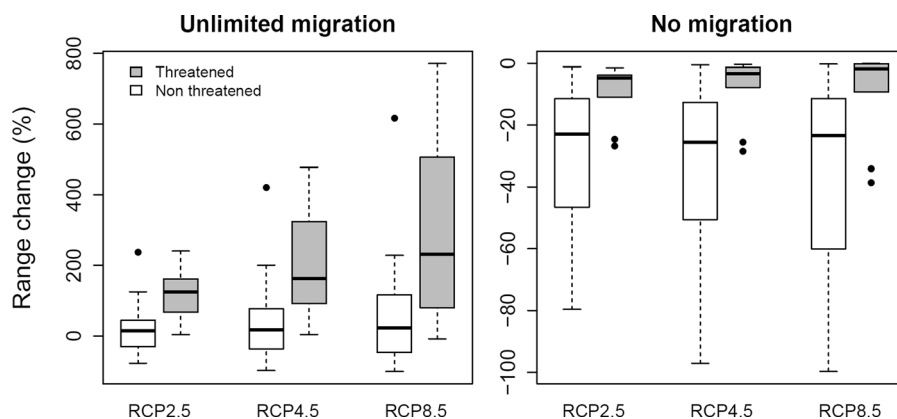
Predictions under all RCPs Online resource 5

N total number of occurrences and final number of occurrences used for modeling, Area predicted area, DES Central Desert, MAG Magdalena, MED Mediterranean, M/D transition Mediterranean-central desert, PEN Peninsula, TROPTR tropical transition, TROP tropical, C/B columnar/barrel, G globular, O opuntoid

Table 3 Predictions of range change in the endemic cacti species of the Baja California range according to the three alternative representative concentration pathways (RCP)

	RCP2.5	RCP4.5	RCP8.5
Mean range change			
Unlimited migration	46%	83%	123%
No migration	– 23%	– 24%	– 28%
More extreme scenario (# sp.)			
Unlimited migration	3	5	32
No migration	18	3	19
# species increasing/decreasing range			
Unlimited migration	30/10	29/11	28/12

three RCPs considered yielded the same patterns in terms of the objectives of the work; although, in absolute terms, changes in the predicted extent of the species increased with increasing radiative forcing values (i.e. largest under RCP8.5; Table 3; Fig. 2). This was particularly true for the unlimited migration scenario although differences for the no migration scenario were more limited, with 45% of the species showing maximum range reductions under the lowest radiative forcing value (RCP2.5) (Table 3; Fig. 2). Unless otherwise noted, results presented in this section refer to the intermediate RCP4.5. A detailed analysis of stable, lost and gained area for each species is shown in Online Resource 5.

**Fig. 2** Differences in rate of range change (%) between threatened and non-threatened endemic cacti species of the Baja California for the two considered migration scenarios (unlimited and no migration) and three representative concentration pathways (RCPs)

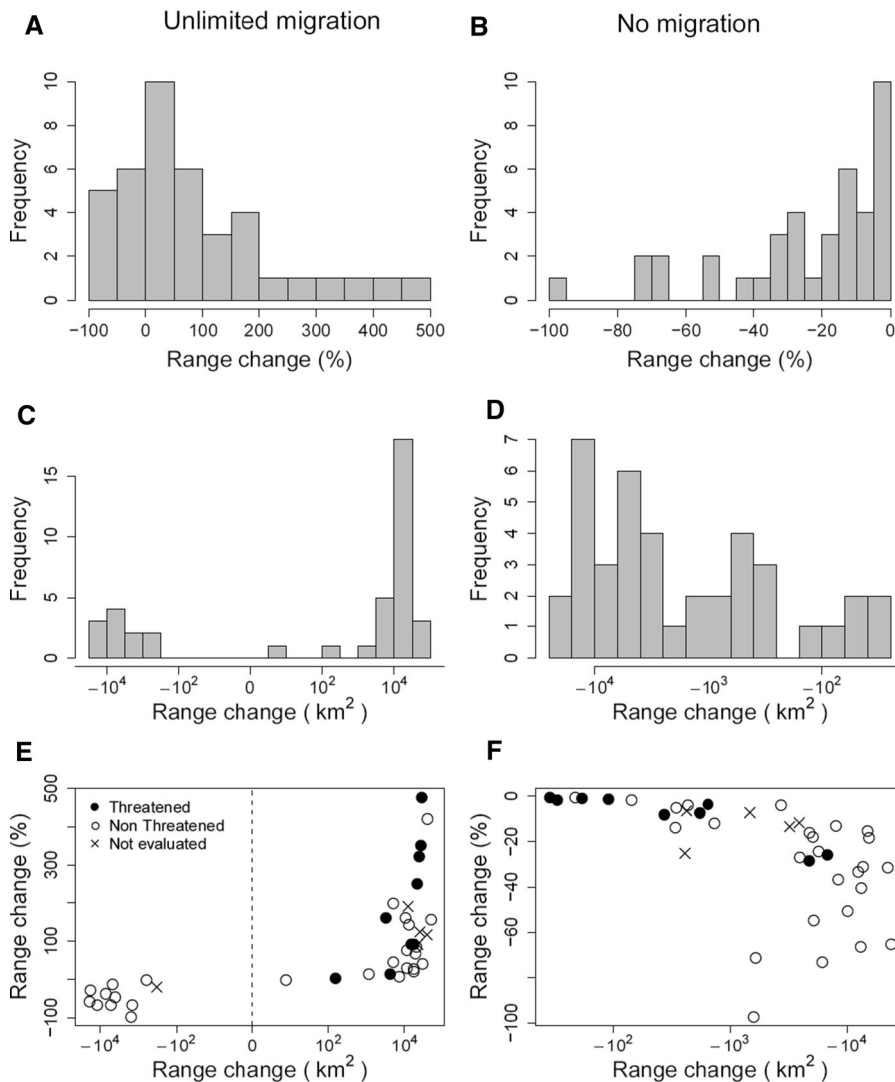


Fig. 3 a–d Frequency distribution of predicted range change in absolute and relative terms under unlimited and no migration and RCP4.5. e, f Relationship between the relative and absolute values of range change

Under the full climate change tracking scenario, predicted species’ range change by year 2070 varied between 478 and -97% (mean = 82.91% ; Table 3, Fig. 3a). In particular, 29 species (73%) were predicted to increase their range size, with a mean increase of 131%. Species that show habitat contraction (the remaining 27%) show an average reduction of its range of 45%. In absolute values, half of the range changes, both positive and negative, were between 10^4 and 10^5 km² (Fig. 3c).

Under the no migration scenario, predicted range change varied between -0.3 and -97.1% (mean = -24% ; Table 3, Fig. 3b). Out of the 40 species, 14

are predicted to lose $< 10\%$ of their current range. On the other extreme, our model predicts that 18% of all species ($n = 7$) lose half or more of their current range under future climate change scenarios. In absolute values, for half of the species (52%, $n = 21$) the predicted current range that will persist under future climate conditions is between 10^4 and 10^5 km². Resulting ranges under the no migration scenario was below 100 km² for one species (*Opuntia pycnantha*) and were below 2500 km² for five species (*Echinocereus pensilis*, *E. mombergeria*, *Mammillaria peninsularis*, *M. phitauiana* and *Stenocereus eruca*) (Fig. 3d–f).

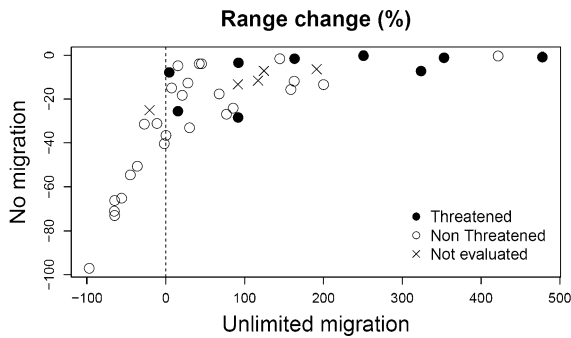


Fig. 4 Relationship between rate of range change (%) in the two considered scenarios (unlimited and no-migration) for the endemic cacti species of the Baja California under RCP4.5

Range change under unlimited and no migration scenarios showed a close asymptotic relationship (Fig. 4), with species predicted to increase their range under full climate tracking also predicted to have larger range change under a no-migration scenario. For species that were not predicted to increase in range, even under full climate change tracking, range change under no migration was predicted to be approx. an average of -30 to -40% . This value was consistent across RCPs. We found seven species particularly impacted by climate change, showing the highest values of range contraction on both migration scenarios. *Opuntia pycnantha* was the most affected species with 97% of range contraction under both the full migration and no migration scenarios, followed by *Stenocereus eruca* (65% and 73%), *Echinocereus pensilis* (65% and 71%), *Cochemeia setispina* (65% and 66%), *Ferocactus gracilis* (56% and 65%), *Echinocereus pacificus* (45% and 55%) and *Ferocactus rectispinus* (36% and 51%) (Table 2). The identification of these seven species as the most affected by climate change in their distribution was also consistent across RCPs (Online Resource 5).

Correlation with species' conservation status and traits

Out of the 40 endemic cacti species considered in our analyses, 9 were classified by IUCN as threatened, 26 as non-threatened, and 4 have not been assessed or were data deficient (Table 2). The proportion of evaluated threatened species in our case study (26%) is thus similar to that described globally for the family (31%; Goettsch et al. 2015). For the three RCP

considered, our models showed that threatened species exhibited larger increases in their distribution ranges than non-threatened species under the full climate change tracking ($p < 0.05$ and $R^2 = 22\%$ in the three cases), thus rejecting our null hypothesis (Fig. 2). In a similar vein, under the no-migration scenario, where positive responses to climate change are not possible, threatened species were significantly less affected by climate change than non-threatened species ($p < 0.05$, $R^2 = 12\text{--}14\%$) (Fig. 2). None of the seven species identified above as particularly impacted by climate change are currently considered threatened.

Regression models showed that chorotype was the main trait correlated with interspecific differences in sensitivity to climate change ($p < 0.05$, $R^2 = 40\%$ and 39% for unlimited and no migration scenarios, respectively). Both migration scenarios showed the same pattern: under the unlimited migration scenario, tropical and tropical transition species are expected to experience the largest increase in the climatic suitable area (190 and 156%, respectively), whereas under the no migration scenario these species are expected to experience the least contraction in their suitable area (-14 and -11%) (Fig. 5). Both scenarios also agreed that species from the Magdalena Plains chorotype were most negatively impacted by climate change with an average decrease in the range of species of 81% and 85% for the unlimited and no migration scenarios, respectively (Fig. 5). The spatial distribution of those species increasing and decreasing

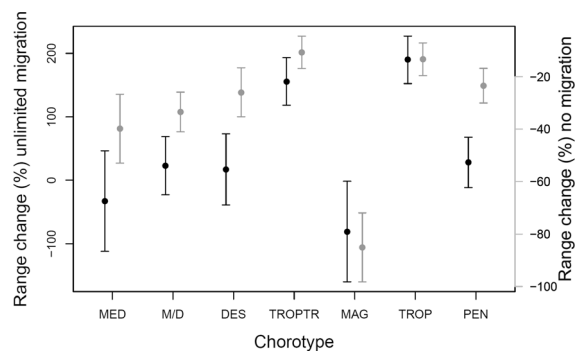


Fig. 5 Range change by chorotype for the endemic cacti species of the Baja California under two migration scenarios (unlimited and no migration) under RCP4.5 (*DES* Central Desert; *MAG* Magdalena; *MED* Mediterranean; *M/D* transition Mediterranean-central desert; *PEN* Peninsula; *TROPTR* tropical transition; *TROP* tropical)

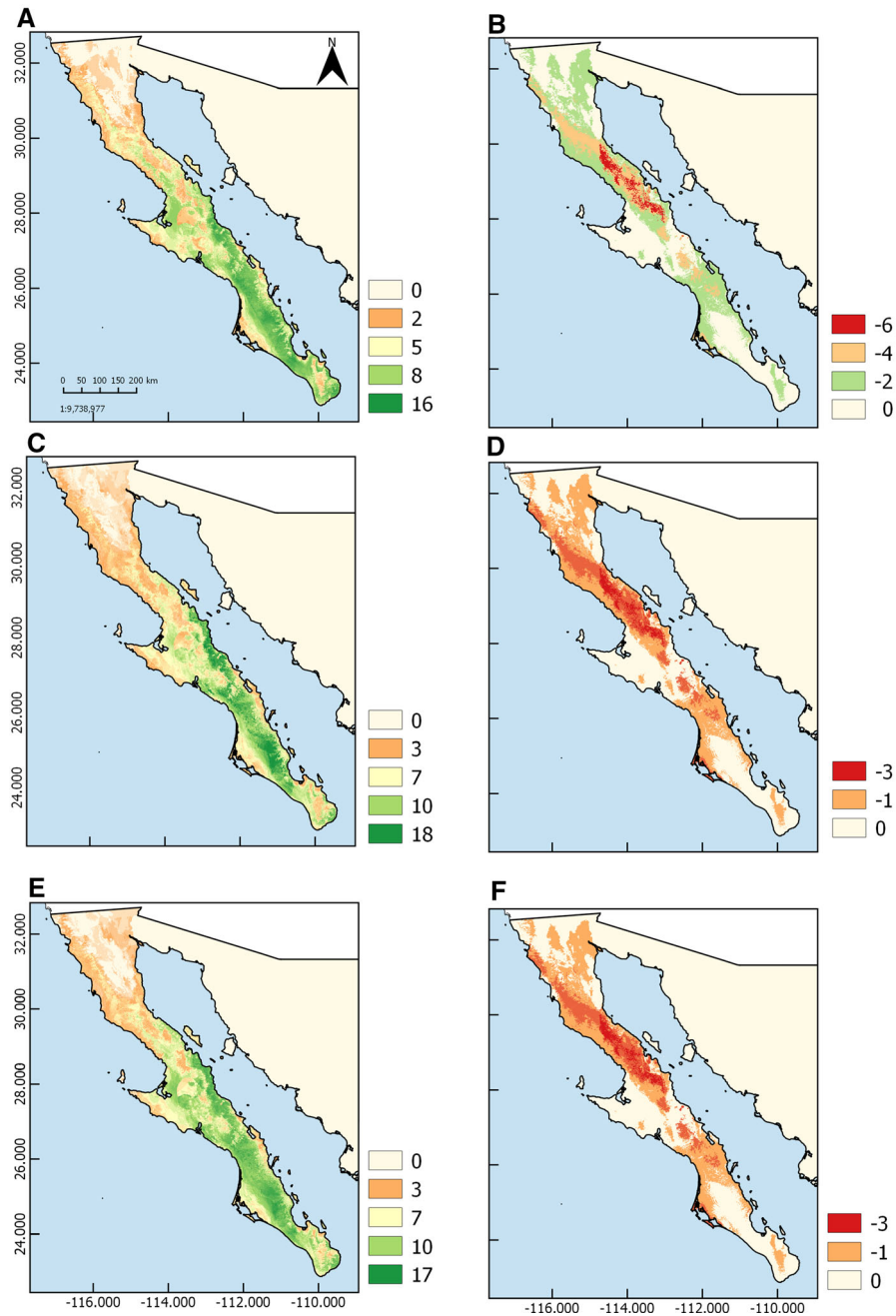


Fig. 6 Number of cacti species per pixel decreasing (right) or increasing (left) their range under the unlimited migration scenario and RCP8.5 (top), RCP4.5 (middle) and RCP2.5 (bottom)

their range under the unlimited migration scenarios is shown in Fig. 6.

Simple regression models showed that predicted range change under unlimited migration was also related to growth form ($p < 0.05$, $R^2 = 8\%$), as

globose species benefited more from climate change. This variable however was not included in a multivariate model including chorotype, suggesting that this response is due to a correlation between chorotype and growth form (i.e. globose species are particularly

abundant in tropical and tropical transition areas). No significant relationship was found between range change and niche breadth, area of occurrence, or environmental driver.

Discussion

Impact of climate change on cacti species' distribution

The Cactaceae family represents a compelling case study on the impacts of climate change, as this taxon is one of the most representative plant groups of the arid and semi-arid areas of the Americas, and it has been identified as the fifth most threatened groups of species on the planet (Goetsch et al. 2015). In addition to current major threats (land conversion and collection) our work shows that, under diverse anthropogenic emission scenarios, climate change poses potential deep impacts for this taxon in the study area. Notably, the present study fills an important taxonomic and geographic gap, since the impact of climate change on arid and semiarid tropical systems has been far less studied and predicted than on other biomes (Lenoir and Svenning 2015), despite their large global extent and their ecological singularity. In particular, our work represents the first effort to evaluate future climate change impacts on plants inhabiting arid and semi-arid systems in the Baja California Peninsula, a biodiversity hotspot for succulent plants in North America (Rebman 2001).

Overall, our results should be taken with caution given the different sources of uncertainty in model assembling (Thuiller et al. 2019) and our correlative approach that does not consider explicit migration and biotic community level processes (Pearson and Dawson 2003). However, our work considered the uncertainty linked to representative concentration pathways, climate change projections (i.e. GCMs), and dispersal constraints. In this sense, the matching results of our two extreme migration scenarios (no-migration and complete tracking) and across the three RCPs modeled suggest that the obtained patterns in relation to the impact of climate change on the distribution of cacti species' ranges might be robust to migration uncertainties and climate change projections (Franklin 2010).

Regarding the most conservative scenario of no migration, and consistently across RCPs, almost one-fifth of the 40 endemic cacti species in the Baja California are expected to lose > 50% of their current distribution range. Remarkably, in contrast to other case studies (e.g. Midgley et al. 2002) where a third of the Proteaceae species analyzed in South Africa suffered complete range dislocations (absence of stable habitat between current range and future projected range), none of the studied Cacti species presented this phenomenon. Nonetheless, even in the absence of total range dislocation, one species (*Opuntia pycnantha*) showed extremely low values of stable home range in relative (3%) and absolute values (47 km²) (specific values for RCP4.5). Three other species (*S. eruca*, *E. pensilis*, *E. pacificus*) with low values of range stability (28–45%) also showed small stable ranges in absolute terms (600–4200 km²). In contrast, three other species (*E. mombergerianus*, *M. phitauiana*, *E. sciurus*) with reduced range stability in absolute terms (1200–3100 km²) presented large relative stability values (75–92%).

Under the more optimistic scenario of unlimited migration, we found that although range expansion predominates, a significant proportion of species (25–30%) show potential contraction in their suitable area (with values ranging from 2 to 97% of habitat reduction for RCP4.5) consistently across RCPs. Most species showed large increases or decreases in their ranges with the most frequent value of change being of the order of 10,000 km² (positive or negative). This result clearly suggests a scenario of winner (i.e. species with large increase on their suitable areas) and loser species (i.e. species that lose a significant portion of their suitable areas), as evidenced in Fig. 3c. The spatial distribution of winner and loser species is shown in Fig. 6.

Interestingly, when jointly analyzing the outcomes of the complete climate tracking and the no-migration scenarios we found a strong non-linear relationship (Fig. 4). The relationship is close to linear for those species negatively impacted by climate change (left part of the plot). This result is highly informative from a conservation perspective because it indicates that the ranking of species negatively impacted by climate change, and thus the prioritization of conservation measures, is robust to the uncertainties associated to migration processes.

Conservation status and traits

Under the identified scenario of winner and loser species, the distribution of threatened species was not random. Across RCPs, species considered threatened by IUCN (*Endangered* or *Vulnerable*) showed significantly larger increases in their distribution range than non-threatened species under the unlimited migration scenario and smallest range contractions when no migration was considered. Specifically when considering full climate change tracking, average predicted increase for non-threatened species across RCPs is 21–57%, whereas it is 111–294% for threatened species. When considering no migration, non-threatened species were predicted to reduce their range by 28–36%, whereas threatened species reduced by 8–10%. Considering unlimited migration, none of the nine threatened species are expected to decrease their range under RCP2.5 and RCP4.5 and only one under RCP8.5 (*E. maritimus*, – 8%).

The modeling approach show that impact of climate change is very strongly correlated with the chorotype of the species. This result is expected because chorotypes have an obvious climatic signal. What is more informative and less predictable is how climate change will impact the different chorotypes. Models indicate that in the Baja California most of the cacti species that have an arid affinity are expected to be negatively affected in the extent of their suitable areas whereas species exhibiting tropical affinity might benefit from climate change. Our results in this sense match the studies developed in the South African cape region (Erasmus et al. 2002; Midgley et al. 2003; Broennimann et al. 2006), that revealed higher vulnerability to climate change in plant species occurring predominantly in arid areas. By contrast, Thuiller et al. (2005) suggest that European flora species occurring preferentially in warm and dry areas should benefit from climate change, conserving their initial habitats and/or expanding to new suitable habitats, whereas species occurring in more temperate regions should either disappear because of a loss of suitable habitat, or migrate north towards new potential habitat. Overall, the inconsistent results found in the different areas of the world reflect the idiosyncratic nature of climate change impacts when local effects and precipitation mediated processes are taken into account (e.g. Anadón et al. 2015). Our models also indicated that globose cacti species are expected to

particularly benefit from climate change, because this growth form is particularly abundant in the tropical areas of the Baja California (i.e. due to a correlation with chorotype). Ecological generalization, including niche breadth and range size, has been identified as one of the key species attributes to indicate risk of extinction due to climate change or any other perturbation (e.g. Pöyry et al. 2009; Angert et al. 2011; Broennimann et al. 2006; Thuiller et al. 2005). However, our models did not find any relationship between and climate change impact and climatic niche breadth or range size.

Conservation implications

Our work depicts a scenario of winner and loser species in the impact of climate change on the distribution of cacti species in Baja California Peninsula. Our models show that most winner species have a tropical affinity, and consequently globose growth, whereas loser species are in arid and Mediterranean systems (Fig. 6). The tropical (and tropical transition) region in Baja California includes most of the cacti identified as threatened by the IUCN due to agricultural and urban development as well as illegal collection (Goettsch et al. 2015). In addition, the tropical Baja California is home to a large number of micro-endemisms (Riemann and Ezcurra 2005), where restricted distribution increases their vulnerability to other threatening factors. Thus, currently threatened cacti species, mainly tropical, globose and with restricted distributions, are expected to benefit from climate change. In contrast, the group of species predicted to be most threatened by climate change is diverse in chorology and growth form; having only in common that they are not currently considered as threatened by the IUCN.

From a broader conservation perspective, the results obtained coincide with previous studies that present new challenges posed by climate change in terms of evaluating extinction risks (Gillson et al. 2013). National and international conservation frameworks for assessing species threats have not been developed in the context of climate change, so they may fail to recognize the species' vulnerability arising from this phenomenon (Thomas et al. 2010). For the studied species, our results show that the currently threatened species are not expected to be additionally impacted by climate change, since the present

threatening factors (development, collection) and future factors do not overlap in the biogeographical and taxonomic space for these species. However, our results expose a worrisome horizon at supraspecific levels for the study area; hence, the total number of endangered species may increase considerably in the future. Therefore, we highlight the need to implement complementary conservation frameworks that take into account factors related to habitat loss and collection, and those mediated by climate change, to correctly assess species vulnerability.

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References

- Abdelaal M, Fois M, Fenu G, Bacchetta G (2019) Using MaxEnt modeling to predict the potential distribution of the endemic plant *Rosa arabica* Crép. in Egypt. *Ecol Inform* 50:68–75
- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38(5):541–545
- Anadón JD, Graciá E, Botella F, Giménez A, Fahd S, Fritz U (2015) Individualistic response to past climate changes: niche differentiation promotes diverging Quaternary range dynamics in the subspecies of *Testudo graeca*. *Ecography* 38(9):956–966
- Anderson RP, Raza A (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *J Biogeogr* 37(7):1378–1393
- Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species’ traits predict recent shifts at expanding range edges? *Ecol Lett* 14(7):677–689
- Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecol Lett* 14(5):484–492
- Auer SK, King DI (2014) Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob Ecol Biogeogr* 23(8):867–875
- Barthlott W, Burstedde K, Geffert JL, Ibsch PI, Korotkova N, Miebach A, Rafiqpoor MD, Stein A, Mutke J (2015) Biogeography and biodiversity of cacti. *Schumannia* 7:208
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol Evol* 3:327–338
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol Model* 222(11):1810–1819
- Broennimann O, Thuiller W, Hughe G, Migdley GF, Alekemade RJM, Guisan A (2006) Do geographic distribution, niche property and life form explain plants’ vulnerability to global change? *Glob Change Biol* 12:1079–1093
- Brown JH (1995) *Macroecology*. The University of Chicago Press, Chicago
- Buckley LB, Kingsolver JG (2012) Functional and phylogenetic approaches to forecasting species’ responses to climate change. *Annu Rev Ecol Syst* 43:205–226
- Burnham KP, Anderson DR (1998) *Model selection and inference: a practical information-theoretical approach*. Springer, New York
- Butler CJ, Wheeler EA, Stabler LB (2012) Distribution of the threatened lace hedgehog cactus (*Echinocereus reichenbachii*) under various climate change scenarios. *J Torrey Bot Soc* 139(1):46–55
- Cactaceae in GBIF Secretariat (2019) GBIF Backbone Taxonomy. Checklist dataset <https://doi.org/10.15468/39omei>. Accessed via GBIF.org on December 2014.
- Carrillo-Angeles IG, Suzán-Azpiri H, Mandujano MC, Golubov J, Martínez-Ávalos JG (2016) Niche breadth and the implications of climate change in the conservation of the genus *Astrophytum* (Cactaceae). *J Arid Environ* 124:310–317
- Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? *Trends Ecol Evol* 28(8):482–488
- Comisión Nacional Forestal (2014) *Inventario Nacional Forestal y de Suelos*. CONAFOR, Guadalajara, Jal., México
- CONABIO (2015) *Red Mundial de Información sobre Biodiversidad* http://www.conabio.gob.mx/remib_ingles/doctos/remib_ing.html. Downloaded on December 2017
- Cortes L, Domínguez I, Lebgue T, Viramontes O, Melgoza A, Pinedo C, Camarillo J (2014) Variation in the distribution of four cacti species due to climate change in Chihuahua, Mexico. *Int J Environ Res Public Health* 11(1):390–402
- Dávila P, Téllez O, Lira R (2013) Impact of climate change on the distribution of populations of an endemic Mexican columnar cactus in the Tehuacán-Cuicatlán Valley, Mexico. *Plant Biosyst Int J Deal Asp Plant Biol* 147(2):376–386
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* 332:53–58
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17(1):43–57
- Erasmus BFN, Van Jaarsveld AS, Chown SL, Kshatriya M, Wessels KJ (2002) Vulnerability of South African animal taxa to climate change. *Glob Change Biol* 8:679–693
- Estrada A, Meireles C, Morales-Castilla I, Poschlod P, Vieites D, Araújo MB, Early R (2015) Species’ intrinsic traits

- inform their range limitations and vulnerability under environmental change. *Glob Ecol Biogeogr* 24(7):849–858
- Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. *Divers Distrib* 16(3):321–330
- Galante PJ, Alade B, Muscarella R, Jansa SA, Goodman SM, Anderson RP (2018) The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. *Ecography* 41(5):726–736
- García RA, Araújo MB, Burgess ND, Foden WB, Gutsche A, Rahbek C, Cabeza M (2014) Matching species traits to projected threats and opportunities from climate change. *J Biogeogr* 41(4):724–735
- Goettsch B, Hilton-Taylor C, Cruz-Piñón G et al (2015) High proportion of cactus species threatened with extinction. *Nat Plants* 15142:1–7
- González-Abraham Ch, Garcillán PP, Ezcurra E (2010) Ecoregions of Baja California peninsula: a synthesis. *Boletín de la Sociedad Botánica de México* 87:69–82
- Gillson L, Dawson TP, Jack S, McGeoch MA (2013) Accommodating climate change contingencies in conservation strategy. *Trends Ecol Evol* 28(3):135–142. <https://doi.org/10.1016/j.tree.2012.10.008>
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol J R Meteorol Soc* 25(15):1965–1978 (**IUCN 2018**)
- IPCC (2013) Climate change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp. doi:<https://doi.org/10.1017/CBO9781107415324>
- IUCN (2019) The IUCN Red List of Threatened Species. Version 2019-3. <https://www.iucnredlist.org>. Downloaded on December 2019
- Johnson CN (1998) Species extinction and the relationship between distribution and abundance. *Nature* 394(6690):272
- Lenoir J, Svenning JC (2015) Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* 38(1):15–28
- Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *J Biogeogr* 40(4):778–789
- Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modeling. *Divers Distrib* 15(1):59–69
- Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol Conserv* 112:87–97
- Midgley GF, Hannah L, Rutherford MC, Powrie LW (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Glob Ecol Biogeogr* 11:445–451
- Morin X, Thuiller W (2009) Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90(5):1301–1313
- Mourelle C, Ezcurra E (1997) Differentiation diversity of Argentine cacti and its relationship to environmental factors. *J Veg Sci* 8:547–558
- Parra JL, Monahan WB (2008) Variability in 20th century climate change reconstructions and its consequences for predicting geographic responses of California mammals. *Glob Change Biol* 14:2215–2231
- Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34(1):102–117
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12(5):361–371
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. *Ecol Model* 190:231–259
- Pöyry J, Luoto M, Heikkinen RK, Kuussaari M, Saarinen K (2009) Species traits explain recent range shifts of Finnish butterflies. *Glob Change Biol* 15:732–743
- Rebman J (2001) Succulent diversity in Lower California Mexico. *Cactus Succul J (US)* 73:131–138
- Riahi K, Rao S, Krey V, Cho C, Chirkov V, Fischer G, Kindermann G, Nakicenovic N, Rafaj P (2011) RCP 8.5—a scenario of comparatively high greenhouse gas emissions. *Clim Change* 109(1–2):33
- Riemann H, Ezcurra E (2005) Plant endemism and natural protected areas in the peninsula of Baja California, Mexico. *Biol Conserv* 122(1):141–150
- Santos-Díaz MS, Pérez-Molphe-Balch E, Ramírez-Malagón R, Núñez-Palenius HG, Ochoa-Alejo N (2010) Mexican threatened cacti: current status and strategies for their conservation. In: Tepper GH (ed) Species diversity and extinction. Nova Science Publishers, Inc., New York, pp 1–60
- Senay SD, Worner SP, Ikeda T (2013) Novel three-step pseudo-absence selection technique for improved species distribution modelling. *PLoS One* 8(8):e71218
- Shreve F, Wiggins I (1964) Vegetation and flora of the Sonoran Desert, I. Stanford University Press, Stanford, California
- Téllez-Valdés O, Vila-Aranda PD (2003) Protected areas and climate change: a case study of the cacti in the Tehuacán-Cuicatlán biosphere reserve, México. *Conserv Biol* 17:846–853
- Thomas CD, Hill JK, Anderson BJ, Bailey S, Beale CM, Bradbury RB, Yardley T (2010) A framework for assessing threats and benefits to species responding to climate change. *Methods Ecol Evol* 2(2):125–142
- Thuiller W, Lavorel S, Araujo MB (2005) Niche properties and geographic extent as predictors of species sensitivity to climate change. *Glob Ecol Biogeogr* 14:347–357
- Thuiller W, Lavorel S, Sykes MT, Araujo MB (2006) Using niche based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12:49–60
- Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019) Uncertainty in ensembles of global biodiversity scenarios. *Nat Commun* 10(1):1446

- Wiggins IL (1980) *Flora of Baja California*. Stanford University Press, Stanford
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* 6(12):e325
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working

Group (2008) Effects of sample size on the performance of species distribution models. *Divers Distrib* 14(5):763–773

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