Science of the Total Environment 785 (2021) 147399

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Climate exposure shows high risk and few climate refugia for Chilean native vegetation

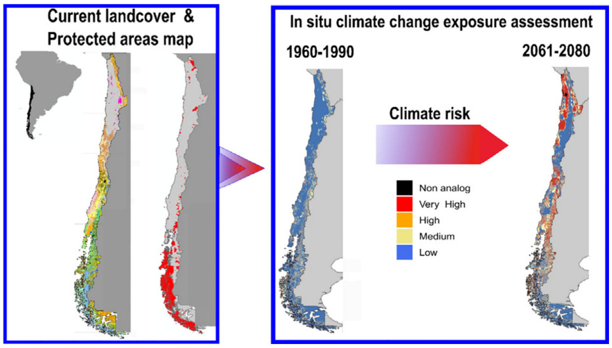
Andrés Muñoz-Sáez [a,b,*], Hyeyeong Choe [c], Ryan M. Boynton [d], Paul R. Elsen [e], James H. Thorne [d]

[a] *Facultad de Ciencias Agronómicas, Universidad de Chile, Av. Santa Rosa 11315 La Pintana, Santiago 8820808, Chile*
[b] *Center of Applied Ecology and Sustainability (CAPES), Santiago 7820244, Chile*
[c] *Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul 08826, Republic of Korea*
[d] *Department of Environmental Science and Policy, University of California, Davis 95616, USA*
[e] *Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA*

HIGHLIGHTS

- We provide an in situ climate risk analysis of vegetation and protected areas (PAs).
- Under RCP8.5, 27.8–43.6% of PAs and 32.2–43.6% of non-PAs face high climate risk.
- Most vegetation types face high climate risk (e.g. *Nothofagus* and *Araucaria* forests).
- Elevation and latitudinal patterns of climate risk changed with the GCM used.
- Climate refugia were identified in the central Andes, in Patagonia, and for some coastal areas.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 February 2021
Received in revised form 8 April 2021
Accepted 22 April 2021
Available online 29 April 2021

Editor: Elena Paoletti

Keywords:
Climate change
Climate risk assessment
Conservation planning
Gondwanic forest
Protected areas management
Latitudinal patterns

ABSTRACT

The many Gondwanic vegetation types found across the extensive latitudes and elevation gradients of South America's southern cone contribute to Chile's global biodiversity hotspot ranking. Species loss in global biodiversity hotspots is an ongoing climate change concern and land managers need spatially explicit climate risk maps to adapt conservation strategies to climate change in these areas. We modeled future climate risk for Chile's terrestrial vegetation using a high-resolution vegetation map and tested the relationship to climate risk for each type's latitudinal and elevation range. We found that 43.6% of all vegetation has high climate risk in Global Circulation Models (GCMs) under a high emissions scenario (RCP8.5). All forest types in the country, including Southern Beech (*Nothofagus* sp.), Alerce (*Fitzroya cupressoides*), Araucaria (*Araucaria araucana*), and Sclerophyllous, as well as the Valdivian rainforest, Altiplanic Steppes, and Salares, face high levels of climate risk. Tests for trends in risk across elevation and latitude showed that exposure for all types increased with elevation based on the MIROC5 GCM, and decreased with latitude based on the Had2GEM-ES GCM. Our results suggest that vegetation types with smaller latitudinal ranges typically have higher levels of climate risk, but a type's elevation range is not significantly correlated with risk of exposure. We identified climatically stable areas which could act as vegetation refugia in Patagonia, the central Andes mountains between latitudes 27.5°S and 32.5°S, and some coastal areas. Conservation strategies in Chile should include the protection of climatically stable areas to safeguard current Gondwanic biodiversity and active habitat restoration in climatically exposed areas to facilitate vegetation shifts.

---

* Corresponding author.
E-mail address: andrmunoz@uchile.cl (A. Muñoz-Sáez).

https://doi.org/10.1016/j.scitotenv.2021.147399

1. Introduction

Climate change impacts are of particular concern for the world's biodiversity hotspots because of the potential vulnerability of their high numbers of endemic species (Malcolm et al., 2006; Myers et al., 2000). This has led to a focus on individual biodiversity hotspots to assess their species' vulnerability to climate change (e.g. Midgley et al., 2002) and to the development of climate-adaptive conservation plans (Hannah et al., 2007). Chile is one of 35 global biodiversity hotspots (Myers et al., 2000), harbors three of the 200 top priority ecoregions for conservation (Olson and Dinerstein, 2002), and six of the 14 terrestrial biomes (Dinerstein et al., 2017). The country's wide range of elevations (0–6893 m) and great latitudinal extent (18–55°S) along the western flanks of the Andes Mountains create many ecological niches (Moreira-Munoz, 2011). Combined with its climatic and geographical isolation, this has resulted in a unique flora, including 4985 plant species, with nearly 50% endemism (Moreira-Munoz, 2011; Scherson et al., 2017), a level also found in Chile's vertebrate fauna (Simonetti, 1999). Many of the plant species form unique Gondwanic vegetation types (Iglesias et al., 2011), including forests dominated by species in the genus *Nothofagus* that make up roughly 58% of the area of all of Chile's native forests and that occupy most of the latitudinal gradient of the southern temperate rainforest (DellaSala et al., 2011; Segovia and Armesto, 2015). *Nothofagus* forests are critical for forest ecosystem functions (Rodríguez et al., 2018) and are an important component in the study of biogeographic theories (Scherson et al., 2017). In contrast, Chile's Gondwanic conifer forests, dominated by *Araucaria* and *Alerce*, exhibit narrow spatial distributions, which, along with their long lifespans, make them vulnerable to climate change (Camarero and Fajardo, 2017). Other vegetation types also support unique biotic communities, such as the highly endemic Sclerophyllous forest of central Chile (Alaniz et al., 2016), and salt flat wetlands ("salares"), which serve as key habitat for migratory bird species (Lobos et al., 2018). Few studies of endemic vegetation types have tested climate change relationships across such wide latitudinal and elevation gradients as these, though examples of such an approach are found from Canada (Boisvert-Marsh et al., 2019), China (Wan et al., 2018) and tropical South America (Fadrique et al., 2018).

Recent climate change studies of Chilean vegetation have focused on potential range shifts and phylogenetic diversity (Fuentes-Castillo et al., 2020; Fuentes-Castillo et al., 2019; see Supporting Information Appendix 1 for full bibliography of studies), but a holistic and comprehensive study for all of Chile's endemic vegetation types is still lacking. The range shifts modeled in recent studies report species shifting southward and to higher elevations, which are consistent with general global predictions (Chen et al., 2011). However, to date there have been no studies explicitly assessing changes in climatic conditions for Chile's Gondwanic vegetation types within their current geographic distributions, that is, their in situ climate risk, based on existing patterns of vegetation across the full extent of the country. For climate adaptation planning, such spatially-explicit climate change refugia (Keppel et al., 2015; Morelli et al., 2020) can provide additional context to species range modeling approaches by showing potential climate-driven physiological stress for vegetation patterns in their current sites under future climatic conditions, and because land managers need tools that enable them to differentiate relative risks to extant vegetation within the static boundaries of existing conservation lands (Thorne et al., 2020). This approach can inform a major decision confronting natural resource managers: whether to invest limited funding and available effort in the retention of existing vegetation, or to permit transition to other vegetation types (Millar and Stephenson, 2015).

Here, we examine climate risk for each of Chile's 38 landcover types that include 24 vegetation types (including 11 forest types, 5 shrublands and succulent types, 4 grasslands types, and 4 wetlands types) using a novel climate exposure approach (Choe and Thorne, 2019; Thorne et al., 2020) not yet applied to Chile that integrates projected future climate conditions with the satellite-derived spatial patterns of each existing dominant vegetation type. We mapped in situ climate exposure of each pixel of each vegetation type, and classified the overall level of risk for each type under different future emissions scenarios (Thorne et al., 2017a). Locations within each vegetation type with highest climate exposure have climate conditions that differ the most from its baseline climate conditions. We then tested for geographic and biogeographic patterns of climate risk by relating our exposure output to elevation and latitude across vegetation types. In line with theoretical and empirical estimates of climate warming, we expected that the level of climate exposure would increase with both latitude and elevation (Nolan et al., 2018; Pepin et al., 2015). We also expected that vegetation types with more restricted latitudinal and elevational distributions would be at higher risk of exposure, as these aspects of geographic range size are typically powerful predictors of vulnerability and extinction risk for various taxonomic groups (Pacifici et al., 2017).

2. Material and methods

2.1. Input data

2.1.1. Vegetation/land cover and conservation lands maps

We used a government-produced vegetation map of Chile covering 725,650 km^2 that used aerial photography (1997–2015; scale 1:50,000) and on-the-ground verification (Conaf-Conama-Birf, 1999). The minimum mapping unit is 0.5 ha for forested areas and 1 ha for non-forested areas. We analyzed 38 land cover types (24 corresponded to natural vegetation types), including forests, matorral (scrubland), grasslands, wetlands, succulents, exotic forest plantations, mixed exotic-native forest, urban areas, industrial areas, hydric sources, bare lands, and glacier areas (Fig. 1, Supporting Information Appendix S2 Table S1). To provide more details about different matorral vegetation types, we also analyzed them according to their vertical structure (Supporting Information Appendix S2).

We used a governmental map of various types of protected areas (hereafter PAs) (BCN, 2020) that we combined to identify conservation lands and non-protected lands at national scale. The terrestrial PAs cover about 131,000 km^2 (18.1%) of the country (Appendix S2, Table S1).

2.1.2. Climate data

We obtained baseline and future climate conditions and 19 bioclimatic variables at a spatial resolution of 30 arc-seconds from the WorldClim database version 1.4.

(https://www.worldclim.org/data/v1.4/cmip5_30s.html; Hijmans et al., 2005) (Supporting Information Appendix S3). We evaluated potential change in climate on a per-pixel basis between the baseline conditions (1960–1990 and a WorldClim-provided future period (2061–2080). We evaluated 17 Global Circulation Models (GCM) outputs and selected two, based three criteria: i) their previous use (HadGEM2-ES) in Chilean government climate change reports (Ministerio del Medio Ambiente, 2016); ii) their predictions of change (minimum temperature and precipitation) bracket the predicted future climates from 17 of the GCMs on the WorldClim website (Thorne et al., 2018); and iii) their satisfactory simulation of precipitation and atmospheric circulation over South America (Almagro et al., 2017). All but one GCM predict a drier and hotter climate pattern (Figs. S1, S2, Table S4).

We selected MIROC5 https://www.worldclim.org/data/v1.4/cmip5_30s.html and HadGEM2-ES (Collins et al., 2011) (Supporting Information Appendix S3, Figs. S1 & S2). We selected two emission scenarios (the Representative Concentration Pathways RCP4.5 and RCP8.5) to compare change from baseline conditions with projected future conditions. The RCP4.5 is roughly equivalent to Paris accord emission reductions and the RCP8.5 is supposed to represent current rates of emissions (Schwalm et al., 2020).

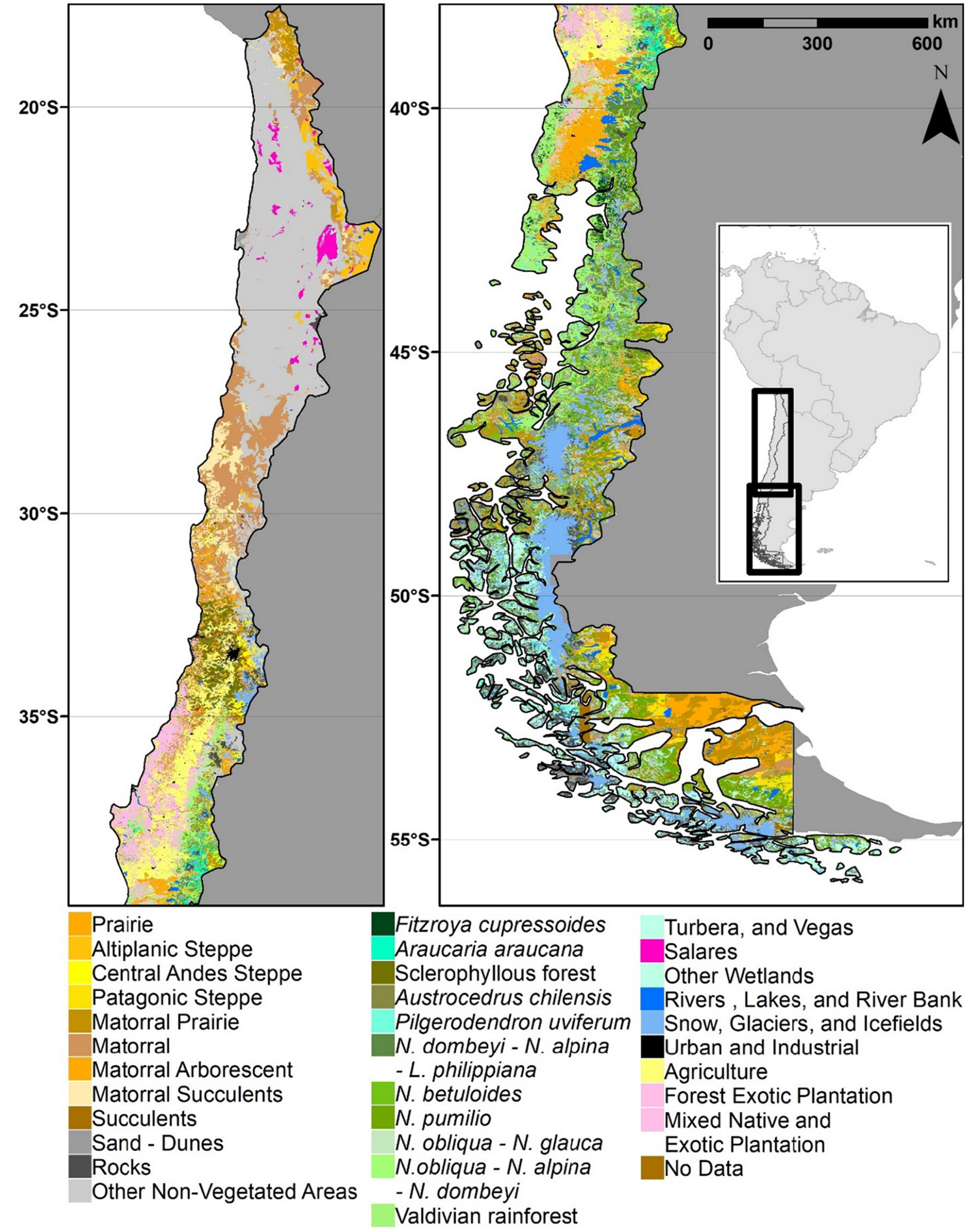


Fig. 1. Map of classification of land cover types based on the National Forestry Cadaster (www.sitconaf.cl).

2.2. Analyses

2.2.1. Climate change model

We randomly selected 100,000 grid cells across the country, equivalent to 13.11% of the country's area (Supporting Information Appendix S3 Table S5), and extracted the baseline and future climate and bioclimatic variables as inputs for four principal components analyses (PCA). The baseline and each of the four futures (2 climate models × 2 emissions scenarios) were put into a principal components analysis using the 'prcomp' base function in R version 3.3.3 (R Development, 2017). We used PCA to reduce the number of bioclimatic variables to two dimensions constituting the first two principal components (Supporting Information Appendix S3 Table S7, Fig. S3), and representing the current and future climate conditions. For each PCA, we zero-centered all climate variables and scaled them to have the same unit variance (Choe and Thorne, 2019). On average, the first two axes represent 75.5% of the variation (Supporting Information Appendix S3), with baseline and future climate conditions values at every grid cell of the country.

2.2.2. Climate change exposure for each vegetation and landcover type

We resampled the vegetation types in the vegetation map to match the resolution of the baseline and future climate data by using the majority sample rule in ArcGIS (ESRI v. Pro) to go from 30 m pixel size to a 30 arc-seconds, the operational grid scale for the analysis. We linked the resulting vegetation type in each pixel to its corresponding climate data from each of the four climate models developed in the PCA models.

To categorize the level of climate exposure for Chile as a whole and for each vegetation type, we first analyzed the frequency of occurrence of baseline climate conditions (Choe and Thorne, 2019; Thorne et al., 2017a). The frequency of baseline climate conditions in the mapped extent of each vegetation type was calculated using a two-dimensional kernel density estimation, the 'kde2d' function in the 'MASS' package in R (Venables and Ripley, 2003), resulting in a baseline climate frequency distribution in 5% increments, with the most frequent, or commonly occurring conditions, found in the center of the distribution. We used the distribution to define five categories of climate stress (hereafter called climate risk). We assumed that the baseline climate conditions found 80% of the time within each vegetation type represents the least physiological risk for that vegetation type (Thorne et al., 2017a; Williams et al., 2018). This central 80% (most commonly occurring) of a vegetation type's climate frequency distribution was defined as 'low risk'; the class from the center, the 80–95% of the distribution was treated as a buffer between low and high exposure, and called 'medium risk'; the marginal 95–99% were classed as 'high risk'; the last (outer) 1% of the frequency distribution was considered 'very high risk', and cells with future-climate conditions not currently found in Chile were classed as 'non-analog'.

Classifying the baseline climate exposure classes for each type identified a range of PCA values associated with each of the five classes. We then examined the future climate PCA values of each grid cell in each vegetation type to see in which class, defined from the baseline time period, the cell's future climate was in. For example, grid cells that retained climate conditions in the central 80% of baseline conditions were considered low risk locations and are potential areas of conservation interest for maintaining current vegetation, whereas grid cells with climate conditions in the high- or very-high climate risk categories are areas that may experience a shift in dominant vegetation (Thorne et al., 2020). This was done for each vegetation type individually, to identify the areas that become highly exposed and those that remain climatically suitable. The climate risk categories of all the vegetation types under each of the four future projections were then mapped to visualize and measure climatic risk across the whole country.

2.2.3. Assessing latitudinal and elevation patterns of exposure across vegetation types

We analyzed the latitudinal and elevation effects of climate on each vegetation type and assessed the degree of vegetation climate exposure for the major forest types, including the Gondwanic *Nothofagus*, *Araucaria*, *Austrocedrus*, *Fitzroya*, and Sclerophyllous forests.

We extracted raster values from a digital elevation model (DEM) at the same spatial resolution of our climate variables (30 arc-seconds), as well as the associated latitudes for all pixels of each vegetation type's range and calculated its mean elevation and latitude. We related these values to the baseline (1960–1990) climate conditions for each vegetation type's pixels, using the 5% frequency values. We also calculated the elevation and latitudinal range as the maximum elevation/latitude minus the minimum elevation/latitude for each vegetation type.

We assessed relationships between mean elevation, mean latitude, elevational range, and latitudinal range on exposure across vegetation types by fitting separate linear models with each geographic parameter as a univariate predictor and mean exposure as the response variable. We repeated these analyses for exposure calculated from each future climate forecast.

3. Results

The RCP4.5 scenario presented lower climate risk than the RCP8.5 scenario, with 16.5–24.18% of the country under high-risk categories (high, very high, and non-analog) by 2080. By comparison, 31.4–43.6% of Chile was classified as high risk under the 'business-as-usual' (RCP8.5) scenario. While lower emissions may eventually be achieved, we focus the paper on the currently more accurate RCP8.5 scenario (Schwalm et al., 2020). We provide results for the RCP4.5 scenario in Supporting Information (Appendix S4 Table S8, Fig. S4). Models showed greater climate exposure under HadGEM2-ES than in MIROC5 (Fig. 2, Supporting information Appendix S4, Fig. S4). Under RCP8.5, 27.8–43.6% of the current protected areas (PAs) and 32.2–43.6% of the non-protected areas are in higher risk categories (Fig. 3, Supporting information Appendix S2 Table S1).

3.1. Vegetation climate risk exposure

There were marked differences in the level of climate exposure among vegetation types under RCP8.5 (supporting information Appendix S5). We found that most of the main vegetation types both within and outside of the protected areas are in high climate risk (Table 1). This is particularly relevant for the case of *Nothofagus* forests that represent nearly 50% of the forested areas of the country, 52–100% of the area of these types within PAs are at high climate risk, with a similar level of exposure (43–99%) for areas outside PAs. For example, the entire extent (100%) of *N. obliqua-N. glauca* (34 km^2) in PAs is under high climate risk as well as over 99% of its total distribution (Table 1, Fig. 4a). A limited area of low climate risk in its southern distribution in the Andes mountains at 36.5°S represents a possible conservation target (Fig. 4a). The situation is not quite a dire for *N. obliqua – N. alpina – N. dombeyi* forests, which have 52–61% of their extent in PAs is at high climate risk, but which have an additional 2043–3032 km^2 outside PAs in areas of low climate risk (Table 1). Chile's Gondwanic coniferous forests have small ranges and all are already endangered (IUCN, 2020). For example, *Araucaria araucana* and *Fitzroya cupressoides* forests, which are well represented in protected areas (44.8% and 63.8% of their range respectively), face high climate risk for >95% of their extents not only within PAs but also beyond PAs (Table 1, Fig. 4b, c). However, we did identify climate refugia in the coastal mountain range at 37.9°S for *A. araucana* and at 41°S for *F. cupressoides* (Fig. 4b, c). Finally, the core biodiversity hotspot of Chile's Winter Rainfall forests, the Sclerophyllous forest and Valdivian rainforest, differ in protected area and climate risk. Only 1.7% (238 km^2) of Sclerophyllous forest is under protection, of which 29% faces high climate risk (Table 1, Fig. 5a). Our analysis identifies two climate refugia for this type, one in the Coast mountains (33°S) and other in the Andes (34.5°S) (Fig. 5a). About 38% (9259 km^2) of Valdivian rainforest is currently protected, of which 33.4–35.3% is under high climate risk (Table 1, Fig. 5b). For Valdivian rainforest, we found climate refugia in National Parks, at Chiloé 42°S and southern Isla Magdalena 44–47°S (Fig. 5b). More information about other vegetation type can be found in the supplementary information (Appendix S6).

3.2. Latitudinal and elevation patterns of exposure across vegetation types

Climate change risk has latitudinal and elevation patterns across Chile, but these depend to some degree on the GCM considered. For example, exposure risk increases with elevation when considering MIROC5 ($\beta_{\text{mean elev}} = 0.072$, 95% confidence interval (CI) = [0.015, 0.131]), and the highest elevation vegetation type, Altiplanic Steppe, had among the highest risk of exposure (Fig. 6e, Fig. S12). However, while exposure risk also increased with elevation when considering HadGEM2-ES, this relationship was not statistically significant ($\beta_{\text{mean elev}} = 0.061$, 95% CI = [−0.046, 0.168]; Fig. 6a). This is perhaps due to a higher degree of variance of exposure for vegetation types with mean elevations <2000 m based on that GCM.

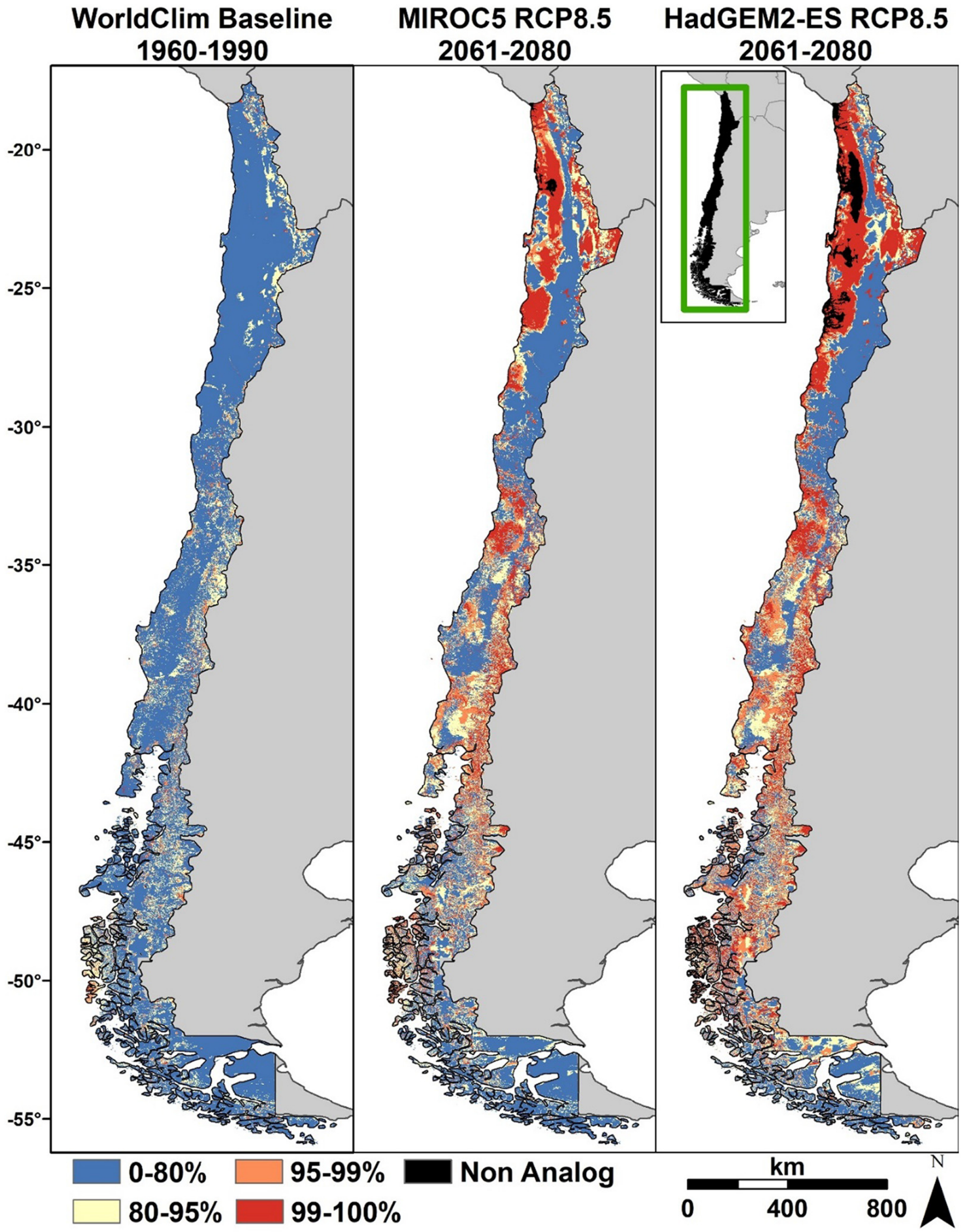


Fig. 2. Projected future climate exposure for Chile: a) Baseline (1960–1990) baseline scenario, b) future (2061–2080) MIROC5 RCP8.5 and HadGEM2-ES RCP8.5 emission scenario. Yellow, orange, red and black colors represent increasing levels of climate risk (Low, Medium, High, Very High, Non-Analog, respectively). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We also found that mean exposure had strong latitudinal patterns when considering projections based on HadGEM2-ES with vegetation types towards the south having increasing risks of exposure ($\beta_{\text{mean lat}} = -0.01$, 95% CI = $[-0.02, -0.001]$; Fig. 6c). For example, Patagonic Steppe is one of the most southerly distributed vegetation types (mean latitude = 50.28°S), and had a mean exposure of 0.94 considering based on HadGEM2-ES. Yet, for the MIROC5 GCM, we did not find a statistically significant relationship between latitude and exposure ($\beta_{\text{mean lat}} = 0.002$, 95% CI = $[-0.005, 0.007]$ Fig. 6g). That said, results from both models indicated that some northerly distributed vegetation types are also at high climate risk, notably Altiplanic Steppe (Supporting information, Fig. S8).

Generally speaking, vegetation types with narrower elevation ranges had higher mean exposure rates, although these trends were not statistically significant with either GCM (MIROC5: $\beta_{\text{elev size}} = -0.022$, 95% CI = $[-0.053, 0.007]$; HadGEM2-ES: $\beta_{\text{elev size}} = -0.034$, 95% CI = $[-0.086, 0.019]$; Fig. 6b, f). Many vegetation types with small elevational ranges had high risk of exposure, such as *Araucaria araucana* (Fig. 4b), Alerce (Fig. 4c), and Patagonic Steppe (Table 1) But we found a few exceptions, such as some Cypress forests that were very narrowly distributed with only moderately high risk of exposure.

Similarly, we found the general trend that vegetation types with smaller latitudinal range sizes had higher mean exposure rates, but this finding was only statistically significant based on results from the MIROC5 GCM ($\beta_{\text{lat size}} = -0.006$, 95% CI = $[-0.009, -0.003]$; Fig. 6h). Results from the HadGEM2-ES qualitatively matched this pattern, but were not statistically significant ($\beta_{\text{lat size}} = -0.006$, 95% CI = $[-0.012, 0.001]$; Fig. 6d).

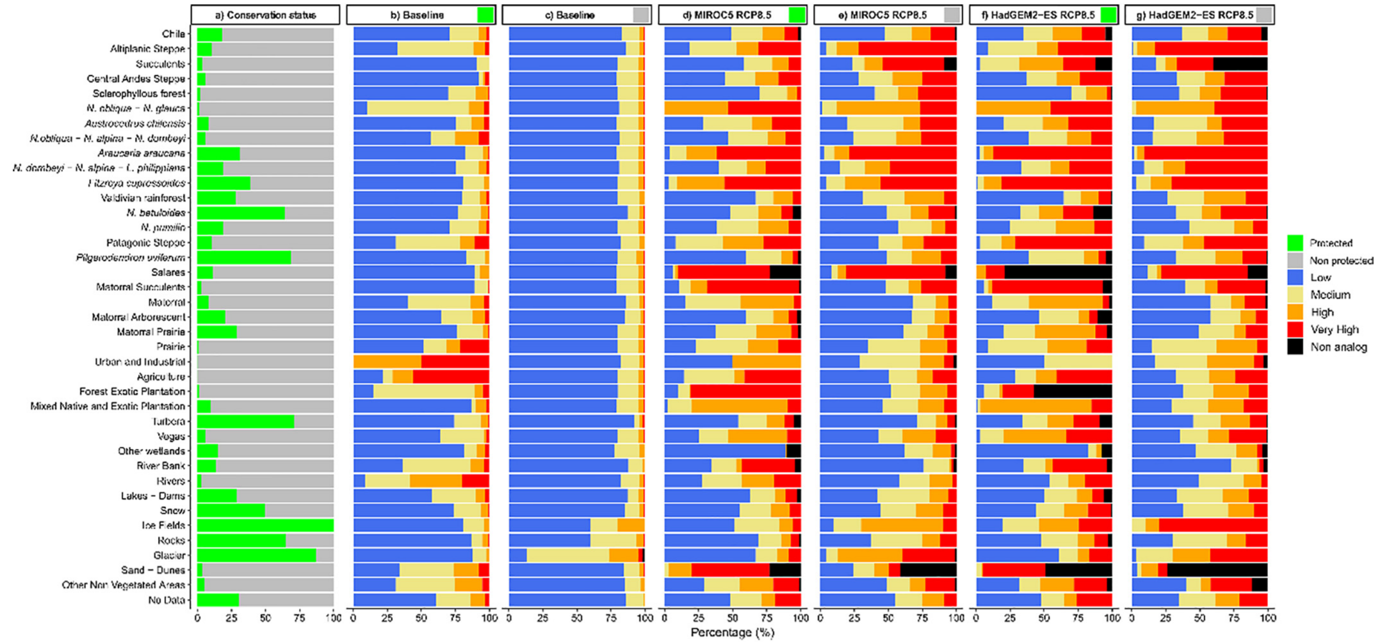


Fig. 3. Land cover types of Chile projected in different climate risk categories at the end of the century for the RCP8.5 emission scenarios for PAs (green) and non-PAs (grey). The categories are based on the percentage of pixels for a given land cover or vegetation type that are with the Baseline period (1960–1990) in terms of the percentage of change of exposure: low (blue, 0%–80%, central 80% of the baseline frequency distribution of climate for a type); medium (yellow, 80%–95%); high (orange, 95%–99%); very high (red, 99%–100%); and non-analog (black, outside 100%). Scores shown values for the two global circulation models (GCMs) evaluated under the Baseline, and RCP8.5 emissions scenario (Supporting Information). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

As mentioned above, there are some notable exceptions to these general patterns in latitude and elevation (Fig. 2). The Andes mountains show high climate risk from central Chile (33°S) to northern Patagonia (43°S), coinciding with their decreasing elevation. Between latitude 43°S to 50°S in the Andes, we found a mixed pattern of low-exposure and high-exposure that coincided with differences in elevation. Likewise, some geographically flat areas show high risk, such as in the north of the country, mainly in and around of the Atacama Desert and coastal areas (21°S). Similarly, in central Chile, the intermediate flat depression ("central valley") between the coastal mountain range and the Andes mountains (33°S–35°S) showed high climate exposure. Finally, we found climatically stable areas in the high Andes between 27.5°S and 32.5°S and in the austral Tierra del Fuego island in Patagonia (55°S). Transverse valleys that cross from the Andes Mountains to the coast (latitude 29°S–31°S) also show low climate exposure and relative stability.

Nevertheless, when controlling for all four factors considered (mean elevation, mean latitude, elevational range size, and latitudinal range size) in a single model, the mean elevation of a vegetation type is a consistently positive and significant indicator of climate exposure risk under either climate change scenario, and is perhaps the most important predictor. The mean latitude of a vegetation type is also an important predictor (i.e., more southerly distributed vegetation types are generally at greater climate exposure risk), especially under the HadGEM2-ES GCM.

4. Discussion

We found that climate risk for vegetation in Chile is widespread across all latitudes, with 31.4–43.6% of the entire land area projected to move into high climate exposure categories. Our results provide evidence to consider for country-level conservation and adaptation planning and evidence-based decision-making, and can be used to identify and manage priorities for individual vegetation types.

Our results offer information for climate change adaptation and mitigation for Chile's natural vegetation types (Table 1, Figs. 2–3). We also

Table 1
Future climate risk exposure (year 2060–2080) for the main vegetation types for both GCMs in RCP8.5. For detailed information see Fig. 3 and Supplementary information.

Vegetation type	Non-protected			Protected		
	Area [km^2]	Low climate risk (%)	High climate risk (%)	Area [km^2]	Low climate risk (%)	High climate risk (%)
Altiplanic Steppe	13,433	1.4–3.6	96.4–98.6	1548	9.2–18.3	81.7–90.8
Succulents	659	18.4–23.3	76.6–81.6	27	2.9–58.7	41.3–97.1
Central Andes Steppe	4947	28.5–33.0	67.0–71.5	292	36.6–44.0	56.0–63.4
Sclerophyllous forest	13,675	35.1–40.4	59.6–64.9	238	70.4–70.4	29.6–29.6
N. obliqua - N. glauca	2087	0.1–0.9	99.1–99.9	34	0.0–0.0	100–100
Austrocedrus chilensis	550	16.0–20.4	79.6–84.0	50	20.2–27.9	72.1–79.8
N. obliqua - N. alpina - N. dombeyi	13,357	15.3–24.2	75.8–84.7	793	38.5–47.3	52.7–61.5
Araucaria araucana	1840	2.0–3.5	96.5–98.0	824	2.8–4.5	95.5–97.2
N. dombeyi - N. alpina - L. philippiana	7003	8.6–14.1	85.9–91.4	1653	33.4–39.5	60.5–66.6
Fitzroya cupressoides	1320	2.8–4.5	95.5–97.2	842	1.1–2.7	97.3–98.9
Valdivian rainforest	24,058	26.4–31.4	68.6–73.6	9259	64.7–66.6	33.4–35.3
N. betuloides	5900	32.6–49.1	50.9–67.4	10,568	31.9–48.0	52.0–68.1
N. pumilio	29,394	42.0–57.0	43.0–58.0	6961	24.6–38.3	61.7–75.4
Patagonic Steppe	6010	8.8–42.9	57.1–91.2	362	2.8–8.3	91.7–97.2
Pilgerodendron uviferum	1311	33.0–48.9	51.1–67.0	2845	38.8–60.3	39.7–61.2
Salares	7340	7.7–12.4	87.6–92.3	954	0.0–6.0	94.0–100.0

highlight the need to increase the representativeness of vegetation types in the country's PAs (Table 1) the majority of which have climate refugia predominantly outside the current stablished areas, whether by expanding current PAs or establishing new PAs depending on the vegetation type. This information is relevant for the establishment of new protected areas and may help inform national efforts for conservation planning (e.g. Chile's National Strategy for Climate Change and Vegetation Resources (ENCCRV, 2017), and National Protection Plan of Wetlands (MMA, 2018)). At the national scale, our climate risk maps can be used to identify which governmental administrative units need to be coordinated for climate adaptive measures (Choe and Thorne, 2019). For individual types, such as *N. obliqua-N. glauca* (Fig. 4a) and Salares (Fig. S9), their small extent of climate refugia within current protected areas and few opportunities for future climate stability outside PAs, suggest more localized research is needed to ensure their survival. For example, *Araucaria araucana* and *Fitzroya cupressoides*, are well-represented in Chile's PAs (Table 1), but show high climate risk within the national reserves and few opportunities for climate refugia outside them. For vegetation types such as these, climate adaptive conservation and management strategies such as increasing connectivity (Stralberg et al., 2020) and land management treatments intended to increase climate resilience (Millar and Stephenson, 2015; O'Donnell et al., 2018) are critical. Both forests types that comprise Chile's Winter Rain biodiversity hotspot (Sclerophyllous forest and Valdivian rainforest) have climate refugia outside current PAs, highlighting the need to stablish new protected parks and private protected areas. Such actions would also support Chile's obligation to the Aichi-Convention on Biological Diversity goal of 17% of protection of each ecosystem, to be reflected in national policy (MMA, 2017). This is particularly relevant for these two forest types, whose high endemism are the result of long periods of climate stability, which increases their vulnerability to climate change (Trew and Maclean, 2021). Finally, some of the vegetation types analyzed here are well represented within PAs that have climate refugia within them (e.g., *N. betuloides*, *Pilgerodendron uviferum*).

Conservation planning that integrates multiple approaches is likely more effective than planning that relies on a single analytical approach, especially under changing conditions (Schmitz et al., 2015). Our in situ climate risk assessment provides a tool for conservation planning nationally that can complement current efforts based on species distribution models (Supporting information Appendix S1). For example, predictions of gains in species richness and increased species turnover along increasing elevation in the Andes mountains of central Chile (35°S) (Fuentes-Castillo et al., 2019) contrasted with our results. This is likely related to different study objectives (species versus vegetation types) and the modeling approach employed (i.e., spatially-dynamic species distribution models versus in situ vegetation risk). However, our approach facilitates identifying areas predicted to have high climate exposure, which is consistent with areas Fuentes-Castillo et al. (2020) identified as more likely to experience high ecological turnover, and where species from other vegetation types may be able to competitively establish. Additionally, areas we identify as climate-stable vegetation refugia (Thorne et al., 2020), including the pristine native vegetation in Southern Patagonia (Terra del Fuego 53°S), are similar to locations where other studies suggest plant species richness may increase in the future under climate change (Fuentes-Castillo et al., 2020). In this case, our study can provide context for land managers as they decide if they whether or not to try to invest in retaining existing dominant vegetation, or to allow some areas to transition to other vegetation (Millar and Stephenson, 2015).

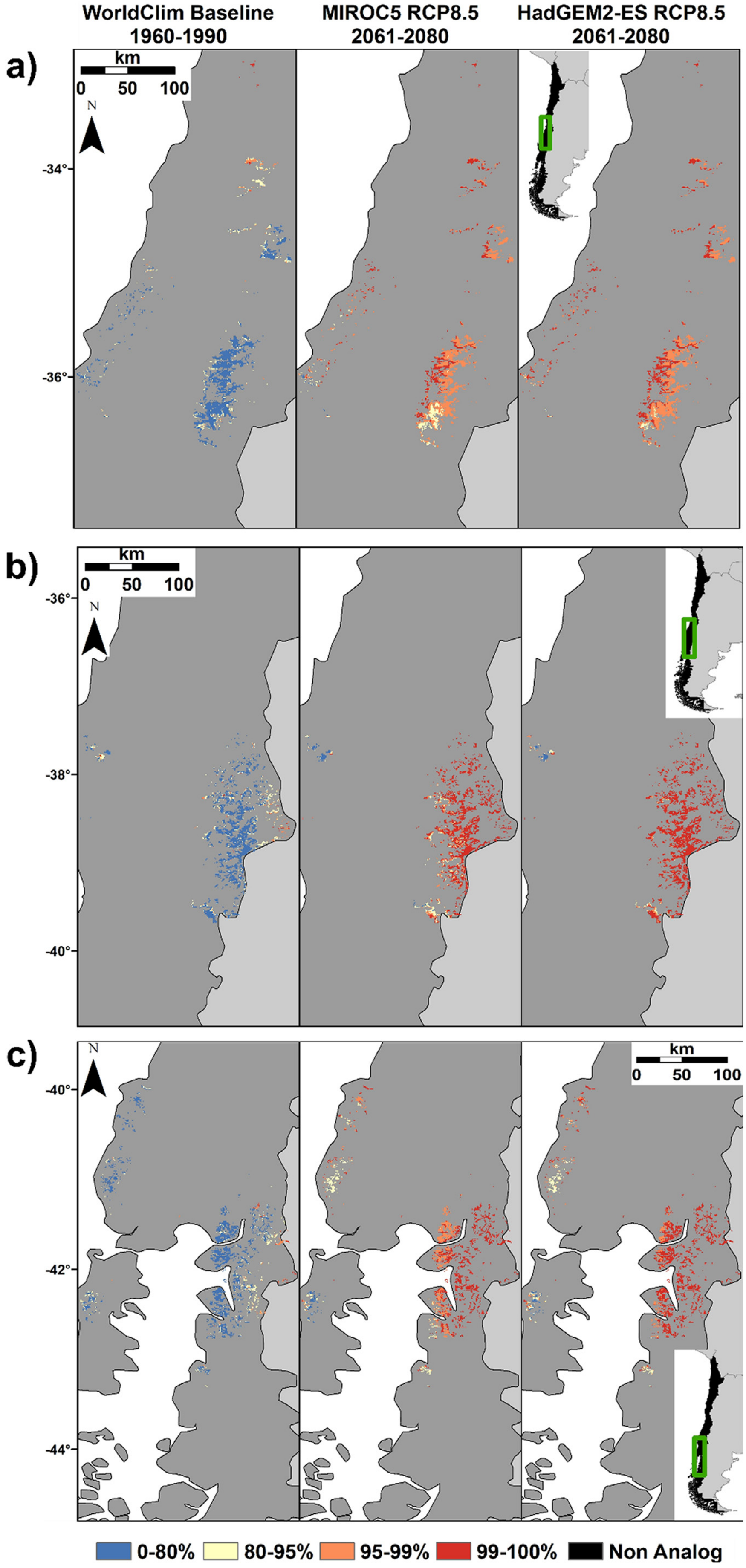
Portions of the Andes mountains in Chile are thought to act as climate refugia due to the large elevational gradients (Elsen et al., 2018). Our results suggest that the Andes will be climate-stable only between latitudes 19°S to 31°S, representing both a warning of low overall refugia potential generally in Chile, but also a time-sensitive opportunity for conservation planning in the identified possible refugia that do exist. Context is key to achieving conservation objectives (Jarzyna and Jetz, 2018), and we observed that some agricultural, ranching and forested landscapes are expected to be climatically stable. These areas, at relatively low elevation (150–400 m a.s.l.) and with flat topography, were predicted to have lower future climate risk at latitude 39°S (agriculture and exotic forest plantations) and around latitude 41°S (grazed grasslands). These climate-stable areas may have substantial adaptation benefits to biodiversity, so regulatory, incentive, or voluntary actions to support biodiversity without sacrificing livelihood potential in these areas could be viable conservation strategies, such as the implementation of sustainable silvopastoral systems (Garibaldi et al., 2020; Kremen and Merenlender, 2018).

Regions in Chile with high climate exposure are likely to face species turnover, with associated changes in ecosystem function, community composition, and biodiversity patterns (Williams and Jackson, 2007). Conservation strategies for these areas could include: management to increase resilience of existing vegetation (Watson et al., 2018); the development of migration corridors (Keeley et al., 2018), restoration of degraded habitat (Meyer et al., 2021), potentially with plant species anticipated to be adapted to future climate conditions; and policies that promote a diversity of land cover types with heterogeneous climate niches (Elsen et al., 2020a). For example, retaining intact native forests with high canopy cover that can resist seed invasion in *Nothofagus* forests (Gómez et al., 2019) could also provide thermal buffering for multiple taxonomic groups (Scheffers et al., 2014). Similarly, stronger government regulation of the frequent practice of leaf-litter removal in central Chile for horticultural purposes could increase resilience to climate change in Sclerophyllous forest and prevent the advance of desertification (Fuentes et al., 2014).

Our assessment of latitudinal patterns of exposure was partially consistent with previous studies that found higher warming rates at high latitude (Nolan et al., 2018). We found that vegetation types restricted to a smaller range of latitudes tended to have higher risk of exposure, at least under the MIROC5 GCM (Fig. 4). We also found elevational gradients of climate risk when based on the MIROC5 GCM, with exposure increasing with elevation, especially for species with a restricted latitudinal range of distribution, but not when based on HadGEM2-ES (Fig. 4). However, apparent differences we observed could be related to the interaction of latitude and elevation, as the Andes reach their highest elevation at Mt. Aconcagua (6962 m above sea level, around 33°S) and decrease in elevation towards southern latitudes. The relationship between latitude and exposure was also influenced by the GCM considered, as we found different spatial patterns of risk between HadGEM2-ES and MIROC5 for vegetation types that have large latitudinal distributions. Therefore, for climate adaptive conservation planning, we caution that climate risk assessments can be sensitive to both the spatial scale considered and choice of modeled climate data (Fordham et al., 2011). In addition to elevation and latitude, maritime influence is another factor potentially influencing the location of low climate-exposure areas in Chile. While this potentially confounded our analysis of elevation range size and climate exposure (Johnstone and Dawson, 2010), we did identify coastal areas of vegetation refugia, located at 31°S and 53°S.

Our results are consistent with previous research that predicted novel climates at low elevations (Mahony et al., 2018). We also found locations of non-analog climates at lower elevations near the coast in the central north of the country, particularly in the Atacama Desert (Fig. 3). It is likely that non-analog conditions in the Atacama desert will increase the already stressful climate that these plants are adapted to with detrimental consequences for their conservation (Díaz et al., 2019), opposite to the relaxation in environmental conditions found in other non-analog climates (Mahony et al., 2018).

Finally, our analysis may also inform vegetation risk status for similar vegetation types. Some of the Altiplanic steppe vegetation is shared in the north of the country with Perú, Bolivia and Argentina, as well as, part of the Nothofagus forest is also found in Argentina (Moreira-


WorldClim Baseline
1960-1990
MIROC5 RCP8.5
2061-2080
HadGEM2-ES RCP8.5
2061-2080
a)
b)
c)
km
0
50
100
N
-34°
-36°
-36°
-38°
-40°
-40°
-42°
-44°
0-80%
80-95%
95-99%
99-100%
Non Analog

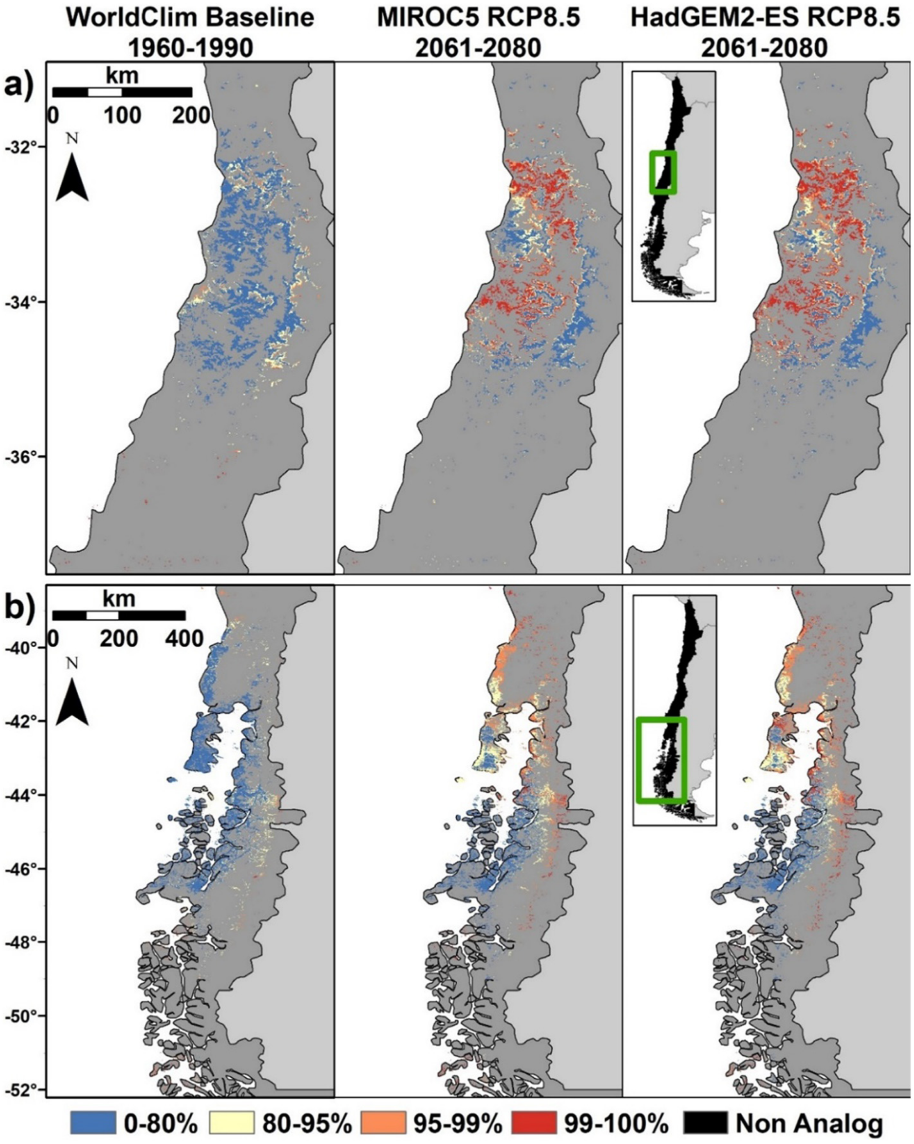


Fig. 5. Projected future climate exposure for Sclerophyllous forest (a) and Valdivian rainforest (b) for Baseline scenario (1960–1990), and future (2061–2080) emission scenarios MIROC5 RCP8.5, and HadGEM2-ES RCP8.5 emission scenario. Yellow, orange, red and black colors represent increasing levels of climate risk. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Munoz, 2011). Performing similar analysis in these countries can also inform and unite conservation planning efforts for the southern cone of Latin America.

4.1. Caveats and future research

The arid and hotter conditions predicted by the GCMs we used (Fig. 2, Supporting Information Appendix S3, Figs. S1, S2, Tables S3, S4) were consistent with an observed increase in wildfires over the past two decades (Úbeda and Sarricolea, 2016). Recently, wildfires have burned large areas of central Chile (CONAF, 2018), and these burned areas were not considered in our current assessment, indicating that the climate risk we report is likely a conservative estimate. Additionally, colonization success in burned areas by invasive species used for forest plantations (*Pinus* and *Eucalyptus*) can increase threats to native forests by competition displacement and increase wildfire risk (highly flammable species) (Bowman et al., 2019). Given the need for conservation planning to implement over the next few decades, another round of climate exposure analysis for more near-term impacts, compared to our predictions for 2070, such as conducted by Thorne et al. (2017a), may be useful for Chilean governments. Future studies could also integrate changes in species distributions, biotic interactions, species adaptability to future climates, and land use projections to our maps of climate risks for native vegetation (Mantyka-Pringle et al., 2015). For example, plant adaptability could also play a key role under climate change, with some plants able to persist even under future climate conditions. In this regard, place-based species and community-level monitoring and experiments focused on phenological and demographic dynamics can help to improve climate risk predictions (Parmesan and Hanley, 2015). Threats from climate change are likely to interact with threats from land use change (Elsen et al., 2020b; Thorne et al., 2017b), especially in mountainous regions

Fig. 4. Projected future climate exposure for *N. obliqua-N. glauca* (a), *Araucaria araucana* (b), and *Fitzroya cupressoides* (c) for Baseline scenario (1960–1990), and future (2061–2080) emission scenarios MIROC5 RCP8.5, and HadGEM2-ES RCP8.5 emission scenario. Yellow, orange, red and black colors represent increasing levels of climate risk. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

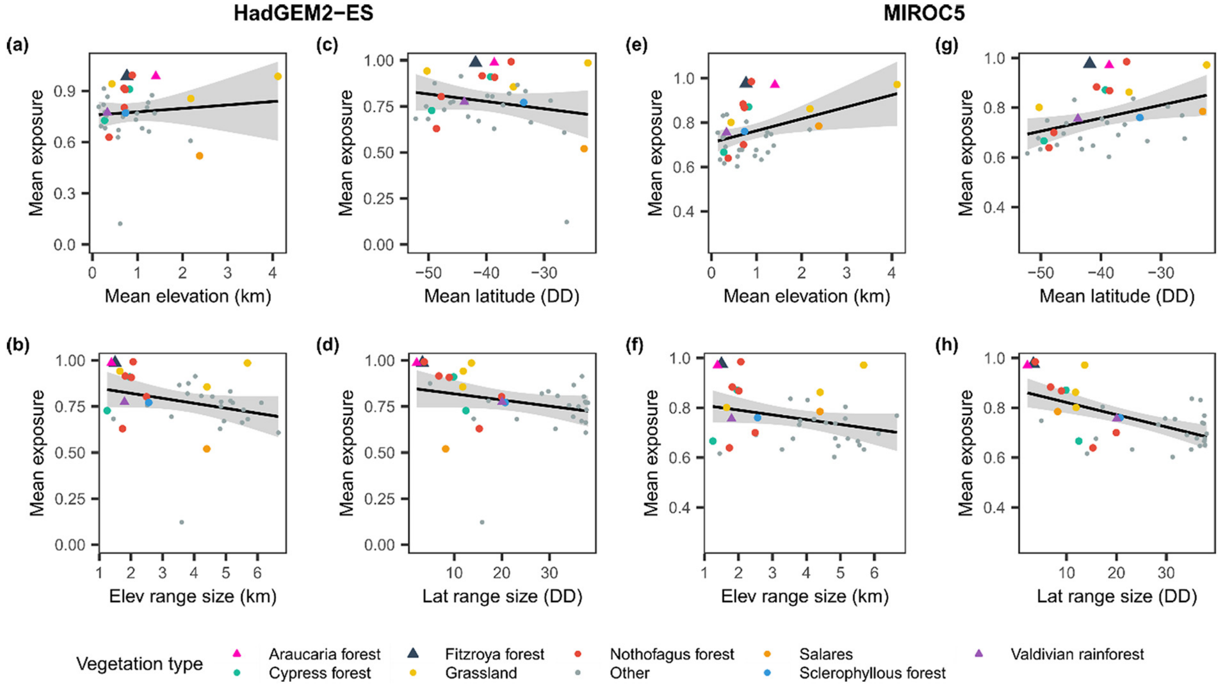


Fig. 6. Climate exposure relationships across vegetation types considering elevation (mean and range), and latitude (mean and range) for HadGEM2-ES (a–d) and MIROC5 (e–h) GCMs. Black lines are linear model fits with shaded regions depicting 95% confidence intervals. Note that Sand Dunes is omitted in the figure for display purposes only but is included in the linear model fits.

where intact vegetation may become suitable for agriculture in the future (Hannah et al., 2013). The implications of these gaps should be considered and complemented with other approaches in future research to effectively guide conservation planning.

Despite these limitations, our approach is uniquely capable of evaluating with precision the climate risk for all of Chile's major vegetation and land cover types. Moreover, our climate risk assessment can be coupled with other data sets (e.g., soil maps, hydrology models, species distribution models) in order to provide a comprehensive risk evaluation (Thorne et al., 2017a).

5. Conclusions

Our results agree that biodiversity hotpots present few climate refugia under climate change (Brown et al., 2020) and are at high risk from climate change (Aukema et al., 2017; Bellard et al., 2014; Le Roux et al., 2019). We found that narrowly distributed vegetation types have higher climate risk, but that for some types, maritime influence, topographic, and microclimatic conditions may provide areas of refuge (e.g. *A. araucana* and *F. cupressoides*). The lower-risk areas highlighted in this study are potential “vegetation refugia” (Thorne et al., 2020), areas that are conservation and restoration priorities, with the goal of maintaining current ecosystem functioning and patterns of biodiversity.

CRediT authorship contribution statement

Andrés Muñoz-Sáez: Conceptualization, Validation, Investigation, Software, Resources, Writing – original draft. **Hyeyeong Choe:** Methodology, Investigation, Software, Writing – review & editing. **Ryan M. Boynton:** Methodology, Software. **Paul R. Elsen:** Investigation, Software, Writing – review & editing. **James H. Thorne:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank L. Renwick for helping with manuscript clarity. We also thank three anonymous reviewers and the editor for helpful comments that improved this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147399.

References

Alaniz, A.J., Galleguillos, M., Perez-Quezada, J.F., 2016. Assessment of quality of input data used to classify ecosystems according to the IUCN Red List methodology: the case of the central Chile hotspot. Biol. Conserv. 204, 378–385. https://doi.org/10.1016/j.biocon.2016.10.038.

Almagro, A., Oliveira, P.T.S., Nearing, M.A., Hagemann, S., 2017. Projected climate change impacts in rainfall erosivity over Brazil. Sci. Rep. 7, 8130. https://doi.org/10.1038/s41598-017-08298-y.

Aukema, J.E., Pricope, N.G., Husak, G.J., Lopez-Carr, D., 2017. Biodiversity areas under threat: overlap of climate change and population pressures on the world's biodiversity priorities. PLoS One 12, e0170615. https://doi.org/10.1371/journal.pone.0170615.

BCN, 2020. Áreas Silvestres Protegidas [WWW Document]. Inf. Territ. Mapoteca - Bibl. del Congr. Nac. Chile URL. https://www.bcn.cl/siit/mapas_vectoriales (accessed 11.30.20).

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. Glob. Ecol. Biogeogr. 23, 1376–1386. https://doi.org/10.1111/geb.12228.

Boisvert-Marsh, L., Périé, C., de Blois, S., 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. J. Ecol. 107, 1956–1969. https://doi.org/10.1111/1365-2745.13149.

Bowman, D.M.J.S., Moreira-Muñoz, A., Kolden, C.A., Chávez, R.O., Muñoz, A.A., Salinas, F., González-Reyes, Á., Rocco, R., de la Barrera, F., Williamson, G.J., Borchers, N., Cifuentes, L.A., Abatzoglou, J.T., Johnston, F.H., 2019. Human–environmental drivers and impacts of the globally extreme 2017 Chilean fires. Ambio 48, 350–362. https://doi.org/10.1007/s13280-018-1084-1.

Brown, S.C., Wigley, T.M.L., Otto-Bliesner, B.L., Rahbek, C., Fordham, D.A., 2020. Persistent quaternary climate refugia are hospices for biodiversity in the Anthropocene. Nat. Clim. Chang. https://doi.org/10.1038/s41558-019-0682-7.

Camarero, J.J., Fajardo, A., 2017. Poor acclimation to current drier climate of the long-lived tree species *Fitzroya cupressoides* in the temperate rainforest of southern Chile. Agric. For. Meteorol. 239, 141–150. https://doi.org/10.1016/j.agrformet.2017.03.003.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026. https://doi.org/10.1126/science.1206432.

Choe, H., Thorne, J.H., 2019. Climate exposure of East Asian temperate forests suggests transboundary climate adaptation strategies are needed. Clim. Chang. 156, 51–67. https://doi.org/10.1007/s10584-019-02493-8.

Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A., Woodward, S., 2011. Development and evaluation of an Earth-System model – HadGEM2. Geosci. Model Dev. 4, 1051–1075. https://doi.org/10.5194/gmd-4-1051-2011.

CONAF, 2018. Estadísticas históricas de incendios forestales en Chile [WWW Document]. Corporación Nac. For URL. http://www.conaf.cl/incendios-forestales/incendios-forestales-en-chile/estadisticas-historicas/ (accessed 5.19.19).

Conaf-Conama-Birf, 1999. Catastro y evaluación de recursos vegetacionales nativos de Chile. 89 p. Comisión Nacional del Medio Ambiente, Corporación Nacional Forestal, Santiago, Chile http://bibliotecadigital.ciren.cl/handle/123456789/10656.

DellaSala, D.A., DellaSala, D.A., Alaback, P., Spribille, T., von Wehrden, H., Nauman, R.S., 2011. Just what are temperate and boreal rainforests? Temperate and Boreal Rainforests of the World: Ecology and Conservation. Island Press/Center for Resource Economics, Washington, DC, pp. 1–41 https://doi.org/10.5822/978-1-61091-008-8_1

Díaz, F.P., Latorre, C., Carrasco-Puga, G., Wood, J.R., Wilmshurst, J.M., Soto, D.C., Cole, T.L., Gutiérrez, R.A., 2019. Multiscale climate change impacts on plant diversity in the Atacama Desert. Glob. Chang. Biol. 25, 1733–1745. https://doi.org/10.1111/gcb.14583.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C.J.C.J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B.P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 67, 534–545. https://doi.org/10.1093/biosci/bix014.

Elsen, P.R., Monahan, W.B., Merenlender, A.M., 2018. Global patterns of protection of elevational gradients in mountain ranges. Proc. Natl. Acad. Sci. 115, 6004–6009. https://doi.org/10.1073/pnas.1720141115.

Elsen, P.R., Farwell, L.S., Pidgeon, A.M., Radeloff, V.C., 2020a. Landsat 8 TIRS-derived relative temperature and thermal heterogeneity predict winter bird species richness patterns across the conterminous United States. Remote Sens. Environ. 236, 111514. https://doi.org/10.1016/j.rse.2019.111514.

Elsen, P.R., Monahan, W.B., Merenlender, A.M., 2020b. Topography and human pressure in mountain ranges alter expected species responses to climate change. Nat. Commun. 11, 1–10. https://doi.org/10.1038/s41467-020-15881-x.

ENCCRV, 2017. Estrategia Nacional de Cambio Climático y Recursos Vegetacionales [WWW Document]. Minist. Agric., Chile URL. https://www.enccrv.cl/. (Accessed 4 May 2021).

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia, L., Silman, M., Farfán-Ríos, W., Malhi, Y., Young, K.R., Cuesta, C.F., Homeier, J., Peralvo, M., Pinto, E., Jadan, O., Aguirre, N., Aguirre, Z., Feeley, K.J., 2018. Widespread but heterogeneous responses of Andean forests to climate change. Nature 564, 207–212. https://doi.org/10.1038/s41586-018-0715-9.

Fordham, D.A., Wigley, T.M.L., Brook, B.W., 2011. Multi-model climate projections for biodiversity risk assessments. Ecol. Appl. 21, 3317–3331. https://doi.org/10.1890/11-0314.1.

Fuentes, J.P., Bown, H.E., Perez-Quezada, J.F., Franck, N., 2014. Litter removal in a sclerophyll forest: short- and medium-term consequences for soil properties. Soil Sci. Soc. Am. J. 78, 634–644. https://doi.org/10.2136/sssaj2013.03.0100.

Fuentes-Castillo, T., Scherson, R.A., Marquet, P.A., Fajardo, J., Corcoran, D., Román, M.J., Pliscoff, P., 2019. Modelling the current and future biodiversity distribution in the Chilean Mediterranean hotspot. The role of protected areas network in a warmer future. Divers. Distrib. 25, 1897–1909. https://doi.org/10.1111/ddi.12988.

Fuentes-Castillo, T., Hernández, H.J., Pliscoff, P., 2020. Hotspots and ecoregion vulnerability driven by climate change velocity in Southern South America. Reg. Environ. Chang. 20, 27. https://doi.org/10.1007/s10113-020-01595-9.

Garibaldi, L.A., Oddi, F.J., Miguez, F.E., Bartomeus, I., Orr, M.C., Jobbágy, E.G., Kremen, C., Schulte, L.A., Hughes, A.C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D.G., Díaz, S., Dicks, L.V., Ellis, E.C., Goldenberg, M., Huaylla, C.A., Kuperman, M., Locke, H., Mehrabi, Z., Santibañez, F., Zhu, C., 2020. Working landscapes need at least 20% native habitat. Conserv. Lett., 1–10 https://doi.org/10.1111/conl.12773.

Gómez, P., Murúa, M., Martín, J.S., Goncalves, E., Bustamante, R., 2019. Forest canopy, a proxi of light intensity, arrests *Pinus radiata* invasion: basic science to conserve the Coastal Maulino forest, Central Chile. bioRxiv, 512194 https://doi.org/10.1101/512194.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5, 131–138. https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2.

Hannah, L., Roehrdanz, P.R., Ikegami, M., Shepard, A.V., Shaw, M.R., Tabor, G., Zhi, L.L., Marquet, P.A., Hijmans, R.J., 2013. Climate change, wine, and conservation. Proc. Natl. Acad. Sci. 110, 6907–6912. https://doi.org/10.1073/pnas.1210127110.

Hijmans, R.J., Camron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 965–978.

Iglesias, A., Artabe, A.E., Morel, E.M., 2011. The evolution of Patagonian climate and vegetation from the Mesozoic to the present. Biol. J. Linn. Soc. 103, 409–422. https://doi.org/10.1111/j.1095-8312.2011.01657.x.

IUCN, 2020. The IUCN Red List of Threatened Species [WWW Document]. Int. Union Conserv. Nat. Nat. Resour URL. https://www.iucnredlist.org/.

Jarzyna, M.A., Jetz, W., 2018. Taxonomic and functional diversity change is scale dependent. Nat. Commun. 9, 1–8. https://doi.org/10.1038/s41467-018-04889-z.

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proc. Natl. Acad. Sci. U. S. A. 107, 4533–4538. https://doi.org/10.1073/pnas.0915062107.

Keeley, A.T.H., Ackerly, D.D., Cameron, D.R., Heller, N.E., Huber, P.R., Schloss, C.A., Thorne, J.H., Merenlender, A.M., 2018. New concepts, models, and assessments of climate-wise connectivity. Environ. Res. Lett. 13, 073002. https://doi.org/10.1088/1748-9326/aacb85.

Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. Front. Ecol. Environ. 13, 106–112. https://doi.org/10.1890/140055.

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 362, 1–9. https://doi.org/10.1126/science.aau6020.

Le Roux, J.J., Hui, C., Castillo, M.L., Iriondo, J.M., Keet, J.-H., Khapugin, A.A., Médail, F., Rejmánek, M., Theron, G., Yannelli, F.A., Hirsch, H., 2019. Recent anthropogenic plant extinctions differ in biodiversity hotspots and coldspots. Curr. Biol. 29, 2912–2918 e2. https://doi.org/10.1016/j.cub.2019.07.063.

Lobos, G., Rebolledo, N., Sandoval, M., Canales, C., Perez-Quezada, J.F., 2018. Temporal gap between knowledge and conservation needs in high Andean anurans: the case of the Ascotán salt flat frog in Chile (Anura: Telmatobiidae: Telmatobius). South Am. J. Herpetol. 13, 33–43. https://doi.org/10.2994/sajh-d-16-00062.1.

Mahony, C.R., MacKenzie, W.H., Aitken, S.N., 2018. Novel climates: trajectories of climate change beyond the boundaries of British Columbia's forest management knowledge system. For. Ecol. Manag. 410, 35–47. https://doi.org/10.1016/J.FORECO.2017.12.036.

Malcolm, J.R., Liu, C., Neilson, R.P.R.P., Hansen, L., Hannah, L., Malcom, J.R., Liu, C., Neilson, R.P.R.P., Hansen, L., Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conserv. Biol. 20, 538–548. https://doi.org/10.1111/j.1523-1739.2006.00364.x.

Mantyka-Pringle, C.S., Visconti, P., Di Marco, M., Martin, T.G., Rondinini, C., Rhodes, J.R., 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biol. Conserv. 187, 103–111. https://doi.org/10.1016/j.biocon.2015.04.016.

Meyer, M.D., Long, J.W., Safford, H.D., Sawyer, S.C., North, M.P., White, A.M., 2021. Principles of postfire restoration. In: Meyer, M.D., Long, J.W., Safford, H.D. (Eds.), Postfire Restoration Framework for National Forests in California. USDA Forest Service, pp. 1–30 PSW-GTR-270.

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Glob. Ecol. Biogeogr. 11, 445–451. https://doi.org/10.1046/j.1466-822X.2002.00307.x.

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826. https://doi.org/10.1126/science.aaa9933.

Ministerio del Medio Ambiente, 2016. Tercera Comunicación Nacional de Chile ante la Convención Marco de las Naciones Unidas sobre Cambio Climático 2016 (In Spanish).

MMA, 2017. Estrategia Nacional de Biodiversidad 2017–2030 (Santiago, Chile).

MMA, 2018. Plan Nacional de Protección de Humedales 2018–2022 (Santiago).

Moreira-Munoz, A., 2011. Plant Geography of Chile, 5th Ed, Plant and Vegetation. Springer Netherlands, Dordrecht https://doi.org/10.1007/978-90-481-8748-5.

Morelli, T.L., Barrows, C.W., Ramirez, A.R., Cartwright, J.M., Ackerly, D.D., Eaves, T.D., Ebersole, J.L., Krawchuk, M.A., Letcher, B.H., Mahalovich, M.F., Meigs, G.W., Michalak, J.L., Millar, C.I., Quiñones, R.M., Stralberg, D., Thorne, J.H., 2020. Climate-change refugia: biodiversity in the slow lane. Front. Ecol. Environ. 18, 228–234. https://doi.org/10.1002/fee.2189.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Kim, S.H., Latorre, C., Leydet, M., Lézine, A.M., Liu, K.B., Liu, Y., Lozhkin, A.V., McGlone, M.S., Marchant, R.A., Momohara, A., Moreno, P.I., Müller, S., Otto-Bliesner, B.L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P.E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., Jackson, S.T., 2018. Past and future global transformation of terrestrial ecosystems under climate change. Science 361, 920–923. https://doi.org/10.1126/science.aan5360.

O'Donnell, F.C., Flatley, W.T., Springer, A.E., Fulé, P.Z., 2018. Forest restoration as a strategy to mitigate climate impacts on wildfire, vegetation, and water in semiarid forests. Ecol. Appl. 28, 1459–1472. https://doi.org/10.1002/eap.1746.

Olson, D.M., Dinerstein, E., 2002. The global 200: priority ecoregions for global conservation author(s). Source Ann. Missouri Bot. Gard. 89, 199–224.

Pacifici, M., Visconti, P., Butchart, S.H.M., Watson, J.E.M., Cassola, F.M., Rondinini, C., 2017. Species' traits influenced their response to recent climate change. Nat. Clim. Chang. 7, 205–208. https://doi.org/10.1038/nclimate3223.

Parmesan, C., Hanley, M.E., 2015. Plants and climate change: complexities and surprises. Ann. Bot. https://doi.org/10.1093/aob/mcv169.

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Chang. 5, 424–430. https://doi.org/10.1038/nclimate2563.

R Development, C.T., 2017. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput., R Foundation for Statistical Computing https://doi.org/10.1111/j.1439-0531.2012.02096.x.Epigenetic.

Rodríguez, J., Cristian, E., Carlos, E., Morales, O.L., Rodríguez-Echeverry, J., Echeverría, C., Oyarzún, C., Morales, L., 2018. Impact of land-use change on biodiversity and ecosystem services in the Chilean temperate forests. Landsc. Ecol. 33, 439–453. https://doi.org/10.1007/s10980-018-0612-5.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. Glob. Chang. Biol. 20, 495–503. https://doi.org/10.1111/gcb.12439.

Scherson, R.A., Thornhill, A.H., Urbina-Casanova, R., Freyman, W.A., Pliscoff, P.A., Mishler, B.D., 2017. Spatial phylogenetics of the vascular flora of Chile. Mol. Phylogenet. Evol. 112, 88–95. https://doi.org/10.1016/j.ympev.2017.04.021.

Schmitz, O.J., Lawler, J.J., Beier, P., Groves, C., Knight, G., Boyce, D.A., Bulluck, J., Johnston, K.M., Klein, M.L., Muller, K., Pierce, D.J., Singleton, W.R., Strittholt, J.R., Theobald, D.M., Trombulak, S.C., Trainor, A., 2015. Conserving biodiversity: practical guidance about climate change adaptation approaches in support of land-use planning. Nat. Areas J. 35, 190–203. https://doi.org/10.3375/043.035.0120.

Schwalm, C.R., Glendon, S., Duffy, P.B., 2020. RCP8.5 tracks cumulative CO_2 emissions. Proc. Natl. Acad. Sci. https://doi.org/10.1073/PNAS.2007117117.

Segovia, R.A., Armesto, J.J., 2015. The Gondwanan legacy in South American biogeography. J. Biogeogr. 42, 209–217. https://doi.org/10.1111/jbi.12459.

Simonetti, J. a, 1999. Diversity and conservation of terrestrial vertebrates in mediterranean Chile. Rev. Chil. Hist. Nat. 72, 493–500.

Stralberg, D., Arseneault, D., Baltzer, J.L., Barber, Q.E., Bayne, E.M., Boulanger, Y., Brown, C.D., Cooke, H.A., Devito, K., Edwards, J., Estevo, C.A., Flynn, N., Frelich, L.E., Hogg, E.H., Johnston, M., Logan, T., Matsuoka, S.M., Moore, P., Morelli, T.L., Morissette, J.L., Nelson, E.A., Nenzén, H., Nielsen, S.E., Parisien, M., Pedlar, J.H., Price, D.T., Schmiegelow, F.K., Slattery, S.M., Sonnentag, O., Thompson, D.K., Whitman, E., 2020. Climate-change refugia in boreal North America: what, where, and for how long? Front. Ecol. Environ. 18, 261–270. https://doi.org/10.1002/fee.2188.

Thorne, J.H., Choe, H., Boynton, R.M., Bjorkman, J., Albright, W., Nydick, K., Flint, A.L., Flint, L.E., Schwartz, M.W., 2017a. The impact of climate change uncertainty on California's vegetation and adaptation management. Ecosphere 8, e02021. https://doi.org/10.1002/ecs2.2021.

Thorne, J.H., Santos, M.J., Bjorkman, J., Soong, O., Ikegami, M., Seo, C., Hannah, L., 2017b. Does infill outperform climate-adaptive growth policies in meeting sustainable urbanization goals? A scenario-based study in California, USA. Landsc. Urban Plan. 157, 483–492. https://doi.org/10.1016/j.landurbplan.2016.08.013.

Thorne, J.H., Choe, H., Stine, P.A., Chambers, J.C., Holguin, A., Kerr, A.C., Schwartz, M.W., 2018. Climate change vulnerability assessment of forests in the Southwest USA. Clim. Chang. 148, 387–402. https://doi.org/10.1007/s10584-017-2010-4.

Thorne, J.H., Gogol-Prokurat, M., Hill, S., Walsh, D., Boynton, R.M., Choe, H., 2020. Vegetation refugia can inform climate-adaptive land management under global warming. Front. Ecol. Environ. 18, 281–287. https://doi.org/10.1002/fee.2208.

Trew, B.T., Maclean, I.M.D., 2021. Vulnerability of global biodiversity hotspots to climate change. Glob. Ecol. Biogeogr. 30, 768–783. https://doi.org/10.1111/geb.13272.

Úbeda, X., Sarricolea, P., 2016. Wildfires in Chile: a review. Glob. Planet. Change 146, 152–161. https://doi.org/10.1016/j.gloplacha.2016.10.004.

Venables, W.N., Ripley, B.D., 2003. Modern applied statistics with S. Technometrics, Fourth. ed Springer, New York https://doi.org/10.1198/tech.2003.s33.

Wan, J.-Z., Wang, C.-J., Qu, H., Liu, R., Zhang, Z.-X., 2018. Vulnerability of forest vegetation to anthropogenic climate change in China. Sci. Total Environ. 621, 1633–1641. https://doi.org/10.1016/j.scitotenv.2017.10.065.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. Nat. Ecol. Evol. 2, 599–610. https://doi.org/10.1038/s41559-018-0490-x.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5, 475–482. https://doi.org/10.1890/070037.

Williams, J.N., Rivera, R., Choe, H., Schwartz, M.W., Thorne, J.H., 2018. Climate risk on two vegetation axes—Tropical wet-to-dry and temperate arid-to-moist forests. J. Biogeogr. 45 (10), 2361–2374. https://doi.org/10.1111/jbi.13413.