

Projected climate change threatens significant range contraction of *Cochemiea halei* (Cactaceae), an island endemic, serpentine adapted plant species at risk of extinction

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Abstract

Aim: Threats faced by narrowly distributed endemic plant species in the face of the Earth's sixth mass extinction and climate change exposure are especially severe for taxa on islands. We investigated the current and projected distribution and range changes of *Cochemiea halei*, an island endemic cactus. This taxon is of conservation concern, currently listed as vulnerable on the International Union for the Conservation of Nature Red List and as a species of special concern under Mexican federal law. The goals of this study are to 1). identify the correlations between climate variables and current suitable habitat for *C. halei*; 2). determine if the species is a serpentine endemic or has a facultative relationship with ultramafic soils; 3). predict range changes of the species based on climate change scenarios. **Location:** The island archipelago in Bahía Magdalena on the Pacific coast, Baja California Sur, Mexico. **Methods:** We used temperature and precipitation variables at 30 arcsecond resolution and soil type, employing multiple species distribution modeling methods, to identify important climate and soil conditions driving current habitat suitability. The best model of current suitability is used to predict possible effects of four climate change scenarios based on best case to worst case representative concentration pathways, with projected climate data from two general circulation models, over two time periods. **Main conclusions:** The occurrence of the species is found to be strongly correlated with ultramafic soils. The most important climate predictor for habitat suitability is annual temperature range. The species is predicted to undergo range contractions from 21% to 53%, depending on the severity and duration of exposure to climate change. The broader implications for a wide range of narrowly adapted, threatened and endemic plant species indicate an urgent need for threat assessment based on habitat suitability and climate change modeling.

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BIOGRAPHICAL SKETCH

Peter B. Breslin began PhD studies in the fall of 2014, investigating questions regarding the biogeography and evolution of Cactaceae. Under the advisement of Martin Wojciechowski, with the help of committee members Lucas Majure, Shannon Fehlberg, Fabio Albuquerque and Jon Rebman, Breslin pursued research into the molecular phylogenetics, ancestral biogeography, climate change impacts on habitat suitability and population viability of the *Mammillaria* and *Cochemiea*(Cactaceae) of Baja California and adjacent regions.

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ABSTRACT

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Keywords : climate change, species distribution modeling, biodiversity, biogeography, range shifts, serpentine adaptation, island endemism, Cactaceae, endangered species

INTRODUCTION

Cactaceae are the 5th most endangered plant or animal family to be globally assessed to date by the International Union for the Conservation of Nature (Goettsch et al., 2015). The primary known threats to populations of cactus species are poaching of wild populations for the horticultural trade, small scale farming and ranching, mining operations, and the effects of climate change (Anderson, Taylor, Montes, & Cat-tabriga,1994; Hernández & Godínez-Álvarez 1994; Oldfield, 1997; Bárcenas-Luna, 2003; Godínez-Álvarez,

Valverde & Ortega Baes, 2003; Téllez-Valdés & Dávila-Aranda, 2003; Martorell & Peters 2005; Ureta & Marti 2012; Goettsch et al.). Aside from these threats, increased risk of extinction in Cactaceae due to climate change exposure is not well understood (Goettsch et al.). This study aims to help fill this gap, using predictive modeling to anticipate the extinction risk due to current conditions and climate change impacts, faced by an island endemic, threatened cactus.

Temperature and precipitation have been shown to be strong correlates for the distribution of plant species (e.g., Guisan & Zimmerman, 2000; Guisan & Thuiller, 2005; Hawkins et al., 2003; Elith & Franklin, 2013). Cacti are often narrowly adapted to specific thermal niches, as well as highly sensitive to seasonal precipitation patterns; for example, the bi-seasonal winter/summer precipitation cycles of the Sonoran Desert region, as well as longer precipitation cycles caused by shifts in the California current and other factors (Gibson & Nobel, 1986; Anderson, 2001). Islands often have both thermal and precipitation differences from their nearest peninsular or continental land masses, and these factors have been shown to contribute to island endemism and increased risk to island biodiversity (Kreft, Jetz, Mutke, Kier, & Barthlott, 2008; Humphreys, Govaerts, Ficinski, Lughadha, & Vorontsova, 2019). Island climates are often significantly distinct from those of adjacent land masses, and, as a result, islands harbor a significant amount of plant biodiversity (e.g., Kreft et al., Kier et al., 2009), yet island ecosystems also host endemic plant species subject to a rate of extinction 500 to 1000 times higher than the background rate (Humphreys et al.).

Ultramafic soils, predominant in the distribution of *C. halei*, such as ophiolite, amphibolites, serpentine, and gabbros, have been shown to drive plant endemism (Kruckberg 1951; Kazakou, Dimitrakopoulos, Baker, Reeves, & Troumbis, 2008; Botha & Slomka 2017). These soils contain high proportions of heavy metals and low quantities of plant nutrients, and are toxic to most plant species. Consequently, species adapted to these soils have a competitive edge and are able to colonize areas that other plants cannot (Brady, Kruckberg, & Bradshaw, 2005; Harrison, Safford, Grace, Viers, & Davies, 2006; Anacker, Whittall, Goldberg, & Harrison, 2011). To date, no studies of habitat suitability of cacti associated with ultramafic soils have been done, and the importance of this substrate to the distribution of *C. halei* is unknown.

Climate change is likely to affect the future distribution of many plant species due to shifts in temperature and precipitation (Bakkenes, Alkemade, Ihle, Leemans, & Latour, 2002; Walther et al., 2002; Kelly & Goulden, 2008; Urban, 2015; Warren, Price, Vanderwal, Cornelius, & Sohl, 2018). Prior to 2019, there were very few studies of habitat suitability and the potential effects of climate change in Cactaceae (Téllez-Valdés & Dávila-Aranda, 2003; Martorell & Peters, 2005; Butler, Wheeler, & Stabler, 2012; Albuquerque, Benito, Rodríguez, & Gray, 2018). In particular, climate projections under all representative concentration pathways (RCPs) of atmospheric “greenhouse gasses” and particulates, show increased mean temperatures ranging from 1.5 C to 4.5 C globally, and increased aridification of existing deserts due to larger areas subject to lower amounts of annual rainfall (Collins et al., 2013). Although cacti are adapted to arid conditions, prior studies have shown that they are vulnerable to projected changes in both temperature and precipitation under climate change scenarios (Téllez-Valdés & Dávila-Aranda, Martorell and Peters, Butler et al., Albuquerque et al.). The effect of climate change on the future suitable habitat of *C. halei* is unknown.

Our investigations include identifying the environmental variables that determine the habitat suitability of *Cochemia halei*. Abiotic correlates for the distribution of rare, narrowly restricted endemic species can provide important insight into suitable habitat, possible threats to the persistence of populations, and the potential effects of future climate change (Hawkins et al., 2003; Hijmans & Graham, 2006; Benito, Martínez-Ortega, Muñoz, Lorite, & Peña, 2009; Franklin 2010; Albuquerque, Castro-Díez, Rodríguez, & Cayuela, 2011; Albuquerque, Astudillo-Scalia, Loyola, & Beier, 2019; Albuquerque, Rodríguez, Búrquez, & Astudillo-Scalia, 2019).

Our specific goals are to investigate: 1). the environmental correlates to the distribution of *C. halei*; 2). whether populations of *C. halei* are more likely to occur on ultramafic soil; 3). whether the species is likely to colonize the peninsula, or if it is more likely to remain isolated on the islands; 4). the effect of varying levels of climate change on the future range and as a contributor to the risk of local and global extinction of *C. halei* over the next 30 to 50 years. This study will help provide background for urgently needed future

analyses of the specific risks faced by narrowly distributed, endemic and endangered cacti and other island endemic plant species.

METHODS

The study site

Bahía Magdalena is an ecologically significant embayment along the Pacific coast of the southern Baja California peninsula (Bizzarro, 2008). In contrast to the adjacent coastal plains, the island archipelago in Bahía Magdalena is part of the North American cordillera, and has mountainous, rocky terrain as a result (Rangin, 1978; Blake, Jayco, & Moore, 1984; Sedlock, 1993). (Fig. 1).

The islands range in elevation from sea level along the bay coastline to nearly 1000 m. (Blake et al., 1984). Several topographical variations on the islands create heterogeneous terrain, including flats, sand dunes, gravel coastlines and highly eroded arroyos. Westerly cliffs drop to the Pacific, at angles as steep as 90°. These cliffs are predominantly exposed ultramafic rock and gravel (Rangin, 1978; Blake et al., 1984).

The main soil mineralogical composition is serpentine rock and its eroded derivatives or non-ultramafic basalt and sand (Rangin, 1978; Blake et al., 1984; Sedlock, 1993). The mountainous ridges consist of ultramafic, oceanic crustal rock formed through tectonic plate collisions estimated to have occurred from the Late Jurassic to the Late Cretaceous periods (Sedlock, 1993, Zaitsev, Sanchez-Montante, & Robinson 2007).

Climate data from WorldClim v. 2.0 (Fick & Hijmans, 2017) shows biseasonal summer and winter precipitation, with autumn and spring being the dry months of the year. The moderating effects of the California current system create narrower diurnal and annual temperature ranges, increased precipitation and cooler seasonal averages for the islands than for the adjacent peninsula (Hickey, 1979; Bakun, 1990; Robinson, Gomez-Gutierrez, & Gomez-Aguirre, 2007; Bizzarro, 2008). From 2010 to 2018, 13 tropical storms or hurricanes occurred in the study region, with the majority occurring in the hottest month, September (National Hurricane Center; Hurricane Research Division; Central Pacific Hurricane Center).

The vegetation of the Bahia Magdalena region features 18 endemic angiosperm taxa; the endemic cacti represent 33% of the plant endemism in the area (Leon de la Luz, Medel-Narvez, & Dominguez-Cadena, 2015). The area is recognized as one of nine regions of high plant endemism in Baja California (Reimann & Ezcurra 2007). The primary vegetative regime is fog crassicaulescent and sarcocaulous scrub, that is, a combination of leaf and stem succulents, such as the endemic *Agave margaritae* Brandege and scrub vegetation, generally less than 8 m high (Rebman & Roberts, 2012, Leon de la Luz et al.).

Cochemiea halei Walton, the study species, is a mat forming stem succulent with straight spines and presumably hummingbird pollinated flowers (Craig, 1945; Pilbeam, 1999). *C. halei* is of conservation concern, assessed as vulnerable by the IUCN, and protected by Mexican law. The factors leading to its classification as vulnerable are the narrow geographic range, the low overall population size, and evidence of declining populations (IUCN). No formal studies of its population viability or quantified risk of extinction have been conducted previously, however.

Survey methods

Occurrence data was gathered over a four year period with eight surveys, in both winter and spring. Random points within the smallest convex polygon around Isla Magdalena and Isla Santa Margarita were generated using ArcMap (v. 10.6.1, ESRI, inc.). The random points were used as centers of survey transects (Elzinga, Salzer, & Willoughby, 1998; Bonham, 2013). In addition to occurrence data, we recorded soil type data and other topographical information, and the latitude and longitude of occurrences was marked using a handheld GPS device (eTrex 30X, Garmin Ltd. Olathe KS). A different surveying technique was employed on Cabo San Lazaro due to the much smaller area of that land mass. At that site, a belt transect method was used, with individuals counted within a 300 m radius along a 3 km segment that covered the entire habitat of *Cochemiea halei* (Bonham). The only known peninsular population, with six individuals, (Gorelick, 2007), was included in all analyses.

Presence points were spatially thinned to a minimum separation of 1 km to reduce sampling bias (Tessarolo, Rangel, Araujo, & Hortal, 2014; Stolar & Neilsen, 2015). A point raster layer of presence/absence locations was generated with 1 km grid squares and multiple records per square were reduced to at most a single record. Point pattern analysis was performed using Ripley’s K statistic to measure the degree of spatial correlation of presence/absence records (Baddely, 2008).

Environmental variables

To investigate correlations between the distribution of *Cochemiea halei* and its environment, we chose 19 energy and precipitation variables from WorldClim V. 2.0, averages from 1970 to 2000, at 30 arcsec resolution (Fick & Hijmans, 2017). Soil type was determined during field surveys using a Munsell soil identification color scale (Munsell Color, Grand Rapids, MI), categorizing soils into ultramafic (2.5Y hue with various color values and chroma) versus either “non-serpentine,” (approximately 7.5YR to 10YR), or sand (Roberts, 1980). Dense sampling of occurrences of *C. halei* with soil type data was performed in order to reduce error when interpolating for missing values (Carl & Kuhn, 2007; Dormann & McPherson, 2007; Dormann et al. 2013). The soil type data from the field was mapped onto zones of ultramafic versus non-ultramafic substrate, as indicated in the geological map of Isla Magdalena and Isla Margarita by Rangin (1978). The soil type raster was generated using inverse distance weighted interpolation (Goncalves, 2006; Grunwald, 2009) and improved using root mean squared error and 5-fold cross validation (Goncalves, 2006).

Four representative concentration pathways (RCPs) were used in climate change projections: 2.6, representing the best case future concentration of carbon in the atmosphere, through intermediate levels 4.5 and 6.0, to the worst case scenario of 8.5, as outlined in the Intergovernmental Panel on Climate Change’s Fifth Assessment Report (IPCC 2013; Liddicoat, Jones, & Robertson, 2013). The climate data itself was derived from two general circulation models (GCMs). The GCMs used were the Hadley Center Global Environmental Model version 2-ES (HadGEM2-ES) and the Community Climate System Model v. 4 (CCSM4), both of which are frequently used in studies of climate change effects on habitat suitability (e.g., Bellouin et al., 2011; Leclere et al. 2014; McQuillan & Rice, 2015; Albuquerque et al., 2018). The HadGEM2-ES model scenarios include projections of changes in ocean temperature and sea ice, and are especially recommended for use in predicting changes in coastal habitat (Collins et al. 2008, Caesar et al., 2013).

Variable preparation

Reduction of multicollinearity for all variables was performed by constructing a correlation matrix and performing hierarchical cluster analysis, which groups variables according to their mutually related correlations (Benito, Cayuela, & Albuquerque, 2013; Sarstedt & Mooi, 2014; Albuquerque et al., 2018). A cutoff of 0.5 Pearson’s correlation index was used; all variables correlated higher than 0.5 were discarded (Albuquerque et al.). Biserial correlation analysis, with variables correlated to presence/absence data for *Cochemiea halei*, was performed for all variables below 0.5 (Kraemer, 2006; Stolar & Nielsen, 2015, Albuquerque et al.). From each cluster of correlated variables as derived from the hierarchical cluster analysis, the variable with the highest correlation to the distribution of *C. halei* was chosen for use in modeling.

Modeling methods

Three methods were used for building models: boosted regression trees (BRT), generalized linear models of the binomial family (GLM) and maximum entropy (Maxent) (Hijmans & Graham, 2006; Elith, Leathwick, & Hastie, 2008; Franklin, 2010). Models used field survey presence and 200 randomly generated pseudoabsence background points (Franklin, 1995; Franklin, 2010; Elith, Kearney, & Phillips, 2010; Elith & Franklin, 2013; Phillips & Elith, 2013, Guillera-Arroita et al., 2015).

BRT is an iterative machine learning optimization method, in which the deviance residuals from a prior decision tree are used as the data for the next step (called “boosting”); the decision tree building process continues until residual deviance is no longer decreased by iterations (De’ath, 2007; Franklin, 2010). Decision trees, the underlying algorithm of BRT, also known as classification and regression trees, perform well with both continuous and categorical variables, and, unlike with GLM, for example, they are robust to a

lack of independence among predictors (De'ath, 2007; Elith & Leathwick, 2009; Elith & Leathwick, 2017; Albuquerque et al., 2018).

GLM is a well known regression method that uses maximum likelihood as the measure of the contribution of a variable to a prediction of the “state” of a dependent variable, in this case the binary outcome of presence/absence (Nelder & Wedderburn, 1972; Guisan, Edwards, & Hastie, 2002).

Maximum entropy (Maxent) is a machine learning method that employs multinomial logistic regression to estimate the probability of the distribution of a species according to the “maximum entropy” of the distribution, i.e., the most uniform distribution of a species possible given the limits imposed by the predictor variables (Phillips, Anderson, & Schapire, 2006; Elith et al. 2011, Phillips, Anderson, Dudik, Schapire, & Blair, 2017).

Model evaluation

For BRT models, evaluation of model performance included measures of residual deviance, k-fold cross validation and the area under the receiver operator characteristic curve (AUC) (De'ath, 2007; Elith & Leathwick, 2009). GLM model performance was evaluated with AUC and adjusted D^2 (a measure of the difference between null deviance and model deviance adjusted for degrees of freedom) and Akaike information criterion (Guisan et al., 2002; Franklin, 2010). Maxent models were evaluated by comparative training and test AUC, and omission on test and training samples against random prediction (specificity-sensitivity curves) (Hijmans, 2012; Elith & Leathwick, 2017).

For predictions of current habitat suitability, maps showing the predicted probabilities of presence or absence are presented for the best model with soil type and without soil type. Plots of the partial response of *C. halei* to each of the environmental variables and the proportional contribution of each variable to model performance are also presented.

Climate change modeling

Climate change scenarios were projected using the best predictive model for current habitat suitability, for the periods 2009-2049 and 2009-2069. Current predicted suitable habitat was subtracted from composite binary presence/absence maps using both general circulation models (GCM's), with range differences counted as contractions if a current presence was projected as a future absence, refuge if current presences remained presences and expansion if current unsuitable habitat was projected as suitable in the future (Elith et al., 2010; Hatten et al., 2016; Albuquerque et al., 2018). Box plots showing the two most significant environmental predictors and their influence on range changes are presented. The proportion of expansion or contraction of future ranges relative to current habitat suitability were calculated and are shown. Prediction maps are also presented with visualizations of projected expansion and contraction.

RESULTS

Survey results

A total of 1227 records were recorded in the field, with accompanying soil type. After separating occurrence points by a minimum distance of 1 km and removing duplicate records, the occurrence and randomly generated pseudoabsence data set used in modeling consisted of 44 presences and 207 pseudoabsences.

Variable selection

The variables that were below the 0.5 correlation threshold in the cluster analysis but most strongly correlated to the occurrence of *Cochemiea halei* in the biserial correlation analysis were annual temperature range, mean temperature of the warmest quarter, precipitation of the warmest quarter and precipitation of the coldest quarter. These variables, along with soil type, were used in the species distribution models. Annual temperature range differs on the islands versus the peninsula, with island temperature ranges of approximately 20* C and the peninsular range 10* wider at 30* C. Mean temperature of the warmest quarter ranges from 24* C in the northwestern region of Isla Magdalena to approximately 30* C at the lowest

elevation in the center of Isla Margarita and on the peninsula. Precipitation of the warmest quarter ranges from 20–40 mm on the islands, except for the highest elevations on Isla Margarita at 70 mm. The majority of peninsular precipitation is also at 70 mm. Precipitation of the coldest quarter is from 20–30 mm on the islands, to slightly over 40 mm on the peninsula. (Fig. 2)

Modeling Results

The three modeling methods of generalized linear models, boosted regression trees and maximum entropy all generated fair to excellent results, as measured by AUC values, with values ranging from 0.80–0.88. Boosted regression trees (BRT) produced the best models, as measured by AUC values, 10-fold cross validation, model deviance versus null deviance and relevance of information regarding predictors and their contributions to the models. The model results presented below are derived from BRT analysis. The first model presented here is a model that included soil type, which was the best performing BRT model. The map of predicted suitable habitat shows a low probability of colonization of the peninsula, especially to the east of localized, immediately adjacent regions on the western edge of Bahia Magdalena. The highest predicted probabilities on the peninsula are near the town of Puerto San Carlos, where the only known peninsular population occurs. (Fig. 3).

Annual temperature range, a simple subtraction of the annual high temperature minus the annual low temperature, has the highest marginal response, which shows a sudden drop in the suitability of habitat for *Cochemiea halei* under an annual temperature range greater than approximately 21.5° C. The optimal mean temperature of the warmest quarter is ranges from 24° C to 26° C, with an increased contribution to occurrence at 26° C, but then a sharp drop off, with temperatures above approximate 26.5° C negatively correlated to occurrence. Precipitation of the warmest quarter is positively correlated with occurrence below 30 mm, but negatively correlated above 30 mm. Precipitation of the coldest quarter shows approximately the same response of precipitation of the warmest quarter. (Fig. 4).

The percent relative contributions for each variable to the predictive ability of the model described above show that the most significant predictor is annual temperature range, accounting for nearly 66% of model performance. Thermal energy in general is a strong predictor of suitable habitat, with the top two predictors accounting for 78.3% of model performance. (Fig.5).

In order to gauge the impact of soil type on the habitat suitability of *C. halei*, a model was created with the same predictor variables as the above model, but without soil type. The habitat suitability map without soil type shows a higher probability of occurrence on the peninsula, where the species does not occur in any large populations and where ultramafic soils do not occur. A higher suitability is also predicted within the islands themselves overall, with a higher saturation in general of suitable habitat. Suitable habitat is also predicted on some pure sand features, such as the sand that connects Isla Magdalena with Cabo San Lazaro. There is also a higher predicted probability on basalt and non-ultramafic soil types on the islands. The low, sandy trough in the middle of Isla Margarita, however, remains an area of low suitability, as does the peninsular region to the east of the small footholds predicted for *C. halei*. The 10-fold cross-validated AUC of this model was .85, slightly lower than the model with soil type. (Fig. 6)

The effects of climate change on the range of *Cochemiea halei*

For all projections, loss of between 21%–53% of suitable habitat is predicted for the species. In the case of the lower representative concentration pathways (RCPs), range contraction is partially offset by expansion into previously unsuitable habitat. As the climate change scenarios increase in RCP, especially over the longer time period to 2070, expansion is reduced significantly. (Table 1) The range maps showing projected future areas of contraction and expansion for *C. halei* indicate the greatest potential loss of habitat is on Isla Margarita, with regions on that island accounting for 40% to 65% of the total contraction. Only two scenarios predict expansion to the peninsula under the effects of climate change, and in both cases, the predicted new suitable habitat is an isolated patch. (Figs. 7 and 8).

Boxplots of the effect of the two most important predictors, annual temperature range and mean tempera-

ture of the warmest quarter, on future habitat suitability indicate significant changes for all climate change projections to 2070. The greater variability of annual temperature range for range contraction areas is consistent with the species having more suitable habitat within a narrower temperature range. The significantly higher mean temperatures of the warmest quarter for all projected future areas also contribute to habitat loss. Predicted areas of expansion also feature higher temperatures, which is a result of temperatures across the study site increasing due to climate change. (Fig. 9).

DISCUSSION

We investigated the effects of environmental and soil variables on the distribution of *Cochemiea halei*, as well as the possible impacts of climate change, using species distribution models. Our results show significant factors affecting the current distribution of the species and potential threats to the persistence of the species under climate change as a result of significant range contraction.

The island endemism of *Cochemiea halei* is strongly correlated with both soil and climate effects. The island archipelago in Bahia Magdalena, the primary suitable habitat for *C. halei*, has significantly different soil and climate from the nearby peninsula. These contrasting conditions are similar in other island habitats near coastal areas along the Pacific Ocean, where conditions are significantly different even a short distance inland (Reimann & Ezcurra, 2005; Bizzarro, 2008; Ratay, Vanderplank, & Wilder, 2014).

Cochemiea halei occupies a narrow range of temperature and precipitation correlates. The moderating temperature effects of the California current system (Hickey, 1979; Huyer, 1983; Bakun, 1990; Robinson et al. 2007) are important to habitat suitability for the species. The two most influential climate variables in the best model were annual temperature range and average temperature of the warmest quarter, accounting for approximately 73% of the model's predictive power. Both of these variables show significantly lower values on the islands than on the peninsula, patterns typical of coastal areas moderated by the upwelling of the California current system, especially in summer (Bakun, 1990). The temperature range on the islands is approximately 10°C narrower than on the peninsula, and the mean temperature of the warmest quarter is 4°C cooler. The bi-seasonal precipitation patterns of the Sonoran Desert region (Shreve & Wiggins, 1964) are represented by the influence on model performance of the precipitation of both the warmest and coldest quarters. However, precipitation is lower on the islands than inland, during both seasons, with the most significant differences occurring during the warmest quarter. These localized effects have been shown to drive endemism (Hijmans & Graham 2006; Snyder, Sloan, Diffenbaugh, & Bell, 2003; Gogol-Prokurat, 2011; Humphreys et al., 2019). *C. halei* is an example of a species that has a localized, well-defined climate response, with the highest probability of suitable habitat predicted to be within a relatively narrow band of thermal and precipitation parameters.

In addition to strong climate influences on the current distribution of *Cochemiea halei*, soil type plays an important role. Narrowly restricted endemic plant species, including cacti, have been shown to be strongly dependent on soil types for habitat suitability (Kruckberg, 1951; Kruckberg & Rabinowitz, 1985; Harrison et al., 2006). Several studies of plant distributions have determined the importance of ultramafic soils in particular as a driver of plant endemism (e.g., Kruckberg, Kazakou et al., 2008; Botha & Slomka, 2017). While *C. halei* does not appear to be an obligate endemic to ultramafic soils, the species is more likely to occur on those soil types, with 60% of occurrences on ultramafic soil. This is similar to other species in the Cactaceae that occur on ultramafic soils, in particular on the islands of Cuba and Puerto Rico (Reyes-Fornet, Fornet-Hernandez, & Martinez Ondaro, 2019). Obligate and facultative adaptations to ultramafic soils have been shown to provide a competitive advantage (Brady et al., 2005; Anacker et al., 2011; Harrison et al., 2006; Pollard, Reeves, & Baker, 2014). The model with soil type had stronger predictive performance, and indicated a more fragmented, lower habitat suitability for areas in our surveys where population density was low, suggesting that ultramafic soils are an important constraint on the distribution of the species.

Cochemiea halei's observed establishment on virtually unweathered ultramafic rock and exposed gravel, in addition to lower precipitation on the islands than on the peninsula, suggest that the species is adapted to evaporation of soil moisture and drier conditions, a common characteristic of cacti distributed in rocky

environments (Gibson & Nobel 1986). In summary, *C. halei* favors cooler, drier habitat, on ultramafic rock and soil, with a moderated annual temperature range, a suite of abiotic predictors that characterize the island habitat in contrast to the nearby peninsula.

Consequently, *Cochemiea halei* is not likely to migrate to the peninsula except for small foothold regions along the peninsular shore. This characterizes *C. halei* as a “stranded” endemic, making its persistence more vulnerable to changes in climate (Crawford & Stuessy, 1997; Cowie & Holland, 2006; Stuessy, Takayama, Lopez-Sepulveda, & Crawford, 2014). The only known peninsular population of *C. halei* consists of approximately six individuals limited to a patch of sand measuring 150 m². At that site, there is no sign of dispersal in the surrounding area, in spite of the plants being large, seed bearing and apparently well-established (Gorelick, 2007).

The suitable habitat for *Cochemiea halei* is a patchwork of sites even within its narrow range on the islands. Major geographical distinctions within the islands that are illustrated on the prediction map from the model with the best predictive ability (Fig. 4) include two distinct regions on Isla Margarita, zones of less suitable habitat on Isla Magdalena, and a narrow zone of suitability at Cabo San Lazaro, with few areas of on-the-ground connectivity between suitable habitats. Endemic plant species often occur in fragmented habitat with geographical barriers and low connectivity between sites (Rabinowitz, 1981; Kotliar & Wiens, 1990). As a narrowly restricted endemic, essentially stranded on the islands, the species is at increased risk for stochastic environmental, demographic and genetic setbacks (Ellstrand & Ellam, 1993; Lande, 1993; Menges, 1992; Matthies, Brauer, Maibom, & Tscharnke, 2004; Melbourne & Hastings, 2008; Mubayi, Kribs, Arunachalam, & Castillo-Chavez, 2019). Even without the impacts of climate change exposure, the species appears to be at elevated risk for local extinction events, population bottlenecks and increased fragmentation.

Climate change

Future climate change scenarios indicate a contraction of *Cochemiea halei*’s range of 21% to 53%, depending on the severity of climate change and the length of time the species is exposed to climate change effects (Table 1). The range contraction reduces suitable habitat on the islands, and the species is unlikely to expand to the peninsula within the climate change conditions and time periods projected here. The unique adaptations of narrowly distributed endemic plant species such as *C. halei* also make them vulnerable to changing climate conditions, as those adaptations are often in response to significantly different local climates or soil types that are unsuitable for related species (Damschen, Harrison, Ackerly, Fernandez-Going, & Anacker, 2012).

Specifically, each of the climate change scenarios projected in this study indicates a widening of the annual temperature range on the islands, which significantly increases the range contraction and limits expansion. The areas of predicted contraction under all scenarios are lower elevation, mostly bayside, leeward flats (Figs. 7 and 8). The areas of expansion are mostly into the higher elevation ridges, especially on Isla Margarita. But the opportunity to expand into these higher elevation locales is greatly reduced as climate change becomes more severe, or persists for a longer time period.

Projections under all climate change scenarios are for a higher mean temperature of the warmest quarter, ranging from approximately 3* C to as high as 6* C. Precipitation of the warmest and coldest quarters is projected to decrease by from 10 mm to 15 mm for regions of predicted range contraction. The wider thermal span and the warmer mean temperature from July–September, along with reduced precipitation, are combined factors that contribute to range contraction, driven by hotter, drier climate. Predicted range contractions are consistent with *Cochemiea halei*’s narrow adaptation to a distinct island climate.

For the first time, temperature and precipitation correlates are identified that drive the fragmented, highly restricted distribution of an island endemic, vulnerable cactus. We used multiple modeling methods to determine the correlations between topographical and climate variables and the habitat suitability of *Cochemiea halei*, a little-studied, island isolated cactus. Our results support the following conclusions: (1) both the moderating effects of Pacific coastal island climate and ultramafic soils unique to the islands strongly determine suitable habitat, which is fragmented, (2) the species is unlikely to disperse to the peninsula, (3) the species has a facultative but not obligate relationship with ultramafic soils, (4) climate change in all

scenarios is likely to contract the range of the species, as a result of greater variability in annual temperature range, higher mean temperatures in the summer and reduced precipitation. Our findings indicate that this narrowly restricted endemic cactus is at increased risk of extinction, and populations should be carefully monitored over at least the next 50 years.

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Data Accessibility Statement : The data that support the findings in this paper, including locality data and raster files of the climate variables used in modeling, are available at the Dryad data repository.

Tables :

Table 1. Percent expansion, contraction and net habitat loss of *Cochemiea halei* under four representative concentration pathway (RCP) climate change scenarios and two time periods.

| Time Period | RCP | expansion | contraction | net habitat loss |
|-------------|-----|-----------|-------------|------------------|
| 2050 | 2.6 | 19% | -46% | -27% |
| | 4.5 | 10% | -48% | -38% |
| | 6.0 | 14% | -47% | -33% |
| | 8.5 | 25% | -52% | -27% |
| 2070 | 2.6 | 29% | -50% | -21% |
| | 4.5 | 5% | -50% | -45% |
| | 6.0 | 6% | -50% | -44% |
| | 8.5 | 2% | -55% | -53% |

Figures:

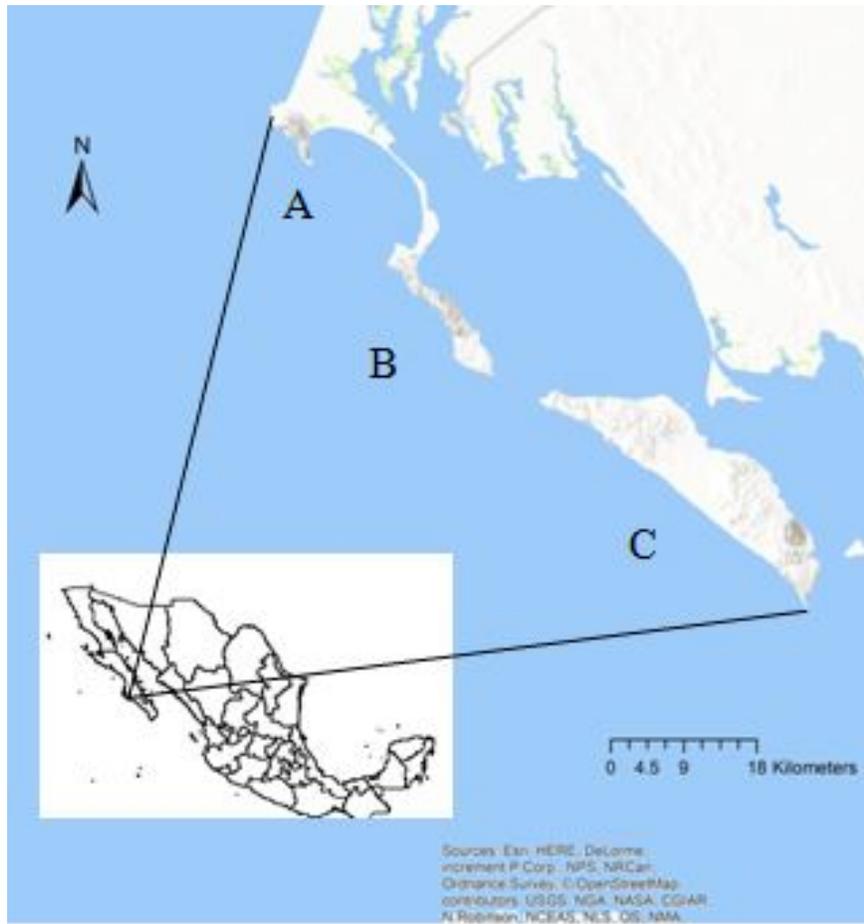


Fig. 1: The Bahía Magdalena region and islands, the known area of distribution of *Cochemia halei*. The islands and named land masses in Bahía Magdalena: (A): Cabo San Lazaro, the most northwesterly land mass of the islands. (B): The main land mass of Isla Magdalena. (C): Isla Margarita. Map created using ArcGIS® software by Esri. ArcGIS® and ArcMap are the intellectual property of Esri and are used herein under license. Copyright (c) Esri. All rights reserved.

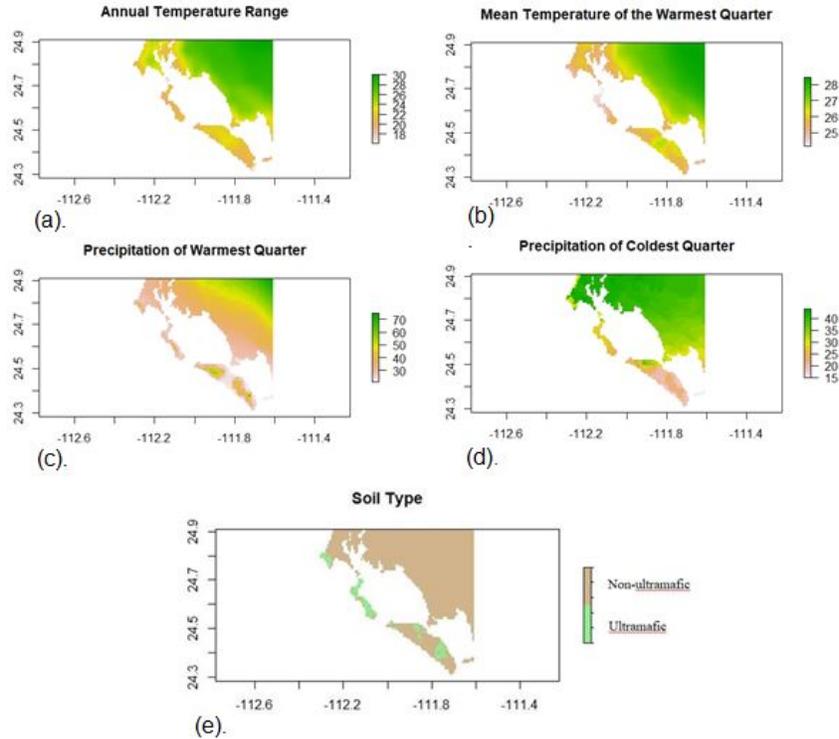


Fig. 2: Maps of the environmental variables used in model building. (a): annual temperature range; the difference between the maximum temperature of the warmest month (September) and minimum temperature of the coldest month (January). (b): mean temperature of the warmest quarter of the year, July–September. (c): precipitation of the warmest quarter of the year, July–September. (d): precipitation of the coldest quarter of the year, December–February. (e): soil type; light green areas are ultramafic soils and tan are all other soil types, including basalt and the sand of the Magdalena Plains on the peninsula. Temperature variables are in degrees C, and precipitation in mm.

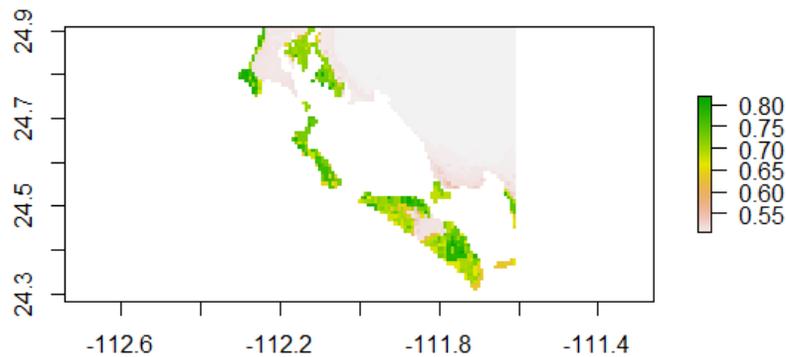


Fig. 3: Predictions of suitable habitat for *Cochemiea halei* . The map is of predictions of habitat suitability, on a scale of zero (transparent) to 1 (dark green). The model predictions derive from a BRT method, using WorldClim V. 2.0 data at 30 arcsec resolution. 44 presences and 207 pseudoabsences were used. The following variables were used: annual temperature range, the mean temperature of the warmest quarter (July-September), precipitation of the warmest quarter (July-September), precipitation of the coldest quarter (December-February), and soil type. The model fitted 4950 trees, with a 10-fold cross-validated AUC of .88. The parameters used for the boosted regression tree analysis were a tree complexity of 2, a learning rate of .0007, bag fraction of .7 and a step size of 25.

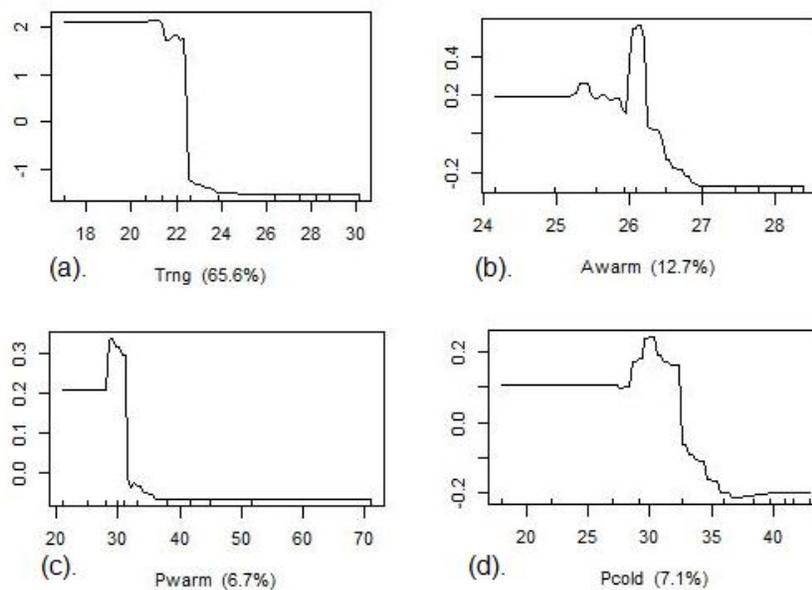


Fig. 4: Partial response plots of climate variables used in species distribution modeling for *Cochemiea halei* .

The plots show the marginal response of *C. halei* to each variable. The variables are (a): annual temperature range, “Trng”, (b): average temperature of the warmest quarter, “Awarm”, (c): precipitation of the warmest quarter, “Pwarm”, and (d): precipitation of the coldest quarter. The *y*-axis for each plot is on a logit scale, showing the relative impact of values of the variable on the probability of occurrence. The *x*-axis for the temperature variables, (a) and (b), is in degrees C. Precipitation variables, (c) and (d), are in mm. The *x*-axis is marked with a decile rug plot.

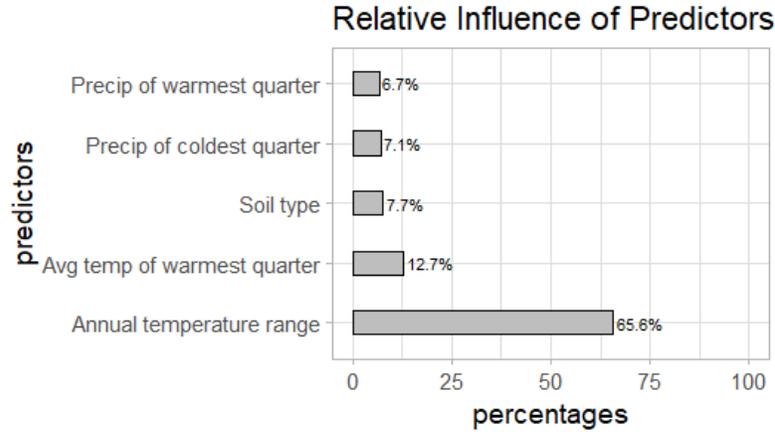


Fig. 5: Percent contributions of predictors to model performance. Percent influence: annual temperature range, 65.6%; average temperature of the warmest quarter, 12.7%; soil type, 7.7%, precipitation of the coldest quarter (December-February), 7.1%; precipitation of the warmest quarter (July-September), 6.7%.

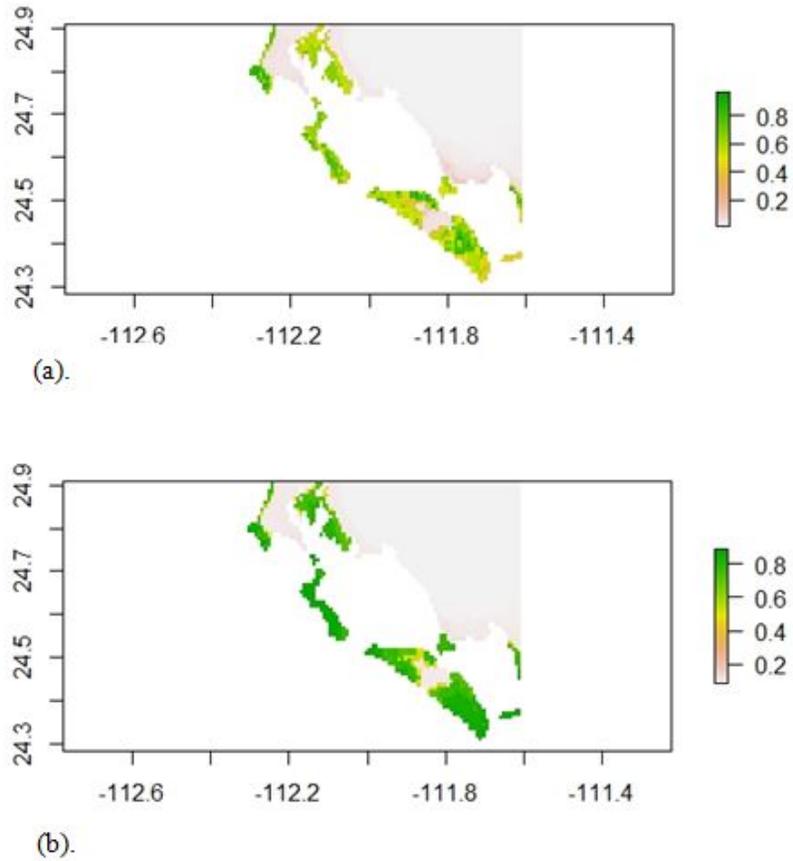


Fig. 6: Comparison of predicted suitable habitat with soil type as a predictor and without soil type as a predictor.(a). the prediction map resulting from the best BRT model with soil type, the same results shown in Fig. 4. (b). the map from the best BRT without soil type. Variables are identical in both models except for omission of soil type in model B: annual temperature range, the mean temperature of the warmest quarter (July-September), precipitation of the warmest quarter (July-September), and precipitation of the coldest quarter (December-February). The best model without soil type fitted 2270 trees, with a 10-fold cross-validated AUC of .85. The parameters used for the boosted regression tree analysis were a tree complexity of 1, a learning rate of .0007, bag fraction of .7 and a step size of 15.

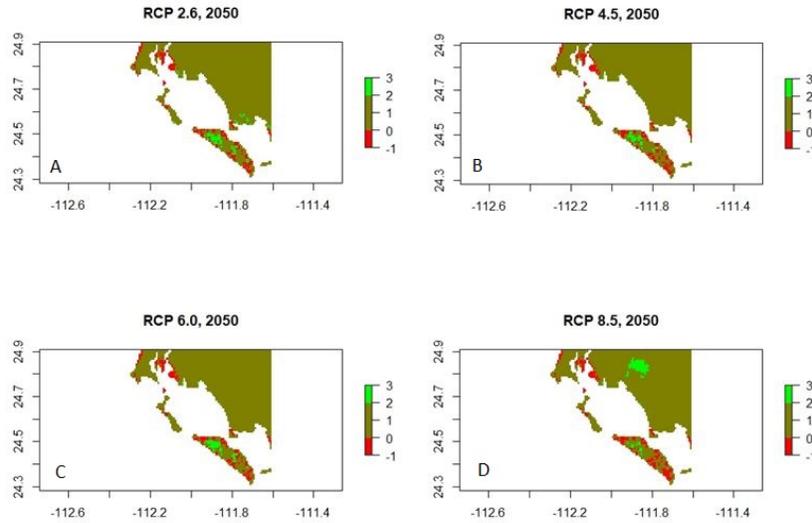


Fig. 7: Predictions of range expansion, refuge, and contraction for *Cochemiea halei*, to 2050. Light green areas represent projected areas of range expansion (from 2 to 3 on the scale), red areas represent projected areas of range contraction (from 0 to -1 on the scale). Increasing representative concentration pathways (RCP) are indicated at the top of each map; increased RCP corresponds to increased severity of climate change exposure. (a): RCP 2.6, (b): RCP 4.5, (c): RCP 6.0, and (d): RCP 8.5.

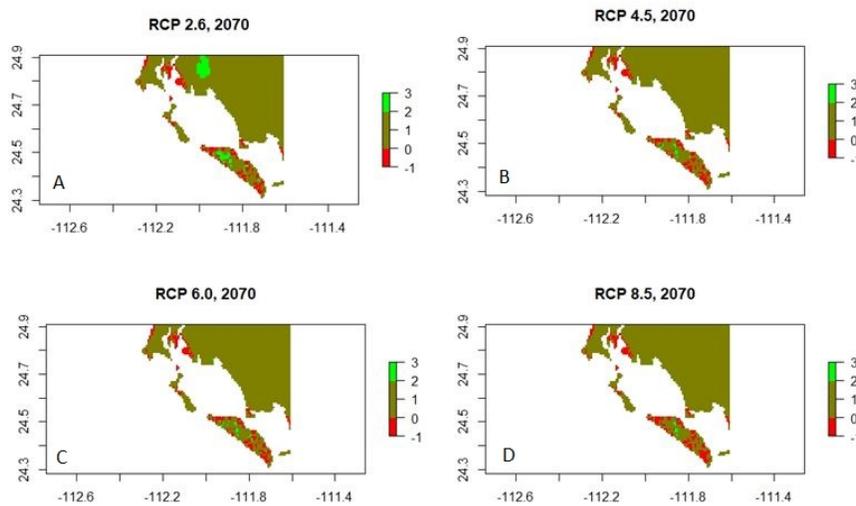


Fig. 8: Predictions of range expansion, contraction and refuge of *Cochemiea halei*, to 2070. Predicted range changes for the four representative concentration pathways are shown for climate scenarios projected to 2070. Light green areas represent projected areas of range expansion (from 2 to 3 on the scale), red areas represent projected areas of range contraction (from 0 to -1 on the scale). Increasing representative concentration pathways (RCP) are indicated at the top of each map; increased RCP corresponds to increased severity of climate change exposure. (a): RCP 2.6, (b): RCP 4.5, (c): RCP 6.0, and (d): RCP 8.5.

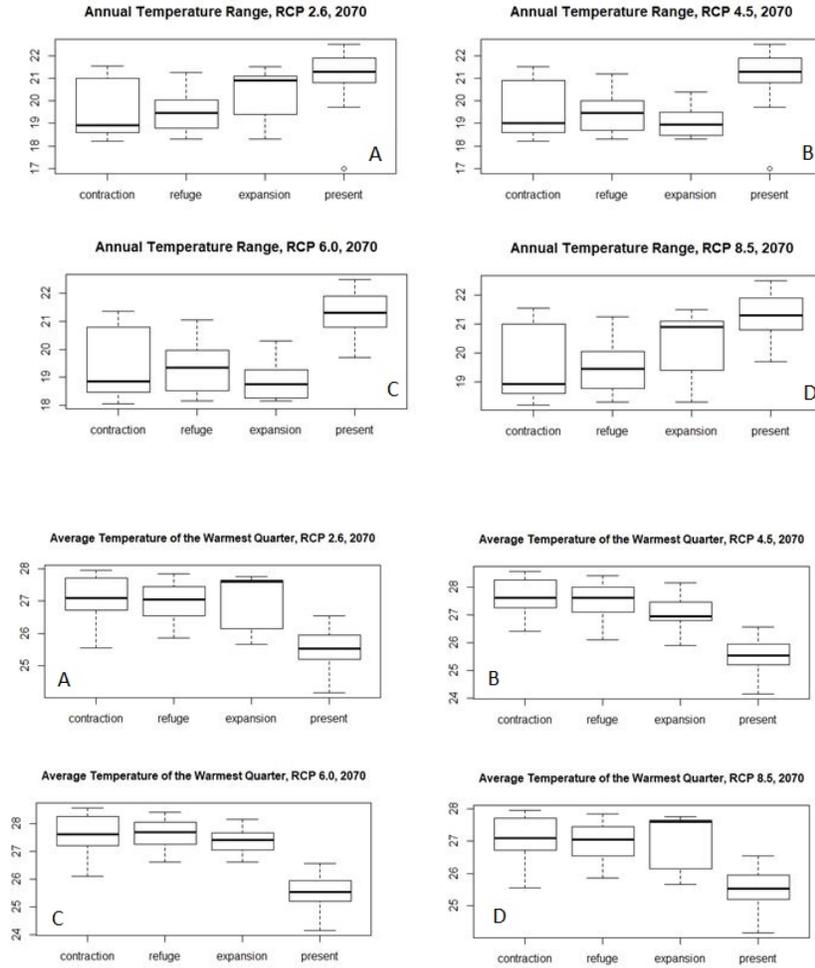


Fig 9: Influence of the two strongest climate predictors on habitat contraction, refuge, and expansion, for *Cochemiea halei*, for four representative concentration pathway scenarios, projected to 2050 and 2070. Each box plot shows the range, 1st quartile, median and 3rd quartile of annual temperature ranges and average temperature of the warmest quarter for each type of predicted future habitat prediction: contraction, refuge, expansion and the present habitat. The *y*-axes are degrees C. All data is from the projections to 2070.