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The impact of climate change on the future geographical distribution range of the endemic relict tree *Gleditsia caspica* (Fabaceae) in Hyrcanian forests

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ABSTRACT

The Caspian locust (*Gleditsia caspica*) is an endemic relict tree that occurs in Hyrcanian forests. Many of its habitats have been destroyed in the last half-century. This study was performed to map past geographic distributions and estimate the suitable areas and potential risks of remaining populations under future climate change. Eight bioclimatic scenarios (one with current conditions, three with future climates, and four with past conditions) were tested using the maximum entropy algorithm. The most significant factors influencing the distributions of *G. caspica* were precipitation in the driest month and temperature seasonality. Even under the most optimistic model (RCP2.6), many stands of *G. caspica* may become endangered in the eastern and central parts of the range, and the distribution of this species will probably shift to the west of the Hyrcanian forest area. Considering the increasing destruction of habitats of this species due to human activities and the expected negative effects of climate change in the future, it is recommended that nature reserves be established to protect the habitat of *G. caspica*. Additionally, ex situ conservation strategies, such as storing seeds using cryopreservation techniques, can ensure the long-term survival of this species in the future.

1. Introduction

The natural distribution and location of forest tree species are influenced by climatic events and anthropogenic factors, which change over time (Dyderski and Pawlik 2020; Roces-Díaz et al. 2018). Species retreat to areas with suitable macro- and microclimatic conditions, described as refugia, as a consequence of these complex changes (Stewart et al. 2010; Svenning et al. 2015). The deleterious effects of the intensification of environmental stresses become even more alarming when we account for the dynamic changes that currently occur in the natural ranges of endemic species and the proportion of plant species that may go extinct (Becklin et al. 2016; Menezes-Silva et al. 2019; Wiens 2016). Detailed knowledge of the distribution of a species is usually a prerequisite for its rehabilitation in any ecosystem and habitat conservation program (Yang et al. 2013; Zhang et al. 2019). Understanding the dispersal pattern of forest tree species in their refugia is important for threatened species management because this information is critical for planning conservation strategies or reforestation programs (Krebs et al. 2004; Vessella et al. 2015).

The northern section of the Alborz Mountain range in Iran, covered by Hyrcanian forests, is located in the Euro-Siberian phytogeographical region and is one of the few remnants of natural closed-canopy deciduous forests in the world (Akhani 1998; Zohary 1973). Hyrcanian forests are known as refuges for many Arcto-Tertiary relict taxa, which are grouped into Hyrcanian and Euxino-Hyrcanian elements (Akhani et al. 2010). The presence of endemic floristic elements, such as *Parrotia persica* (DC.) C.A. Mey., *Pterocarya fraxinifolia* (Lamb.) Spach, *Zelkova carpinifolia* (Pall.) K. Koch and *Gleditsia caspica* Desf., which survived the

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last glacial period only in Hyrcanian forests, makes this area a unique relict ecosystem preserving the phylogenetic heritage of the late Cenozoic (Browicz 1989; Gholizadeh et al. 2020; Scharnweber et al. 2007).

The endemic relict flora is considered especially sensitive to climate changes (Song et al. 2021; Taleshi et al. 2019; Walas et al. 2019), which are frequently followed by marginal extinction at the warm edge of the range and growth at the cold edge, due to its low biotic complexity (Parmesan 2006; Pauli et al. 2007). In total, 256 endemic and near-endemic taxa belonging to 50 families and 152 genera of flowering plants have been identified in Hyrcanian forests (Ghorbanalizadeh and Akhani 2021) as especially sensitive to climate change (Ahmadi et al. 2020; Alavi et al. 2019; Limaki et al. 2021). Hyrcanian forests were important refugia for temperate broad-leaved trees during the Quaternary glaciations (Akhani et al. 2010; Leroy et al. 2007; Zohary 1983). During the past five decades, increasing temperatures have been observed at many synoptic weather stations in Iran, including in the Caspian area (Azizi and Roshani 2008; Jafari 2008; Molavi-Arabshahi et al. 2016), with the average temperature increasing by 0.74 °C over the past 20 years (Attarod et al. 2017). Therefore, climate change may threaten the geographical distribution and habitat suitability of many species (Mohammadi et al. 2019) with high extinction risk, especially relicts of the Arcto-Tertiary forest, by eliminating their contemporary habitat (Ledig et al. 2012; Walther et al. 2002). Therefore, the prediction of suitable habitat under climate change provides important information for the conservation management of rare and endangered Cenozoic relict tree species (Qin et al. 2017).

Gleditsia caspica Desf. (Leguminosae), one of these relics, is endemic throughout Hyrcanian forests; it is endangered by intense human activity and habitat destruction (Milani et al. 2017; Schnabel and Krutovskii 2004). This pioneer and highly important species is a deciduous legume and is found along the southern coastal plain of the Caspian Sea and lower mountain slopes in southeastern Azerbaijan and northwestern Iran (Akhani 2006; Nourmohammadi et al. 2019). Caspian locust trees are common throughout their range, native exclusively to temperate lowland forests and found from sea level to 500 m a.s.l. within the Hyrcanian ecoregion (Scharnweber et al. 2007). The natural habitats of this species are threatened by loss and fragmentation due to excessive felling of trees for agriculture and grazing, conversion of forestlands to residential areas and farmland, and hybridization with introduced species (*Gleditsia triacanthos* L.) (Schnabel and Krutovskii 2004). Therefore, *G. caspica* is currently found only as individual stems and/or in small communities around row crop and cattle farms (Nourmohammadi et al. 2016; Nourmohammadi et al. 2019). In the most recent assessments, this species is included on the list of endangered species (IUCN evaluation, 2022; under review). Determination of the distribution range of threatened plants in response to climate changes and demarcation of past, contemporary, and future climate refugia of relict plants can be useful for developing valuable conservation efforts and management strategies (Tang et al. 2017; Zhang et al. 2014).

An increase in atmospheric carbon dioxide concentration, associated with the expanded use of fossil fuel for industrial activities and land cover changes, will have a strong impact on average temperature (Gitz and Ciais 2004; Popp et al. 2012). Projected future changes in climate include a rise in temperature (by between 1.4 and 5.8 °C) and a change in the amount and frequency of precipitation until 2100 (Alavi et al. 2019; Beckage et al. 2008). The prediction of species richness and the explanation of evolutionary processes are two of the main challenges of biological science (Huston 1994; Tang et al. 2018). The dispersal, migration, evolution, adaptation, and extinction of species are strongly controlled by environmental variables and climate change (Hampe and Petit 2005; Pearson and Dawson 2003). Species distribution modeling (SDM) is a geographically explicit approach that combines species occurrence data with environmental variables to produce spatially explicit and comprehensive maps that are valuable for identifying areas where conservation efforts and management strategies are most needed (Roberts and Hamann 2012; Tang et al. 2017). SDM is a very powerful approach that has been applied to estimate past distributions of relict species in relevant areas, model their present potential distribution range, and predict vulnerability under future climate change (Tang et al. 2017). This methodology is useful for forecasting conservation areas (especially for designing zones for species protection, restoration, translocation, and reintroductions) and for asking questions regarding the patterns of niche evolution (Araújo and Peterson 2012). MAXENT is one of the most popular software programs for species range estimation (Phillips et al. 2006; Phillips et al. 2019). This tool uses the maximum entropy algorithm, a set of species locations and a set of environmental variables that may shape the species range.

One of the most important priorities in biodiversity protection is the conservation and management of rare and threatened relict species. Reliable data on the natural population abundance, dynamics, and genetic resources of vulnerable and endangered species are crucial for any conservation program (Sękiewicz et al. 2020). SDM was performed in this study to (1) map past geographic distributions of climatically relevant areas and estimate the suitable areas that may serve as potential new habitats and (2) predict the impact of future climate change on the species distribution and evaluate the potential risks involved.

2. Materials and methods

2.1. Study species

Gleditsia caspica Desf. (Leguminosae) is a dioecious, endemic, and critically endangered tree that occurs in the Hyrcanian ecoregion. This species is native exclusively to lowland forests, typically below an altitude of 800 m a.s.l. (Boulos et al. 1994; Frey and Probst 1986).

2.2. Sources of data and statistical analysis

Data on the presence of *G. caspica* in Hyrcanian forests, along with the approximate area of the habitat, were taken from the data center of the Iranian Forest Organization (attached Excel file). Overall, 141 locations were collected: 74 in Gilan, 24 in West Mazandaran, and 43 in East Mazandaran (Fig. 1).

The models of the potential distribution of *G. caspica* were created using the maximum entropy algorithm implemented in MAXENT 3.4.1. (Phillips et al. 2006; Phillips et al. 2019). We tested eight bioclimatic scenarios: one with current conditions, three with future climates using the CCSM4 model (Representative Concentration Pathway (RCPs) 2.6, 4.5, and 8.5; (Collins et al. 2013; Gent et al. 2011)), and four with past conditions (Last Interglacial – LIG, approximately 130 ka BP; Last Glacial Maximum – LGM, approximately 21 ka BP; Younger Dryas – YD, between 12.9 and 11.7 ka BP; and Middle Holocene – MH, between 8.326 and 4.2 ka BP). Additionally, to assess the importance of soil type, one edaphic–bioclimatic scenario was included for the current conditions. Rasters for 19 bioclimatic variables were downloaded from two databases: CHELSA (LGM, current climate, and future conditions (Karger et al. 2017; Karger et al. 2018)) and PaleoClim (LIG, YD, and MH (Brown et al. 2018; Fordham et al. 2017; Otto-Bliesner et al. 2006)). The soil type raster (World Reference Base soil classification, TAXNWBR) was downloaded from the SoilGrids database (http://soilgrids.org (Hengl et al. 2017)).

The spatial resolution of the rasters was 30 arc-seconds for CHELSA and 2.5 arc-min for PaleoClim. Ten variables were excluded from the analyses because of strong correlations, which were estimated using the *vif* function in the package 'usdm' in R (Naimi et al. 2014; RCoreTeam 2021). Each analysis was conducted using bootstrapping with logistic output and 100 replications, 10,000 maximum iterations, and a 10^{-5} convergence threshold. The 'random seed' option was used, with 20% of the stands treated as test points to provide a random test partition. The receiver operating characteristic (ROC) curve and area under the curve (AUC) were used as criteria for model accuracy (Mas et al. 2013; Wang et al. 2007). The MAXENT results were visualized in QGIS 3.16.4

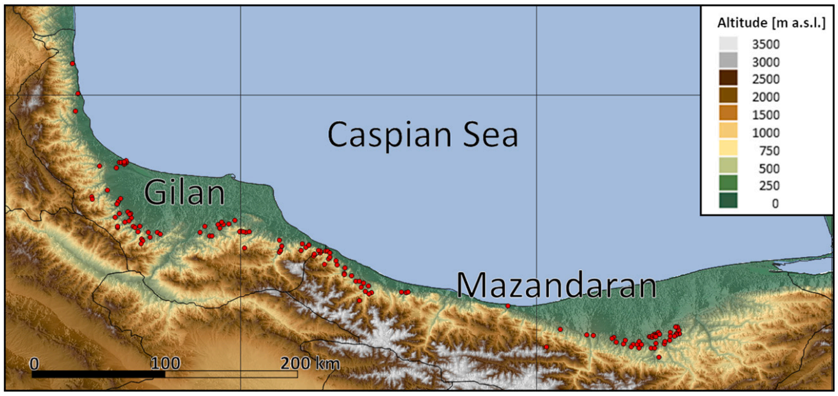

Fig. 1. Location of all stands under study used in Maxent modeling.

'Hannover' (QGISDevelopmentTeam 2020). The area of the potential range and values of the bioclimatic variables were calculated using SAGA GIS software (Conrad et al. 2015).

The environmental differences between the three geographical regions were estimated using principal component analysis (PCA), which was conducted using the '*prcomp*' function in R. The analysis was performed on a dataset of stands of species based on standardized values of the bioclimatic variables used in MAXENT modeling.

3. Results

3.1. Evaluation of models

The obtained models had high AUC values; for most models, this value was 0.992. The exceptions were the two models of current conditions (with and without soil), with an AUC of 0.993, and the LGM model, with an AUC of 0.982.

3.2. Current potential distribution

Gleditsia caspica is endemic to Hyrcanian forests; it usually occurs in broad-leaved forest and sometimes grows on riverside terraces and forest edges. According to data on species stands used in the MAXENT analyses, the average size of the stands is approximately 610 ha (the smallest is 3 ha, and the largest is 6500 ha). Most of the stands occur at low altitudes (78 populations below 500 m a.s.l.); only 16 are in areas above 1000 m a.s.l. The potential range of *G. caspica* covers most of Gilan Province, as well as a large part of Mazandaran Province (Fig. 2A). For the bioclimatic model, the suitable area (>0.05) was only 27,610.46 km^2, approximately half of which had moderate or good suitability (Table 1). The model with an additional soil raster showed almost the same potential range (Fig. S1). Within an estimated range, two regions with high suitability were observed: one stretched along a strip from the Talysh Mountains in the north to West Mazandaran in the south, and the other is located in the foothills of the Alborz Mountains in eastern Mazandaran. The most important variables in the MAXENT bioclimatic models were precipitation of the driest month (average

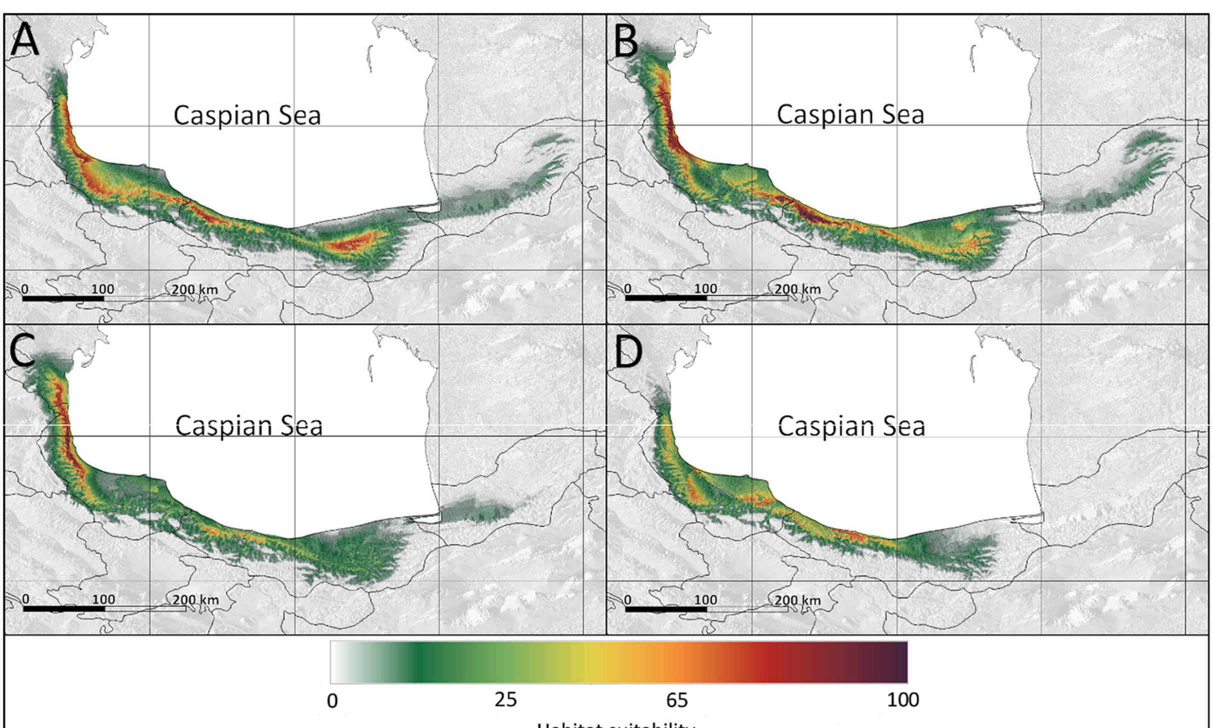

Fig. 2. The potential range of *Gleditsia caspica*; A - current conditions, B - future, model RCP2.6, C - future, model RCP4.5, D - future, model RCP8.5.

Table 1
Potentially suitable area for *Gleditsia caspica* in each tested scenario.

Model	Suitability			
	Weak (0.05–0.25)	Moderate (0.25–0.50)	Good (>0.5)	**Sum**
Current	13,809.41	6929.78	6871.27	**27,610.46**
Current with soil	14,595.92	6828.52	6595.31	**28,019.75**
RCP2.6	17,234.37	9675.87	7173.09	**34,083.33**
RCP 4.5	18,606.95	4942.41	3377.59	**26,926.95**
RCP 8.5	10,663.98	6637.25	2382.05	**19,683.28**
LIG	20,805.05	7838.52	1440.73	**30,084.30**
LGM	2798.43	0.00	0.00	**2798.43**
YD	29,904.38	1376.89	0.00	**31,281.27**
MH	15,963.34	1678.09	0.00	**17,641.43**

contribution 74.9%) and temperature seasonality (12.7%). Although the soil data did not significantly affect the potential range, in the bioclimatic–edaphic model, soil type was more important than temperature seasonality (10.9 and 8.9%, respectively). The most suitable soil types for *G. caspica* were luvisols, phaeozems, and kastanozems.

The PCA of the current bioclimatic variables used in the MAXENT analysis supported environmental differentiation between stands from the eastern part of the range (East Mazandaran) and populations from the western part (Gilan and West Mazandaran, Fig. 3).

3.3. Future species range

Predicted future climate change will negatively impact the natural stands of *G. caspica.* Although in the most optimistic model (RCP2.6), the area suitable for *G. caspica* is even larger than that of today, many stands in eastern Mazandaran and central Gilan may become endangered (Table 1, Fig. 4). In the more pessimistic scenarios RCP4.5 and RCP8.5, the conditions in these regions will be even worse. There is some possibility of a range shift to the north, as the Talysh Mountains became more suitable in scenarios RCP 2.6 and 4.5; additionally, conditions in coastal areas could be better than those of today (Fig. 4).

The most important factor in all tested models was precipitation of the driest month (bio14). In Gilan and western Mazandaran, precipitation would be higher than that of today in scenario RCP2.6, and even in the pessimistic scenario, RCP8.5, it does not fall below 30 mm (Fig. 5A). In eastern Mazandaran, which has different environmental conditions, the situation is more pessimistic. Precipitation in the future may drop significantly there, below the level that is suitable for *Gleditsia,* as 30 mm

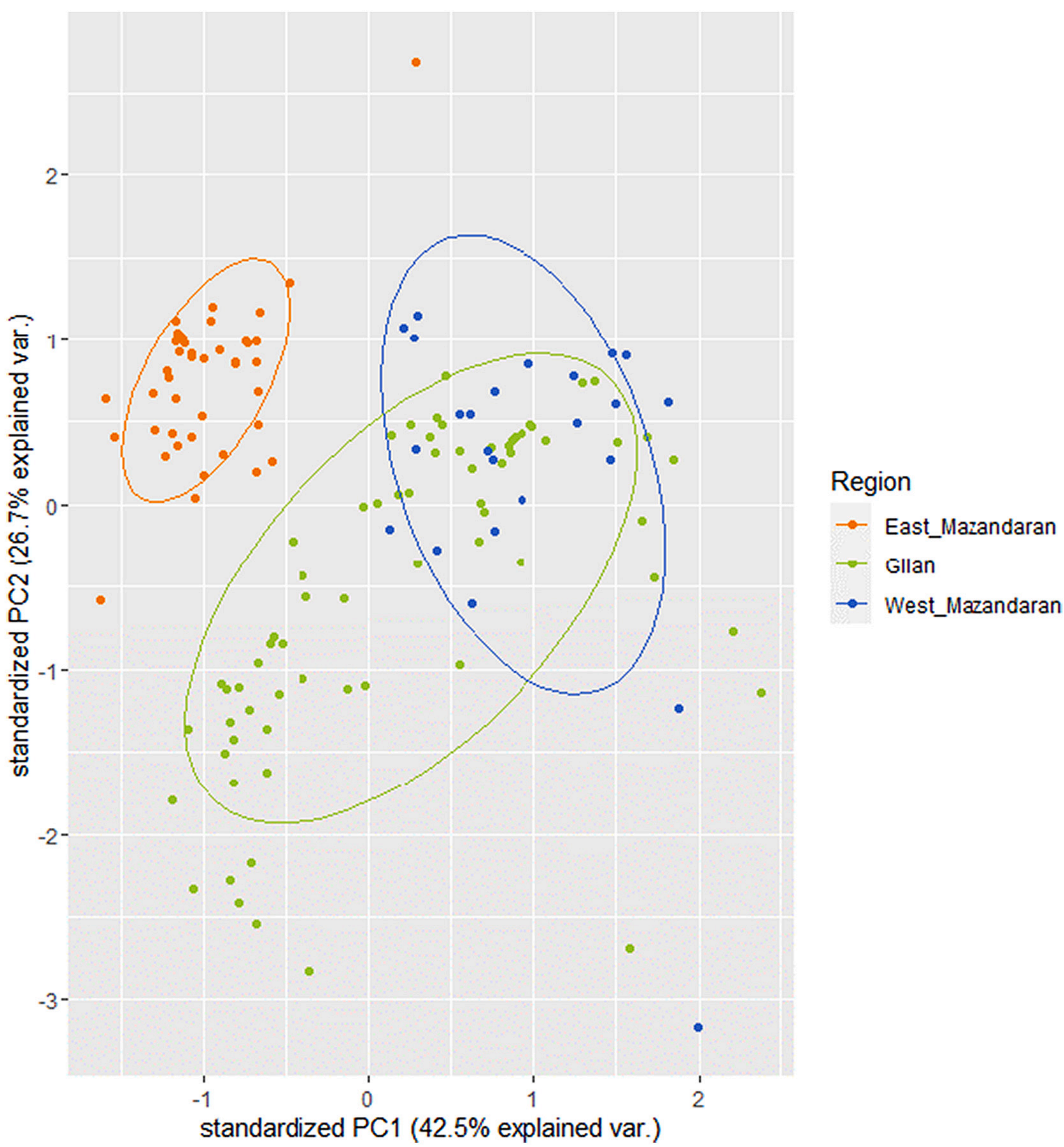

Fig. 3. Ordination plot for the first two principal components from a PCA on environmental variables for each stand; ellipses indicate geographical regions.

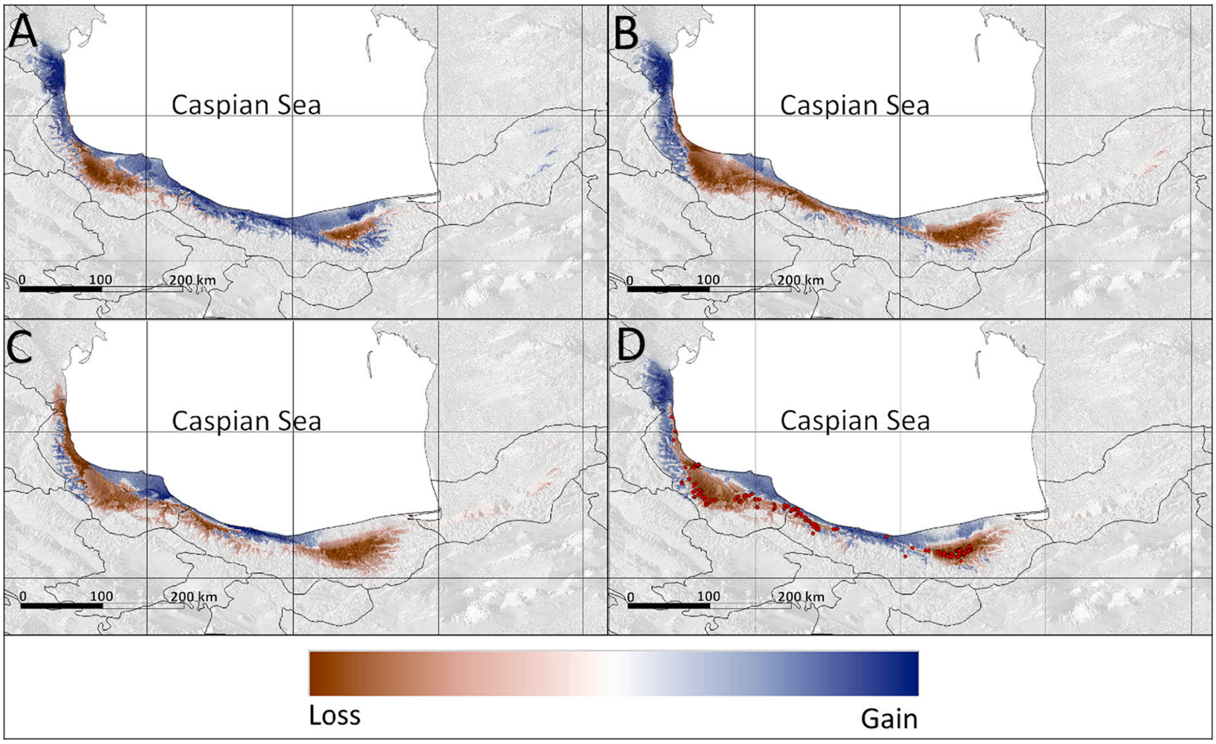

Fig. 4. Change in suitability between current conditions and future scenarios; A - change according to model RCP2.6, B - change according to model RCP4.5, C - change according to model RCP8.5, D - average change with localization of stands.

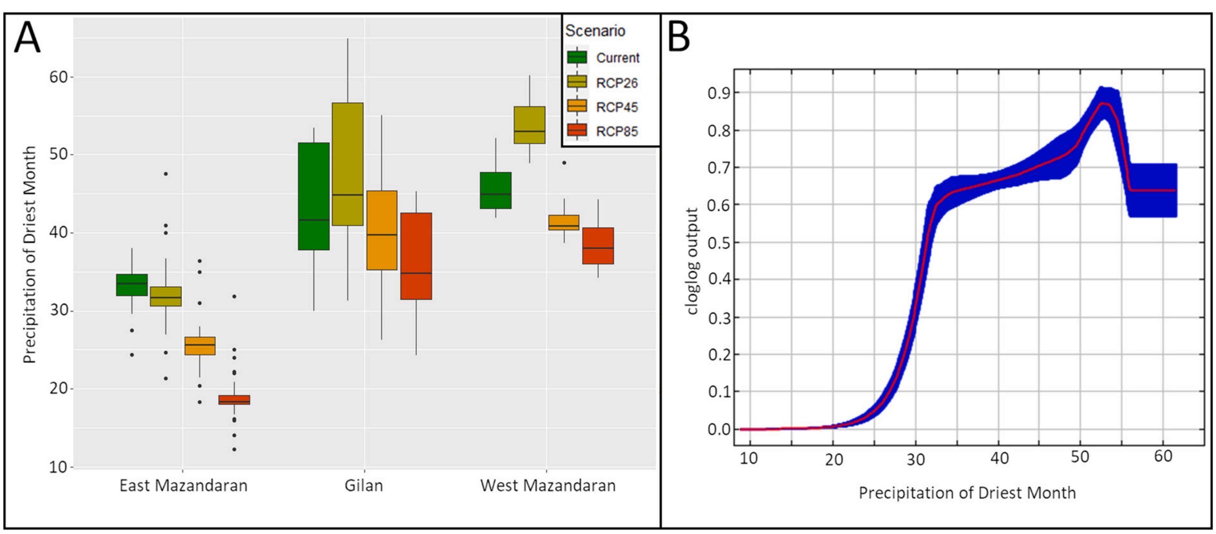

Fig. 5. Values and importance of precipitation of the driest month (bio14); A – precipitation in mm according to the region and tested scenario; B - response curve for bio14 in the model of the current climate.

of rainfall during the driest month yields a potential suitability of approximately 30% when bio14 is treated as the only predictor (Fig. 5B).

3.4. Past species range

During the LIG period, the potential range of *G. caspica* was wide (covering >30,000 km^2) and quite similar to the current potential range. However, in the glacial period, *Gleditsia* was probably pushed into refugia due to unfavorable climatic conditions. Only approximately 10% of the current potential range was suitable for the species during this period (Table 1). The MAXENT analyses revealed two main areas where the species could survive: a larger area in northern Gilan and a second, smaller area in southern Mazandaran (Fig. 6). Interestingly, the locations of these two refugia are similar to the current division between the western and eastern parts of the species range, which have different climatic conditions (Fig. 3). After the LGM, the climate became more favorable, and the species started to expand; during the YD, the potential range was similar to the current range, although suitability was lower. During the Holocene, the species could have occurred in similar areas, and changes in the range were associated mostly with transgressions of the Caspian Sea, which was visible in the Middle Holocene model (Fig. 6D).

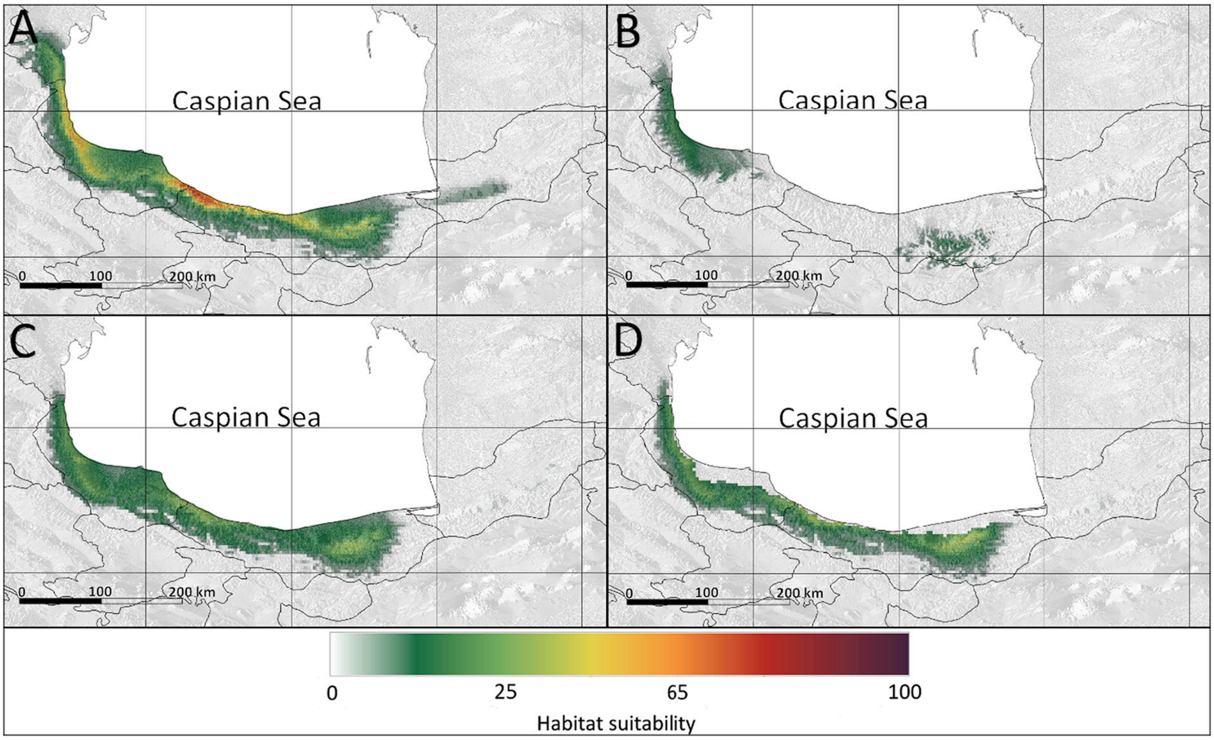

Fig. 6. The potential range of *Gleditsia caspica* in the past: A - Last Interglacial (130*k*), B - Last Glacial Maximum (21*k*), C - Younger Dryas (12.9–11.7 k), D - Middle Holocene (8.326–4.2 k).

4. Discussion

4.1. Model accuracy and current distribution

Climatic variables are important environmental factors that shape sustainability in ecosystems and affect levels of biodiversity, from the organism to biome levels (Bellard et al. 2012; Liu et al. 2015). The ecological niches of tree species and their distribution patterns are determined by multiple components that work altogether and will be influenced by future climate change (Wang et al. 2019). **Refugia** facilitate the persistence of species during large-scale and long-term climatic change and offer suitable conditions in time and space for particular species (Keppel et al. 2015). Regarding fossil evidence, *Gleditsia* expanded throughout the Caucasus during the Miocene and part of the Pliocene (Schnabel and Krutovskii 2004; Shakryl 1992). Pack (1982) argues that *G. caspica* once had a wider range than it has now, but repeated Pleistocene glaciations led to range contractions and pushed the species into isolated refugia such as the southern Caucasus (Pack 1982). The results of the estimated models provided accurate predictions of the current potential distributions of *G. caspica* in Iran. The AUC values that we obtained for the models in this research were very high (> 0.9), similar to those of other studies on potential distributions (Chakraborty et al. 2016; Taleshi et al. 2019; Tejedor Garavito et al. 2015; Trisurat et al. 2009). The predicted species habitat suitability under different climate conditions in our study showed that the suitable area of *G. caspica* will expand due to predicted future climate change under the RCP2.6 scenario, and some new areas could become potential habitats, while under RCP8.5, *G. caspica* will lose approximately 29% of its suitable area.

An increase in the suitable area of *G. caspica,* which was predicted under the RCP2.6 scenario, may be associated with relatively mild climate change, considering the low concentration of greenhouse gas emissions in this scenario. Theoretical precipitation in most of the current range of the species will be even higher than that of today, and in the wet area of Hyrcania, high temperature may even have a positive impact by accelerating phenological processes and prolonging the growing season (Zhang et al. 2018). In the most pessimistic scenario (RCP8.5), the suitable range of *G. caspica* decreased, which is consistent with the results of previous studies conducted on different plant species worldwide (Ma and Sun 2018; Peng et al. 2019; Zhang et al. 2018). Many endemic species are included on the IUCN Red List of threatened species; with narrow geographic distributions and extremely restricted habitats, these species have limited adaptability to the ecological impact of strong climate change in comparison with broadly distributed species, and they are in danger of global extinction (Abdelaal et al. 2019; Abolmaali et al. 2018; Zhang et al. 2015). A significant increase in temperature, as well as lower precipitation, might have a negative effect on their distribution (Xu and Xue 2013). Our results show a more severe influence of climate change on the eastern part of Mazandaran (warmer and drier). Similar findings were also presented in the study by Taleshi et al. (2019), who showed that *G. caspica* will lose at least 70% of its suitable habitats under the RCP4.5 future scenario, while under RCP8.5, it will lose at least 83% of its suitable habitats by 2070.

4.2. Model limitations

Although the models presented in our work showed high AUC values and covered the entire range of the species, it should be noted that the method used has limitations. The soil raster could be used for a model of the contemporary range but not for models of the past because such data are not available; however, soil type was not a determining factor for *Gleditsia*. Additionally, species distributions are influenced not only by climatic and edaphic variables but also by habitat factors such as the occurrence of competition between species. The relationships between individual species can be very complex and affect potential ranges to varying degrees, but using them as variables in modeling is very difficult. In addition, considerations for predicting range shifts also require taking into account factors related to the biology of the tested species, such as seed dispersal, which affects the ability to colonize new areas. An additional factor that can hinder analyses in the Hyrcanian region is strong human influence; large changes in vegetation cover due to management can disrupt a species' natural range and artificially narrow its ecological requirements.

4.3. Range shift in response to climate change

The average climate conditions across the geographic range of *G. caspica* are different from the west to the east of the Hyrcanian ecoregion (Akhani et al. 2010). Mean annual rainfall decreases from the west (1350 mm) to the east (530 mm), while the mean annual temperature increases from the west (15 °C) to the east (17.5 °C) (Sagheb-Talebi et al. 2014; Taleshi et al. 2019). Over the last five decades, an increase in temperature has been recorded at synoptic stations in the Caspian Sea, with 0.74 °C warming over the past 20 years (Attarod et al. 2017; Jafari 2008). Ahmadi et al. (2019) reported an increasing trend in the mean annual temperature in Hyrcanian forests compared to the current climate, with increases of approximately 2.9 and 4.3 °C by 2050 and 2070, respectively. Additionally, they predicted a 9.6% and 19.2% decrease in precipitation in the driest month by 2050 and 2070, respectively.

Of the different factors related to climate conditions, precipitation in the driest month and temperature seasonality appeared to be the most influential with regard to the realized niche of *G. caspica*. A decrease in precipitation in the driest month implies severe drought conditions in summer (Trisurat et al. 2011). Some studies have shown that younger trees are expected to be even more susceptible to drought effects triggered by ongoing climate change (Dell'Oro et al. 2020; Stojanović et al. 2015; Stojanović et al. 2018). Additionally, the normal physiology of seeds could be affected by insufficient water availability, making germination difficult because of the induction of seed dormancy (Chen et al. 2020). Under the conditions of high temperatures and water scarcity, the seeds of *G. caspica* were found to be damaged by pests and diseases (Semenyutina and Melnik 2021), which can be tracked with signs of reduced growth and dieback in tree species (Allen et al. 2010). Precipitation during the driest month is different between the eastern and western parts of the *G. caspica* range. From the west to the east in Hyrcanian forests, the dry season lengthens from one to three months, and *G. caspica* presence appears to be limited by summer dryness. Thus, *G. caspica* is not naturally distributed at the eastern boundary of the Hyrcanian forest area, where annual rainfall is approximately 500 mm and temperature is higher (Alavi et al. 2019; Sagheb 2016). Temperature variables also played a significant role in the *G. caspica* range, which is a common pattern for plant species distributions (Linares et al. 2011; Long et al. 2021; Song et al. 2021; Tang et al. 2017).

Latitudinal and elevational shifts in distribution patterns in response to 20th-century climate change have been **reported** for many species around the world (Büntgen and Krusic 2018; Kaky et al. 2020; Lenoir and Svenning 2015; McLaughlin et al. 2017; Rapacciuolo et al. 2014; Wolf et al. 2016), but this effect is more significant for relict tree species (Koo et al. 2017; Long et al. 2021; Tang et al. 2017). Future distribution scenarios in this study show the possibility of the *G. caspica* range shifting to the north, while the Talysh Mountains become more suitable as a species refugium; additionally, conditions in coastal areas could be more suitable than they are today. Upward shifts are one of the most frequent types of range shifts reported in response to contemporary climate change (Lenoir and Svenning 2015). In recent years, climate change-related range shifts of many plant species have been reported by several authors worldwide (Beckage et al. 2008; Gatti et al. 2019; Lenoir et al. 2008; Ogawa-Onishi et al. 2010; Vessella et al. 2017), with special attention on Hyrcanian forest ecoregions (Ahmadi et al. 2020;Alavi et al. 2019; Limaki et al. 2021; Taleshi et al. 2019). The results of the studies conducted in Hyrcanian forests are largely consistent with our findings and have confirmed elevational shifts in Hyrcanian species distributions in response to global climate change (Alavi et al. 2019; Limaki et al. 2021; Taleshi et al. 2019). An expected rise in the average temperature in northern Iran and an approximately 9% precipitation decrease by the end of the century (Azizi and Roshani 2008; Babaeian et al. 2010; Jafari 2008) will probably lead to tree species shifts to higher altitudes, which are currently not favorable for the growth of many tree species due to lower temperatures and lasting cold in spring (Ahmadi et al. 2017). The expected shift of the geographical range of *G. caspica* toward the coastal areas observed in this study is probably associated with cool, relatively wet, and moderate climate conditions, a narrow range of temperature extremes, a high frequency of clouds and fog, and higher annual precipitation in the coastal area (DellaSala et al. 2015). However, if the potential range of this species shifts to the western areas of Hyrcanian forests, there is a lack of forest habitat for the presence of this species in these areas due to significant land-use change (agricultural and urban planning).

4.4. Management implications

One of the most important analytical–statistical tools in spatial ecology, land management (Williams et al. 2009), conservation biology (Watling et al. 2015), and species extinction risk assessment (Fordham et al. 2012) is SDM. The range size of plant species is related to their vulnerability to climate change, and the widespread decrease in species habitat could even drive them to extinction (Di Marco and Santini 2015; Zu et al. 2021). Our findings suggest that climate change severely exacerbates contraction of the distribution range of *G. caspica* in the lowlands and may increase the risk of local extinction for this species. Dispersed populations, particularly in places with fragmented forests, may experience reduced connection and gene flow, resulting in unsuccessful regeneration.

Additionally, low-longevity seeds in the soil bank (Fazli et al. 2020) cannot stabilize population dynamics by spreading out risk and diminishing large fluctuations in response to short-term environmental perturbations. However, due to the high intensity of degradation and land-use change in the plains region of Hyrcanian forests, it may be impossible to find a suitable habitat for the restoration of this tree species in the future, especially in the central parts of the range. Due to the severity of habitat destruction in the previous three decades, the development of conservation techniques, both in situ and ex situ, including seed storage by cryopreservation, is an urgent requirement for this species (Wade et al. 2016). Although the results of this study suggested widespread correspondence between the distribution range of *G. caspica* and environmental conditions over time, other factors, such as competition, natural selection, dispersal limitation, and human-caused degradation, can also affect the species' distribution in its habitat.

5. Conclusions

Gleditsia capsica is one of the most emblematic climate relicts of western Eurasia. The species is an endemic and threatened tree growing naturally only in the Hyrcanian forest ecoregion of Iran and Azerbaijan. Our work is the first to estimate the potential range of *G. caspica* under past, current, and future (2070) climate conditions and the relationship between the regional distribution of the species and climate change. MAXENT models supported the hypothesis that after the LGM, the tree species began to expand its range, reaching nearly the present potential range during the YD, especially in the eastern part of the range. Today, two refugia for *G. caspica* exist: a larger one in Gilan Province and a second one in the eastern part of Mazandaran Province. The results of the future climate analyses, combined with our database of current occurrence sites, indicated that populations of *G. capsica* occurring in the eastern part of the Hyrcanian forest ecoregion will be most threatened by climate change. However, a strong reduction in the species' range is also expected in Mazandaran, the second refugial area. With the loss of at least 50% of suitable habitat area over the next half-century, an ex situ conservation strategy is recommended, particularly due to the good seed storage capacity of the genus *Gleditsia* under cryopreservation conditions.

Declaration of Competing Interest

None.

Data availability

Data will be made available on request.

References

Abdelaal, M., Fois, M., Fenu, G., Bacchetta, G., 2019. Using MaxEnt modeling to predict the potential distribution of the endemic plant Rosa arabica Crép. In Egypt. Ecol. Informat. 50, 68–75.

Abolmaali, S.M.-R., Tarkesh, M., Bashari, H., 2018. MaxEnt modeling for predicting suitable habitats and identifying the effects of climate change on a threatened species, Daphne mucronata, in Central Iran. Ecol. Inform. 43, 116–123.

Ahmadi, K., Alavi, S.J., Kouchaksaraei, M.T., 2017. Constructing site quality curves and productivity assessment for uneven-aged and mixed stands of oriental beech (Fagus oriental Lipsky) in Hyrcanian forest, Iran. For. Sci. Technol. 13, 41–46.

Ahmadi, K., Alavi, S.J., Amiri, G.Z., Hosseini, S.M., Serra-Diaz, J.M., Svenning, J.-C., 2020. The potential impact of future climate on the distribution of European yew (Taxus baccata L.) in the Hyrcanian Forest region (Iran). Int. J. Biometeorol. 64, 1451–1462.

Akhani, H., 1998. Plant Biodiversity of Golestan National Park, Iran. Biologiezentrum des OÖ Landesmuseums.

Akhani, H., 2006. Flora Iranica: facts and figures and a list of publications by KH Rechinger on Iran and adjacent areas. Rostaniha 7, 19–61.

Akhani, H., Djamali, M., Ghorbanalizadeh, A., Ramezani, E., 2010. Plant biodiversity of Hyrcanian relict forests, N Iran: an overview of the flora, vegetation, palaeoecology and conservation. Pak. J. Bot. 42, 231–258.

Alavi, S.J., Ahmadi, K., Hosseini, S.M., Tabari, M., Nouri, Z., 2019. The response of English yew (Taxus baccata L.) to climate change in the Caspian Hyrcanian Mixed Forest ecoregion. Reg. Environ. Chang. 19, 1495–1506.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.T., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684.

Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93, 1527–1539.

Attarod, P., Kheirkhah, F., Khalighi Sigaroodi, S., Sadeghi, M., Bayramzadeh, V., 2017. Trend analysis of meteorological parameters and reference evapotranspiration in the Caspian region. Iran. J. Forest 9, 171–185.

Azizi, G., Roshani, M., 2008. Study of climate change on southern coast of the Caspian Sea with Mann-Kendall method. Physical Geography Res. 64, 13–28.

Babaeian, I., Najafinik, Z., ZABOL, A.F., ADAB, H., Malbousi, S., 2010. Climate Change Assessment over Iran during 2010–2039 by Using Statistical Downscaling of ECHO-G Model.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T., Perkins, T., 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proc. Natl. Acad. Sci. 105, 4197–4202.

Becklin, K.M., Anderson, J.T., Gerhart, L.M., Wadgymar, S.M., Wessinger, C.A., Ward, J. K., 2016. Examining plant physiological responses to climate change through an evolutionary lens. Plant Physiol. 172, 635–649.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

Boulos, L., Miller, A.G., Mill, R.R., Hamilton, A.C., 1994. Regional overview: South West Asia and the Middle East. In: Davis, S.D., Heywood, V.H. (Eds.), Centres of Plant Diversity. A Guide and Strategy for their Conservation. Volume 1, Europe, Africa, South West Asia, and the Middle East. The World Wide Fund for Nature and IUCN – The World Conservation Union, Cambridge, UK, pp. 293–348.

Browicz, K., 1989. Chorology of the Euxinian and Hyrcanian element in the woody flora of Asia. Plant Syst. Evol. 162, 305–314.

Brown, J., Hill, D., Dolan, A., Carnaval, A., Haywood, A., 2018. Paleoclim, high spatial resolution paleoclimate surfaces for global land areas. Sci. Data 5, 1–9.

Büntgen, U., Krusic, P.J., 2018. OPINION PIECE non-traditional data and innovative methods for autumn climate change ecology. Clim. Res. 75, 215–220.

Chakraborty, A., Joshi, P., Sachdeva, K., 2016. Predicting distribution of major forest tree species to potential impacts of climate change in the central Himalayan region. Ecol. Eng. 97, 593–609.

Chen, Q., Yin, Y., Zhao, R., Yang, Y., Teixeira da Silva, J.A., Yu, X., 2020. Incorporating local adaptation into species distribution modeling of Paeonia mairei, an endemic plant to China. Front. Plant Sci. 10, 1717.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., 2013. Long-Term Climate Change: Projections, Commitments and Irreversibility, Climate Change 2013-The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 1029–1136.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for automated geoscientific analyses (SAGA) v. 2.1. 4. Geosci. Model Dev. 8, 1991–2007.

DellaSala, D.A., Brandt, P., Koopman, M., Leonard, J., Meisch, C., Herzog, P., Alaback, P., Goldstein, M.I., Jovan, S., MacKinnon, A., 2015. Climate Change May Trigger Broad Shifts in North America's Pacific Coastal Rainforests. Reference Module in Earth Systems and Environmental Sciences.

Dell'Oro, M., Mataruga, M., Sass-Klaassen, U., Fonti, P., 2020. Climate change threatens on endangered relict Serbian spruce. Dendrochronologia 59, 125651.

Di Marco, M., Santini, L., 2015. Human pressures predict species' geographic range size better than biological traits. Glob. Chang. Biol. 21, 2169–2178.

Dyderski, M.K., Pawlik, Ł., 2020. Spatial distribution of tree species in mountain national parks depends on geomorphology and climate. For. Ecol. Manag. 474, 118366.

Fazli, M., Akbarinia, M., TABARI, K.S.M., Yousefzadeh, H., Moslemi, S.M.S., 2020. The Effect of Scarification Treatments on Seed Germination of Persian Honey Locust.

Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., 2012. Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? Glob. Chang. Biol. 18, 1357–1371.

Fordham, D.A., Saltré, F., Haythorne, S., Wigley, T.M., Otto-Bliesner, B.L., Chan, K.C., Brook, B.W., 2017. PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. Ecography 40, 1348–1358.

Frey, W., Probst, W., 1986. A synopsis of the vegetation in Iran. In: Kürschner, H. (Ed.), Contribution to the Vegetation of Southwest Asia. Dr. Ludwig Reichert Verlag, Wiesbaden, Germany, pp. 9–43.

Gatti, R.C., Callaghan, T., Velichevskaya, A., Dudko, A., Fabbio, L., Battipaglia, G., Liang, J., 2019. Accelerating upward treeline shift in the Altai Mountains under last-century climate change. Sci. Rep. 9, 1–13.

Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R., Lawrence, D.M., Neale, R.B., Rasch, P.J., Vertenstein, M., 2011. The community climate system model version 4. J. Clim. 24, 4973–4991.

Gholizadeh, H., Naqinezhad, A., Chytrý, M., 2020. Classification of the Hyrcanian forest vegetation, Northern Iran. Appl. Veg. Sci. 23, 107–126.

Ghorbanalizadeh, A., Akhani, H., 2021. Plant diversity of Hyrcanian relict forests: an annotated checklist, chorology and threat categories of endemic and near endemic vascular plant species. Plant Diversity.

Gitz, V., Ciais, P., 2004. Future expansion of agriculture and pasture acts to amplify atmospheric CO 2 levels in response to fossil-fuel and land-use change emissions. Clim. Chang. 67, 161–184.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467.

Hengl, T., Mendes de Jesus, J., Heuvelink, G.B., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS One 12, e0169748.

Huston, A., 1994. The coexistence of species on changing landscapes. Page Biol. Divers. 483–557.

Jafari, M., 2008. Investigation and Analysis of Climate Change Factors in Caspian Zone Forests for Last Fifty Years.

Kaky, E., Nolan, V., Alatawi, A., Gilbert, F., 2020. A comparison between ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. Ecol. Inform. 60, 101150.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 1–20.

Karger, D., Conrad, O., Böhner, J., 2018. Data from: Climatologies at High Resolution for the earth's Land Surface Areas, 7266827510 bytes.

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.

Koo, K.A., Kong, W.-S., Park, S.U., Lee, J.H., Kim, J., Jung, H., 2017. Sensitivity of Korean fir (Abies koreana Wils.), a threatened climate relict species, to increasing temperature at an island subalpine area. Ecol. Model. 353, 5–16.

Krebs, P., Conedera, M., Pradella, M., Torriani, D., Felber, M., Tinner, W., 2004. Quaternary refugia of the sweet chestnut (Castanea sativa Mill.): an extended palynological approach. Veg. Hist. Archaeobotany 13, 145–160.

Ledig, F.T., Rehfeldt, G.E., Jaquish, B., 2012. Projections of suitable habitat under climate change scenarios: implications for trans-boundary assisted colonization. Am. J. Bot. 99, 1217–1230.

Lenoir, J., Svenning, J.C., 2015. Climate-related range shifts–a global multidimensional synthesis and new research directions. Ecography 38, 15–28.

Lenoir, J., Gégout, J.-C., Marquet, P., De Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science.

Leroy, S.A., Marret, F., Gibert, E., Chalié, F., Reyss, J.-L., Arpe, K., 2007. River inflow and salinity changes in the Caspian Sea during the last 5500 years. Quat. Sci. Rev. 26, 3359–3383.

Limaki, M.K., Nimvari, M.E.-H., Alavi, S.J., Mataji, A., Kazemnezhad, F., 2021. Potential elevation shift of oriental beech (Fagus orientalis L.) in Hyrcanian mixed forest ecoregion under future global warming. Ecol. Model. 455, 109637.

Linares, J.C., Tíscar, P.A., Camarero, J.J., Taïqui, L., Viñegla, B., Seco, J.I., Merino, J., Carreira, J.A., 2011. Tree Growth Decline on Relict Western-Mediterranean Mountain Forests: Causes and Impacts. Nova Science Publishers Inc., Hauppauge, NY, USA, pp. 1–20.

Liu, J., Mooney, H., Hull, V., Davis, S.J., Gaskell, J., Hertel, T., Lubchenco, J., Seto, K.C., Gleick, P., Kremen, C., 2015. Systems integration for global sustainability. Science 347.

Long, T., Tang, J., Pilfold, N.W., Zhao, X., Dong, T., 2021. Predicting range shifts of Davidia involucrata Ball. under future climate change. Ecol. Evol. 11, 12779–12789.

Ma, B., Sun, J., 2018. Predicting the distribution of Stipa purpurea across the Tibetan Plateau via the MaxEnt model. BMC Ecol. 18, 1–12.

Mas, J.-F., Soares Filho, B., Pontius, R.G., Farfán Gutiérrez, M., Rodrigues, H., 2013. A suite of tools for ROC analysis of spatial models. ISPRS Int. J. Geo Inf. 2, 869–887.
McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. Glob. Chang. Biol. 23, 2941–2961.
Menezes-Silva, P.E., Loram-Lourenço, L., Alves, R.D.F.B., Sousa, L.F., Almeida, S.E.D.S., Farnese, F.S., 2019. Different ways to die in a changing world: consequences of climate change for tree species performance and survival through an ecophysiological perspective. Ecol. Evol. 9, 11979–11999.
Milani, E., Saeidi Mehrvarz, S., Gholizadeh, H., 2017. Floristic, life form and chorological studies of the Abshar protected area, Shirgah, Mazandaran Province, north of Iran. Caspian J. Environ. Sci. 15, 165–180.
Mohammadi, S., Ebrahimi, E., Moghadam, M.S., Bosso, L., 2019. Modelling current and future potential distributions of two desert jerboas under climate change in Iran. Ecol. Inform. 52, 7–13.
Molavi-Arabshahi, M., Arpe, K., Leroy, S., 2016. Precipitation and temperature of the Southwest Caspian Sea region during the last 55 years: their trends and teleconnections with large-scale atmospheric phenomena. Int. J. Climatol. 36, 2156–2172.
Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37, 191–203.
Nourmohammadi, K., Rahimi, D., Naghdi, R., Kartoolinejad, D., 2016. Effects of physical and chemical treatments of seed dormancy breaking on seedling quality index (QI) of Caspian locust (Gleditsia caspica Desf.). Austrian J. Forest Sci. 133, 157–171.
Nourmohammadi, K., Kartoolinejad, D., Naghdi, R., Baskin, C.C., 2019. Effects of dormancy-breaking methods on germination of the water-impermeable seeds of Gleditsia caspica (Fabaceae) and seedling growth. Folia Oecol. 46, 115–126.
Ogawa-Onishi, Y., Berry, P.M., Tanaka, N., 2010. Assessing the potential impacts of climate change and their conservation implications in Japan: a case study of conifers. Biol. Conserv. 143, 1728–1736.
Otto-Bliesner, B.L., Marshall, S.J., Overpeck, J.T., Miller, G.H., Hu, A., members, C.L.I.P, 2006. Simulating Arctic climate warmth and icefield retreat in the last interglaciation. Science 311, 1751–1753.
Pack, J., 1982. Gleditsia caspia, not a distinct species (Leguminosae). Taxon 31, 336–339.
Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.
Pauli, H., Gottfried, M., Reiter, K., Klettner, C., Grabherr, G., 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. Glob. Chang. Biol. 13, 147–156.
Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371.
Peng, L.-P., Cheng, F.-Y., Hu, X.-G., Mao, J.-F., Xu, X.-X., Zhong, Y., Li, S.-Y., Xian, H.-L., 2019. Modelling environmentally suitable areas for the potential introduction and cultivation of the emerging oil crop Paeonia ostii in China. Sci. Rep. 9, 1–10.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.
Phillips, S.J., Dudík, M., Schapire, R.E., 2019. Maxent Software for Modeling Species Niches and Distributions (Version 3.4. 1).
Popp, A., Krause, M., Dietrich, J.P., Lotze-Campen, H., Leimbach, M., Beringer, T., Bauer, N., 2012. Additional CO2 emissions from land use change—forest conservation as a precondition for sustainable production of second generation bioenergy. Ecol. Econ. 74, 64–70.
QGISDevelopmentTeam, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
Qin, A., Liu, B., Guo, Q., Bussmann, R.W., Ma, F., Jian, Z., Xu, G., Pei, S., 2017. Maxent modeling for predicting impacts of climate change on the potential distribution of Thuja sutchuenensis Franch., an extremely endangered conifer from southwestern China. Global Ecol. Conserv. 10, 139–146.
Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh, R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D., 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Glob. Chang. Biol. 20, 2841–2855.
RCoreTeam, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Roberts, D.R., Hamann, A., 2012. Predicting potential climate change impacts with bioclimate envelope models: a palaeoecological perspective. Glob. Ecol. Biogeogr. 21, 121–133.
Roces-Díaz, J.V., Jiménez-Alfaro, B., Chytrý, M., Díaz-Varela, E.R., Álvarez-Álvarez, P., 2018. Glacial refugia and mid-Holocene expansion delineate the current distribution of Castanea sativa in Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 491, 152–160.
Sagheb, K., 2016. FORESTS OF IRAN: A Treasure from the Past, a Hope for the Future. Springer.
Sagheb-Talebi, K., Pourhashemi, M., Sajedi, T., 2014. Forests of Iran: A Treasure from the Past, a Hope for the Future. Springer.
Scharnweber, T., Rietschel, M., Manthey, M., 2007. Degradation stages of the Hyrcanian forests in southern Azerbaijan. Archiv für Naturschutz und Landschaftsforschung 46, 133–156.
Schnabel, A., Krutovskii, K.V., 2004. Conservation genetics and evolutionary history of Gleditsia caspica: inferences from allozyme diversity in populations from Azerbaijan. Conserv. Genet. 5, 195–204.
Sękiewicz, K., Walas, Ł., Beridze, B., Fennane, M., Dering, M., 2020. High genetic diversity and low future habitat suitability: will Cupressus atlantica, endemic to the High Atlas, survive under climate change? Reg. Environ. Chang. 20, 1–19.
Semenyutina, A., Melnik, K., 2021. Генеративные и репродуктивные качества у таксонов рода Gleditsia в засушливых условиях. Greening Rev. 11.
Shakryl, A.K., 1992. Leguminosae species from the tertiary of Abkhazia. In: Advances in Legume Systematics, Part 4, pp. 189–206.
Song, Y.-G., Walas, Ł., Pietras, M., Sâm, H.V., Yousefzadeh, H., Ok, T., Farzaliyev, V., Worobiec, G., Worobiec, E., Stachowicz-Rybka, R., 2021. Past, present and future suitable areas for the relict tree Pterocarya fraxinifolia (Juglandaceae): integrating fossil records, niche modeling, and phylogeography for conservation. Eur. J. For. Res. 1–17.
Stewart, J.R., Lister, A.M., Barnes, I., Dalén, L., 2010. Refugia revisited: individualistic responses of species in space and time. Proc. R. Soc. B Biol. Sci. 277, 661–671.
Stojanović, D., Levanič, T., Matović, B., Orlović, S., 2015. Growth decrease and mortality of oak floodplain forests as a response to change of water regime and climate. Eur. J. For. Res. 134, 555–567.
Stojanović, D., Levanič, T., Matović, B., Stjepanović, S., Orlović, S., 2018. Growth response of different tree species (oaks, beech and pine) from SE Europe to precipitation over time. Dendrobiology 79, 97–110.
Svenning, J.-C., Eiserhardt, W.L., Normand, S., Ordonez, A., Sandel, B., 2015. The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. Annu. Rev. Ecol. Evol. Syst. 46, 551–572.
Taleshi, H., Jalali, S.G., Alavi, S.J., Hosseini, S.M., Naimi, B., Zimmermann, N.E., 2019. Climate change impacts on the distribution and diversity of major tree species in the temperate forests of northern Iran. Reg. Environ. Chang. 19, 2711–2728.
Tang, C.Q., Dong, Y.-F., Herrando-Moraira, S., Matsui, T., Ohashi, H., He, L.-Y., Nakao, K., Tanaka, N., Tomita, M., Li, X.-S., 2017. Potential effects of climate change on geographic distribution of the tertiary relict tree species Davidia involucrata in China. Sci. Rep. 7, 1–18.
Tang, C.Q., Matsui, T., Ohashi, H., Dong, Y.-F., Momohara, A., Herrando-Moraira, S., Qian, S., Yang, Y., Ohsawa, M., Luu, H.T., 2018. Identifying long-term stable refugia for relict plant species in East Asia. Nat. Commun. 9, 1–14.
Tejedor Garavito, N., Newton, A.C., Golicher, D., Oldfield, S., 2015. The relative impact of climate change on the extinction risk of tree species in the montane tropical Andes. PLoS One 10, e0131388.
Trisurat, Y., Alkemade, J., Arets, E., 2009. Projecting forest tree distributions and adaptation to climate change in northern Thailand. J. Ecol. Nat. Environ. 1, 55–63.
Trisurat, Y., Shrestha, R.P., Kjelgren, R., 2011. Plant species vulnerability to climate change in peninsular Thailand. Appl. Geogr. 31, 1106–1114.
Vessella, F., Simeone, M.C., Schirone, B., 2015. *Quercus suber* Range Dynamics by Ecological Niche Modelling.
Vessella, F., López-Tirado, J., Simeone, M.C., Schirone, B., Hidalgo, P.J., 2017. A tree species range in the face of climate change: cork oak as a study case for the Mediterranean biome. Eur. J. For. Res. 136, 555–569.
Wade, E.M., Nadarajan, J., Yang, X., Ballesteros, D., Sun, W., Pritchard, H.W., 2016. Plant species with extremely small populations (PSESP) in China: a seed and spore biology perspective. Plant Diversity 38 (5), 209–220.
Walas, Ł., Sobierajska, K., Ok, T., Dönmez, A.A., Kanoğlu, S.S., Dagher-Kharrat, M.B., Douaihy, B., Romo, A., Stephan, J., Jasińska, A.K., 2019. Past, present, and future geographic range of an oro-Mediterranean tertiary relict: the juniperus drupacea case study. Reg. Environ. Chang. 19, 1507–1520.
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.
Wang, Z., Chang, Y.-C.I., Ying, Z., Zhu, L., Yang, Y., 2007. A parsimonious threshold-independent protein feature selection method through the area under receiver operating characteristic curve. Bioinformatics 23, 2788–2794.
Wang, L., Wang, W.J., Wu, Z., Du, H., Zong, S., Ma, S., 2019. Potential distribution shifts of plant species under climate change in Changbai Mountains, China. Forests 10, 498.
Watling, J.I., Brandt, L.A., Bucklin, D.N., Fujisaki, I., Mazzotti, F.J., Romanach, S.S., Speroterra, C., 2015. Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. Ecol. Model. 309, 48–59.
Wiens, J.J., 2016. Climate-related local extinctions are already widespread among plant and animal species. PLoS Biol. 14, e2001104.
Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M., Schwartz, M.W., 2009. Using species distribution models to predict new occurrences for rare plants. Divers. Distrib. 15, 565–576.
Wolf, A., Zimmerman, N.B., Anderegg, W.R., Busby, P.E., Christensen, J., 2016. Altitudinal shifts of the native and introduced flora of C alifornia in the context of 20th-century warming. Glob. Ecol. Biogeogr. 25, 418–429.
Xu, M., Xue, X., 2013. Analysis on the effects of climate warming on growth and phenology of alpine plants. J. Arid Land Resour. Environ. 27, 137–141.
Yang, X.-Q., Kushwaha, S., Saran, S., Xu, J., Roy, P., 2013. Maxent modeling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in lesser Himalayan foothills. Ecol. Eng. 51, 83–87.
Zhang, Y., Wang, Y., Zhang, M., Ma, K., 2014. Climate change threats to protected plants of China: an evaluation based on species distribution modeling. Chin. Sci. Bull. 59, 4652–4659.
Zhang, H., Wang, X., Zhang, Y., Hu, R., Pan, Y., Chen, N., 2015. Responses of plant growth of different life forms to rainfall amount changes in an arid desert area. Chinese J. Ecol. 34, 1847–1853.
Zhang, K., Yao, L., Meng, J., Tao, J., 2018. Maxent modeling for predicting the potential geographical distribution of two peony species under climate change. Sci. Total Environ. 634, 1326–1334.

Zhang, K., Zhang, Y., Zhou, C., Meng, J., Sun, J., Zhou, T., Tao, J., 2019. Impact of climate factors on future distributions of Paeonia ostii across China estimated by MaxEnt. Ecol. Inform. 50, 62–67.

Zohary, M., 1973. Geobotanical Foundations of the Middle East. Fischer.

Zohary, M., 1983. Geobotanical Foundation of the Middle East; Gus. Fischer-Verlag, Stuttgart, Germany.

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., Luo, A., Li, Y., Ji, C., Peng, S., 2021. Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. Sci. Total Environ. 783, 146896.