

Distribution of drought-tolerant plant species under future climate change in Iran

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Abstract

The potential suitable habitats for ten drought-tolerant plant species were identified in Iran based on bioclimatic variables using MaxEnt. The impact of climate change on habitat suitability of the species was modeled using the GFDL-ESM2G climate scenario, which predicts warmer and slightly wetter conditions, and the CCSM4 scenario, which predicts warmer and slightly drier conditions for the mid century (2041 to 2060). The drought tolerance level of the species was determined by the de Martonne aridity index based on temperature and precipitation. *Cornulaca monacantha* was classified as the most drought-tolerant species, followed by *Hammada salicornica*, *Seidlitzia rosmarinus*, *Zygophyllum eurypterum*, *Haloxylon persicum*, *Haloxylon ammodendron*, *Cousinia stocksii*, *Halocnemum strobilaceum*, *Gymnocarpus decander* and *Cousinia cylindracea*. The highest suitable habitat gains were predicted to occur for *C. cylindracea* and *H. strobilaceum*, whereas the highest losses in habitat suitability were predicted for *H. persicum* and *C. stocksii* under both scenarios of climate change. Soil attributes, type and intensity of interaction between species and intensity of grazing may significantly influence the habitat losses and gains and can be considered as parameters for modeling of species distributions.

Key words: bioclimatic variables, climate change, drought-tolerant plant species, suitable habitat.

Abbreviations: AMT, annual mean temperature; AP, annual precipitation; AUC, area under curve; GCM, global climate model; Iso, isothermality; PS, precipitation seasonality; PWQ, precipitation of warmest quarter; RCP, representative concentration pathways; ROC, receiver operating characteristic curve; TAR, temperature annual range.

Introduction

Modeling of species distributions is important in ecology and has been used for studying species-environment relationships (Buckley et al. 2016) and evaluating the impact of climate and land use changes on species distribution (Mousaei Sanjerehei, Rundel 2017). It has also been effectively applied for quantifying environmental niches of species (Dallas, Hastings 2018), selection of appropriate species for ecological restoration (Wood et al. 2018), as well as assessing habitat potential for conserving rare and endemic species (Queiroz et al. 2012).

Species distribution models relate species data to environmental variables (Guisan, Zimmermann 2000). The species data can be presence, presence-absence or frequency observations obtained using random or systematic sampling (Guisan, Thuiller 2005).

The environmental predictors that have frequently been used for modeling of species-environment relationships include climatic, topographic and edaphic variables (Beauregard, de Blois 2014; Mousaei Sanjerehei, Rundel 2017). In addition to the environmental variables, competition and facilitation between species can play an important role in distribution of species (Mousaei

Sanjerehei et al. 2011; Mpakairi et al. 2017). Therefore, presence or absence of data for competitor and facilitator species can influence the efficiency of predictive modeling.

Climate change has been identified as one of the most effective drivers of species habitat losses and gains (Riordan, Rundel 2014; Mousaei Sanjerehei, Rundel 2017), species richness (Boutin et al. 2017), distributions (Mathys et al. 2018) and community shifts (Dieleman et al. 2015). The projected global climate models (GCMs) predict an increase of 0.3 to 1.7 °C in temperature for the lowest greenhouse gas concentration trajectory and a temperature increase of 2.6 to 4.8 °C for the highest greenhouse gas concentration trajectory by the end of 21st century (Stocker et al. 2013). Therefore, modeling of species-environment relationships under climate change is useful for predicting the impact of future climate change on species and ecosystems.

There are a variety of methods that have been extensively used for modeling species-environment relationships. These include artificial neural networks (Pearson et al. 2002), Bayesian analysis (de Rivera et al. 2018), climatic envelope (Pearson, Dawson 2003), classification and regression trees (McDermid, Smith 2008), ecological niche factor analysis (Hirzel et al. 2002), generalized additive models (Lehmann et al. 2002), generalized linear models

(Guisan et al. 2002), binary logistic regression (Mousaei Sanjerehei 2014) and maximum entropy (Phillips et al. 2006). Selection of an appropriate method for modeling species distribution depends on type of response variables, collinearity between predictors, type of species and spatial scale of study (Guisan, Thuiller 2005).

MaxEnt (maximum entropy) is a general-purpose machine-learning method which calculates probability distributions based on incomplete data (Phillips et al. 2006) and does not require absence data, making it appropriate for modeling species distribution based on presence only data. Maxent generates a probability distribution, starting from the uniform distribution and repeatedly improving the fit to the data, which is called the training gain. The gain is defined as the average log probability of the presence samples, and indicates how closely the model is concentrated around the presence samples; for example, if the gain is 2, it means that the average likelihood of the presence samples is $\exp(2) \approx 7.4$ times higher than that of a random background pixel (Phillips 2005). MaxEnt has a variety of advantages over other modeling methods such as high performance with both limited species presence data (Pearson et al. 2007) and spatially biased data (Loiselle et al. 2008).

The objectives of this study were to determine the current potential suitable habitat of ten drought-tolerant plant species in Iran, to detect the most important bioclimatic factors influencing the distribution of the species and to model the impact of projected climate change on the distribution of the species by the mid-century.

Materials and methods

The current and future potential distribution of ten drought-tolerant plant species (*Cornulaca monacantha*, *Cousinia cylindracea*, *Cousinia stocksii*, *Haloxylon ammodendron*, *Halocnemum strobilaceum*, *Haloxylon persicum*, *Hammada salicornica*, *Seidlitzia rosmarinus*, *Gymnocarpus decander* and *Zygophyllum eurypterum*) were determined in Iran for 2000 (1950 to 2000) and 2050 (2041 to 2060). The main important uses of the studied species are presented in Table 1. Presence data of the species and bioclimatic variables were used for modeling of the species distributions using Maximum Entropy (MaxEnt).

Presence data for the plant species were obtained from maps of Iranian vegetation types. In the vegetation types where a studied plant species was dominant, a number of points were approximately uniformly selected as the occurrence localities of the species. The number of records used to model individual species was 1650 for *H. salicornica*, 1332 for *Z. eurypterum*, 527 for *S. rosmarinus*, 490 for *C. stocksii*, 473 for *H. ammodendron*, 453 for *G. decander*, 264 for *C. monacantha*, 260 for *C. cylindracea*, 254 for *H. persicum* and 250 for *H. strobilaceum*. The difference in the number of occurrence points does not create any problem, because Maxent is among the least sensitive algorithms to sample size (Wisiz et al. 2008).

The current (2000) and future (2050) bioclimatic layers with 30-arcsec resolution were obtained from the WorldClim website (www.worldclim.org). These include 19 bioclimatic variables, which have been found to significantly

Table 1. Main importance of the studied plant species

Plant species	Importance	Reference
<i>Cornulaca monacantha</i> Delile	Forage for camel grazing, sand fixation, wind erosion control	Zare Chahouki, Shafizadeh Nasrabadi (2008)
<i>Cousinia cylindracea</i> Boiss.	Forage for sheep grazing	Zarekia et al. (2017)
<i>Cousinia stocksii</i> C. Winkl.	Medicinal uses	Maleki, Akhiani (2018); Shahreyary Nejad, Fathi (2018)
<i>Gymnocarpus decander</i> Forssk.	Soil protection, forage production	Karampoor et al. (2015)
<i>Halocnemum strobilaceum</i> M. B.	Restoration and rehabilitation of saline lands, forage for livestock grazing, soil conservation, medicinal uses	Gibbons et al. (1999); Vali, Ghazavi (2003); Toranjzar, Fathi (2016); Ehsani et al. (2017)
<i>Haloxylon ammodendron</i> (C. A. Mey.) Bunge	Sand fixation, erosion control	Zandi et al. (2011); Xu et al. (2014)
<i>Haloxylon persicum</i> Bge. ex Boiss.	Sand fixation, erosion control	Abdi et al. (2019)
<i>Hammada salicornica</i> (Moq.) Iljin	Soil protection, forage and fodder production,	Yousefi, Yarahmadi (2015)
<i>Seidlitzia rosmarinus</i> (Ehrh.) Bge.	Rehabilitation of saline lands, camel forage, industrial uses	Hadi et al. (2007); Baghestani, Zare (2009); Heydarnezhad et al. (2015)
<i>Zygophyllum eurypterum</i> Boiss. & Buhse	Soil conservation, livestock grazing, medicinal and industrial uses	Ahmad et al. (2006); Fatemi et al. (2015); Khalasiahwazi, Zare (2015); Khosravi et al. (2017)

influence biological functions of plants (Riordan, Rundel 2014). There is a high correlation between some of these bioclimatic variables (for example between annual mean temperature and maximum temperature of warmest month or between annual precipitation and precipitation of wettest month) in Iran (Mousaei Sanjerehei, Rundel 2017). In order to avoid model overfitting and collinearity between the bioclimatic variables, a correlation matrix consisting of all the bioclimatic variables covering Iran was constructed and a subset of variables with a low (< 0.8) and non-significant correlation coefficient ($a > 0.05$) was selected for the MaxEnt modeling (Riordan, Rundel 2014; Mousaei Sanjerehei, Rundel 2017). The six bioclimatic variables with the resolution of 30 arc-seconds (1 km) (1950 to 2000) kept for modeling were: annual mean temperature (AMT), annual precipitation (AP), isothermality (Iso), temperature annual range (TAR), precipitation seasonality (PS) and precipitation of warmest quarter (PWQ). The relationship between the presence localities of the species and the six bioclimatic variables for 2000 was modeled in MaxEnt. Maximum background pixels, maximum number of iterations and convergence threshold were set to 10000, 500 and 10^{-5} , respectively. Sixty percent of the presence localities of species were selected for model training and 40% for model testing. The MaxEnt logistic model was used to estimate the probability (between 0 and 1) of species presence. Performance of the model was evaluated using the area under curve (AUC) of the receiver operating characteristic curve (ROC). The ROC curve measures a model's ability to correctly predict presence and absence, plotting the model sensitivity (false negative) against $1 - \text{specificity}$ (false positive). The AUC represents the probability that a presence site will be ranked above an absence, or in the other word, above random background site when presence only data are used (Phillips et al. 2006). AUC ranges from 0 to 1 with 0.5 indicating random prediction and 1 indicating complete fitness. Maximum sensitivity plus specificity threshold was used to produce a map of suitable and unsuitable conditions for the species. Maximum sensitivity plus specificity is an efficient threshold to convert the continuous probability of an occurrence map into a binary presence/absence map (Liu et al. 2005).

The impact of climate change on the potential habitat of the species for 2050 (2041 to 2060) can be modeled using global climate models (GCMs) under four representative concentration pathways (RCPs) (Stocker et al. 2013).

To select the most efficient climate models representing the future climatic conditions of Iran in terms of temperature and precipitation, we used the results of studies that investigated the climate change of Iran in a period of 55 years from 1951 to 2005 (Kousari et al. 2011; Kousari, Zarch 2011). These studies indicated significant increase in the annual mean temperature and a lack of significant increase/decrease in annual precipitation in arid and

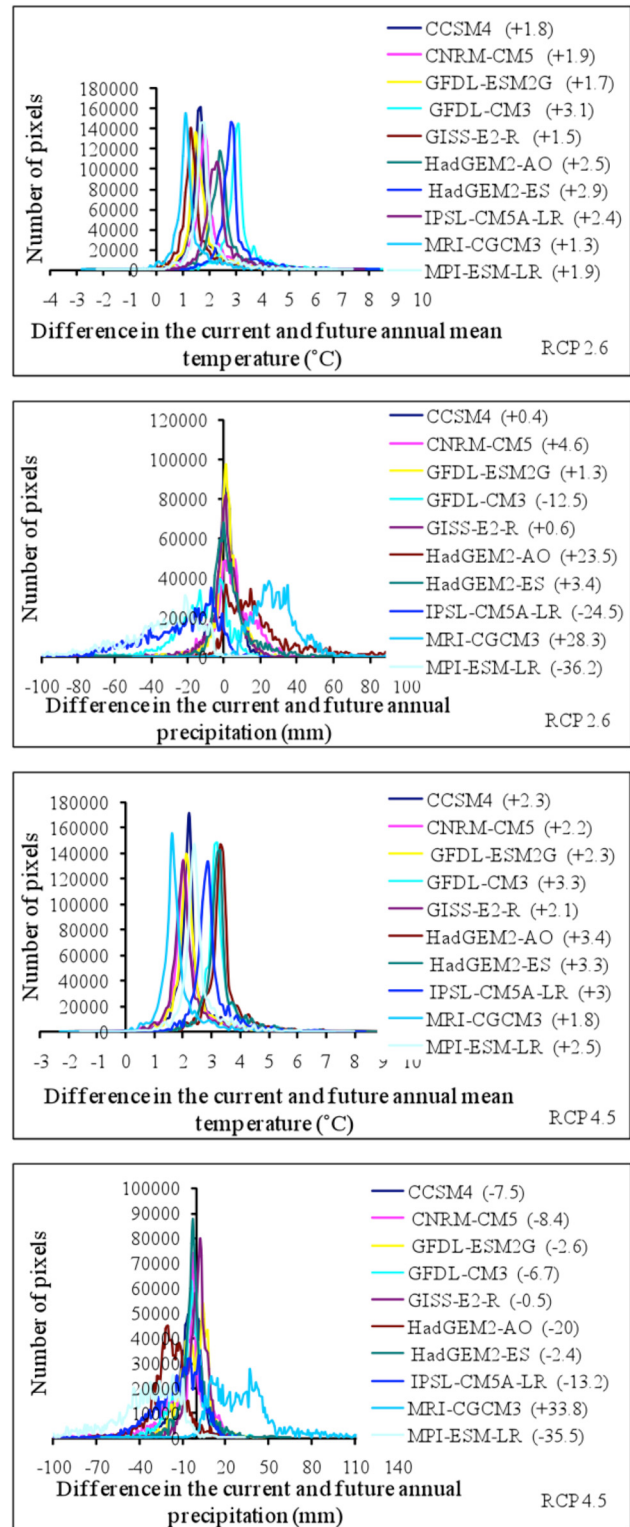


Fig. 1. Histogram of difference in the current (2000) and future (2050) annual mean temperature and annual precipitation in the potential habitats of the species. The future annual temperature and precipitation were obtained from ten global climate models (RCP 2.6 and 4.5) for 2050. The values in parenthesis show the mean difference in the current and future temperature and precipitation for each climate model.

semiarid parts of Iran in the 55-year period (1951 to 2005).

To obtain the changes of temperature and precipitation in the presence locations of the species from 2000 to 2050, the produced maps of current potential distribution of the species were overlaid with the current (2000) annual temperature and precipitation layers and the future (2050) annual temperature and precipitation layers of ten climate models including CCSM4, CNRM-CM5, GFDL-CM3, GFDL-ESM2G, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-LR and MRI-CGCM3 (WorldClim databases). Based on the histogram of changes in temperature and precipitation from 2000 to 2050 (Fig. 1), two climate models including GFDL-ESM2G under RCP2.6 and CCSM4 under RCP4.5 were selected as the best representatives of future climatic conditions of arid and semiarid parts of Iran. GFDL-ESM2G (RCP2.6) predicts an increase of 1.7 °C (95% confidence intervals 0.8 to 2.7) in annual mean temperature (AMT) and an increase of 1.3 mm (95% CI -4 to 7) in annual precipitation (AP) indicating warmer and slightly wetter conditions. CCSM4 (RCP 4.5) predicts an AMT increase of 2.3 °C (95% CI 1.4 to 3.2) and an AP decrease of 7.5 mm (-18 to 3) indicating warmer and slightly drier conditions in arid and semiarid parts of Iran by the mid century.

The model trained on the current (2000) bioclimatic data in MaxEnt was projected by applying it to the future (2050) bioclimatic data obtained from GFDL-ESM2G and CCSM4 models. The maps of current and future suitable habitat for the species were overlaid with the reference land cover map of Iran (Mousaei Sanjerehei 2014) to remove non-rangeland cover types (rock, wetland, water, farmlands) from the maps and to determine parts of the rangelands predicted as suitable habitat for the plant species.

To obtain percentage of losses and gains in the habitat of the plant species from 2000 to 2050, the map of current suitable habitat for the species was overlaid with the map of future suitable habitat produced using the GFDL-ESM2G and CCSM4 models for 2050.

Since elevation has been identified as one of the most important drivers of species distribution in many ecological studies, the elevational ranges of the species were determined by excluding AMT from the MaxEnt model and including elevation to the model due to a correlation coefficient of > 0.8 between elevation and AMT in Iran.

The degree of tolerance of the species to drought was classified using the de Martonne aridity index (de Martonne 1926). This index is a measure of habitat climate based on temperature and precipitation, which shows a strong correlation with plant species attributes such as distribution, production and leaf thickness (Tian et al. 2016; Bhuyan et al. 2017):

$$I = P / 10 + T,$$

where P is annual precipitation (mm) and T is annual mean temperature (°C). The values of $I < 5$ indicate arid, 5 to 10 semi-arid, 10 to 20 semi-humid, 20 to 30 humid and > 30

perhumid climate. All of the analyses and calculations were performed by ILWIS and MaxEnt.

Results

Model performance and predictor contributions

The AUC for the MaxEnt models was in a range of 0.899 to 0.991 indicating good model performance and a narrow ecological niche for the plant species. The highest test AUC for the models using six bioclimatic variables was for *C. cylindracea* (0.991) followed by *H. persicum* (0.984), *H. strobilaceum* (0.979), *C. stocksii* and *C. monacantha* (0.977), *H. ammodendron* (0.956), *S. rosmarinus* and *G. decander* (0.942), *H. salicornica* (0.917) and *Z. eurypterum* (0.899) (Table 2). The higher the value of AUC, the narrower the niche range of species. The model AUC using five bioclimatic variables together with elevation was approximately similar to that using six bioclimatic predictors. The results of the Jackknife test showed the importance of each climatic variable in the model of species distribution. By a Jackknife test, a number of models are created. Each variable is excluded in turn, and a model is created with the remaining variables. Then a model is created using each variable in isolation. In addition, a model is created using all variables, as before (Phillips 2005). According to the Jackknife test using six bioclimatic variables, annual precipitation was the most effective variable for predicting the suitable conditions for *C. monacantha*, *H. salicornica*, *S. rosmarinus* and *Z. eurypterum*, annual mean temperature for *H. ammodendron* and *H. strobilaceum*, temperature annual range for *C. cylindracea*, precipitation seasonality for *G. decander* and isothermality for *C. stocksii* and *H. persicum*. The variables with the least influence on predicting the species suitable habitat were precipitation seasonality for *C. cylindracea*, *C. stocksii* and *H. ammodendron*, precipitation of the warmest quarter for *H. strobilaceum*, *H. persicum* and *G. decander*, temperature annual range for *H. salicornica*, *S. rosmarinus* and *Z. eurypterum* and isothermality for *C. monacantha* (Table 2). For the models made with five bioclimatic variables together with elevation, annual mean temperature was replaced by elevation in the Jackknife test result with no changes in the order of the importance of the predictors.

Response curves

Response curves showed how each environmental variable affects the MaxEnt prediction. Environmental thresholds for the growth and distribution of species can be characterized using response curves. The most suitable habitat for the studied plant species was predicted to occur in areas with annual precipitation of 50 to 200 mm, except for *C. cylindracea* and *H. strobilaceum* which had the highest probability of presence with annual precipitation range of 175 to 275 and 125 to 375, respectively (Table 2). Therefore, *C. cylindracea* and *H. strobilaceum* have a lower

Table 2. The AUC for the model of species distribution using six bioclimatic variables, order of variables from most (left) to least (right) important in predicting the distribution of the species according to the Jackknife test, range of each variable (AP, AMT, TAR, PS, PWQ, ISO and elevation) in which the response (probability of presence) of species is high, and the percentage area of rangelands of Iran (A) predicted as suitable habitat for the species. AMT, annual mean temperature (°C); AP, annual precipitation (mm); Iso, isothermality (%); TAR, temperature annual range (°C); PS, precipitation seasonality (%); PWQ, precipitation of warmest quarter (mm)

Plant species	AUC	Order of the variables from most (left) to least (right) important for each species										Range of each variable in which the species response (occurrence) probability is high										A (%)
		AP	AMT	PWQ	TAR	PS	ISO	AP	AMT	TAR	PS	ISO	PWQ	PS	ISO	PWQ	ISO	E				
<i>C. monacantha</i>	0.977	AP	AMT	PWQ	TAR	PS	ISO	50-150	16-22	37-42	>75	<5	>36	900-1800	9.7							
<i>C. cylindracea</i>	0.991	TAR	AP	AMT	ISO	PWQ	PS	175-275	7-14	41-44	78-95	<10	38-39.5	>2100	1.3							
<i>C. stocksii</i>	0.977	ISO	TAR	AP	AMT	PWQ	PS	100-200	14-24	30-37.5	82-117	<10	>41	1300-2200	3.4							
<i>H. ammodendron</i>	0.956	AMT	AP	ISO	PWQ	TAR	PS	75-180	16-23	36.5-42	65-105	<10	>36.5	500-1250	9.6							
<i>H. strobilaceum</i>	0.979	AMT	TAR	PS	AP	ISO	PWQ	125-375	>24	25-30	105-130	10-70	28-37	<150	1.4							
<i>H. persicum</i>	0.984	ISO	TAR	AP	PS	AMT	PWQ	75-150	16-27	34-37.5	85-115	<15	41.5-45	500-2000	3.9							
<i>H. salicornica</i>	0.917	AP	AMT	ISO	PS	PWQ	TAR	50-150	>18	25.5-43	85-125	<15	37.5-45	500-1600	10.8							
<i>S. rosmarinus</i>	0.942	AP	AMT	ISO	PWQ	PS	TAR	50-180	17-24	34-43	67-105	<10	36.5-41.5	600-1500	16.1							
<i>G. decander</i>	0.942	PS	AP	AMT	TAR	ISO	PWQ	50-200	16-26	25-38	85-125	<10	>37	100-1900	13.9							
<i>Z. eurypterum</i>	0.899	AP	PS	AMT	ISO	PWQ	TAR	50-200	14-25	26-42	85-122	<10	>38.5	50-2100	17							

tolerance to an arid climate, but are more likely to occur in wetter conditions compared to the other species.

The suitable conditions for all plant species occurred at precipitation of the warmest quarter (PWQ) of less than 10 to 15 mm, except for *H. strobilaceum* whose suitable conditions were predicted to occur at a PWQ of 10 to 70 mm. However, PWQ was the least important driver of *H. strobilaceum* distribution based on the Jackknife test and therefore it was not useful for estimating the suitable habitat of this species. The most suitable habitat for the studied species occurred at an annual mean temperature of 15 to 25 °C, except for *H. strobilaceum*, *H. salicornica* and *C. cylindracea*. For *H. strobilaceum* and *H. salicornica*, the most suitable habitat was predicted to occur at an annual mean temperature of more than 24 and 18 °C, respectively, indicating the tolerance of the two species to high temperatures. *C. cylindracea* is more likely to prefer colder conditions (annual mean temperature of 7 to 14 °C) than other species (Table 2).

The widest and narrowest temperature annual range was respectively related to the habitat of *G. decander* (25 to 38 °C) and *C. cylindracea* (41 to 44 °C). Considering that temperature annual range was the most effective driver of *C. cylindracea* distribution, the smallest predicted habitat for this species may be due to its narrow temperature annual range.

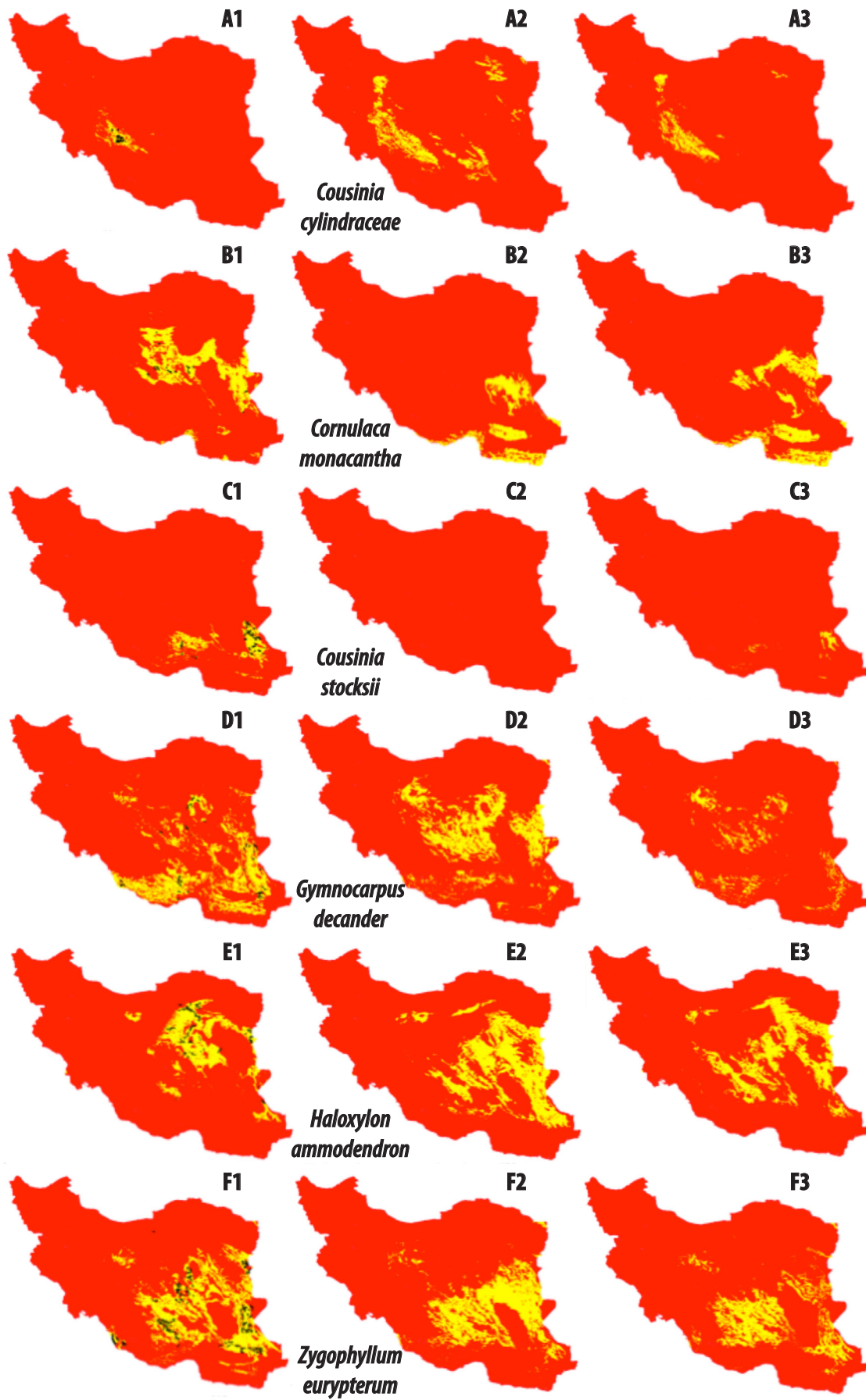
Range of precipitation seasonality was rather similar for the habitat of all species and therefore it was not a suitable indicator for distinguishing the niche of the species.

Z. eurypterum and *G. decander* had highest probability of occurrence in a wide range of elevation (50 to 2300 m) and were able to occur in lower elevations than *C. stocksii*, *C. monacantha*, *H. ammodendron*, *H. salicornica*, *S. rosmarinus* and *H. persicum* species, which did not seem to appear at elevations of less than 500 m. The locations with an altitude of more than 2100 m and less than 150 m were the most suitable habitats for *C. cylindracea* and *H. strobilaceum*, respectively. *C. cylindracea* and *H. strobilaceum* can therefore be classified respectively as high elevation and low elevation plant species.

Current and future habitat of species

Maps of current (2000) suitable habitats for the plant species using six bioclimatic variables are presented in Fig. 2. Based on the predictive maps, 17% of the area of rangelands of Iran was predicted as suitable habitat for *Z. eurypterum*, 16.1% for *S. rosmarinus*, 13.9% for *G. decander*, 10.8% for *H. salicornica*, 9.7% for *C. monacantha*, 9.6% for *H. ammodendron*, 3.9% for *H. persicum*, 3.4% for *C. stocksii*, 1.4% for *H. strobilaceum* and 1.3% for *C. cylindracea*.

The suitable habitat for each species under the GFDL-ESM2G model, which indicates a warmer and slightly wetter condition, and the CCSM4 model, which indicates a warmer and slightly drier condition for 2050, is presented in Fig. 2. The highest habitat gains and losses were predicted



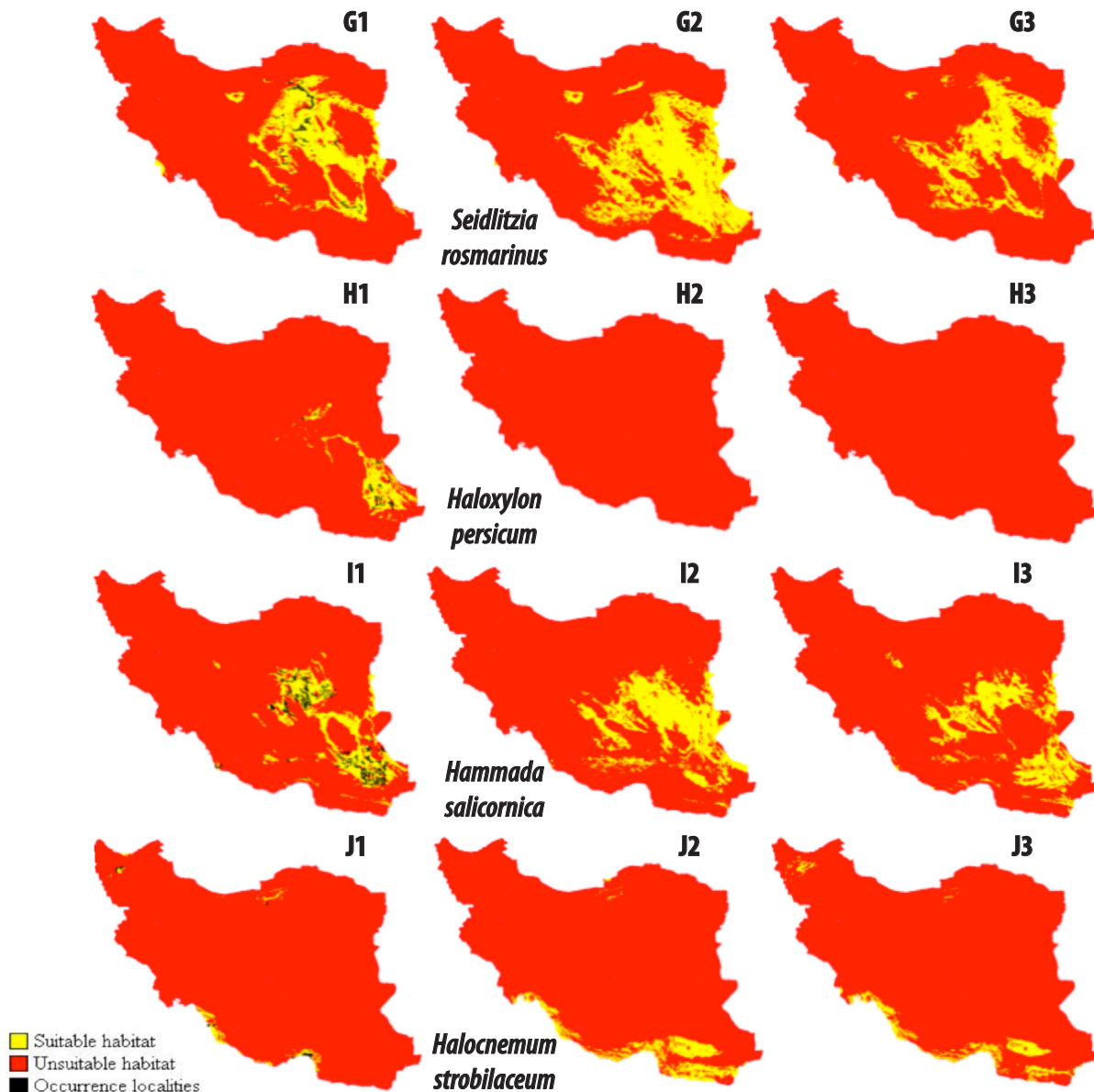


Fig. 2. Predictive maps of (1) current suitable habitat (1950 to 2000) and future suitable habitat (2041 to 2060) under (2) GFDL-ESM2G (RCP2.6) scenario (warmer and slightly wetter conditions) and (3) CCSM4 (RCP4.5) scenario (warmer and slightly drier conditions) for the species using six bioclimatic variables. Occurrence localities for each plant species are shown in the map of current suitable habitat.

to occur for *C. cylindracea* and *H. persicum* under GFDL-ESM2G and for *H. strobilaceum* and *H. persicum* under CCSM4, respectively. Climate change under the projection of GFDL-ESM2G was predicted to cause losses of 85% and gains of 48% in the potential habitat of *C. monacantha* by 2050. Therefore this species is likely to lose $85 - 48 = 37\%$ of its suitable habitat under a warmer and slightly wetter condition by the mid century (Fig. 3). The percentage habitat losses and gains were respectively 14.5 and 406.3 for *C. cylindracea*, 100 and 0.05 for *C. stocksii*, 36.1 and 110.2 for *H. ammodendron*, 24.8 and 340.5 for *H. strobilaceum*, 99.99 and 0.01 for *H. persicum*, 32.7 and 74.6 for *H. salicornica*, 25.5 and 89.4 for *S. rosmarinus*, 62.6 and 69.3 for *G. decander* and 37.3 and 29.7 for *Z. eurypterum*. Therefore warmer and

slightly wetter conditions are predicted to cause a habitat decrease of 99.95% for *C. stocksii*, 99.99% for *H. persicum* and 7.3% for *Z. eurypterum*, and a habitat increase of 391.8% for *C. cylindracea*, 315.7% for *H. strobilaceum*, 63.9% for *S. rosmarinus*, 74.1% for *H. ammodendron*, 41.9% for *H. salicornica*, and 6.7% for *G. decander* by 2050 (Fig. 3).

The projected climate change under CCSM4 predicting a warmer and slightly drier condition in arid and semiarid parts of Iran is likely to decrease the suitable habitat of *C. monacantha* by 9.7% (65.8% loss - 56.1% gain), *C. stocksii* by 78% (80.5 - 2.5), *H. persicum* by 100% (100 - 0), *G. decander* by 62.5% (77.2 - 14.7) and *Z. eurypterum* by 32.5% (51.5 - 19.0) and to increase the suitable habitat of *C. cylindracea* by 135.4% (137.4% gain - 2% loss), *H.*

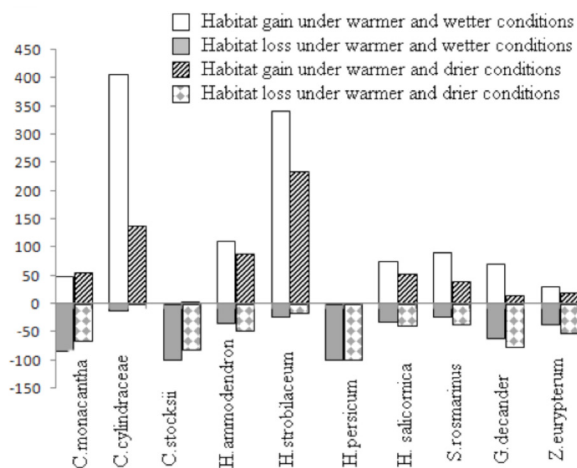


Fig. 3. The percentage losses and gains in the habitat of the plant species under the GFDL-ESM2G (warmer and slightly wetter conditions) and the CCSM4 climate scenarios (warmer and slightly drier conditions).

ammodendron by 41.6% (88.9 – 47.3), *H. strobilaceum* by 217.6% (234.2 – 16.6), *H. salicornica* by 14.7% (54.1 – 39.4) and *S. rosmarinus* by 3.9% (40.5 – 36.6) by mid century (Fig. 3).

Climate of the species habitats

Fig. 4 shows classification of the climate of the species habitat based on the de Martonne aridity index. The classification indicated a semiarid climate for the habitat of *C. cylindracea* and an arid climate for the habitats of other species. *C. monacantha* can be classified as the most drought tolerant species followed by *H. salicornica*, *S. rosmarinus*, *Z. eurypterum*, *H. persicum*, *H. ammodendron*, *C. stocksii*, *H. strobilaceum*, *G. decander* and *C. cylindracea*.

Discussion

The results of MaxEnt modeling provided important information on the environmental tolerance and habitat suitability of the studied plant species. The area under the ROC curve (AUC) was almost higher for the Maxent model of all species. This suggests that the bioclimatic variables alone provided useful information about the habitat requirements of the species and that the species have narrow ecological niches (Elith et al. 2011; Mousaei Sanjerehei, Rundel 2017). A narrow ecological niche has been identified for *C. monacantha* and *S. rosmarinus* using MaxEnt modeling in arid and semiarid Poshtkhoh rangelands of Yazd, Iran (Chahouki, Sahragard 2016).

Annual precipitation was the most effective climatic variable in predicting the suitable habitat for almost half of the plant species (*C. monacantha*, *H. salicornica*, *Z. eurypterum* and *S. rosmarinus*). The importance of precipitation has been identified in distribution of arid plant species such as *H. salicornica*, *S. rosmarinus* and

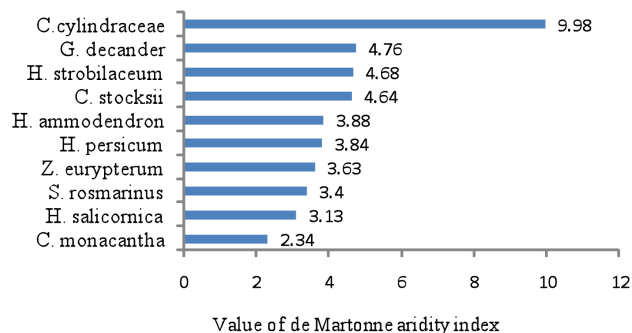


Fig. 4. Classification of tolerance of the plant species to drought based on the de Martonne aridity index (I). I < 5 (arid), 5 to 10 (semi-arid), 10 to 20 (semi-humid), 20 to 30 (humid) and > 30 (perhumid).

C. monacantha (Abdelahi et al. 2006; Fatemi et al. 2015; Yousefi, Yarahmadi 2015; El-Maboud 2016).

Although at a regional scale (throughout Iran), climatic variables were found to present important information about the habitat suitability of the plant species, at local scale (eg., watershed) soil properties can provide complementary information about the distribution of plant species and as a result enhance accuracy of predictive models (Beauregard, de Blois 2014).

Studies have indicated a strong correlation between soil calcium carbonate content and the occurrence of *Z. aurypterum* (Mousaei Sanjerehei 2012; Khalasiahwazi, Zare 2015), and between soil salinity and the occurrence of *H. strobilaceum* and *S. rosmarinus* (Kurkova et al. 2002; El-Ghani, Amer 2003; Vali, Ghazavi 2003; Hosseini, Shahmoradi 2011). *C. monacantha* and *H. salicornica* were the most drought-tolerant plant species in arid climates. *H. salicornica* has been identified as a xerophytic species, and *C. monacantha* as both a xerophytic and psammophytic species in arid climates (El-Ghani, Amer 2003; Ehsani, Ghasriani 2015).

High drought tolerance of *C. monacantha* may be due to accumulation of total carbohydrate and organic osmolytes like proline and glycinebetaine (El-Maboud 2016). The accumulation of osmolytes like proline and glycinebetaine in cells is known to protect plants against abiotic stresses via osmoregulation or osmoprotection (Giri 2011; El-Maboud 2016).

The high tolerance of *H. salicornica* to drought stress may be due to osmoregulation through an increase in absorption of potassium and sodium by this species (Mosleh et al. 2016).

Two species of *Haloxylon*, *H. persicum* and *H. ammodendron*, were also found to have high and approximately similar tolerance to drought. Studies have shown that inorganic ions, especially Na⁺, are important in osmoregulation for *H. ammodendron* to adapt to a saline and arid environment, while organic solutes, especially soluble sugars, play an important role in drought adaptation in the xerophyte, *H. persicum* (Song et al. 2006).

C. cylindracea was classified as a semi-arid and the least drought tolerant species adapted to a higher elevation and colder and wetter conditions, compared to other plant species. At local scales, suitable habitat for *C. cylindracea* has been reported to occur in low temperature and high elevation semi-steppe regions (Ghehsareh et al. 2010; Tahmasebi et al. 2017).

The climate change under both GFDL-ESM2G and CCSM4 scenarios is predicted to drive losses and gains in the habitat of the plant species. More habitat gains by species are likely due to higher adaptation of the species to a wide range of environmental conditions. However, habitat gains and losses under future climatic conditions may be influenced by several factors like soil properties, ability of species for establishment and growth in new habitats, species interactions and intensity of grazing in the current and future species habitats (Beauregard, de Blois 2014; Mpakairi et al. 2017).

H. strobilaceum was one of the species with the most area gains under future warmer/slightly drier and warmer/slightly wetter conditions. This may be because annual mean temperature is the most effective driver of *H. strobilaceum* distribution, and also because this species can tolerate high temperatures (> 24 °C). Therefore, this species is likely to benefit from temperature increase under climate change. Small seeds of *H. strobilaceum* with high germination rate can facilitate habitat gains by this species (Hosseini, Shahmoradi 2011). In addition, *H. strobilaceum* has been identified as one of the most saline tolerant species, and therefore presence of saline soils in new habitats can increase probability of the species expansion into new habitats (El-Ghani, Amer 2003; Hosseini, Shahmoradi 2011).

S. rosmarinus was predicted to benefit from habitat gains under warmer and slightly wetter conditions, and studies have shown that presence of saline soils can facilitate gains of habitat by this species (Hadi et al. 2007; Baghestani, Zare 2009).

Intensity of competition and facilitation between plant species can also significantly influence species habitat gains and losses under climate change. For example, a negative association (competition) has been detected between *Z. eurypterum* and *Artemisia sieberi* in Nodushan arid rangelands of Yazd, Iran (Mousaei Sanjerehei et al. 2011). Therefore, losses of *Z. eurypterum* habitat in these regions may be accelerated under climate change due to competition between *Z. eurypterum* and *A. sieberi*. In addition, the ability of *Z. eurypterum* for gaining new habitats under climate change is likely to decrease if *A. sieberi* occurs in the new habitats. However, due to high preference of *Z. eurypterum* and low preference of *A. sieberi* for calcareous soils, presence of calcareous soils may assist the survival of *Z. eurypterum* or its establishment and expansion in new habitats (Mousaei Sanjerehei 2012).

Intensity of grazing is another important factor that

can significantly influence the future distribution of plant species. A study conducted in the habitats of *C. cylindracea*, the species with the most area gains under both scenarios of climate change, showed that continuous sheep grazing can result in the complete exclusion of *Artemisia sieberi* and *Salsola laricina*, two palatable species accompanying *C. cylindracea*, and the expansion of *C. cylindracea*, the less palatable species (Zarekia et al. 2017).

In contrast to *C. cylindracea*, *H. salicornica* and *Z. eurypterum* are sensitive and intolerant arid species to overgrazing (Ehsani, Ghasriani 2015; Khosravi et al. 2017). Therefore, intense grazing where habitat losses were predicted to occur for *H. salicornica* and *Z. eurypterum* under climate change may increase the probability of their habitat losses.

Two species of *Haloxylon* showed different responses to the projected climate change. *H. persicum* was predicted to lose its whole habitat and to gain no new habitat under both scenarios of climate change, whereas *H. ammodendron* was likely to benefit from both scenarios of climate change and to gain more habitats. This may be due to the narrow range of isothermality (42 to 45%) and temperature annual range (34 to 37 °C) for the habitat of *H. persicum* as the most important drivers of the distribution of this species. The future climate conditions may lead to a decrease in the optimum isothermality and temperature annual range for *H. persicum* and as a result to an extensive loss of its habitat. Although optimum isothermality and temperature annual range for *H. persicum* may be created in some regions of the country under climate change, the other climatic variables such as annual precipitation may be not in the tolerance range of the species in those regions.

Nevertheless, morphological and physiological properties of *H. persicum* can help the survival of this species under climate change. *H. persicum* allocates a high percentage of its biomass to roots and has a high specific root length and area. These traits may enable *H. persicum* to tolerate high water and drought stress and survive in some parts of its habitat (Xu et al. 2014).

Undoubtedly, there are some other factors such as soil attributes, type and intensity of interactions between species and grazing intensity that are important in species distribution and shaping species ranges that were not included in our study. At coarse spatial scales, however, such factors become less influential relative to climate (Franklin 1995; Pearson et al. 2004; Luoto et al. 2007; Riordan, Rundel 2017). The bioclimatic variables used in this study are strongly related to the physiological tolerances of species and directly affect distribution of species (Franklin 1995; Guisan, Zimmermann 2000).

Although the effects of climate changes on the future species habitat gains were modeled in this study, habitat fragmentation may cause a strong barrier to distribution of species, strongly limiting the ability of species to disperse across a landscape. Therefore, limiting land use

changes activities that may lead to habitat conversion and fragmentation is very useful both in preventing further barriers to dispersal, such that species are more likely to keep pace with climate change, and in maintaining patches of habitat above the thresholds beyond which species become locally extinct due to climate change.

The accuracy of species predictive modeling under climate change depends on the selection of appropriate climate scenarios that can efficiently predict the future climatic conditions of a study area. In this study, two efficient climate models which can best represent the future climate of arid and semiarid parts of Iran in terms of temperature and precipitation were selected for modeling. In addition the drought tolerance of the plant species was determined based on an aridity index that can complement the results of Maxent modeling.

In conclusion, species distribution modelling has reasonable potential for helping the current and future preservation of arid land plant species by enhancing the success of restoration activities through selection of suitable habitats and better prediction of the impacts of future climate changes on these distributions.

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