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; Svening 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 (Akhanzi 1998; Zohary 1973). Hyrcanian forests are known as refuges for many Arcto-Tertiary relict taxa, which are grouped into Hyrcanian and Euxino-Hyrcanian elements (Akhanzi 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
last glacial period only in Hycranian 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 Hycranian forests (Ghorbanalizadeh and Akhani 2021) as especially sensitive to climate change (Ahmadi et al. 2020; Alavi et al. 2019; Limaki et al. 2021). Hycranian 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 relics 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 Hycranian 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 Hycranian 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 Giais 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 conservation (Huntley 1994; Tang et al. 2019). 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 (Scharnweber et al. 2005). 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 Hycranian 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 Hycranian 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.
‘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 km², 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. 1. Location of all stands under study used in Maxent modeling.](image1)

![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.](image2)
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...

### Table 1

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

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

*Fig. 3.* Ordination plot for the first two principal components from a PCA on environmental variables for each stand; ellipses indicate geographical regions.
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 km²) 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).
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 Hycranian 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 Hycranian 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; Stoianovic et al. 2015; Stoianovic 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 Hycranian 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 Hycranian 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 relic 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. 2016; Vessella et al. 2017), with special attention on Hycranian 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 Hycranian forests are largely consistent with our findings and have confirmed elevational shifts in Hycranian 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. 2018; 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 (DellaSalà et al. 2015). However, if the potential range of this species shifts to the western areas of Hycranian 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, long-lifecycle 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 Hycranian 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 caspica is one of the most emblematic climate relics of western Eurasia. The species is an endemic and threatened tree growing naturally only in the Hycranian 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 Mazzandaran Province. The results of the future climate analyses, combined with our database of current occurrence sites, indicated that populations of G. caspica occurring in the eastern part of the Hycranian forest ecoregion will be most threatened by climate change. However, a strong reduction in the species’ range is also expected in Mazzandaran, 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.


