Niches and climate-change refugia in hundreds of species from one of the most arid places on Earth

Milen Duarte1,2, Pablo C. Guerrero3, Mary T.K. Arroyo1,2 and Ramiro O. Bustamante1,2

1 Departamento de Ciencias Ecológicas, Universidad de Chile, Santiago, Chile
2 Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile
3 Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

ABSTRACT

Background and Aims: Global climate change is a major threat to biodiversity worldwide. Several arid areas might expand in the future, but it is not clear if this change would be positive or negative for arid-adapted lineages. Here, we explore whether climatic niche properties are involved in the configuration of climate refugia and thus in future species trends.

Methods: To estimate putative climate refugia and potential expansion areas, we used maximum entropy models and four climate-change models to generate current and future potential distributions of 142 plant species endemic to the Atacama and mediterranean Chilean ecosystems. We assessed the relationship between the similarity and breadth of thermal and precipitation niches with the size of climate refugia and areas of potential expansions.

Key Results: We found a positive relationship between breadth and similarity for thermal niche with the size of climate refugia, but only niche similarity of the thermal niche was positively related with the size of expansion areas. Although all lineages would reduce their distributions in the future, few species are predicted to be at risk of extinction in their current distribution, and all of them presented potential expansion areas.

Conclusion: Species with a broad niche and niche dissimilarity will have larger refugia, and species with niche dissimilarity will have larger expansion areas. In addition, our prediction for arid lineages shows that these species will be moderately affected by climate change.

INTRODUCTION

Global climate change is one of the main factors impacting terrestrial and marine biodiversity in this century (Barnosky et al., 2011). Among the mechanisms that cause biotic impoverishment are the fragmentation and contraction of the geographical distribution of species, which can lead to increases in the degree of threat to these species (Parmesan, 1996; Bakkenes et al., 2002; Thuiller et al., 2008). The contraction of the
distribution of species may be due to climate conditions, insofar as associated changes may not meet species’ climatic niche requirements; therefore, a given species may suffer local and/or global extinction (Walther et al., 2002; Thomas et al., 2004; Jiguet et al., 2010; Wiens, 2016). On the other hand, species that will disperse to and track new climatic conditions can expand their distribution (Alarcón & Cavieres, 2015) and move their distribution limits (Felde, Kapfer & Grytnes, 2012).

The responses of organisms to climate change are limited and depend on the speed and intensity of climate change, as well as on biological variables such as physiological tolerance, morpho-functional traits, and life history (Araújo et al., 2013; Parmesan & Hanley, 2015). Predictions of ongoing climate change suggest that abiotic variables will be substantially altered in large geographic areas in a short time period, and species may not be able to adapt to these new conditions (Quintero & Wiens, 2013b; Wiens, 2016). Moreover, the dispersal potential of many species is limited, particularly in low-mobility groups such as terrestrial plants (Higgins & Richardson, 1999; Dullinger, Dirnböck & Grabherr, 2004; Dullinger et al., 2015), and few studies have shown models of dispersion that favor species distribution (Alarcón & Cavieres, 2015). Besides, dispersal of propagules is heavily constrained by habitat destruction and human-induced changes in land use (Hermy & Verheyen, 2007), which act as steadfast barriers to the movement of propagules between unconnected biotopes.

The climatic niche of species can be characterized by evaluating properties such as niche breadth and similarity (Colwell & Futuyma, 1971; Wiens et al., 2009). Climatic niche breadth is the climatic amplitude where one species can exist (Thuiller et al., 2005b). It is possible to distinguish the degree of similarity between these climatic conditions across different localities of the same species, evaluating how similar or different these localities are (Quintero & Wiens, 2013a). Additionally, this niche dimension can be projected onto geographic space (e.g., biotope), thus identifying all suitable areas where species can persist (Soberón & Peterson, 2005; Peterson, 2006; Colwell & Rangel, 2009). This spatial projection has been used to predict changes in the distribution of species predicted by current global climate change (Parmesan & Yohe, 2003; Pearson & Dawson, 2003; Thomas et al., 2004; Thuiller, Lavorel & Araújo, 2005a; Tingley et al., 2009). Thus, changes in the spatial distribution of biotopes enable the identification of the geographical areas that maintain climatic conditions that are suitable for various species after climate change and/or their geographical areas may expand. Furthermore, a comparison of current and future predicted distributions (expected by climate change) can allow for the identification of stable zones that can act as refuge areas for the species (Barnosky, 2008; Trivedi et al., 2008; Williams et al., 2008; Ashcroft, 2010; Keppel et al., 2012; Alamir, Mukul & Turton, 2015; Serra-Diaz et al., 2015; Stralberg et al., 2015). The size distribution of refugia are relevant for species conservation, since species with small refugia face a greater probability of extinction (Thuiller, Lavorel & Araújo, 2005a).

In the southwestern Andes, it is expected that climate change will modify rainfall regimes, which will increase in summer and decrease in winter (Vera et al., 2006; Sánchez et al., 2015). In recent decades, the western side of the Andes in the Southern Cone has seen cooling in some coastal areas coupled with an increase in temperature at high altitudes.
This tendency is likely to continue according to predictions made by the Intergovernmental Panel on Climate Change (IPCC, 2013); by the year 2080, on average, temperatures may rise by 3 °C, and annual rainfall may decrease by 6% in the Atacama Desert, an area that is one of the driest places on Earth (Guerrero et al., 2013). The impact of climate changes will be greater in the mediterranean area of Chile, where a decrease of 50% in annual rainfall and an increase of 2.5 °C in temperature are expected; in contrast, the annual precipitation and temperature in temperate forests of southern South America may increase by 5% and 1 °C, respectively (Christensen et al., 2007).

In this study, we characterized the climatic niche, the size of refugia areas, and the potential expansion size area for 142 plant species from arid western South America. The core task of our study was to evaluate the relationship between niche breadth and similarity of arid-adapted plant species with the size of climatic refugia and potential expansion areas.

**MATERIALS AND METHODS**

**Dataset and study region**

This study was conducted in western South America between 25° and 47° latitude, on 142 species from six plant genera: *Chaetanthera* (Asteraceae), *Eriosyce* (Cactaceae), *Malesherbia* (Passifloraceae), *Schizanthus* and *Nolana* (Solanaceae), and *Leucocoryne* (Alliaceae). These genera have received substantial attention by botanists (Gengler-Nowak, 2003; Meudt & Simpson, 2006; Pérez, Arroyo & Medel, 2007; Dillon et al., 2009; Davies, 2010; Guerrero et al., 2011; Guerrero, Durán & Walter, 2011; Jara-Arancio et al., 2014), meaning that good occurrence data are available. To characterize climatic niches and to estimate species distributions, we used the occurrence data obtained directly from a Chilean herbaria (CONC, Herbarium University of Concepción and SGO, National Museum of Natural History), the literature (Guerrero et al., 2013; Jara-Arancio et al., 2014), field trips, and other databases (i.e., the PhD thesis of Meudt, 2004). Bioclimatic variables were obtained from Worldclim (Hijmans et al., 2005). To select variables, we performed a Pearson correlation analysis in ENMTools (Warren, Glor & Turelli, 2010), discarding those variables correlated by over 0.9. A total of 10 variables were retained: mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter. The resolution of all climatic layers was 1 km². Managing climatic layers was performed with ArcGIS v. 10.0 (Esri, Redlands, CA, USA).

The future climatic variables were obtained from the National Science Foundation and its project Community Climate System Model, with the CCSMS4.0 model. We used the four representative concentration pathways (Moss et al., 2010), named after a predictable range of radiative values in the year 2100 relative to pre-industrial values in 1750: ~2.6, ~4.5, ~6.0 and >8.5 W m⁻². These are the most recent global model climate projections that are used in the Fifth Assessment IPCC report (Pachauri et al., 2014).
Inferring climate refugia

We constructed species distribution models (SDMs) using climate data for current and future 2080 climate conditions. For the future climate condition, we used four scenarios: 2.6, 4.5, 6.0, and 8.5 (in order of increasing gas concentration). SDMs were constructed using MAXENT (Phillips, Anderson & Schapire, 2006; Merow, Smith & Silander, 2013). We correlated occurrence points with 10 climatic variables and used 75% of data for training purposes and 25% model performance. We obtained the model from 10 replicates and a cross-validation procedure for replicate adjustment. Both training and test models obtained area under the curve (AUC) values. For SDM regularization, we selected the average model.

We overlapped the current distribution model of each species with the future projection according to models 2.6, 4.5, 6.0, and 8.5, obtaining four refugia models for each species. All spatial analyses were developed using ArcGIS 10.1 and SDM Toolbox 1.c.1. Finally, we obtained four possible results: range expansion areas (projected areas that are not currently occupied by the species); refugia areas (areas where the current distribution coincides with the future projection); and areas of contraction (current distribution areas, but which are not occupied in the projection figure).

Climatic niche characterization

To assess niche properties, we selected variables that account for the minimum and maximum ranges of the precipitation and temperature (i.e., the minimum temperature of the coldest month, maximum temperature of the wettest month, precipitation of the wettest quarter, and precipitation of the driest quarter) to describe niche breadth as niche tolerance (Quintero & Wiens, 2013a); further, niche similarity can be described as the variance in niche position of the breadth of the species in all localities.

The climatic niche breadth and similarity of species were assessed with the raw climate values extracted directly from WorldClim using occurrence data (Hijmans et al., 2005). Since it is possible to assess the niche characteristic directly, following Quintero & Wiens (2013a), we calculated the temperature niche breadth as the difference between the minimum temperature of the coldest month and the maximum temperature of the wettest month, as well as the precipitation niche breadth as the difference between the precipitation of the wettest quarter and the precipitation of the driest quarter. Then, the temperature and precipitation within each locality niche breadth were calculated as the differences between their maximum and minimum values; we also calculated their variances and the variance in the position of each locality on the niche axis for all localities in each species as the niche similarity between localities. The raw data can be found in Appendix 1.

Finally, we related the climatic niche results with the size of the refugia and expansion area of each species using generalized lineal models (GLM). For this, we used niche breadth variance (niche breadth) and niche position variance (niche similarity). Refugia and expansion area were the dependent variables, and niche similarity and breadth were the predictor variables.
RESULTS

We characterized the niche of the species (Appendix 2). For temperature axes, we found species currently occupying from −12.2 °C to 31.4 °C; for annual precipitation, we found species occupying from 0 mm to 1,104 mm. The spatial analyses indicated that current
and future (refugia) species distribution areas were significantly different (t-test) for the 4.5, 6.0 and 8.5 models (Fig. 1; p < 0.05).

Spatial analyses indicated that the suitable habitat area for species distribution demonstrated reductions of 0%–99.8% for the 2.6 model, 0%–93.9% for the 4.5 model, 0%–100% for the 6.0 model, and 0%–100% for the 8.5 model. We found a potential expansion area of 0%–224.7% for the 2.6 model, 0%–461.1% for the 4.5 model, 0%–406.8% for the 6.0 model and 0%–828.8% for the 8.5 model. The 2.6 model showed one possible extinction (N. intonsa) and another species refugia between 0.02%–100%. The 4.5 model showed a 6.10%–100% refugia area; the 6.0 model showed one possible extinction (E. iquiquensis) and 0%–100% refugia area; and the 8.5 model showed one possible extinction (L. purpurea) and 0%–100% refugia area. Therefore, the least conservative scenario for the three measures used (contraction, refugia, and distribution expansion) is

Figure 2 Histogram of contraction area (red), refugia (green) and future expansion (gray) for each species. (A) 2.6 greenhouse scenario model, (B) 4.5 model, (C) 6.0 model, and (D) 8.5 model.

Full-size DOI: 10.7717/peerj.7409/fig-2
the 8.5 model (Fig. 2), which shows high percentages of contraction (up to 100%), narrow climatic refugia (from 0%), and high expansion values (up to 828.8% of the current distribution).

Significant relationships between temperature niche similarity and the size of refugia were detected for all SDMs (Table 1). The GLM analysis indicated a positive relationship between temperature niche similarity and the four emission scenarios (2.6, 4.5, 6.0, and 8.5), and a positive effect between niche breadth in temperature and the two emission scenarios (6.0 and 8.5). Moreover, we detected positive relationships between niche similarity in temperature for all models and expansion areas (Table 1).

**DISCUSSION**

Niche breadth is positively correlated with the geographic distribution of species (Slatyer, Hirst & Sexton, 2013) and the survival of species (Saupe et al., 2015). In terms of climate change, we found that climatic niche breadth and similarity are positively correlated with refugia size and temperature, a result consistent with previous evidence (Thuiller, Lavorel & Araújo, 2005a). In our arid lineages, species with wide climatic niches and more dissimilar niches (non-grouping niche position) would be less affected by global warming compared to species with more narrow climatic niches. In addition, species with narrow distributions or habitat specialist species may be more prone to extinction after climate change (Johnson, 1998), since there is a positive relationship between the size of the distribution area and species abundance (Brown, 1984; Gaston, 1996).

| Table 1 | Relationship between niche breadth and refugia size and size expansion to the four greenhouse scenarios (2.6, 4.5, 6.0, and 8.5). Gray values represent significant results; \( p < 0.05 \). |
| --- | --- | --- | --- | --- |
| **Tests of significance for size refugia (GLM, III)** |  |  |  |  |
|  |  |  |  |  |
| **2.6** |  |  |  |  |
| F  | p  | F  | p  | F  | p  | F  | p  |
| Temperature  |  |  |  |  |  |  |  |
| Breadth  | 0.006  | 0.940  | 2.320  | 0.130  | 4.581  | 0.034  | 17.298  | 0.000 |
| Position  | 11.613  | 0.001  | 18.594  | 0.000  | 17.740  | 0.000  | 25.509  | 0.000 |
| Precipitation  |  |  |  |  |  |  |  |  |
| Breadth  | 0.040  | 0.842  | 0.023  | 0.881  | 0.268  | 0.605  | 0.849  | 0.359 |
| Position  | 0.012  | 0.913  | 0.006  | 0.939  | 0.032  | 0.859  | 0.170  | 0.681 |
| **Tests of significance for size expansion (GLM, III)** |  |  |  |  |
|  |  |  |  |  |
| **2.6** |  |  |  |  |
| F  | p  | F  | p  | F  | p  | F  | p  |
| Temperature  |  |  |  |  |  |  |  |  |
| Breadth  | 1.589  | 0.210  | 1.581  | 0.211  | 1.682  | 0.197  | 1.274  | 0.261 |
| Position  | 17.402  | 0.000  | 16.139  | 0.000  | 16.591  | 0.000  | 14.243  | 0.000 |
| Precipitation  |  |  |  |  |  |  |  |  |
| Breadth  | 0.376  | 0.541  | 0.412  | 0.522  | 0.342  | 0.560  | 0.111  | 0.740 |
| Position  | 0.061  | 0.805  | 0.083  | 0.774  | 0.062  | 0.804  | 0.111  | 0.739 |
We believe that for species with narrow climatic niches, the presence of climate refugia can be subject to the magnitude of climate change in their geographic area. Alarcón & Cavieres (2018) found a positive relationship between niche breadth and change in species’ distribution with increasing elevation; however, as the latitude increases, the relationship is reversed, and species with wide niches present greater changes in their distribution, which reaffirms the idea that the niche breadth–refugia relationship could be modified by the magnitude of change in a specific geographical area. It is important to incorporate other factors, such as latitude or gradients in future studies.

As a consequence of the fact that species hold limited potential to adapt to the warmer and drier climatic conditions, together with dispersion constraints, the number of species threatened by global warming should increase in the future (Thomas et al., 2004; Thuiller et al., 2005b, 2006; Keppel et al., 2012). Although our study in arid lineages showed significant differences between the current distribution and potential future areas (refugia) only some species present a high risk of extinction under expected future climate-change scenarios: for the most conservative scenario (2.6), 63% of the evaluated species will retain over 80% of their distribution, 19% will retain between 60% and 80%, 14% will retain between 40% and 60%, 3% will retain between 20% and 40%, and only 1% will retain less than 20% of its distribution. For the IUCN (2012), a species is considered endangered if its population has reduced by at least 50% in 10 years or has a extent of occurrence less than 5,000 km², or has an area of occupancy less than of 500 km²; hence, our results suggest that the species studied should not be at high risk. Although there are few studies in SDMs for semi-arid and arid ecosystems, our results are similar to those found in Namibia, for example. In that study, it was predicted that less than 5% of the species could experience a complete range reduction by 2080, although it is expected that more than 47% will have a range reduction of at least 30% by the year 2080 (Thuiller et al., 2006). However, in our study, species that showed a greater than 50% reduction in their distribution were species of importance due to their high extinction risk. *E. chilensis* and *E. recondita* are considered endangered in their endemic distribution.

From an evolutionary perspective, a study based on the effects of climate change on endemic species in Sahara-Sahel showed that some groups with a high capacity to adapt to global change (for example, those with a high dispersal capacities) may be able to colonize distinct areas, while groups with low adaptive capacity may be more vulnerable to extinction (Vale & Brito, 2015). This result is consistent with the finding from study on arid-adapted plants, where desert plants may be resilient to climate change since they presented with positive population growth rates (Salguero-Gómez et al., 2012). Also, at an intraspecific level, semiarid plants could present a better response to climate change in more arid populations because of the greater phenotypic plasticity of these populations in comparison with more mesic populations (Lázaro-Nogal et al., 2015). Persistence against climate change may be favored by species with seed dormancy, since seeds may resist long periods of drought (Clauss & Venable, 2000), while rapid life cycles and fast reproductive processes allow species to take advantage of short windows of ecological opportunities when resources are abundant, such as episodic rainfalls (Aronson et al., 1993), which allow water to be retained in water-scarce conditions. However, there is
evidence of an evolutionary lag time for Chaetanthera, Malesherbia and Nolana to adapt to new, more severe arid conditions, and thus rapid adaptation to ongoing climate change may be unlikely (Guerrero et al., 2013). This tells us that the study of arid lineages and their future in the face of climate change is still in process. Therefore, describing these evolutionary advantages is also important when evaluating the future distributions of various species. For example, in our study, some species of the genus Leucocoryne (geophite) showed a large niche breadth and low similarity; at the same time, it is known that these plants have bulbous structures that enable it to store water in prolonged droughts (Jara-Arancio et al., 2014).

By detecting areas of possible expansion for species distribution, it is possible to propose areas that could potentially benefit from conservation efforts and ecological restoration, as reforestation with those species that present expansion in those areas (Padonou et al., 2015) and human-assisted introductions to maximize the native forests’ connectivity (Hannah et al., 2008), could attenuate the impact generated by the contraction of natural species distribution. This conservation method is currently being incorporated for conservation planning and ecological restoration (Yang et al., 2013; Ardestani et al., 2015; Remya, Ramachandran & Jayakumar, 2015). In our case, this could be very useful for arid lineages, due to the intensification of mining activity in the western Andes (Cisternas & Gálvez, 2014), and this study could serve as the impetus for initiating restoration in that area. Proposing areas of expansion for these arid lineages would counteract the effect of global change and, in turn, fill gaps in conservation, as in the case of groups such as cacti, which are poorly conserved in non-take areas (Duarte et al., 2014). Therefore, areas of both refugia and expansion could be subject to concrete conservation efforts, and they may also be used in environmental policies and conservation planning.

CONCLUSIONS
This work provides new knowledge on which properties could define the future distribution of species throughout the course of global climate change. We have found that species with a broad niche and niche similarity will have a larger refuge. In addition, those species with niche similarity will have larger expansion areas than species with low similarity. The species evaluated belong to semi-arid ecosystems, which seldom been evaluated in relation to their future distribution. Our prediction in arid lineages shows that these species will be moderately affected by climate change. For this reason, we suggest taking conservative measures to protect these lineages in the places where they are currently distributed, which will serve as future areas of refuge in the face of climate change.

ACKNOWLEDGEMENTS
We thank the Chilean Herbaria (CONC, SGO) curators who provided access to their plant collections used in this study. We also thank Heidi Meudt and Alison Davies for providing occurrence data and taxonomic literature. English-language editing of this manuscript was provided by Journal Prep Services.
ADDITIONAL INFORMATION AND DECLARATIONS

Funding
This research was supported by grants ICM P02-005 and PBF-23. Pablo Cesar Guerrero’s research was supported by FONDECYT 1160583. Milen Duarte Muñoz’s research was supported by CONICYT 21140099. Ramiro O. Bustamante’s research was supported by FONDECYT 1180193. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures
The following grant information was disclosed by the authors:
ICM: P02-005 and PBF-23.
FONDECYT: 1160583.
CONICYT: 21140099.
FONDECYT: 1180193.

Competing Interests
The authors declare that they have no competing interests.

Author Contributions
- Milen Duarte conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Pablo C. Guerrero contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Mary T.K. Arroyo contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Ramiro O. Bustamante contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft, analysis.

Data Availability
The following information was supplied regarding data availability:
The raw data are available in the Supplemental File.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.7409#supplemental-information.

REFERENCES
Alamgir M, Mukul SA, Turton SM. 2015. Modelling spatial distribution of critically endangered Asian elephant and Hoolock gibbon in Bangladesh forest ecosystems under a changing climate. Applied Geography 60:10–19 DOI 10.1016/j.apgeog.2015.03.001.
Alarcón D, Cavieres LA. 2015. In the right place at the right time: habitat representation in protected areas of South American Nothofagus-dominated plants after a dispersal
constrained climate change scenario. *PLOS ONE* **10**(3):e0119952
DOI 10.1371/journal.pone.0119952.

Alarcón D, Cavieres LA. 2018. Relationships between ecological niche and expected shifts in elevation and latitude due to climate change in South American temperate forest plants. *Journal of Biogeography* **45**(10):2272–2287 DOI 10.1111/jbi.13377.

Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013. Heat freezes niche evolution. *Ecology Letters* **16**(9):1206–1219 DOI 10.1111/ele.12155.

Ardestani EG, Tarkesh M, Bassiri M, Vahabi MR. 2015. Potential habitat modeling for reintroduction of three native plant species in central Iran. *Journal of Arid Land* **7**(3):381–390 DOI 10.1007/s40333-014-0050-4.

Aronson J, Floret C, Le Floc'h E, Ovalle C, Pontanier R. 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. II. Case studies in Southern Tunisia, Central Chile and Northern Cameroon. *Restoration Ecology* **1**(3):168–187.

Ashcroft MB. 2010. Identifying refugia from climate change. *Journal of Biogeography* 37:1407–1413.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* **8**(4):390–407 DOI 10.1046/j.1354-1013.2001.00467.x.

Barnosky AD. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **105**(1):11543–11548 DOI 10.1073/pnas.0801918105.

Barnosky AD, Matzke N, Tomiya S, Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire KL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth’s sixth mass extinction already arrived? *Nature* **471**(7336):51–57 DOI 10.1038/nature09678.

Brown JH. 1984. On the relationship between abundance and distribution of species. *American Naturalist* **124**(2):255–279 DOI 10.1086/284267.

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon RT, Laprise R, Magña V, Mearns CG, Menendez CG, Raisanen J, Rinde A, Sarr A, Whetton P. 2007. Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. New York: Cambridge University Press.

Cisternas LA, Gálvez ED. 2014. Chile’s mining and chemicals industries. *Chemical Engineering Progress* **110**(6):46–51.

Clauss MJ, Venable DL. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist* **155**(2):168–186 DOI 10.1086/303314.

Colwell RK, Futuyma DJ. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**(4):567–576 DOI 10.2307/1934144.

Colwell RK, Rangel TF. 2009. Hutchinson’s duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America* **106**(19):6519–6565 DOI 10.1073/pnas.0901650106.

Davies A. 2010. A systematic revision of Chaetanthera Ruiz and Pav., and the reinstatement of Oriastrum Poepp. and Endl (Asteraceae: Mutisieae). München: Dissertation der Fakultät für Biologie der Ludwig-Maximilians-Universität.

Dillon MO, Tu T, Xie L, Quipuscoa SV, Wen J. 2009. Biogeographic diversification in *Nolana* (Solanaceae), a ubiquitous member of the Atacama and Peruvian Deserts along the western coast.
of South America. *Journal of Systematics and Evolution* 47(5):457–476
DOI 10.1111/j.1759-6831.2009.00040.x.

Duarte M, Guerrero PC, Carvallo G, Bustamante RO. 2014. Conservation network design for endemic cacti under taxonomic uncertainty. *Biological Conservation* 176:236–242
DOI 10.1016/j.biocon.2014.05.028.

Dullinger S, Dendoncker N, Gattringer A, Leitner M, Mang T, Moser D, Mümker CA, Plutzar C, Rounsevell M, Willner W, Zimmermann NE, Hübner K. 2015. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. *Diversity and Distributions* 21(12):1375–1387 DOI 10.1111/ddi.12370.

Dullinger S, Dirnböck T, Grabherr G. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* 92(2):241–252 DOI 10.1111/j.0022-0477.2004.00872.x.

Falvey M, Garreaud RD. 2009. Regional cooling in a warming world: recent temperature trends in the southeast Pacific and along the west coast of subtropical South America (1979–2006). *Journal of Geophysical Research* 114:D04102 DOI 10.1029/2008JD010519.

Felde VA, Kapfer J, Grytnes J-A. 2012. Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. *Ecography* 35(10):922–932 DOI 10.1111/j.1600-0587.2011.07057.x.

Gaston KJ. 1996. The multiple forms of the interspecific abundance-distribution relationship. *Oikos* 76(2):211–220 DOI 10.2307/3546192.

Gengler-Nowak K. 2003. Molecular phylogeny and taxonomy of Malesherbiaceae. *Systematic Botany* 28:333–344.

Guerrero PC, Arroyo MT, Bustamante RO, Duarte M, Hagemann TK, Walter HE. 2011. Phylogenetics and predictive distribution modeling provide insights into the geographic divergence of *Eriosyce subgen. Neoporteria* (Cactaceae). *Plant Systematics and Evolution* 297(1–2):113–128 DOI 10.1007/s00606-011-0512-5.

Guerrero PC, Durán AP, Walter HE. 2011. Latitudinal and altitudinal patterns of the endemic cacti from the Atacama desert to Mediterranean Chile. *Journal of Arid Environments* 75(11):991–997 DOI 10.1016/j.jaridenv.2011.04.036.

Guerrero PC, Rosas M, Arroyo MTK, Wiens JJ. 2013. Evolutionary lag times and recent origin of the biota of an ancient desert (Atacama-Sechura). *Proceedings of the National Academy of Sciences of the United States of America* 110(28):11469–11474 DOI 10.1073/pnas.1308721110.

Hannah L, Dave R, Lowry PP, Andelman S, Andrianarisata M, Andriamaro L, Cameron A, Hijmans R, Kremen C, MacKinnon J, Randrianasolo HH, Andriambololonerana S, Razafimpahanana A, Randriamahazo H, Randrianarisoa J, Razafinjatovo P, Raxworthy C, Schatz GE, Tadross M, Wilmé L. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters* 4(5):590–594 DOI 10.1098/rsbl.2008.0270.

Hermy M, Verheyen K. 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research* 22(3):361–371 DOI 10.1007/s11284-007-0354-3.

Higgins SL, Richardson DM. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist* 153(5):464–475 DOI 10.1086/303193.

Hijmans RJ, Cameron SE, Parr 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.

IPCC. 2013. Climate change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Nauels A, Tignor MMB, Xia Y, Allen SL, Bex V, Boschung J, Midgley PM, eds. *Contribution of
Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press, 1535.

IUCN. 2012. Guidelines for Application of IUCN Red List Criteria at Regional and National Levels: Version 4.0. Gland, Switzerland and Cambridge, UK: IUCN.

Jara-Arancio P, Arroyo MTK, Guerrero PC, Hinojosa LF, Arancio G, Méndez MA. 2014. Phylogenetic perspectives on biome shifts in Leucocoryne (Alliaceae) in relation to climatic niche evolution in western South America. *Journal of Biogeography* 41(2):328–338. DOI 10.1111/jbi.12186.

Jiguet F, Gregory RD, Devictor V, Green RE, Voříšek P, Van Strien A, Couvet D. 2010. Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology* 16(2):497–505. DOI 10.1111/j.1365-2486.2009.01963.x.

Johnson CN. 1998. Species extinction and the relationship between distribution and abundance. *Nature* 394(6690):272–274. DOI 10.1038/28385.

Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* 21(4):393–404. DOI 10.1111/j.1466-8238.2011.00686.x.

Lázaro-Nogal A, Matesanz S, Godoy A, Pérez-Trautman F, Gianoli E, Valladares F. 2015. Environmental heterogeneity leads to higher plasticity in dry-edge populations of a semi-arid Chilean shrub: insights into climate change responses. *Journal of Ecology* 103(2):338–350. DOI 10.1111/1365-2745.12372.

Merow C, Smith MJ, Silander JA Jr. 2013. A practical guide to MaxEnt for modeling species’ distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069.

Meudt H. 2004. Dissertation Research: Austral Biogeography: The Evolution of Subalpine Ourisia (Scrophulariaceae) in a Phylogenetic Context. National Science Foundation (VA, VA).

Meudt HM, Simpson BB. 2006. The biogeography of the austral, subalpine genus Ourisia (Plantaginaceae) based on molecular phylogenetic evidence: South American origin and dispersal to New Zealand and Tasmania. *Biological Journal of the Linnean Society* 87(4):479–513. DOI 10.1111/j.1095-8312.2006.00584.x.

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

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P, Dubash NK. 2014. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC.

Padonou EA, Teka O, Bachmann Y, Schmidt M, Lykke AM, Sinsin B. 2015. Using species distribution models to select species resistant to climate change for ecological conservation of bowe in West Africa. *African Journal of Ecology* 53(1):83–92. DOI 10.1111/aje.12205.

Parmesan C. 1996. Climate and species’ range. *Nature* 382(6594):765–766. DOI 10.1038/382765a0.

Parmesan C, Hanley ME. 2015. Plants and climate change: complexities and surprises. *Annals of Botany* 116(6):849–864. DOI 10.1093/aob/mcv169.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42. DOI 10.1038/nature01286.
Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12(5):361–371 DOI 10.1046/j.1466-822x.2003.00042.x.

Pérez F, Arroyo MTK, Medel R. 2007. Phylogenetic analysis of floral integration in Schizanthus (Solanaceae): does pollination truly integrate corolla traits? Journal of Evolutionary Biology 20:1730–1738.

Peterson AT. 2006. Uses and requirements of ecological niche models and related distributional models. Biodiversity Informatics 3:59–72 DOI 10.17161/bi.v3i0.29.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190(3–4):231–259 DOI 10.1016/j.ecolmodel.2005.03.026.

Quintero I, Wiens JJ. 2013a. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecology and Biogeography 22(4):422–432 DOI 10.1111/geb.12001.

Quintero I, Wiens JJ. 2013b. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecology Letters 16(8):1095–1103 DOI 10.1111/ele.12144.

Remya K, Ramachandran A, Jayakumar S. 2015. Predicting the current and future suitable habitat distribution of Myristica dactyloides Gaertn. using MaxEnt model in the Eastern Ghats, India. Ecological Engineering 82:184–188 DOI 10.1016/j.ecoleng.2015.04.053.

Salguero-Gómez R, Siewert W, Casper BB, Tielbürger K. 2012. A demographic approach to study effects of climate change in desert plants. Philosophical Transactions of the Royal Society B: Biological Sciences 367(1606):3100–3114 DOI 10.1098/rstb.2012.0074.

Sánchez E, Solman S, Remedio ARC, Berbery H, Samuelsson P, Da Rocha RP, Mourão C, Li L, Marengo J, De Castro M, Jacob D. 2015. Regional climate modelling in CLARIS-LPB: a concerted approach towards twenty first century projections of regional temperature and precipitation over South America. Climate Dynamics 45(7–8):2193–2212 DOI 10.1007/s00382-014-2466-0.

Saupe EE, Qiao H, Hendricks JR, Portell RW, Hunter SJ, Soberón J, Lieberman BS. 2015. Niche breadth and geographic range size as determinants of species survival on geological time scales. Global Ecology and Biogeography 24(10):1159–1169 DOI 10.1111/geb.12333.

Serra-Diaz JM, Scheller RM, Syphard AD, Franklin J. 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. Landscape Ecology 30(6):1039–1053 DOI 10.1007/s10980-015-0173-9.

Slater RA, Hirst M, Sexton JP. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16(8):1104–1114 DOI 10.1111/ele.12140.

Soberón J, Peterson AT. 2005. Interpretation of model of fundamental ecological niches and species’ distribution areas. Bioinformatics 21:1–10.

Stralberg D, Bayne E, Cumming SG, Sólymos P, Song SJ, Schmiegelow FK. 2015. Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: a modified refugia approach. Diversity and Distributions 21(9):1112–1128 DOI 10.1111/ddi.12356.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, De Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld AS, Midgley FG, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. Nature 427(6970):145–148 DOI 10.1038/nature02121.
Thuiller W, Albert C, Araújo MB, Berryc PM, Cabezad M, Guisane A, Hickler T, Midgley GF, Patersonc J, Schurh FM, Sykesf MT, Zimmermanni NE. 2008. Predicting global change impacts on plant species’ distributions: future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9(3-4):137–152 DOI 10.1016/j.ppees.2007.09.004.

Thuiller W, Lavorel S, Araújo MB. 2005a. Niche properties and geographic extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14(4):347–357 DOI 10.1111/j.1466-822X.2005.00162.x.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. 2005b. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102(23):8245–8250 DOI 10.1073/pnas.0409902102.

Thuiller W, Midgley GF, Hughes GO, Bomhard B, Drew G, Rutherford MC, Woodward FI. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. Global Change Biology 12(5):759–776 DOI 10.1111/j.1365-2486.2006.01140.x.

Tingley MW, Monahan WB, Beissinger SR, Moritz C. 2009. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences of the United States of America 106:19637–19643 DOI 10.1073/pnas.0901562106.

Trivedi MR, Berry PM, Morecroft MD, Dawson TP. 2008. Spatial scale affects bioclimatic model projections of climate change impacts on mountain plants. Global Change Biology 14(5):1089–1103 DOI 10.1111/j.1365-2486.2008.01553.x.

Vale CG, Brito JC. 2015. Desert-adapted species are vulnerable to climate change: insights from the warmest region on Earth. Global Ecology and Conservation 4:369–379 DOI 10.1016/j.gecco.2015.07.012.

Vera C, Silvestri G, Liebmann B, González P. 2006. Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. Geophysical Research Letters 33(13):1613 DOI 10.1029/2006GL025759.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. Nature 416(6879):389–395 DOI 10.1038/416389a.

Warren DL, Glor RE, Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33(3):607–611.

Wiens JJ. 2016. Climate-related local extinctions are already widespread among plant and animal species. PLOS Biology 14(12):e2001104 DOI 10.1371/journal.pbio.2001104.

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

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLOS Biology 6(12):e325 DOI 10.1371/journal.pbio.0060325.

Yang X-Q, Kushwaha SPS, Saran S, Xu J, Roy PS. 2013. Maxent modeling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in lesser Himalayan foothills. Ecological Engineering 51:83–87 DOI 10.1016/j.ecoleeng.2012.12.004.