



# Effects of alternative sets of climatic predictors on species distribution models and associated estimates of extinction risk: A test with plants in an arid environment



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## ABSTRACT

The effects of using alternative sets of climatic predictor variables on the performance, spatial predictions and future projections of species distribution models (SDMs) and its consequences on extinction risk estimates have remained insufficiently studied.

Here, we modelled the present and future potential distributions of 13 species of *Heliotropium* sect. *Cochranea*, a plant group with a centre of diversity in the Atacama Desert. We developed and applied a sequential procedure, starting from climate monthly variables, to derive six alternative sets of climatic predictor variables. We used them to fit models with eight modelling techniques within an ensemble forecasting framework, and derived climate change projections for each of them. We evaluated the effects of using these alternative sets of predictor variables on performance, spatial predictions and projections of SDMs using Generalised Linear Mixed Models (GLMM). Our Results show that the use of different sets of climatic predictor variables did not have a significant effect on overall metrics of model performance, but had significant effects on present and future spatial predictions and extinction risk estimates. This form of uncertainty in model-based estimates of extinction risk may need to be better acknowledged and quantified in future SDM studies.

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## 1. Introduction

The identification of the important climatic factors involved in controlling the present distribution of plant species is a key step in assessing extinction risks and making predictions about the potential effects of climate change on species distributions (Guisan and Thuiller, 2005). Species distribution models (SDMs, Guisan and Thuiller, 2005; Franklin, 2009; Peterson et al., 2011) represent an important class of tools in this regard, by allowing to quantify species–environment relationships and using these to predict spatial distributions. As a result, SDMs have been and are still used massively to derive climate change projections of species

distributions (e.g., Engler et al., 2011; Thuiller et al., 2011). However, by being correlative, SDMs cannot formally be used to identify causal species–environmental relationships; they can only provide supporting evidence for pre-established hypotheses on factors controlling species distributions (Austin, 2007; Araújo and Townsend Peterson, 2012). How, then, can we provide guidelines on which climatic factors should be preferentially used to build models, predictions and future projections?

As a first approach, Austin (2007) suggested that previous knowledge about the physiological responses of plants to their environments and general ecological theory (e.g., the law of the minimum) should be used a priori to identify suitable environmental variables for modelling species distributions (from recent past to present). SDMs can then be used to quantify the respective importance of pre-selected environmental factors, or sets of factors, in influencing the distribution of plant species. For instance, a recent study has shown that the use of monthly variables rather than annual means or totals, and the inclusion of variables capturing environmental variations (e.g., extremes), improved SDM

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predictions of tree species (Zimmermann et al., 2009). More generally, Araújo and Guisan (2006), Austin and Van Niel (2011a) and Peterson et al. (2011), in their reviews, identified the selection of environmental predictors as one of the major challenges in SDM research, and recent studies have shown that the selection of predictor variables can significantly affect the performance of and predictions from SDMs (Dormann et al., 2008; Peterson and Nakazawa, 2008; Syphard and Franklin, 2009; Ashcroft et al., 2011; Austin and Van Niel, 2011b; Synes and Osborne, 2011; Triviño et al., 2011; Watling et al., 2012; Williams et al., 2012; Braunisch et al., 2013; Sheppard, 2013).

In practice, however, the choice of predictor variables to be used is often limited by both the availability of information and the scale at which phenomena are studied (Austin and Van Niel, 2011a). Furthermore, it remains difficult to determine a priori which specific variables primarily influence the distribution of a species, unless there is deep knowledge of its ecophysiology. One easy solution would be to include as many variables as are available. However, the inclusion of too many variables in a model can cause serious overfitting problems (Araújo and Guisan, 2006; Thuiller et al., 2008a), generating models too centred on the dataset used to train them, and consequently of limited transferability to other conditions such as future climates (Randin et al., 2006).

A more parsimonious approach is to select alternative subsets of variables with potential ecological relevance to the species under study, with each subset corresponding to a different hypothesis or set of hypotheses on how the environment may control the species' distribution. This type of approach was for instance used by Vicente et al. (2010) to test hypotheses on the factors controlling patterns of alien invasive plant species richness, but it has so far rarely been used for individual species. Another way of defining subsets of factors is to keep as separate sets, variables generated through different published approaches, such as the use of raw monthly values (e.g., Hijmans & Graham, 2006), of more advanced bioclimatic indices (e.g., Broennimann et al., 2007). The effect of the different preparative treatment of climatic and other environmental variables on SDM performance and predictions has so far remained largely untested (Ashcroft et al., 2011; Synes and Osborne, 2011; Bedia et al., 2013; Fernandez et al., 2013).

SDMs have been used for more than a decade to derive climate change scenarios (e.g., Guisan and Theurillat, 2000), but they were only more recently identified as useful tools for determining species status in terms of vulnerabilities and extinction risks (Thuiller et al., 2005; Rödder et al., 2009; IUCN, 2010; Fordham et al., 2012; Crimmins et al., 2013; Fordham et al., 2013; but see Akçakaya et al., 2006), in particular through providing an alternative approach to calculating IUCN's AOO criterion (area of occupancy; IUCN, 2001). However, it is unclear whether the choice of environmental variables can have an effect on the resulting SDM-based extinction risk estimates.

Arid ecosystems have been identified as being among the most sensitive to climate change (Kefi et al., 2007) and climate change ultimately affect the modelled estimates of extinction risks (IUCN, 2001; Fordham et al., 2013). They thus provide appropriate systems to assess the use of SDMs to estimate climate change threat on plants.

Here, we use data on the distribution of rare plant species in an arid landscape in Chile and Perú to address the following questions:

- (1) Are there differences in performance and accuracy among SDMs fitted with different alternative sets of climatic predictor variables?
- (2) Are there differences in the estimates of climate change effects among different sets of climatic predictor variables?

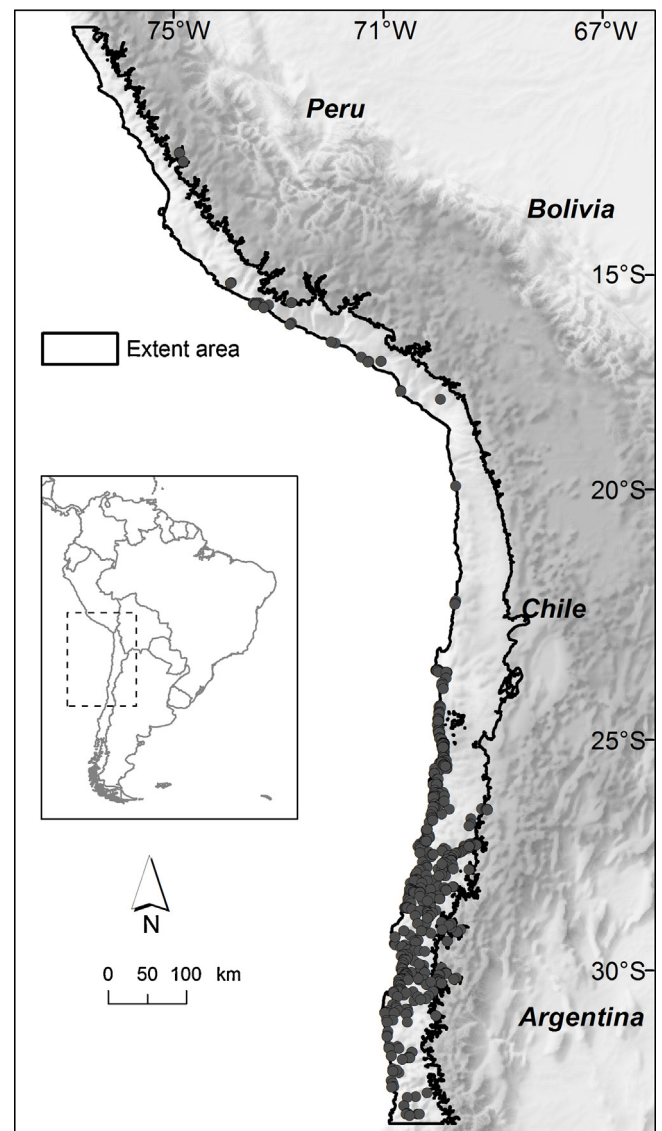


Fig. 1. Extent area indicating the distribution of *Heliotropium* sect. *Cochreana* (circles).

- (3) Do those differences affect model-based estimates of extinction risk for rare species?

To address these questions, we derived six sets of present and future predictors from the same initial monthly climatic variables we previously developed for the area, and applied a sequential procedure to compare the results of using them for fitting SDMs with different modelling techniques.

## 2. Materials and methods

### 2.1. Study system

*Heliotropium* L. sect. *Cochreana* (Miers) Kuntze (Heliotropiaceae, Boraginales) is a group of shrubby and microphyllous plants. Sixteen out of 17 species have a geographical range centred in the Atacama Desert (18°30' S–31°30' S, 0–3 000 a.s.l.; Table 1; Fig. 1). Only one species has its centre of distribution in the Peruvian Desert (*H. krauseanum*), and one species extends its distribution to the Mediterranean woodland zone of central Chile (*H. stenophyllum*). Most species have narrow geographic ranges along the coast

**Table 1**  
 Latitudinal and altitudinal range, total number of herbarium specimens, total number of presence records and occurrences after 1950 for each species of *Heliotropium* sect. *Cochranea*. Species marked with asterisks were not included in the analyses because of their low number of occurrences. Spatial autocorrelation of the presence data (>1950) of each species as measured by Moran's I index (Cliff and Ord, 1981) is indicated in the last column.

Species	Latitude S	Elevation (m)	Occurrences		Moran's I
			Total	>1950	
<i>Heliotropium chenopodiaceum</i> (A.DC.) Clos	26.2–31.5	200–2250	150	81	0.584
* <i>Heliotropium eremogenum</i> I.M.Johnst.	23.4–23.7	100–1000	16	10	
<i>Heliotropium filifolium</i> (Miers) I.M.Johnst.	27.4–28.6	20–530	26	17	0.186
<i>Heliotropium floridum</i> (A.DC.) Clos	26.0–29.3	0–265	66	45	0.706
* <i>Heliotropium glutinosum</i> Phil.	26.3–27.2	1195–2200	18	6	
<i>Heliotropium inconspicuum</i> Reiche	25.1–26.1	100–780	21	13	0.735
* <i>Heliotropium jaffuelii</i> I.M.Johnst.	22.0–22.1	N/A	4	1	
<i>Heliotropium krauseanum</i> Fedde	12.6–19.6	0–1734	39	15	0.444
<i>Heliotropium linariifolium</i> Phil.	24.9–27.1	0–1300	104	55	0.627
<i>Heliotropium longistylum</i> Phil.	27.7–28.4	5–400	22	13	0.557
<i>Heliotropium megalanthum</i> I.M.Johnst.	27.8–28.6	0–620	40	24	0.433
<i>Heliotropium myosotifolium</i> (A.DC.) Reiche	27.1–29.2	170–900	56	30	0.707
* <i>Heliotropium philippianum</i> I.M.Johnst.	24.4–25.1	20–1100	25	6	
<i>Heliotropium pycnophyllum</i> Phil.	23.5–27.1	0–930	141	74	0.759
<i>Heliotropium sinuatum</i> (Miers) I.M.Johnst.	27.7–29.7	0–1500	83	63	0.782
<i>Heliotropium stenophyllum</i> Hook. & Arn.	28.5–32.8	0–1200	204	79	0.307
<i>Heliotropium taltalense</i> (Phil.) I.M.Johnst.	24.4–25.5	50–1060	67	27	0.791
<b>Total</b>	<b>12.6–32.8</b>	<b>0–2250</b>	<b>1082</b>	<b>559</b>	<b>0.586</b>

and are local endemics and geographically rare (Johnston, 1928; Luebert and Wen, 2008). *Heliotropium* sect. *Cochranea* is one of the most diverse plant groups of the Atacama Desert (Luebert and Wen, 2008) and also one of the best studied. Therefore, the entire distribution of these species can be captured, making current and future projections possible (Thuiller et al., 2004).

The study was carried out in an area that includes the complete distribution of *Heliotropium* sect. *Cochranea*: the Peruvian and Atacama Deserts of South America. Most species are restricted to the Pacific coastal range, but a few species reach the foothills of the western slope of the Andes up to ca. 2000 m. Therefore, the extent area was circumscribed to the western side of the Andes of southern Peru and northern Chile between 10° S and 33° S and from the coastline to an elevation of 2500 m (Fig. 1). After a revision of specimens from 22 herbaria, the literature and extensive fieldwork, we do not know of any record of section *Cochranea* species from outside this area.

## 2.2. Climatic data

Climatic surfaces were available for our study area from the widely used WorldClim project (Hijmans et al., 2005), but after a preliminary assessment values obtained from weather stations in the study area and values extracted from WorldClim differed substantially, especially for temperature data. The Global Historical Climate Network Dataset (GHCN, Peterson and Vose, 1997), used as primary source by Hijmans et al. (2005), show a scanty temperature data and does not contain extreme temperature data for our study area. Therefore, we built a new expanded dataset of climatic surfaces that included weather stations from specific Chilean sources. In addition to the Faoclim dataset (FAO, 2001), we used the stations reported by Hajek and di Castri (1975), Amigo and Ramírez (1998), Rivas-Martínez et al. (2003) and Luebert and Plissock (2006). Climatic surfaces were generated for this study using the software Anusplin v.4.36 (Hutchinson, 2006; Xu and Hutchinson, 2013), which implements the methods described in Hutchinson (1995) and is the same algorithm used to derive WorldClim. We modelled monthly data for a time period of 50 years (1950–2000) of precipitation (P), mean temperature (T), mean maximum temperature (M) and mean minimum temperature (m) obtained from a total of 930 weather stations in Chile, Bolivia, Peru and Argentina, to generate climatic surfaces in an area distinctly larger than our

specific extent area, thus avoiding edge effects (Mesquita and Sousa, 2009). Interpolations were fitted with the second-order spline method using elevation as an independent variable (Hutchinson, 2006). The complete dataset of monthly variables at 1 km resolution are available for free download in the ECOSPAT website (<http://www.unil.ch/ecospat/page89413.html>).

## 2.3. Presence data

Herbarium samples of *Heliotropium* sect. *Cochranea* were critically revised and determined at the herbaria A, B, BM, BSB, CONC, DR, EIF, F, G, GH, K, M, MA, MSB, NY, SGO, ULS and US (herbarium codes according to the Index Herbariorum, available at <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>). All specimens with ambiguous locality data were discarded from the analysis. A total of 1082 records, corresponding to 559 unique records from collections after 1950 (the time-frame of the weather station data used to generate the climatic surfaces), were included (Table 1). Only those species with more than 10 unique records (13 species, Table 1) were considered for analysis (Pearson et al., 2007). All species exhibited positive spatial autocorrelation (Table 1), which was significant in all cases ( $P \ll 0.0001$ , data not shown). The Pearson's correlation coefficient calculated between mean True Skill Statistic (TSS) (see below) and Moran I ( $r = 0.0555$ ) was not significantly different from zero ( $t = 0.1844$ ,  $df = 11$ ,  $P = 0.857$ ), suggesting that spatial autocorrelation did not show a linear relationship with predictive power.

## 2.4. Modelling potential distribution

BIOMOD2 version 3.1–25 (Thuiller et al., 2009, 2012) was used to generate species distribution models (SDMs). BIOMOD2 is a library for R (R Development Core Team, 2009) that implements ensemble forecasting (Araújo and New, 2007). Eight modelling techniques implemented in BIOMOD2 were used in our analysis: (1) artificial neural networks (ANN), (2) classification tree analysis (CTA), (3) generalised additive model (GAM), (4) generalised boosted model (GBM), (5) generalised linear model (GLM), (6) multivariate adaptive regression splines (MARS), (7) Random Forest (RF) and (8) Surface Range Envelope (SRE).

The presence dataset was partitioned into a set containing 70% of the data points that was used to calibrate all models (training

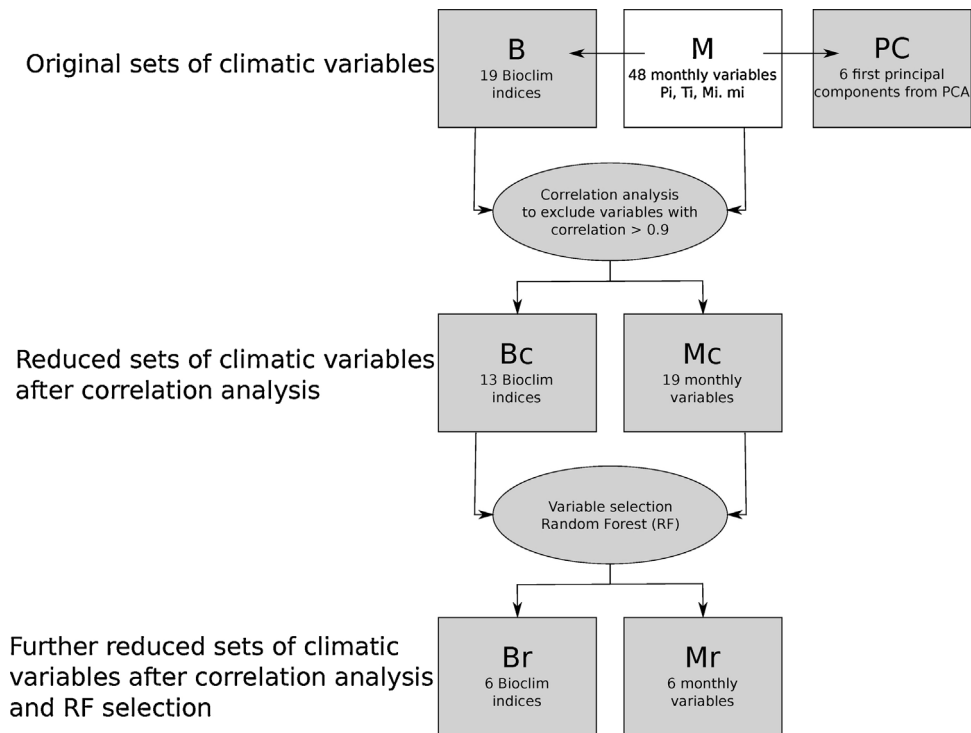


Fig. 2. Overview of the steps followed in the procedure to select the sets of predictor variables used in the analyses.

data) and a set containing 30% of the data points that was used to evaluate the model (test data). Two replicates were done for each of the eight techniques using the 70–30% split-data criteria and presence data was selected randomly by cross-validation. Replicates were rescaled using binomial GLM to make comparable the eight techniques (Thuiller et al., 2009, 2012). The modelling techniques implemented in BIOMOD2 need both presence and absence data. Because our datasets contain only presence data, 10000 pseudo-absence points were randomly selected from the extent and absence points were downweighted, so that the sum of presence-weights equalled the sum of absence-weights (Barbet-Massin et al., 2012). The predictive power was evaluated with the area under the relative operating characteristic curve (AUC) and the true skill statistic (TSS), except for SRE, for which AUC is not available. TSS measures the actual agreement minus the agreement expected by chance while accounting for prevalence. Consensus models were obtained by using the ensemble forecasting approach implemented in BIOMOD2, which uses a weighted average consensus method to reduce model-based uncertainty (Marmion et al., 2009; Thuiller et al., 2009) and excludes the results from techniques with low predictive power. Low predictive power was evaluated on the binary projection of each replicates according to the TSS evaluation method. TSS scores above 0.7 were used to build final consensus models.

## 2.5. Sets of climatic variables

To assess the effects of different sets of climatic variables on modelling outputs, six sets of variables were assembled based on our climatic surfaces. Variable importance on species distribution was evaluated with RF as an integral part of the definition of sets of climatic variables Mr and Br (see below), RF has been widely and successfully implemented for determining variable importance in SDM (Cutler et al., 2007), due to its capacity to select meaningful ecological variables independent of collinearity. The methodology

for selecting those sets of climatic variables is schematically illustrated in Fig. 2. The following sets of variables were defined:

- (1) Mc: Nineteen of the 48 monthly means of Pi, Ti, Mi and mi (where  $i$  is the month number), where only the middle month from each season (DJF [summer], MAM [fall], JJA [winter], SON [spring]) was selected, provided that all correlations within the season were  $> 0.9$ ; when two (three) correlations among variables within the season were  $< 0.9$ , one (two) more variable(s) was (were) selected.
- (2) Mr: One reduced subset of six monthly means from Mc, taken from a selection based on a variable contribution analysis in RF, using the greatest values of mean decreased accuracy (Thuiller et al., 2008b).
- (3) B: The Bioclim set of 19 bioclimatic variables generated with the bioclim-aml script (available at <http://www.worldclim.org/bioclim-aml>).
- (4) Bc: A subset of 13 variables from B resulting from the elimination of one of each pair of variables with correlations  $> 0.9$ .
- (5) Br: One reduced subset of six variables from Bc resulting from a selection based on a variable contribution analysis in RF using the greatest values of mean decreased accuracy (Thuiller et al., 2008b).
- (6) PC: The first six principal components resulting from a PCA of the 48 monthly variables within the full extent.

## 2.6. Comparing models fitted with different sets of climatic variables

All 8 modelling techniques were applied to each of the 6 sets of variables and each of the 13 species (resulting in 624 models). The effects of a set of variables and techniques on predictive performance and spatial projection were evaluated using generalised linear mixed models (GLMM). Monte Carlo simulations with 10000 iterations were performed to obtain  $p$  values. Effects of models on the predictive performance were evaluated using True Skill

Statistics (TSS) as response variables, species as a random effect and the set of variables and techniques as fixed-effects. A second GLMM assesses the effect on spatial projections using 10000 random points extracted from inside the predicted binary distribution of current models for each combination of the set of variables and techniques. Projected values of presence and absence were used as response variables, sets of variables and techniques as fixed-effects and species as a random effect. GLMM analyses and Monte Carlo simulations were applied by using the lme4 R library (Bates and Maechler, 2011) and languageR library (Baayen, 2011). In order to obtain binary models, a probability threshold was estimated by optimising the value of the True Skill Statistics (TSS) using MaxSens + Spec criterion (MaxTSS) available in the PresenceAbsence R library (Freeman and Moisen, 2008). This method showed the best performance in a recent comparison of threshold techniques (Jiménez-Valverde and Lobo, 2007).

### 2.7. Climate change scenarios

We used the HadCM3 (Hadley Centre Coupled Model, version 3) climate change model for the year 2050, with SRES (special report emission scenarios) A2 and B2 (IPCC, 2007). The data were obtained from the GCM downscaled GCM data portal webpage (<http://www.ccafs-climate.org/data/>). Monthly data on precipitation, mean maximum temperature and mean minimum temperature were downloaded. Monthly mean temperature was calculated as the average of the monthly mean minimum and maximum temperature surfaces. We obtained climate change scenarios for our study area following the procedure proposed by Buytaert et al. (2009). The same six sets of variables used for the current climate (Mc, Mr, B, Bc, Br, PC) were created for each climate change scenario (HadCM3 A2 and HadCM3 B2).

Climate change scenarios were used to re-project the models previously calibrated in BIOMOD2, thereby obtaining future projections of species distributions. Range shifts under climate change scenarios were further compared among sets of climatic variables using the kappa ( $\kappa$ ) statistic, as implemented in the Map Comparison Kit Software (Visser and de Nijs, 2006).  $\kappa$  is a measure of spatial agreement between models where the range of possible values is from  $-1$  to  $1$  and was calculated between present and future models, within species, climate change scenarios and sets of variables.

### 2.8. Extinction risk

To assess the extinction risk for each species, predicted areas of occupancy (AOO) were calculated from the binary projections of the final models (see above). To compare the effect of the sets of climatic variables and climate change scenarios on the predicted AOO (pAOO), three GLMM analyses were conducted as described above. The current pAOO, future pAOO, and percentage of change in pAOO between current and future pAOO were used as the response variables. For each analysis, we set species as a random effect, and sets of variables and climate change scenarios as fixed effects.

Extinction risk was evaluated following the recommendations of IUCN (2010). An Anthropogenic land use map (Luebert and Plischoff, 2006; Arino et al., 2008) was used to mask the projected current and future area for all species before the extinction risk criteria were applied. The mask was created reclassifying anthropic and natural land cover classes in two categories (converted and non-converted), transforming the result to raster format and using this final raster binary map to remove converted areas in all the current and future binary models. These calculations were carried out using spatial analyst tools in ArcGIS v.10.3 (ESRI 2012).

Extinction risk was assessed using Criterion A3(c) (IUCN, 2001) using the change in area of occupancy to the year 2050 as a measure of an increase/decrease in population size (Thuiller et al., 2005;

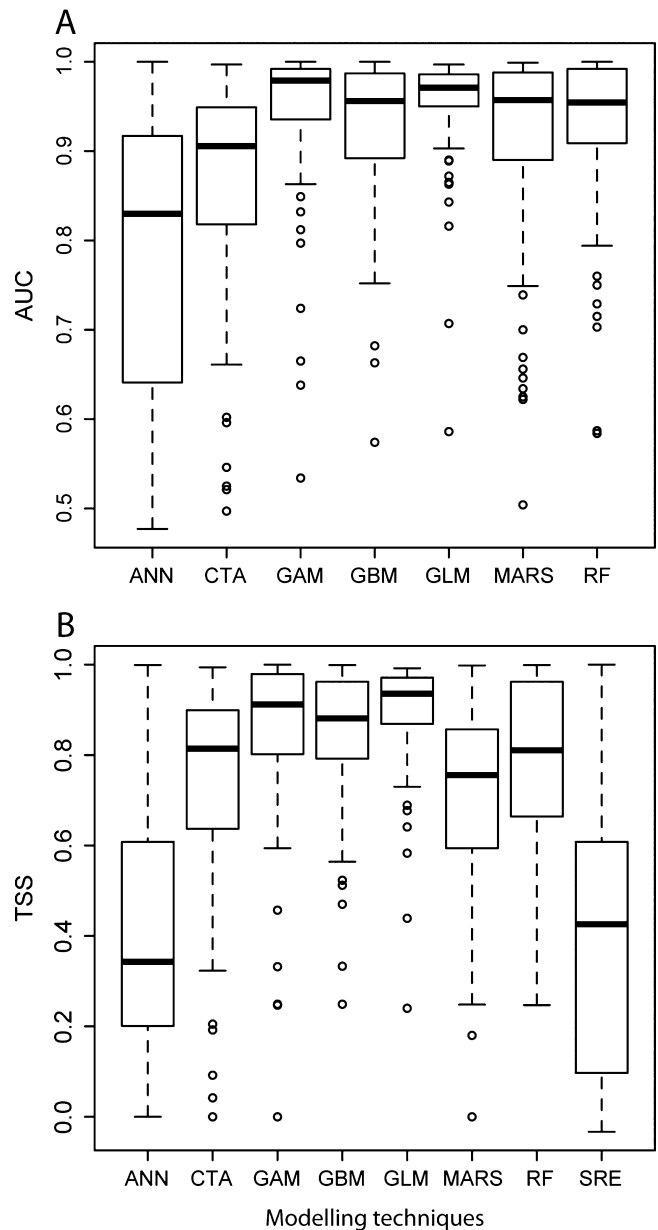


Fig. 3. Boxplots of the predictive performance of the different techniques used for SDMs. (A) AUC and (B) TSS. Values correspond to all species and variable sets.

Nenzén and Araújo, 2011). This approach has been recommended by IUCN (2010). We compared the results of these analyses among sets of climatic variables, computing the number of changes in the extinction risk between pairs of sets of variables.

## 3. Results

### 3.1. Sets of climatic variables

Correlation matrices among monthly variables and among Bio-clim indices are supplied in the Supplementary Appendix A. From the initial full sets of monthly climatic variables, the reduced sets obtained by removing overly correlated variables were:

- Mc (set of own monthly variables reduced after correlation analysis): P1, P3, P4, P5 P7, P9, P11, T1, T4, T7, T10, M1, M4, M7, M10, m1, m4, m7, m10;

**Table 2**

Variables selected from the analysis of variable importance conducted with Random Forest (RF). Mr and Br are different sets of variables for each species. They are subsets of Mc and Bc and differ between species. Mc: reduced set of the newly derived monthly variables (after inspection of the correlation matrix; see Appendix A). Bc: reduced set of the standard Bioclim indices. Numbers 1–6 correspond to the order of importance of the variables according to the RF results, with 1 being the most important and 6 being the least important.

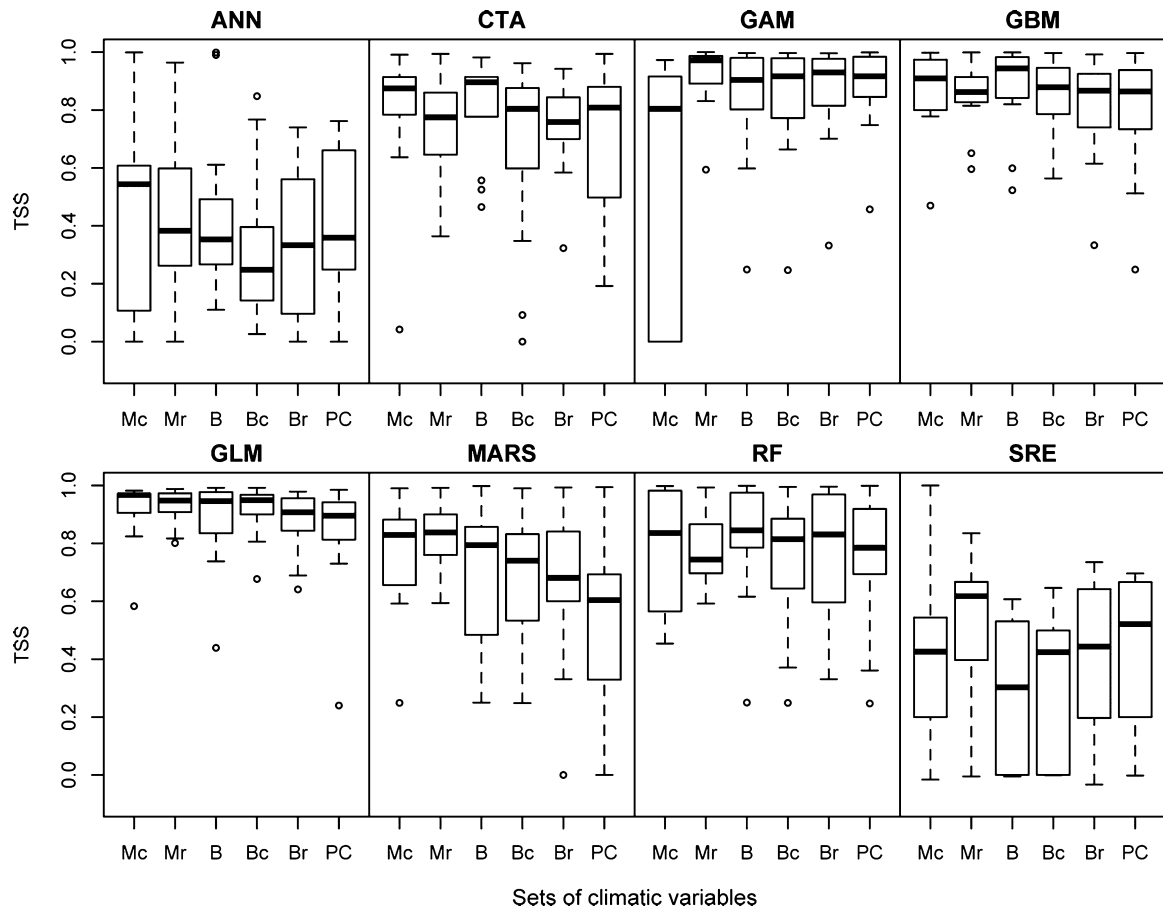
Species	Mr						Br					
	1	2	3	4	5	6	1	2	3	4	5	6
<i>H. chenopodiaceum</i>	P7	M10	m7	M1	M7	M4	BIO19	BIO5	BIO7	BIO2	BIO9	BIO6
<i>H. filifolium</i>	P7	m7	m1	m10	P3	M1	BIO11	BIO3	BIO9	BIO8	BIO19	BIO15
<i>H. floridum</i>	P7	m1	M4	m4	m10	m7	BIO4	BIO3	BIO5	BIO15	BIO9	BIO7
<i>H. inconspicuum</i>	P7	m10	M7	M10	T7	m7	BIO6	BIO19	BIO3	BIO8	BIO11	BIO15
<i>H. krauseanum</i>	M10	M7	P1	P4	P11	m7	BIO18	BIO6	BIO7	BIO5	BIO8	BIO14
<i>H. linariifolium</i>	P7	m10	M10	M1	m1	M7	BIO19	BIO4	BIO6	BIO3	BIO15	BIO5
<i>H. longistylum</i>	m1	P7	m10	M4	P3	P5	BIO3	BIO2	BIO9	BIO7	BIO5	BIO8
<i>H. megalanthum</i>	P7	m1	P5	m7	M10	m4	BIO11	BIO3	BIO9	BIO19	BIO15	BIO8
<i>H. myosotifolium</i>	P7	M10	m1	m7	M1	T1	BIO9	BIO19	BIO2	BIO11	BIO5	BIO6
<i>H. pycnophyllum</i>	m10	M4	T7	M7	P7	M10	BIO19	BIO15	BIO3	BIO6	BIO8	BIO4
<i>H. sinuatum</i>	P7	m1	m7	M7	P5	M10	BIO11	BIO19	BIO5	BIO9	BIO2	BIO8
<i>H. stenophyllum</i>	m7	P7	T1	m4	m1	P3	BIO19	BIO6	BIO9	BIO2	BIO5	BIO7
<i>H. taltalense</i>	T7	m7	P7	M1	m10	M4	BIO6	BIO8	BIO11	BIO19	BIO5	BIO15

- Bc (set of bioclim indices reduced after correlation analysis): BIO2, BIO3, BIO4, BIO5, BIO6, BIO7, BIO8, BIO9, BIO11, BIO14, BIO15, BIO18, BIO19.

The RF analysis of variable contribution conducted on the Mc and Bc sets yielded further reduced sets of climatic variables (Mr and Br) that were different for each species (Table 2). In the Mr set (the set of monthly variables reduced after correlation and RF analyses), winter precipitation (P7) was selected for all species except *Heliotropium krauseanum*, and winter minimum temperature (m7)

was selected for 10 out of 13 species. In the Br set (set of Bioclim indices reduced after correlation and RF analyses), the precipitation of the coldest quarter (BIO19) was selected for 10 species, and the maximum temperature of the warmest month (BIO5) was selected for 9 species.

The first six principal components (eigenvectors and eigenvalues provided in Appendix B) derived from the full sets of monthly variables accounted for 97.2% of the total variance, whereas 71.4% of the variance was accounted for by just the first two principal components.



**Fig. 4.** Boxplots of the predictive performance (TSS) of the models with different sets of climatic variables across modelling techniques. Values of each technique and set of climatic variables correspond to the 13 species analysed.

**Table 3**  
Pairwise comparisons across all species between set of climatic variables (left) and between modelling techniques (right) as obtained from GLMM analyses for predictive power (TSS; upper row) and spatial pattern (Suitable pixels; lower row). Low probability values (highlighted in bold) mean statistically significant differences (<0.05, two-tailed test) for the corresponding comparisons.

	B	BC	BR	MC	MR		
Predictive power/Set of climatic variables							
B							
BC	0.2066						
BR	0.5920	0.4704					
MC	0.7528	0.3268	0.8198				
MR	0.2050	<b>0.0120</b>	0.0706	0.1198			
PC	0.1082	0.7620	0.3232	0.2126	<b>0.0034</b>		
Spatial pattern/Set of climatic variables							
B							
BC	<b>0.0008</b>						
BR	<b>0.0001</b>	<b>0.0001</b>					
MC	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>				
MR	<b>0.0060</b>	<b>0.0048</b>	<b>0.0052</b>	<b>0.0066</b>			
PC	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>		
	ANN	CTA	GAM	GBM	GLM	MARS	RF
Predictive power/Modelling techniques							
ANN							
CTA	<b>0.0001</b>						
GAM	<b>0.0001</b>	<b>0.0378</b>					
GBM	<b>0.0001</b>	<b>0.0016</b>	0.3058				
GLM	<b>0.0001</b>	<b>0.0001</b>	<b>0.0118</b>	0.1366			
MARS	<b>0.0001</b>	0.1758	<b>0.0008</b>	<b>0.0001</b>	<b>0.0001</b>		
RF	<b>0.0001</b>	0.2438	0.3522	<b>0.0550</b>	<b>0.0002</b>	<b>0.0114</b>	
SRE	0.6044	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
	CTA	GAM	GBM	GLM	MARS		
Spatial pattern/Modelling techniques							
CTA							
GAM	<b>0.0001</b>						
GBM	<b>0.0001</b>	<b>0.0001</b>					
GLM	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>				
MARS	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>			
RF	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>		

### 3.2. Species distribution models

GAM and GLM yielded the models with the greatest predictive power (Fig. 3). ANN and SRE showed poor performance according to the TSS statistic. The latter two techniques were therefore excluded from ensemble forecasting.

### 3.3. Comparison among sets of climatic variables

#### 3.3.1. Predictive power

When comparing the predictive power of single modelling techniques across sets of climatic variables, no differences were revealed using TSS (Fig. 4). The results with AUC (Appendix C) followed the same pattern. GLMM analyses (Table 3) also did not show a significant effect of the sets of climatic variables on the predictive power of SDMs, but identified a statistically significant effect of modelling techniques.

#### 3.3.2. Spatial pattern

When comparing the spatial patterns of predictions from binary models among different sets of variables (Fig. 5), all pairwise combinations of different set of predictors had a statistically significant effect over the distribution of suitable pixels (Table 3).

#### 3.3.3. Climate change projections

For most comparisons, no significant change in predicted area of occupancy (pAOO) between the current models and climate change scenarios was detected when averaged across species (present and future estimates of pAOO for each species under different climate

change scenarios and sets of climatic variables are presented in Appendix D). However, when individual species were considered, some trends could be observed (Table 4). Four species (*H. filifolium*, *H. longistylum*, *H. megalanthum* and *H. sinuatum*) were predicted to loose area (reduced pAOO) under all sets of climatic variables and climate change scenarios. *H. floridum* and *H. myosotifolium* showed a decrease in pAOO for all except one combination of predictor sets and climate change scenario. Within climate change scenarios, all other species varied among sets of climatic variables as to whether their surfaces would increase or decrease under climate change scenarios (Table 4).

The corresponding  $\kappa$  statistics as a measure of spatial agreement between present and future models, were very low (mean 0.032) for all sets of climatic variables (Table 5); the maximum value (0.441) was reached by *H. stenophyllum* under scenario B2, set of climatic variables B. This result suggests that under the climate change scenarios analysed, the potential geographic ranges of the species will differ substantially in their spatial pattern (Fig. 6).

#### 3.3.4. Extinction risk

Results of the GLMM analysis in relation to change in pAOO exhibited mostly an absence of statistically significant effects from using different sets of climatic predictor variables on current predicted and future projected distributions. Only the Mc set showed a significant effect in all combinations when the percentage of change was assessed (Table 6).

Under IUCN criterion A3, 50.8% of the corresponding comparisons (i.e., for a given species and climate change scenario) between pairs of sets of climatic variables produced different estimates of

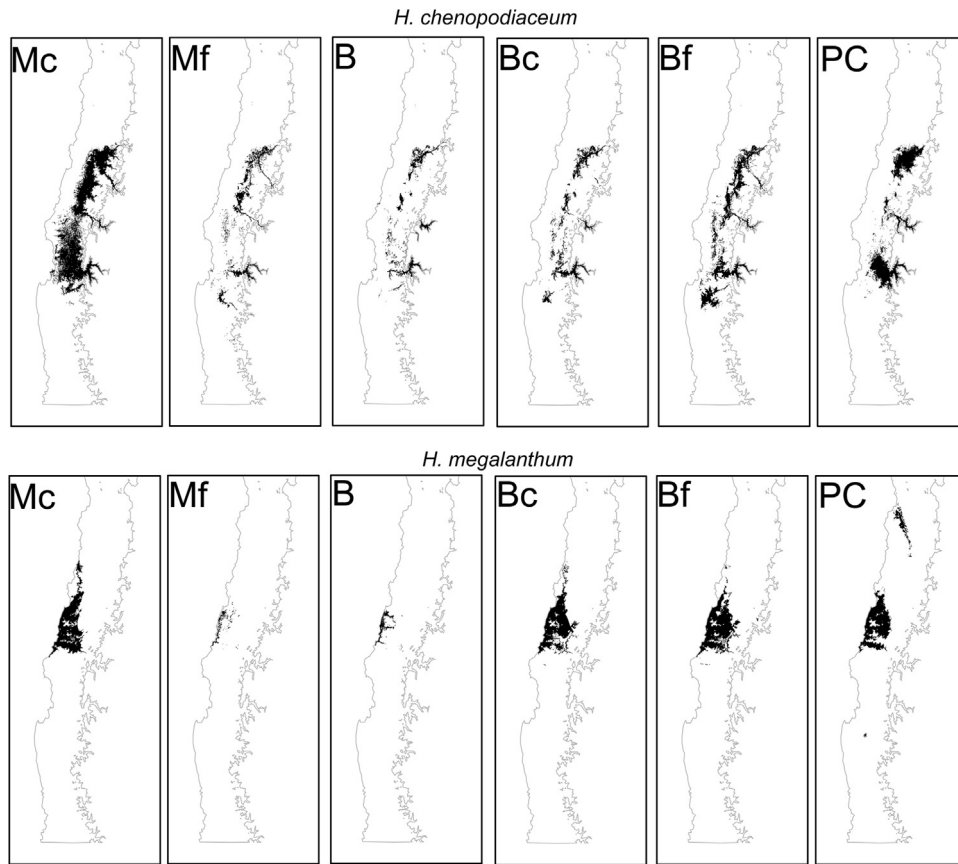


Fig. 5. Final models of *Heliotropium chenopodiaceum* (upper panel) and *H. megalanthum* (lower panel) according to different sets of climatic variables.

Table 4

Percentage of change in the predicted area between current and future projections for the 13 modelled species under two climate change scenarios (B2 or A2) and six sets of climatic variables (Mc, Mr, B, Bc, Br, PC). Increases are shaded to facilitate visual comparison.

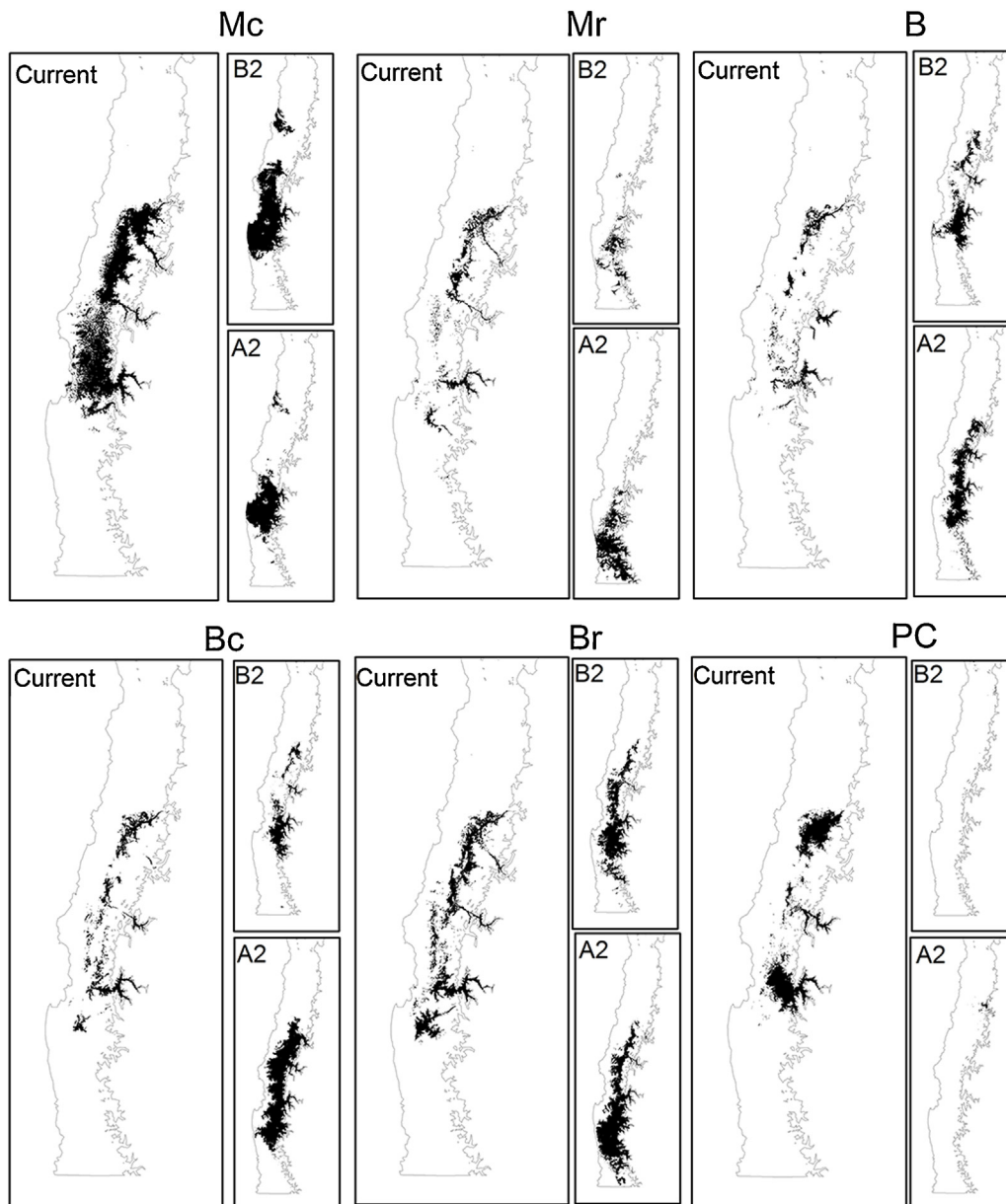
Species	B2						A2					
	Mc	Mr	B	Bc	Br	PC	Mc	Mr	B	Bc	Br	PC
<i>Heliotropium chenopodiaceum</i>	69	6	259	588	138	3	4	227	423	116	234	-93
<i>Heliotropium filifolium</i>	-100	-97	-100	-100	-100	-99	-100	-93	-100	-99	-100	-100
<i>Heliotropium floridum</i>	18	-37	-100	-97	-94	-100	-77	-77	-100	-27	-64	-100
<i>Heliotropium inconspicuum</i>	994	129	97	201	-100	-100	1526	32	11	-99	-100	-100
<i>Heliotropium krauseanum</i>	-55	-100	139	582	822	-16	820	-100	1918	1991	694	-94
<i>Heliotropium linariifolium</i>	378	883	154	358	398	-100	691	649	18	-42	153	-100
<i>Heliotropium longistylum</i>	-100	-100	-100	-100	-76	-100	-100	-100	-100	-100	-74	-100
<i>Heliotropium megalanthum</i>	-69	-97	-100	-82	-44	-36	-34	-100	-100	-91	-80	-62
<i>Heliotropium myosotifolium</i>	-100	-69	-99	-71	-100	-88	-100	-19	-76	20	-57	-100
<i>Heliotropium pycnophyllum</i>	1248	-47	-4	38	-30	-100	1672	213	-98	-82	-73	-100
<i>Heliotropium sinuatum</i>	-100	-4	-92	-86	-58	-31	-100	-30	-92	-96	-63	-89
<i>Heliotropium stenophyllum</i>	229	78	104	306	93	-64	166	67	-100	-28	107	-64
<i>Heliotropium taltalense</i>	131	-72	-85	-100	-100	-100	94	238	-30	-100	-94	-100

Table 5

Kappa statistics as a measure of spatial overlap for the comparisons between current and future potential distributions under scenarios B2 and A2 for different sets of climatic variables. Agreement values over 0.2 are shaded.

Species	B2						A2					
	Mc	Mr	B	Bc	Br	PC	Mc	Mr	B	Bc	Br	PC
<i>Heliotropium chenopodiaceum</i>	0.280	0.071	0.226	0.232	0.319	-0.029	0.213	0.022	0.103	0.182	0.194	-0.003
<i>Heliotropium filifolium</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-0.001	0.000	0.000	0.000	0.000
<i>Heliotropium floridum</i>	0.032	0.103	0.000	-0.001	0.023	-0.001	-0.003	-0.005	0.000	-0.009	0.034	0.000
<i>Heliotropium inconspicuum</i>	0.025	0.012	0.004	0.036	0.000	0.000	0.016	-0.007	0.000	0.000	0.000	0.000
<i>Heliotropium krauseanum</i>	-0.006	0.001	0.025	0.022	0.089	0.062	0.082	0.000	0.040	0.055	0.110	-0.007
<i>Heliotropium linariifolium</i>	0.248	-0.026	0.321	0.003	0.216	0.000	0.115	-0.025	0.151	-0.003	0.046	0.000
<i>Heliotropium longistylum</i>	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.000	0.075	0.000
<i>Heliotropium megalanthum</i>	-0.010	0.000	0.000	-0.002	0.018	-0.017	-0.020	0.000	0.000	-0.002	-0.006	-0.012
<i>Heliotropium myosotifolium</i>	0.000	-0.002	0.000	0.000	0.000	-0.001	0.000	-0.003	-0.005	-0.015	-0.002	0.000
<i>Heliotropium pycnophyllum</i>	0.112	0.219	0.190	0.008	0.104	0.000	0.065	0.021	0.022	0.003	0.043	0.000
<i>Heliotropium sinuatum</i>	0.000	-0.009	0.001	0.000	0.020	-0.005	0.000	-0.035	-0.001	-0.001	-0.009	-0.001
<i>Heliotropium stenophyllum</i>	0.066	0.024	0.441	0.016	0.063	-0.023	0.012	-0.001	0.000	0.000	0.014	-0.023





**Fig. 6.** Comparison of present and climate change projections of *Heliotropium chenopodiaceum* according to different sets of climatic variables. Final binary models are depicted for the present models and for climate change scenarios A2 and B2.

extinction risk (Table 7). The estimated extinction risk for each species, climate change scenario and set of climatic variables are provided in Appendix E.

#### 4. Discussion

Several sources of uncertainty in SDMs have been reported (e.g., Araújo et al., 2005; Barry and Elith, 2006; Pearson et al., 2006; Guisan et al., 2007; Buisson et al., 2010; Beale and Lennon, 2012; Zurell et al., 2012; Swanson et al., 2013). These include modelling techniques, model specification, presence/absence data, extent definition, environmental data, choice of threshold to convert probabilistic predictions into binary ones, or the choice of climate change scenarios. However, the effect of choosing one set of environmental predictors (here climatic) among different alternative ones on SDMs had rarely been assessed so far. Here, we provide comprehensive evidences that the choice of the climatic dataset can have statistically significant effects on SDMs and

the spatial patterns of their predictions. These effects are transferred to the projections of climate change on species distribution and estimates of extinction risk (Fordham et al., 2011; Braunisch et al., 2013; Wenger et al., 2013). A few other studies have also explored the effect of the set of variables on the outcomes of SDMs, and found supporting results (Peterson and Nakazawa, 2008; Syphard and Franklin, 2009; Synes and Osborne, 2011; Watling et al., 2012). These authors stressed that, although predictive performance may all be high for different SDM-building strategies, the spatial arrangement of SDM predictions may vary considerably. They further noted that the use of predictive performance as the sole evaluation metric of SDMs may not be appropriate in all circumstances.

Our results complement these previous findings in three ways. First, we show across many species that the resulting SDMs may vary among the sets of environmental predictors not only when these predictors are of different character (e.g., climate versus soil) or originating from different sources (Broennimann et al., 2007),

**Table 6**

Pairwise comparisons across species from GLMM analysis between predictor sets for the current modelled area (Current), future modelled area (Future) and percentage of change (Change). Low probability values (highlighted in bold) mean statistically significant differences (<0.05, two-tailed test) for the corresponding comparisons.

	B	BC	BR	MC	MR
Current/Set of climatic variables					
B					
BC	0.6842				
BR	0.9510	0.7424			
MC	0.3214	0.1514	0.2610		
MR	0.4956	0.2764	0.4406	0.7082	
PC	0.3524	0.1800	0.2992	0.9246	0.7840
Future/Set of climatic variables					
B					
BC	0.6842				
BR	0.9510	0.7424			
MC	0.3214	0.1514	0.2610		
MR	0.4956	0.2764	0.4406	0.7082	
PC	0.3524	0.1800	0.2992	0.9246	0.7840
Percentage of change/Set of climatic variables					
B					
BC	0.8676				
BR	0.3304	0.4232			
MC	<b>0.0046</b>	<b>0.0022</b>	<b>0.0036</b>		
MR	0.7986	0.9116	0.7892	<b>0.0016</b>	
PC	<b>0.0260</b>	<b>0.0366</b>	<b>0.0250</b>	<b>0.0001</b>	<b>0.0470</b>

but also when they are different subsets or transformed variables derived from the same original dataset, an issue that had rarely been previously addressed in SDMs research (e.g., Synes and Osborne, 2011). Second, despite the generally high predictive performance achieved under all different sets of predictor variables, patterns of spatial predictions can greatly vary between models built with different subsets. Our results also suggest that model evaluation should additionally consider spatial patterns of predictions, which may prove particularly critical for some conservation decisions, such as those derived from SDM-based extinction risk estimates (Schwartz, 2012). Third, we show here for the first time that uncertainty generated by those of predictor variables has impacts on extinction risk estimates.

Akçakaya et al. (2006) commented critically on several potential sources of uncertainty and potential limitations when evaluating extinction risks with SDM-based IUCN (2001) criteria. Uncertainty may for instance relate to temporal scale (i.e., arbitrary definitions of generation times), spatial scale (i.e., including only part of the geographic range of the species or the use of inappropriate spatial

**Table 7**

Number of differences in extinction risk estimate (C) and percentage of differences (%) between pairs of sets of climatic variables for the IUCN criteria of extinction risk A3.

Comparison	C	%
Mc – Mr	11/26	42.3
Mc – B	10/26	38.5
Mc – Bc	12/26	46.2
Mc – Br	14/26	53.8
Mc – PC	18/26	69.2
Mr – B	13/26	50.0
Mr – Bc	12/26	46.2
Mr – Br	16/26	61.5
Mr – PC	20/26	76.9
B – Bc	7/26	26.9
B – Br	11/26	42.3
B – PC	14/26	53.8
Bc – Br	11/26	42.3
Bc – PC	14/26	53.8
Br – PC	15/26	57.7
<b>Total</b>	<b>198/390</b>	<b>50.8</b>

resolution) and abundance patterns (linear relationship between range area and abundance), as usually assessed in many SDM-based evaluation of extinction risk using the IUCN (2001) criteria. These uncertainty dimensions, together with others potentially important ones that are still poorly covered in SDM studies, such as biotic interactions (Araújo and Luoto, 2007), landscape process and local population dynamics (Franklin, 2010) – can yield both under- and over-estimations in predicted distributions, possibly hampering the proper application of SDM-based IUCN criteria to the estimation of extinction risks. New approaches are incorporating more biologically relevant dimensions like population sizes, life history and spatial traits combining SDM with demographic models to estimate extinction risk under climate changes (Keith et al., 2008; Fordham et al., 2013; Guisan et al., 2013; Guisan, 2014; Pearson et al., 2014), these new approaches even address more biologically meaningful variables do not incorporate yet some uncertainties intrinsic to SDM like addressed in our paper.

Our assessment of extinction risk for *Heliotropium* sect. *Cochranea* varied depending on the climate change scenario used and the set of climatic variables used. These variations introduce an additional element of uncertainty into the assessment of extinction risks. At this stage, the question can be seen as whether it is possible to handle this uncertainty (as in Carvalho et al., 2011) so that SDM estimates of IUCN extinction risk remain valid using the IUCN (2001) criteria.

Concluding, this study revealed two main findings:

- (1) The use of different sets of climatic variables in SDMs has a direct influence on the spatial arrangement of suitable pixels in model projections, regardless of the model's predictive power. This uncertainty is transferred to the climate change projections and therefore to the IUCN estimate of extinction risk. In future studies, model evaluations should also take into account the spatial arrangement of predictions to assess these differences.
- (2) SDM-based estimates of extinction risk for *Heliotropium* sect. *Cochranea* under climate change can be highly sensitive to the choice of the set of climatic predictor variables. Estimated change in the predicted area of occupancy (cover area of pixels predicted to be suitable), a direct proxy for extinction risk, varied up to 2000% between sets of climatic variables in our study, and more than 50% of the extinction risk estimates changed when different sets of climatic variables were employed.

This form of uncertainty should be better accounted in future SDM studies.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.06.003>.

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