Climate change and conservation in a warm North American desert: effect in shrubby plants

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ABSTRACT

Background: Deserts are biologically rich habitats with a vast array of animals and plants adapted to xeric conditions, and most deserts are among the planet’s last remaining areas of total wilderness. Among North American deserts, the Chihuahuan Desert has the highest levels of diversity and endemism. To understand the effect of future climate change on plants distributed in this arid land and propose effective conservation planning, we focused on five endemic shrubby species that characterize the Chihuahuan Desert and used an integrative approach.

Methods: Ecological niche-based modeling, spatial genetics and ecological resistance analyses were carried out to identify the effect of global warming on the studied five shrubby species. Key areas that need to be preserved were identified taking into account the existing protected areas within the Chihuahuan Desert.

Results: The extent of future distribution will vary among these species, and on average expansion will occur in the western part of the Chihuahuan Desert. For most species low environmental resistance to gene flow was predicted, while higher future resistance was predicted for one species that would lead to increased population isolation. The highest haplotype diversity was identified in three hotspots. Based on future suitability of habitat and in the haplotype diversity we suggest preserving two hotspots of genetic diversity in the Sierra Madre Oriental, located in areas without protection. The third hotspot was detected in the well preserved Tehuacán-Cuicatlán Man and Biosphere Reserve.

Conclusion: Global climate change will have an effect in arid adapted plants, favoring expansion in the western of the Chihuahuan Desert however negatively affecting others with high ecological resistance disrupting gene flow. Two hotspots of genetic diversity in the Sierra Madre Oriental should be protected.

Subjects Biodiversity, Ecology, Evolutionary Studies, Genetics
Keywords Arid-adapted plants, Chihuahuan desert, Conservation planning, Desert biota, Environmental resistance, Haplotype diversity, Protected natural areas

INTRODUCTION

The effect of future climate change on organisms has been studied from multiple perspectives, in diverse biomes, ecosystems, farming landscapes and for many taxa and functional groups of organisms. The main effects of climate change are associated with...
demographic threats, opportunities for expansion, and positive or negative implications with respect to the size and position of species ranges, as well as the genetic variability of populations, disequilibrium in biotic interactions and a variable capacity of adaptation in natural and agricultural systems (Harris et al., 2006; Kelly & Goulden, 2008; Williams et al., 2010; Thornton et al., 2014; Anadón, Sala & Maestre, 2014; García et al., 2014; Corlett & Westcott, 2013; Skogen, Helland & Kaltenborn, 2018).

Understanding how future climate variation influences ecological and evolutionary processes in organisms is crucial to conservation decision-making. Furthermore, estimating genetic diversity among populations and their spatial distribution is valuable for determining their degree of vulnerability (Sgrò, Lowe & Hoffmann, 2011); areas with high genetic diversity should have priority for conservation owing to its importance for building resiliency in populations (Forester, DeChaine & Bunn, 2013). Often, genetic variability has already decreased where vulnerability to changes in climate is highest, and will deteriorate further precisely in the areas where diversity may be most needed for future persistence (Franks & Hoffmann, 2012). Complementary approaches to the assessment of genetic variation include methods that identify the ecological resistance of populations given that data on dispersal and gene flow are essential for conserving species in fragmented landscapes (McRae & Beier, 2007). It has been demonstrated that gene flow rates in plants vary enormously depending on the species and populations involved (Ellstrand, 2014); moreover, the effect of gene flow might still be significant at distance of thousands of meters acting as a connecting force for local selection of populations (Ellstrand, 2014). Thus, identifying genetic polymorphisms leading to population differentiation depending on genetic flow in populations and their connectivity in future climate scenarios will be practical for setting conservation planning (Ellstrand & Elam, 1993). An additional instrument for estimating the effect of future climate conditions on species is ecological niche-based modeling, which can provide useful ways to integrate future climate scenarios into conservation (Wiens, Stralberg & Jongsomjit, 2009; Forester, DeChaine & Bunn, 2013). Ecological niche and gene flow are causally interrelated with the potential for one to impact the other, thus studying both simultaneously should provide stronger predictions of future species distributions.

Just like any habitat, deserts will be affected by climate change. These biomes are biologically rich habitats with a vast array of animals and plants adapted to xeric conditions, and several deserts are among the Planet’s last remaining areas of total wilderness (Ward, 2009; Cooke, Warren & Goudie, 2013). Although the individual deserts of North America and northern Mexico are very small compared with the vast deserts of the Sahara, Arabia, Australia and Asia, the origin and evolution of their biota have led to a unique, high degree of elevated diversity (Riddle & Hafner, 2006; Wilson & Pitts, 2010). The most diverse of North American Deserts is the warm Chihuahuan Desert whose limits to the north are in the mountains of Arizona-New Mexico, and include western Texas, the Mexican Plateau to Hidalgo and Querétaro and a southern relict area, the Tehuacán Valley (Fig. 1, Henrickson & Johnston, 1986; Wilson & Pitts, 2010). The insularity of the Chihuahuan Desert has produced an area rich in
endemic plant species; of the approximately 3,500 species about one third are endemic (Villarreal-Quintanilla et al., 2017).

There are few protected areas located within boundaries of the Chihuahuan Desert. The largest are the four biosphere reserves—Barranca de Metztitlán, la Michilia, Mapimí, and Tehuacán-Cuicatlán—and there are smaller protected areas such as Cuatrociénegas (National Commission of Natural Protected Areas, CONANP, www.gob.mx/conanp). The little research that there is on the effect of future climate change on the flora of the Chihuahuan Desert has focused on plants such as the cacti (Aragón-Gastélum et al., 2014; Shryock, Esque & Hughes, 2014; Carrillo-Angeles et al., 2016) or on ecosystems such as grasslands that are frequently dominated by *Larrea* and *Prosopis* (Huenneke et al., 2002; Baez et al., 2013; Bell et al., 2014).

Here, we focus on the shrubby plants of the Chihuahuan Desert and using prospective ecological niche-based modeling (ENM) in five endemic species, aim to estimate whether species ranges will vary or remain the same and to identify the areas that are more likely to remain stable. Additionally, by acquiring molecular data we estimate genetic diversity of populations of these species and determine how it is spatially distributed to determine the degree of vulnerability, taking into account the ecological connectivity of the

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**Figure 1** Distribution and images of the studied species. Limits of the Chihuahuan Desert and distribution map and images of the five plant species studied. Main biogeographic areas are indicated in addition to occurrence localities. Areas follow Shreve (1942) and Morafka (1977). (A) Chihuahuan Desert subprovinces and distribution of studied species. (B) Delimitation of the Chihuahuan Desert. (C) *Berberis trifoliolata* (Berberidaceae). (D) *Ephedra aspera* (Ephedraceae). (E) *Setchellanthus caeruleus* (Setchellanthaceae). (F) *Leucophyllum laevigatum* (Scrophulariaceae). (G) *Lindleya mespiloides* (Rosaceae). Images taken by Diego F. Angulo, Israel Loera, Victoria Sosa, Etelvina Gándara and Marilyn Vásquez-Cruz, respectively. Full-size DOI: 10.7717/peerj.6572/fig-1
populations. The goal is to provide guidelines for conservation decision-making based on these data and the existing protected areas.

Using these five indicator endemic shrubby plants we aim to: (1) determine how genetic diversity is spatially distributed in the Chihuahuan Desert; (2) establish the effect of global climate change on their distribution based on predictions of future climate scenarios for 2070; (3) understand how habitat ecological resistance among species might be affected by future climate change; (4) identify the most vulnerable or resilient populations and evaluate if they are located within protected areas; (5) make recommendations for conservation decision-making.

**MATERIALS AND METHODS**

**Field study permissions.** We obtained collecting permits to conduct this work from the Secretaría de Medio Ambiente y Recursos Naturales, Instituto Nacional de Ecología, Dirección General de Vida Silvestre (permit number: Registro de Colección Científica VER-FLO-228-09-09).

**Study species.** We selected five endemic species to the Chihuahuan Desert (Fig. 1). The first is the Mormon tea gymnosperm *Ephedra aspera* Engelm. ex S. Watson, a wind-pollinated species with rugged yellowish stems, dry seed cones and large seeds dispersed by small mammals (*Hollander & Wall, 2009*). The four other species are angiosperms. *Berberis trifoliolata* Moric. (transferred to *Alloberberis* by *Chih-Chieh & Kuo-Fang, 2017*), known as algerita or agarito, is a small to large shrub with gray or blue foliage and leaflets with sharp spines, its yellow flowers are clustered and fragrant (*Angulo, Sosa & GarcíaFranco, 2014*). *Leucophyllum laevigatum* Standl. known as Chihuahuan Sage or blue Texas ranger, is one of the most showy shrubs in the desert and produces exuberant bright violet to purple small flowers that attract butterflies and bees; its plants are cultivated in nurseries and used as ornamentals in Texas and Arizona (*Henrickson & Flyr, 1985*). The rose species *Lindleya mespiloides* Kunth is the only species of a monotypic genus endemic to the Chihuahuan Desert, with a shrubby or tree-like life form with thick leaves, conspicuous white flowers and dry, capsular fruits (*Henrickson, 2012*). *Setchellanthus caeruleus* Brandegee is the sole species of Setchellanthaceae, a family endemic to the Chihuahuan Desert, and is receiving much interest because it produces glucosinolates and belongs to the group of mustard plants. Its shrubs or small trees have corky branches and showy lavender-violet flowers; populations are few and far between and have been collected only in the north of the desert and in the Tehuacán Valley (*Iltis, 1999*).

**Sampling and DNA sequencing.** We collected samples from populations of *E. aspera* and *Leucophyllum laevigatum* in their entire range. Protocols for extraction, amplification and sequencing including the DNA markers with their corresponding primers are the same utilized in previous research (*Gándara & Sosa, 2014*; *Loera, Ickert-Bond & Sosa, 2017*). For the three remaining species we used previously published sequences (*B. trifoliolata: Angulo et al., 2017*, *Lindleya mespiloides: Vásquez-Cruz & Sosa, 2016*; *S. caeruleus: Hernández-Hernández, Colorado & Sosa, 2013*) (Fig. 1; see Table 1 for...
| Sample location          | Code | Berberis trifoliata | Ephedra aspera | Leucophyllum laevigatum | Lindleya mespiloides | Setchellanthus caeruleus |
|--------------------------|------|---------------------|----------------|-------------------------|---------------------|-------------------------|
| México, Acatitlán, Qro   | ACT  | – – – – 21.2 –99.21 0.25 0.001 | – – – – | – – – – | – – – – | – – – – |
| Mexico, Arteaga, Coah    | ART  | 25.40 –100.80 0.5 | – – – – | 0.0004 – – 0 0 | – – – – | – – – – |
| Mexico, borderline Coah-Zac | FCZ | 24.98 –101.18 0 | 24.98 –101.18 0.56 0.0034 0 | – – | 0.47 0.00024 24.68 –101.40 1 0.00457 | – – – – |
| Mexico, C erro El Potosí, NL | CEP | 24.89 –100.19 0.47 | –100.18 24.88 0.77 0.0054 | 0.0008 | – – – – | – – – – |
| Mexico, Chih             | CHIH | 28.60 –106.12 0.39 | – – – – | 0.0003 | – – – – | – – – – |
| Mexico, Cuatro Genegas, Coah | CC | 27.30 –102.61 0.69 | – – – – | 0.001 | – – | 0.66 0.00034 | – – – – |
| México, Galeana, NL      | GAL  | – – – – – – – – | – – – – | – – | 24.75 –100.04 0.4 0.0002 | – – – – |
| Mexico, Guadalcazar, SLP | GUAD | 22.65 –100.43 0.17 | 22.61 –100.47 0.8 0.0038 | 0.0001 | – – – – | – – – – |
| Mexico, Ixmiquilpan, Hgo | IXM  | 20.61 –99.24 0.21 | – – – – | 0.0003 | – – – – | – – – – |
| México, Icotlán, Oax     | IIC  | – – – – 17.78 –97.48 0.53 0.0022 | – – – – | – – – – | – – – – | – – – – |
| México, La Angostura, Coah | ANG | 25.34 –101.05 0 | – – – – | 0 | – – – – | – – – – |
| México, La Gavia, Coah   | LG   | 26.35 –101.36 0.89 | – – – – | 0.001 | – – – – | – – – – |
| México, La Laguna, Qro   | LAG  | – – – – 21.27 –99.21 0.77 0.0039 | – – – – | – – – – | – – – – | – – – – |
| Mexico, La Zarca, Dgo    | ZAR  | – – – – – – – – | – – – – | – | 25.46 –104.60 0 0 | – – – – |
| México, Laguna Seca, SLP | LSE  | – – – – 22.27 –100.81 0.25 0.0005 | – – – – | – – – – | – – – – | – – – – |
| Mexico, Lerdo, Dgo       | LER  | – – – – – – – – | – – – – | – – – – | – – – – | 25.43 –103.7 0 0 |
| México, Maconí, Qro      | MAC  | – – – – 20.85 –99.55 0.9 0.0037 | – – – – | – – – – | – – – – | – – – – |
| Mexico, Mapimí, Dgo      | MAP  | – – – – – – – – | – – – – | – | 26.57 –103.97 0.66 0.00115 25.67 –103.87 0.25 0.00027 | – – – – |
| Mexico, Matehuala SLP    | MAT  | 25.14 –100.69 0.68 | – – – – | 0.002 | – – – – | – – – – |
| Mexico, Ojinaga, Chih    | OJIN | 29.15 –105.39 0.4 | – – – – | 0.0007 | – – – – | – – – – |
| Mexico, Ojuelas, Dgo     | OJU  | 25.80 –103.78 0.4 | 25.79 –103.79 1 0.0083 0.0003 | – – – – | – – – – | – – – – |
| Mexico, Pablillo, NL     | PAB  | 24.61 –100.00 0 | – – – – | 0 | – – – – | – – – – |
| Mexico, Parral, Chih     | PARRL | 27.32 –105.72 0.6 | – – – – | 0.0007 | – – | 0 0 27.32 –105.72 0.4 0.00138 | – – – – |
| Mexico, Parras, Coah     | PARR | 25.36 –102.18 0.91 | 25.36 –102.17 0.6 0.0037 0.002 | – – | 0 0 | – – – – |
| México, Peña Miller, Qro | MIL  | – – – – 21.09 –99.69 0.58 0.0023 | – – – – | – – – – | – – – – | – – – – |
| México, Ramos Anzpe, Coah | RAZ | 25.61 –100.83 0.5 | – – – – | 0.0004 | – – – – | – – – – |

(Continued)
Table 1 (continued).

| Sample location       | Code | Berberis trifoliolata Lat | Long | h | Ephedra aspera Lat | Long | h | Leucophyllum laevigatum Lat | Long | h | π | Lindleya mespiloides Lat | Long | h | π | Setchellanthus caeruleus Lat | Long | h | π |
|-----------------------|------|---------------------------|------|---|-------------------|------|---|---------------------------|------|---|---|--------------------------|------|---|---|----------------------------|------|---|---|
| Mexico, Rancho Jaguey, Coah | RJ   | 25.23                     | -101.02 | 0 | -                  | -    | - | 0                         | -    | - | - | 25.23                     | 25.23 | - | - | -                         | -    | - | - |
| Mexico, Real de Catorce SLP | RC   | 23.74                     | -100.85 | 0.81 | 23.73             | -100.84 | 0.73 | 0.0018                    | 0.002 | 0 | 0 | 23.74                     | 23.74 | - | 0 | 0                         | 0.0016 | - | - |
| Mexico, Rocamontes, Dgo | ROCA | 24.74                     | -101.18 | 0 | 24.62             | -101.23 | 0.6  | 0.00037                   | 0      | 0 | 0 | 24.74                     | 24.74 | - | 0 | 0                         | 0.0003 | - | - |
| Mexico, Rodeo, Dgo    | ROD  | -                        | -      | - | -                 | -    | - | -                         | -    | - | - | 25.11                     | 25.11 | - | - | -                         | -    | - | - |
| Mexico, San Juan del Rio, Dgo | ATO | -                        | -      | - | -                 | -    | - | -                         | -    | - | - | 24.84                     | 24.84 | - | - | -                         | -    | - | - |
| Mexico, San Pedro Iturbide, NL | SPI | 24.72                     | -99.91  | 0.33 | 24.74             | -99.93 | 0.47  | 0.0019                    | 0.0002 | 0 | 0 | -                        | -    | - | - | -                         | -    | - | - |
| Mexico, Santa María del Oro, Dgo | StaMO | 25.99                    | -105.33 | 0 | -                 | -    | - | -                         | 0      | 0 | 0 | 26.00                     | 26.00 | - | - | -                         | -    | - | - |
| México, Santa Teresa, SLP | TER  | -                        | -      | - | -                 | -    | - | -                         | -    | - | - | -                        | -    | - | - | -                         | -    | - | - |
| Mexico, Sierra de San Miguel, NL | SSM | 26.11                     | -100.66 | 0.4 | -                 | -    | - | -                         | 0.001  | 0 | 0 | -                        | -    | - | - | -                         | -    | - | - |
| México, Sierra Mojada, Coah | MOJ | -                        | -      | - | -                 | -    | - | -                         | -    | - | - | 27.26                     | 27.26 | - | 0 | 0                         | 0.007 | - | - |
| México, Tamazulapan, Oax | TAM  | -                        | -      | - | -                 | 17.66 | -97.58 | 0.34  | 0.0007                    | -      | - | - | 18.09                     | 18.09 | - | - | 0.00815                   | -    | - | - |
| Mexico, Teotitlán, Oax | TEO  | -                        | -      | - | -                 | -    | - | -                         | -    | - | - | 18.37                     | 18.37 | - | - | -                         | -    | - | - |
| México, Teotongo, Oax | TT   | -                        | -      | - | -                 | 17.76 | -97.54 | 0.75  | 0.0026                    | -      | - | - | -                        | -    | - | - | -                         | -    | - | - |
| Mexico, Trópico de Cáncer, Zac | TCA | -                        | -      | - | -                 | 23.67 | -101.91 | 0.71  | 0.0049                    | 23.68 | -101.92 | 0 | - | -                        | -    | - | - |
| Mexico, Ventura, SLP | VEN  | 22.38                     | -100.77 | 0.17 | -                 | -    | - | -                         | 0.0001 | - | - | -                        | -    | - | - | -                         | -    | - | - |
| Mexico, Zapotitlán de Salinas Pue | TEH | -                        | -      | - | -                 | 18.37 | -97.47 | 0.83  | 0.0044                    | -      | - | - | 18.31                     | 18.31 | - | - | 0.00163                   | -    | - | - |
| Mexico, Zaragoza, NL | ZAG  | -                        | -      | - | -                 | 23.97 | -99.79 | 0.93  | 0.00045                   | -      | - | - | -                        | -    | - | - | -                         | -    | - | - |
| US Austin, Texas | AUST | 30.14                     | -97.96  | 0 | -                 | -    | - | -                         | 0      | 0 | 0 | -                        | -    | - | - | -                         | -    | - | - |
| US Purola, Texas | PUR  | 30.49                     | -98.2   | 0.85 | -                 | -    | - | -                         | 0.001  | - | - | -                        | -    | - | - | -                         | -    | - | - |

Note: Populations studied, indicating population abbreviation, number of plants, geographic region, latitude and longitude where they were collected, as well as molecular diversity indices and their respective haplotypes. San Luis Potosi (SLP), Coahuila (Coah), Zacatecas (Zac), Nuevo Leon (NL), Durango (Dgo), Chihuahua (Chih), Hidalgo (Hgo), Haplotype diversity (h), nucleotide diversity (π).
localities). The plastid markers sequenced were \textit{trnF-trnL}, \textit{rpl32-trnL}, \textit{trnH-psbA} and \textit{psbI-psbK}. GenBank accessions representing all haplotypes in the populations of each species are listed in Table S1.

**Genetic analyses.** Parameters of population diversity, such as haplotype diversity ($h$) and nucleotide diversity ($\pi$), were estimated for each population using DnaSP (Librado & Rozas, 2009). Haplotype genetic diversity ($h$) was interpolated for each species using a distance weighted interpolation in ArcView v. 3.2 (ESRI, Redlands, CA, USA). In order to visualize the genetic diversity on a map, we plotted this interpolation over a hill shade map obtained from the digital elevation model Hydro1K. We then averaged the genetic diversity of all species to identify the areas that share the highest genetic diversity. Genetic differentiation among populations of the studied species was estimated by pairwise $F_{st}$ with an analysis of molecular variance with ARLEQUIN ver. 3.5.1.2 (Excoffier & Lischer, 2010) with 1,000 simulations performed to test significance of covariance components and fixation indices.

**Ecological niche-based modeling.** The geographical coordinates of the species utilized in this study were collected in the field and complemented with information consulted in the following herbaria: ARIZ, ENCB, MEXU, TEX and XAL as well as from the Global Biodiversity Information Facility GIBIF (www.gbif.org) to carry out Ecological Niche Modeling (ENM). They comprised the entire distribution of species (the number of records used in each species is given in Table S2). \textit{S. caeruleus} is a relict taxon recorded in only two localities with a few individuals, and we considered all occurrences. We used the biogeographic sub-regions of the Chihuahuan Desert proposed by Morafka (1977, 1989) based on climate and distribution data for flora and fauna: Sonora-Cochise, Transpecos, Mapimian, Saladan and Rio Pánuco; we also included the Tehuacán Valley proposed by Shreve (1942) as a satellite area of the Chihuahuan Desert (Fig. 1). Considering a pixel of one km$^2$, ENM was estimated for each species. Environmental inputs were based on the 19 climate variables from the WorldClim data base version 1.4 (Hijmans et al., 2005) at a 2.5 min resolution. These variables represent global precipitation and temperature conditions for the years 1960–1990.

Prior to estimating ENM’s we performed a paired Pearson correlation analysis based on the extracted environmental data of all the occurrence points. Then we selected a set of uncorrelated variables (Pearson correlation coefficients below 0.7) as environmental inputs. The latter resulted in a set of eight bioclimatic variables (i.e., BIO2 = Mean Diurnal Range (Mean of monthly (max temp—min temp), BIO4 = Temperature Seasonality (standard deviation *100), BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO9 = Mean Temperature of Driest Quarter, BIO12 = Annual Precipitation, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation). In addition, a principal component analysis (PCA) analysis was conducted to corroborate the most significant climate variables (see results in Fig. S1) using the statistical software R with the package raster (Thuiller et al., 2016). Species distribution modeling (SDM) were estimated using the maximum
entropy algorithm (MaxEnt) implemented in the R package biomod2 (Thuiller et al., 2016).

For each species, occurrence data was divided using 70% of the records for training the models and 30% for testing them. A total of 10 replicates per each species were used and from these, geographic predictions and performance was averaged per species. Model performance was estimated for the projections in the climatic scenario for the present using the statistical metrics relative operating characteristic (ROC), TSS (true skill statistic) and Kappa. Values for ROC range from zero to one, with values greater than 0.5 meaning the model predicts testing points better than a random expectation. TSS and Kappa values range from −1 to 1 where values close to 0 indicate a prediction not different than random whereas positive values indicate predictions better than random. To integrate most of the variation observed in the bioclimatic variables, we alternatively performed a multivariate analysis. A PCA was performed using 19 bioclimatic variables of all the climatic scenarios used in this study and reduce the observed variation on a set of uncorrelated PC axes. Then, we used the PC scores of these axes to generate raster layers for each climate scenario as environmental inputs to estimate SDMs and perform geographic projections. The first six PC axes explained more than 95% of the observed variation and were used to estimate SDMs. Loading contributions for each of the PC axes used are showed in Table S4. PCA analyses were conducted in the statistical software R using the package raster (Thuiller et al., 2016).

To predict whether suitability conditions of each species might potentially change in the future we projected the estimated ENMs to future climate scenarios (i.e., for the year 2070). We used the “Representative Concentration Pathways” (RCPs) RCP 2.6 and 8.5 climate scenarios that represent the most optimistic and pessimistic scenarios, respectively. The RCPs are coherent with an ample range of probable changes in future human greenhouse gas emissions with the objective or representing their atmospheric concentrations. RCP 2.6 expects that global annual greenhouse gas emissions will reach the highest point between 2010 and 2020, and that they will descend substantially thereafter while the RCP 8.5 expects that emissions continue to rise during the 21st century (Meinshausen et al., 2011). In addition, two different general circulation models (GCMs) for each of these scenarios were used to obtain the geographic predictions. These GCMs were CCSM4 and MIROC-ESM. All future environmental layers were based on the WorldClim database version 1.4 (Hijmans et al., 2005). We averaged the suitability values of the two different climate simulations for each RCP scenario to perform geographic projections under future scenarios.

**Evaluation of protected areas and genetic diversity.** To identify whether the areas with the highest genetic diversity lie within protected areas we also overlaid protected areas on the distribution maps of the sampled populations. Protected area shape files from Mexico were downloaded from the National Commission of Protected Natural Areas (CONANP, www.gob.mx/conanp) and the world database on protected areas (https://www.iucn.org/theme/protected-areas). Protected areas in Texas were obtained from the Texas Parks and Wildlife Department (tpwd.texas.gov). Table 2 includes the protected areas within the Chihuahuan Desert.
| Code | Name                                                | Designation                                      | Designation type                   | Area     |
|------|-----------------------------------------------------|--------------------------------------------------|------------------------------------|----------|
| 0    | Pico de Orizaba                                    | National Park                                   | National                           | 0        |
| 1    | Cofre de Perote                                     | National Park                                   | National                           | 0        |
| 2    | Gogorrón                                            | National Park                                   | National                           | 0        |
| 3    | Cumbres de Monterrey                               | National Park                                   | National                           | 1,773.96 |
| 4    | Cuatrociénegas                                      | Flora and Fauna Protection Area                 | National                           | 843.47   |
| 5    | Maderas del Carmen                                  | Flora and Fauna Protection Area                 | National                           | 2,083.81 |
| 6    | Los Mámoles                                         | National Park                                   | National                           | 231.5    |
| 7    | Sierra Gorda                                        | Biosphere Reserve                               | National                           | 3,835.67 |
| 8    | Cerro El Potosí                                     | Area Subject to Ecological Conservation          | National                           | 9.8938   |
| 9    | Cuenca Alimentadora del Distrito Nacional de Riego  | Natural Resources Protection Area                | National                           | 0        |
| Don Martín                                  |                                                  |                                                  |          |
| 10   | Huiricuta y la Ruta Histórica Cultural del Pueblo   | Not reported                                     | National                           | 1,400    |
| Huichol                                     |                                                  |                                                  |          |
| 11   | Ocampo                                              | Flora and Fauna Protection Area                 | National                           | 3,442.38 |
| 12   | Real de Guadalcázar                                 | Not reported                                     | National                           | 2,570    |
| 13   | Serranía de Zapalinamé                              | Area Subject to Ecological Conservation          | National                           | 257.6868 |
| 14   | Sierra y Cañón de Jimulco                           | Natural protected area and ecological reserve    | National                           | 604.5826 |
| 15   | Zona de Restauración Ecológica del Lobo Mexicano    | Certified                                        | National                           | 0        |
| San Joaquín de Soto                         |                                                  |                                                  |          |
| 16   | Tehuacán-Cuicatlán                                 | Biosphere Reserve                               | National                           | 4,901.87 |
| 17   | Barranca de Metztitlán                              | Biosphere Reserve                               | National                           | 960.43   |
| 18   | Mapimí                                              | Biosphere Reserve                               | National                           | 3,423.88 |
| 19   | Sierra de Alvarez                                   | Flora and Fauna Protection Area                 | National                           | 169      |
| 20   | Rio Sabinas                                         | Ramsar Site, Wetland of International Importance | International                      | 6,031.23 |
| 21   | Laguna de Santiaguillo                              | Ramsar Site, Wetland of International Importance | International                      | 240.16   |
| 22   | Big Bend National Park                              | UNESCO-MAB Biosphere Reserve                     | International                      | 2,832.47 |
| 23   | Black Gap                                           | State Wildlife Management Area                   | National                           | 0        |
| 24   | Mason Mountain                                      | State Wildlife Management Area                   | National                           | 0        |
| 25   | Old Tunnel                                          | State Wildlife Management Area                   | National                           | 0        |
| 26   | Honey Creek                                         | State Natural Area                               | National                           | 0        |
Current and future environmental resistance to gene flow. We estimated ecological resistance among populations using the habitat suitability raster file derived from ecological niche modeling as a conductance matrix in Circuitscape 4.0.5 (McRae & Beier, 2007). Circuitscape considers the landscape to be an electrical circuit in which populations serve as sources or sinks of electrical current, while environmental features either inhibit or assist the flow of that current by providing high or low resistance to the circuit(s) connecting the populations (McRae & Beier, 2007). Environmental resistance was averaged for each species considering current and future climate scenarios and plotted using boxplots.

RESULTS
Genetic diversity and its spatial distribution
Haplotype and nucleotide diversity for every population of each species is included in Table 1 and displayed in Figs. 2A–2F. The B. trifoliolata population with the highest haplotype diversity (h) was located in the Mapimian subprovince in La Gavia and Parras (Fig. 2A); in Leucophyllum laevigatum it was in the Saladan and Mapimian subprovinces (Fig. 2C); S. caeruleus in the Tehuacán Valley (Fig. 2E); E. aspera in the Mapimian subprovince; and Lindleya mespiloides in the Saladan subprovince (Figs. 2B and 2D). The nucleotide diversity $\pi$ of B. trifoliolata coincides with the same localities mentioned above and in the Texas population; for Leucophyllum laevigatum nucleotide diversity was highest in Parral and Rocamontes Durango; S. caeruleus in Tehuacán, E. aspera in Galeana; and Lindleya mespiloides in Hojuelas, Durango (Fig. 2D). Among the populations of all of the species, L. laevigatus and S. caeruleus populations had the highest haplotype diversity. For E. aspera, B. trifoliata, Leucophyllum laevigatum and Lindleya mespiloides the highest haplotype diversity occurred in the Mapimian subprovince (Figs. 2A–2D), and for S. caeruleus in Tehuacán (Fig. 2E). Genetic landscape analysis revealed high haplotype diversity for all species in the northwestern areas of the Chihuahuan Desert with the exception of S. caeruleus for which haplotype diversity was high in the Tehuacán Valley (Fig. 2F). Average haplotype diversity was high along the mountains in localities in Texas, the Sierra Madre Oriental and the Tehuacán Valley (Fig. 2F). Table 3 includes Fst estimations for studied species with their corresponding $P$-values, indicating that S. caeruleus has the highest values with the highest degree of differentiation among populations (Table S3 includes Fst pairwise estimations for populations of every species).

Ecological niche modeling
Model performance evaluated with the ROC is summarized in Table 4, showing similar values for every studied species. Table 5 includes eigenvalues retrieved by the PCA that were utilized to generate SMDs (individual eigenvalues for every species are presented in Table S4). In general, current ENMs accurately predicted the known distribution of every species (Fig. 3), though the models over-predicted ranges of E. aspera, Lindleya mespiloides and S. caeruleus (Fig. 3). Future ENM with RCP2.6 and RCP8.5 models predicted extended ranges for all studied species, although RCP8.5 predicted less considerable areas (Fig. 3). Suitable conditions predicted by current and future climate...
scenarios were identified in the Mexican Plateau, in the areas corresponding to the Mapimian and Saladan subprovinces as well as in the Sierra Madre Oriental. Results with CCSM4 and MIROC-ESM climate scenarios were congruent with RCP2.6 and RCP8.5, respectively (included in Fig. S2).
Current and future environmental resistance

Estimates of environmental resistance based on the prediction of current ecological niche models are displayed in Fig. 4. The most important temperature and precipitation variables were assigned resistance costs ranging from zero (no resistance to movement) to 100 (strong barrier to movement). *B. trifoliolata* and *E. aspera* had the most elevated changes in environmental resistance under present and future climate scenarios with a predicted increase in environmental resistance that would lead to lower gene flow (Fig. 4). The other species have a similar degree of environmental resistance under current and future climate scenarios (Fig. 4).

Protected areas and genetic diversity

For the five species, most of the populations with high genetic diversity are located in unprotected areas, with the exception of the Tehuacán Valley Biosphere Reserve, and the

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Table 3  **Fixation index Fst for populations of the five studied species.** Number of populations, and variance components among populations and within populations is indicated.

| Source of variation | Berberis trifoliolata | Ephedra compacta | Leucophyllum laeavigatum | Lindleya mespiloides | Setchellanthus caeruleus |
|---------------------|-----------------------|------------------|--------------------------|----------------------|-------------------------|
| Sample populations  | 20                    | 9                | 9                        | 20                   | 4                       |
| Among populations   | d.f 19                | 8                | 8                        | 19                   | 3                       |
| Sum of squares      | 101.485               | 62.021           | 70.591                   | 207.293              | 35.833                  |
| Variance components | 1.80299 Va            | 1.95550 Va       | 1.73775 Va               | 1.33925 Va           | 2.20357 Va              |
| Percentage of variation | 55.05         | 94.80            | 64.63                    | 64.59                | 84.57                   |
| Within populations  | d.f 24                | 27               | 32                       | 133                  | 17                      |
| Sum of squares      | 35.33                 | 2.895            | 30.433                   | 97.661               | 6.833                   |
| Variance components | 1.47222 Vb            | 0.10723 Vb       | 0.95104 Vb               | 0.73429 Vb           | 0.40196 Vb              |
| Percentage of variation | 44.95             | 5.20             | 35.37                    | 35.41                | 15.43                   |
| Total               | d.f 43                | 35               | 40                       | 152                  | 20                      |
| Sum of squares      | 136.818               | 64.917           | 101.024                  | 304.954              | 42.667                  |
| Variance components | 3.27521               | 2.06273          | 2.68879                  | 2.07354              | 2.60553                 |
| Percentage of variation | 20                | 42.667           | 2.60553                  |                      |                         |
| Fixation index (Fst) | 0.55049 ***           | 0.94801 ***      | 0.64629 ***              | 0.64587 ***          | 0.84573 ***             |

Note: *** Significant values at P < 0.000, significance tests (1,000 permutations).

Table 4  **Model performance metrics for SDMs using the set of uncorrelated bioclimatic variables.** Results are averages of 10 replicates per species using the 30% of occurrence data to test model performance.

| Species                | Mean Kappa | Mean TSS | Mean ROC |
|------------------------|------------|----------|----------|
| *Berberis trifoliolata*| 0.5241     | 0.5822   | 0.8429   |
| *Ephedra aspera*       | 0.4821     | 0.5575   | 0.8277   |
| *Leucophyllum laeavigatum* | 0.4771  | 0.553    | 0.8252   |
| *Lindleya mespiloides* | 0.5267     | 0.5973   | 0.8461   |
| *Setchellanthus caeruleus* | 0.4823 | 0.5622   | 0.8215   |
southernmost area of the Chihuahuan Desert (Figs. 5A–5C, protected areas 49, 51 and 56, see Table 2 for information on protected areas, their designation and their surface area). In the central area of the Chihuahuan Desert, populations with high genetic diversity lie between two protected areas (Fig. 5, protected area 11 Los Mármoles and 12 Sierra Gorda). In the central-eastern part of the desert there is a high diversity of populations in an area specifically protected for wild wolves, not for the biota in general (Fig. 5, 55 Protected area for the Mexican wolf Zamora). In summary, two zones in the Chihuahuan Desert have the greatest haplotype diversity: the southern region of the Sierra Madre Oriental (between protected areas 42 Sierra Santa Marta de Abajo and 54 Zona de Restauración Ecológica del Lobo Mexicano Potrero de Zamora, Fig. 5B), and the Tehuacán Valley (around protected areas 49 and 56, which correspond to the Tehuacán-Cuicatlán Biosphere Reserve, see Fig. 5C).

DISCUSSION

Genetic diversity and its spatial distribution

In plants, higher genetic diversity has been frequently found in zones that had a stable climate during glacial periods and for which post-glacial migration was identified (Faye et al., 2016; Wolfe et al., 2016), and in contrast, unstable regions are expected to

| PC axes | Eigenvalues  | Variation explained | Cumulative variation explained |
|---------|--------------|---------------------|-------------------------------|
| PC1     | 0.49896854  | 0.013104625         | 0.983323705                  |
| PC2     | 0.32075430  | 0.005663578         | 0.988978283                  |
| PC3     | 0.26855034  | 0.003781631         | 0.992768913                  |
| PC4     | 0.23764228  | 0.002967856         | 0.99573677                   |
| PC5     | 0.1646206   | 0.001423567         | 0.999716036                  |
| PC6     | 0.13549916  | 0.000966317         | 0.999812654                  |
| PC7     | 0.10307274  | 0.000559157         | 0.999875811                  |
| PC8     | 0.10144121  | 0.000545196         | 0.999922740                  |
| PC9     | 0.08939732  | 0.000420625         | 0.999964032                  |
| PC10    | 0.07367577  | 0.000285691         | 0.999993723                  |
| PC11    | 0.03281499  | 5.67E-05            | 0.999999398                  |
| PC12    | 0.01262439  | 8.39E-06            | 0.999998786                  |
| PC13    | 0.01014121  | 4.23E-06            | 0.999998786                  |
| PC14    | 0.00480265  | 1.21E-06            | 1                             |

Note: Rows in bold represent the variables used to generate raster layers to estimate SDMs and perform projection on geographic space.
represent recently colonized areas and thus exhibit lower genetic diversity (Abellán & Svenning, 2014; Caze et al., 2016; Ornelas, Licona-Vera & Vásquez-Aguilar, 2018). Higher genetic diversity has been found as well in environments that fluctuate in time or space, in which different genotypes can be favored at different times or locations and shifting selection can support higher genetic variation in fitness, even when stabilizing selection is acting to reduce genetic variation (Nadeau, Urban & Bridle, 2017). In particular for the Chihuahuan Desert southern areas such like the Mezquital and the Tehuacán Valleys, have been proposed as areas of refugia for the biota of this warm desert because they were isolated during periods of glacial-interglacial cycles, with semi-arid climates and it has been discovered that a number of plants from these areas have high genetic diversity (Loera, Ickert-Bond & Sosa, 2017).
Results here coincide with these findings: (1) high nucleotide diversity was found for populations of *Lindleya mespiloides* and *S. caeruleus* in the southernmost limits of the Chihuahuan Desert areas that have been proposed as refugia; (2) with the exception of *S. caeruleus* the other species studied had high nucleotide diversity in several areas of the Mexican Plateau that had a stable climate during glacial periods, and moreover this species has the highest population differentiation; (3) the average of high haplotype diversity values for the five species along the Sierra Madre Oriental mountain range coincided with those expected for fluctuating environments.

In addition, results here agree with the indicators of genetic variation identified for various plant species distributed in the Chihuahuan Desert, such as *Fouquieria shrevei* (Aguirre-Liguori, Scheinvar & Eguiarte, 2014), *Agave striata* (Trejo, Alvarado-Cárdenas & Scheinvar, 2016), and *A. lechuguilla* (Scheinvar, Gámez & Castellanos-Morales, 2017), in which high genetic diversity was identified in the north coinciding with findings for *E. aspera* and *Leucophyllum laevigatum*. Likewise for *Hunnemannia fumariifolia*, high genetic variation was associated with areas in the vicinity of the Sierra Madre Oriental...
Sosa, Ruiz-Sanchez & Rodríguez-Gómez, 2009), coinciding with results for B. trifoliata and Leucophyllum laevigatum.

**Ecological niche modeling and ecological resistance**

Forecast showed that global warming would favor an expansion mostly in the western range for the five studied species, under the two models RCP2.6 and RCP8.5 (Fig. 3). RCP 2.6 and RCP 8.5 are sets of predictions that exclusively consider the components of radiative forcing, forecasting how energy is transmitted between grids using the laws of thermodynamics, allowing to estimate dozens of environmental variables (Moss et al., 2010). The RCP 2.6 scenario is the best case for limiting anthropogenic climate change in which global CO$_2$ emission peak by 2020 and decline around 2080. The RCP 8.5 scenario is the worst because it considers that emission continue to increase rapidly and by 2100 will stabilize. This scenario is highly energy intensive continuing to grow until the century reaching approximately three times current levels. Even though the latter model is based on higher emissions projecting more elevated future temperature, the ecological modeling did not predict marked differences in range of the studied species.
Results show that ecological resistance for the majority of species is similar in present and future conditions with the exception of *B. trifoliolata* and *E. aspera* where the ecological resistance will increase in future conditions. Ecological resistance can reduce functional connectivity and gene flow between populations (*McRae & Beier, 2007; Spear et al., 2010; Peterman et al., 2014*) and might affect genetic structure. Likewise, lower resistance leads to higher dispersal for individuals (*Cushman et al., 2006*). Thus the rest of species might be affected in connectivity among populations in future scenarios of climate change.

Protected areas, genetic diversity and ecological resistance

On one hand, designing biodiversity conservation strategies should maximize genetic diversity and preserve adaptive potential (*Polfus et al., 2016*). On the other hand, identifying and protecting climate-change refugia is a good approach for conservation, particularly in areas of complex topography (*Brito et al., 2016; Corlett & Westcott, 2013*). Furthermore, mountain ranges constitute important centers of diversification in arid regions and act as species pumps into surrounding areas, in addition to being important reservoirs of cryptic diversity, even of common and widespread species (*García-Porta et al., 2017*).

Thus, we propose the preservation of two areas with high haplotype diversity, identified by ecological niche modeling in the Mexican Plateau and on the slopes of the Sierra Madre Oriental mountain range that will have suitable climate conditions in the future (these areas are indicated in *Fig. 5*). Despite the apparently large number of reserves in the Mexican system of natural areas that are located in the Chihuahuan Desert, only four large biosphere reserves are well managed: Barranca de Meztitlán, Mapimí, Sierra Gorda and Tehuacán-Cuicatlán. The others fall under a different designation, and some of them are small and not actively protected.

CONCLUSIONS

In summary, this study shows that even shrubby species adapted to arid conditions will be affected by climate change; the five species will have suitable climate conditions for expanding their distribution to the west of the Chihuahuan Desert according to the future climate scenarios. However, for species with low ecological resistance, climate change can have the effect of allowing gene flow among populations. Based on suitability of habitat and haplotype diversity, we suggest preserving two hotspots of genetic diversity in the Sierra Madre Oriental, located in areas without protection.

Innovative conservation measures are being currently proposed such like moveable and temporary reserves as well as targeted gene flow (*Reside, Butt & Adams, 2018*). Resilient species to climate change are crucial for understanding genomics of climate change, assessing genes involved with the response to their future environment in view of climate change (*Rellstab et al., 2016*). We suggest these measures of moveable reserves and genomics of climate change should be implemented in the Chihuahuan Desert plants.

Understanding the effect of climate change in plants of the Chihuahuan Desert is crucial: (1) dry tropical areas are extremely understudied compared to the humid biomes (*Muenchow et al., 2018*); (2) species in deserts are preserved evidence of humid past. In particular the woody elements of the warm Chihuahuan Desert formed part of the
Madro-Tertiary Geoglora, a fossil flora from the southwestern United States and North of Mexico so desert species are outstanding repositories of past climate changes; (3) the most decisive climate variables in deserts are related to temperature and precipitation, understanding future changes in both gives insights whether plants will be capable of adaptation to changes in these climate variables.

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Victoria Sosa is an Academic Editor of PeerJ. The rest of the authors declare that they have no competing interests.

Author Contributions
- Victoria Sosa conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Israel Loera performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Diego F. Angulo performed the experiments, analyzed the data, authored or reviewed drafts of the paper, approved the final draft.
- Marilyn Vásquez-Cruz performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Etelvina Gándara performed the experiments, analyzed the data, authored or reviewed drafts of the paper, approved the final draft.

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Data Availability
The following information was supplied regarding data availability:
GenBank accession numbers and newly generated sequences are available in Table S1, and the georeferences are included in the Supplementary Material.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.6572#supplemental-information.

REFERENCES
Abellán P, Svenning J-C. 2014. Refugia within refugia: patterns in endemism and genetic divergence linked to Late Quaternary climate stability in the Iberian Peninsula. Biological Journal of the Linnean Society 113(1):13–28 DOI 10.1111/bij.12309.
Aguirre-Liguori JA, Scheinvar E, Eguiarte LE. 2014. Gypsum soil restriction drives genetic differentiation in Fouquieria shrevei (Fouquieriaceae). American Journal of Botany 101(4):730–736 DOI 10.3732/ajb.1400031.
Anadón JD, Sala OE, Maestre FT. 2014. Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. Journal of Ecology 102(6):1363–1373 DOI 10.1111/1365-2745.12325.
Angulo DF, Amarilla LF, Anton AM, Sosa V. 2017. Colonization in North American Arid lands: the journey of agarito (Berberis trifoliolata) revealed by multilocus molecular data and packrat mound fossil remains. PLOS ONE 12(2):e0168933 DOI 10.1371/journal.pone.0168933.
Angulo DF, Sosa V, García-Franco JG. 2014. Floral movements: stamen motion in Berberis trifoliolata. Botanical Sciences 92(1):14–44 DOI 10.17129/botsci.46.
Aragón-Gastélum JL, Flores J, Yáñez-Espinosa L, Badano E, Ramírez-Tobías HM, Rodas-Ortiz JP, González-Salvatierra C. 2014. Induced climate change impairs photosynthetic performance in Echinocactus platyacanthus, an especially protected Mexican cactus species. Flora—Morphology, Distribution, Functional Ecology of Plants 209(9):499–503 DOI 10.1016/j.flora.2014.06.002.
Báez S, Collins SL, Pockman WT, Johnson JE, Small EE. 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. Oecologia 172(4):1117–1127 DOI 10.1007/s00442-012-2552-0.
Bell CW, Tissue DT, Loik ME, Wallenstein MD, Acosta-Martínez V, Erickson RA, Zak JC. 2014. Soil microbial and nutrient responses to 7 years of seasonally altered precipitation in a Chihuahuan Desert grassland. Global Change Biology 20(5):1657–1673 DOI 10.1111/gcb.12418.
Brito JC, Tarroso P, Vale CG, Martínez-Freiría F, Boratyński Z, Campos JC, Ferreira S, Godinho R, Gonçalves DV, Leite J, Lima VO, Pereira P, Santos X, Ferreira da Silva MJ, Silva TL, Velo-Antón GM Veríssimo J, Crochet PA, Pleguezuelos JM, Carvalho SB. 2016. Conservation biogeography of the Sahara-Sahel: additional protected areas are needed to secure unique biodiversity. Diversity and Distributions 22(4):371–384 DOI 10.1111/ddi.12416.
Carrillo-Angeles IG, Suzán-Azpiri H, Mandujano MC, Golubov J, Martínez-Avalos JG. 2016. Niche breadth and the implications of climate change in the conservation of the genus Astrophytum (Cactaceae). Journal of Arid Environments 124:310–317 DOI 10.1016/j.jaridenv.2015.09.001.
Caze ALR, Mader G, Nunes TS, Queiroz LP, De Oliveira G, Diniz JAF, Bonatto SL, Freitas LB. 2016. Could refuge theory and rivers acting as barriers explain the genetic variability
distribution in the Atlantic forest? *Molecular Phylogenetics and Evolution* **101**:242–251
DOI 10.1016/j.ympev.2016.05.013.

Chih-Chieh Y, Kuo-Fang C. 2017. Why *Mahonia*? Molecular recircumscription of *Berberis* s.l., with the description of two new genera, *Alloberberis* and *Moranothamnus*. *Taxon* **66**(6):1371–1392
DOI 10.12705/666.6.

Cooke R, Warren A, Goudie A. 2013. Deserts of the world. In: Malloy R, Brock J, Floyd A, Livingston M, Webb RH, eds. *Design with the Desert: Conservation and Sustainable Development*. Boca Raton: CRC Press, 3–36.

Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* **28**(8):482–488
DOI 10.1016/j.tree.2013.04.003.

Cushman SA, McKelvey KS, Hayden J, Schwartz MK. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *American Naturalist* **168**(4):486–499
DOI 10.1086/506976.

Ellstrand NC. 2014. Is gene flow the most important evolutionary force in plants? *American Journal of Botany* **101**(5):737–753
DOI 10.3732/ajb.1400024.

Ellstrand NC, Elam DR. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* **24**(1):217–242
DOI 10.1146/annurev.es.24.110193.001245.

Excoffier L, Lischer EL. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* **10**(3):564–567
DOI 10.1111/j.1755-0998.2010.02847.x.

Faye A, Deblauwe V, Mariac C, Richard D, Sonké B, Couvreur TLP. 2016. Phylogeography of the genus *Podococcus* (Palmae/Arecaceae) in Central African rain forests: climate stability predicts unique genetic diversity. *Molecular Phylogenetics and Evolution* **105**:126–138
DOI 10.1016/j.ympev.2016.08.005.

Forester BR, DeChaine EG, Bunn AG. 2013. Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions* **19**(12):1480–1495
DOI 10.1111/ddi.12098.

García RA, Cabeza M, Rahbek C, Araújo MB. 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* **344**(6183):1247579
DOI 10.1126/science.1247579.

García-Porta J, Simó-Riuadlbas M, Robinson M, Carranza S. 2017. Diversification in arid mountains: biogeography and cryptic diversity of *Pristurus rupestris* in Arabia. *Journal of Biogeography* **44**(8):1694–1704
DOI 10.1111/jbi.12929.

Harris JA, Hobbs RJ, Higgs E, Aronson J. 2006. Ecological restoration and global climate change. *Restoration Ecology* **14**(2):170–176
DOI 10.1111/j.1526-100X.2006.00136.x.

Henrickson J. 2012. Systematics of *Lindleya* (Rosaceae: Maloideae). *Journal of the Botanical Research Institute of Texas* **6**:341–360.

Henrickson J, Flyr LD. 1985. Systematics of *Leucophyllum* and *Eremogeton* (Scrophulariaceae). *Sida* **11**:107–172.

Henrickson J, Johnston MC. 1986. Vegetation and community types of the Chihuahuan Desert. In: Barlow A, Powell M, Timmermann BN, eds. *The Second Symposium on Resources of...*
the Chihuahuan Desert Region, United States and Mexico. Alpine: Chihuahuan Desert Research Institute, 20–39.

Hernández-Hernández T, Colorado WB, Sosa V. 2013. Molecular evidence for the origin and evolutionary history of the rare American desert monotypic family Setchellanthaceae. *Organisms Diversity & Evolution* 13(4):485–496 DOI 10.1007/s13127-013-0136-4.

Hijmans R, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15):1965–1978 DOI 10.1002/joc.1276.

Hollander JL, Wall SB. 2009. Dispersal syndromes in North American *Ephedra*. *International Journal of Plant Sciences* 170(3):323–330 DOI 10.1086/596334.

Huenneke LF, Anderson JP, Remmenga M, Schlesinger WH. 2002. Deserti
dication alters patterns of aboveground network production in Chihuahuan ecosystems. *Global Change Biology* 8(3):247–264 DOI 10.1046/j.1365-2486.2002.00473.x.

Iltis HH. 1999. Setchellanthaceae (Capparales), a new family for a relictual, glucosinolate-producing endemic of the Mexican deserts. *Taxon* 48(2):257–275 DOI 10.2307/1224431.

Kelly AE, Goudlen ML. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105(33):11823–11826 DOI 10.1073/pnas.0802891105.

Librado P, Rozas J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25(11):1451–1452 DOI 10.1093/bioinformatics/btp187.

Loera I, Ickert-Bond SM, Sosa V. 2017. Pleistocene refugia in the Chihuahuan Desert: the phylogeographic and demographic history of the gymnosperm Ephedra compacta. *Journal of Biogeography* 44(12):2706–2716 DOI 10.1111/jbi.13064.

McRae BH, Beier P. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academic of Sciences of the United States of America* 104(50):19885–19890 DOI 10.1073/pnas.0706568104.

Meinshausen M, Smith SJ, Calvin K, Daniel JS, Kainuma MLT, Lamarke J-F, Matsumoto K, Montzka SA, Raper SCB, Riahi K, Thompson A, Velders GJM, Van Vuuren DPP. 2011. The RCP greenhouse gas concentration and their extensions from 1765 to 2300. *Climatic Change* 109(1–2):213–241 DOI 10.1007/s10584-011-0156-z.

Morafka DJ. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Dordrecht: Springer Science & Business Media.

Morafka DJ. 1989. An interdisciplinary definition of North America’s Chihuahuan Desert: is it desirable and obtainable? In: *Yearbook, Conference of Latin Americanist Geographers*. Baton Rouge: Louisiana State University, 23–34.

Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, Van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T, Meehl GA, Mitchell JFB, Nakicenovic N, Riahi K, Smith SJ, Stouffer RJ, Thomson AM, Weyant JP, Wilbanks. 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463(7282):747–756 DOI 10.1038/nature08823.

Muenchow J, Dieker P, Kluge J, Kessler M, Von Wherden H. 2018. A review of ecological gradient research in the Tropics: identifying research gaps, future directions, and conservation priorities. *Biodiversity and Conservation* 27(2):273–285 DOI 10.1007/s10531-017-1465-y.

Nadeau CP, Urban MC, Bridle JR. 2017. Climates past, present, and yet-to-come shape climate change vulnerabilities. *Trends in Ecology & Evolution* 32(10):786–800 DOI 10.1016/j.tree.2017.07.012.
Ornelas JF, Licona-Vera Y, Vásquez-Aguilar AA. 2018. Genetic differentiation and fragmentation in response to climate change of the narrow endemic *Psittacanthus auriculatus*. *Tropical Conservation Science* 11:194008291875551 DOI 10.1177/1940082918755513.

Peterman WE, Connette GM, Semlitsch RD, Eggert LS. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. *Molecular Ecology* 23(10):2402–2413 DOI 10.1111/mec.12747.

Polfus JL, Manseau M, Klütsch CFC, Simmons D, Wilson PJ. 2016. Ancient diversification in glacial refugia leads to intraspecific diversity in a Holarctic mammal. *Journal of Biogeography* 44(2):386–396 DOI 10.1111/jbi.12918.

Rellstab C, Zoller C, Walthert L, Lesur I, Pluess Ar, Graf R, Bodénès C, Sperisen C, Kremer A, Gugerli F. 2016. Signatures of local adaptation in candidate genes of oaks (Quercus spp.) with respect to present and future climatic conditions. *Molecular Ecology* 25(23):5907–5924 DOI 10.1111/mec.13889.

Reside AE, Butt N, Adams VM. 2018. Adapting systematic conservation planning for climate change. *Biodiversity and Conservation* 27(1):1–29 DOI 10.1007/s10531-017-1442-5.

Riddle BR, Hafner DJ. 2006. A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *Journal of Arid Environments* 66(3):435–461 DOI 10.1016/j.jaridenv.2006.01.014.

Scheinvar E, Gámez N, Castellanos-Morales G. 2017. Neogene and Pleistocene history of *Agave lechuguilla* in the Chihuahuan Desert. *Journal of Biogeography* 44(2):322–334 DOI 10.1111/jbi.12851.

Sgrò CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* 4(2):326–337 DOI 10.1111/j.1752-4571.2010.00157.x.

Shreve F. 1942. The desert vegetation of North America. *Botanical Review* 8(4):195–246 DOI 10.1007/bf02882228.

Shryock Df, Esque TC, Hughes L. 2014. Population viability of *Pediocactus bradyi* (Cactaceae) in a changing climate. *American Journal of Botany* 101:1944–1953 DOI 10.3732/ajb.140035.

Skogen K, Helland H, Kaltenborn B. 2018. Concern about climate change, biodiversity loss, habitat degradation and landscape change: embedded in different packages of environmental concern? *Journal for Nature Conservation* 44:12–20 DOI 10.1016/j.jnc.2018.06.001.

Sosa V, Ruiz-Sanchez E, Rodriguez-Gómez F. 2009. Hidden phylogeographic complexity in the Sierra Madre Oriental: the case of the Mexican tulip poppy *Hunnemannia fumariifolia* (Papaveraceae). *Journal of Biogeography* 36(1):18–27 DOI 10.1111/j.1365-2699.2008.01957.x.

Spear SF, Balkenhol N, Fortin MJ, McRae BH, Scribner KIM. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology* 19(17):3576–3591 DOI 10.1111/j.1365-294X.2010.04657.x.

Thornton PK, Erickson PJ, Herrero M, Challinor AJ. 2014. Climate variability and vulnerability to climate change: a review. *Global Change Biology* 20(11):3313–3328 DOI 10.1111/gcb.12581.

Thuiller W, Georges D, Engler R, Breiner F, Georges MD, Thuiller CW. 2016. Package “biomod2”: ensemble platform for species distribution modeling. Available at https://cran.r-project.org/web/packages/biomod2/index.html.

Trejo L, Alvarado-Cárdenas LO, Scheinvar E. 2016. Population genetic analysis and bioclimatic modeling in *Agave striata* in the Chihuahuan Desert indicate higher genetic variation and lower differentiation in drier and more variable environments. *American Journal of Botany* 103(6):1020–1029 DOI 10.3732/ajb.1500446.
Vásquez-Cruz M, Sosa V. 2016. New insights on the origin of the woody flora of the Chihuahuan Desert: the case of Lindleya. American Journal of Botany 103(9):1694–1707 DOI 10.3732/ajb.1600080.

Villarreal-Quintanilla JA, Bartolomé-Hernández JA, Estrada-Castillón E, Ramírez-Rodriguez H, Martínez-Amador SJ. 2017. The endemic element of the Chihuahuan Desert vascular flora. Acta Botanica Mexicana 118:65–96 DOI 10.21829/abm118.2017.1201.

Ward D. 2009. The biology of deserts. New York: Oxford University Press, 304.

Wiens JA, Stralberg D, Jongsomjit D. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. Proceedings of the National Academy of Sciences of the United States of America 106(Supplement_2):19729–19736 DOI 10.1073/pnas.0901639106.

Williams AP, Allen CD, Millar Ci, Swetnam TW, Michaelsen CJ, Leavitt SW. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. Proceedings of the National Academy of Sciences of the United States of America 107(50):21289–21294 DOI 10.1073/pnas.0914211107.

Wilson JS, Pitts JP. 2010. Illuminating the lack of consensus among descriptions of earth history data in the North American deserts: a resource for biologists. Progress in Physical Geography: Earth and Environment 34(4):419–441 DOI 10.1177/0309133310363991.

Wolfe AD, Necamp T, Fassnacht S, Blischak P, Kubatko L. 2016. Population genetics of Penstemon albomarginatus (Plantaginaceae), a rare Mojave Desert species of conservation concern. Conservation Genetics 17(6):1245–1255 DOI 10.1007/s10592-016-0857-y.