J Genet Resour2025; 11(2): 203-213 *Homepage: http://sc.journals.umz.ac.ir/*

RESEARCH ARTICLE *DOI: 10.22080/jgr.2025.29178.1438*

Climate Change Impact on the Future Distribution of Rare, Relict and Small Fragmented Populations of *Lilium ledebourii* in the Hyrcanian Forest

Hamed Yousefzadeh[1*], Narjes Amirchakhmaghi[1], Mojtaba Bahrami [2], Mansour Pouramin[3], Gregor Kozlowski[4,5,6], Łukasz Walas[7]

[1] Tarbiat Modares University, Faculty of Natural sciences, Department of Forestry, Tehran, Iran.
[2] Tarbiat Modares University, Faculty of Natural sciences, Department of Environmental science, Tehran, Iran.
[3] Guilan University, Faculty of Natural sciences, Department of Forestry, Rasht, Iran.
[4] Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, Shanghai 201602, China.
[5] Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland.
[6] Natural History Museum Fribourg, Chemin du Musée 6, CH-1700 Fribourg, Switzerland.
[7] Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland.

ARTICLE INFO

Article history:
Received 19 May 2025
Accepted 08 July 2025
Available 25 July 2025

Keywords:
Fragmented populations
Habitat suitability
Hyrcanian forest
Rare species
Refugium forest

****Corresponding authors:***
✉ H. Yousefzadeh
h.yousefzadehseraj@modares.ac.ir

p-ISSN 2423-4257
e-ISSN 2588-2589

ABSTRACT

This study aimed to map the historical geographical range of *L. ledebourii* in the Hyrcanian Forest; assess the current areas inhabited by this species; predict the future geographical distribution of this rare species under various climate change scenarios; and determine the main climatic factors associated with the distribution pattern of *L. ledebourii. Lilium ledebourii* is a rare plant with a very limited and fragmented distribution in the Hyrcanian Forest. A total of 19 spatial points were utilized to model the potential distribution of *L. ledebourii* under both current and projected climate conditions. Bioclimatic variables for present-day conditions were sourced from the CHELSA database, while data for the Last Glacial Maximum were obtained from the NCAR-CCSM4 model. For future climate scenarios, variables were derived from three different models across two distinct projections. The most important variables were precipitation in the warmest quarter, precipitation in the coldest quarter, and precipitation seasonality. The present potential range of the species covers 40,909 km^2, forming a long strip in the Hyrcanian area with the highest suitability in the mountains. During the LGM, the species potential range was approximately 16% greater than the current range. Under future conditions, the potential range of *L. ledebourii* is likely to be drastically reduced, and suitability will decrease significantly. According to the morphological spatial pattern analysis, the future potential range of *L. ledebourii* will be fragmented in both tested scenarios. The connections between these core areas will be very restricted. Considering the shrinking of the habitat areas of *L. ledebourii* due to climate change and the high vulnerability of this species in its habitat (grazing, steep slopes, and soil erosion), ex situ conservation could represent the most effective approach for securing the long-term survival of *L. ledebourii* within the Hyrcanian Forest.

Please cite this paper as: Yousefzadeh, H., Amirchakhmaghi, N., Bahrami, M., Pouramin, M., Kozlowski, G., Walas, Ł. (2025). Climate change impact on the future distribution of rare, relict and small fragmented populations of *Lilium ledebourii* in the Hyrcanian Forest. *Journal of Genetic Resources,* 11(2), *203-213*. doi: 10.22080/jgr.2025.29178.1438

Introduction

The Changes in global climate patterns have created numerous negative impacts on ecosystems and species across the planet, especially native species, and numerous studies are addressing this issue (Zangiabadi *et al.*, 2021).

This phenomenon includes more frequent extreme weather events, intensified greenhouse effects, accelerated melting of glaciers and snow, rising sea levels, risks to biodiversity, and a greater spread of diseases (Kumar *et al.*, 2021), poses significant challenges to species. The morphological structures, growth, and development patterns of plants can be dramatically altered by abiotic factors disrupted by climate change, including temperature, precipitation, soil conditions, and altitude (Garza *et al.*, 2020). These variations also alter the diversity and stability of global ecosystems and the geographical distribution patterns of plants. This forces species to either adapt to changing conditions or adjust their geographical ranges; otherwise, extinction may occur (Kaky and Gilbert, 2019). Locally rare and threatened species with restricted populations, limited geographic distribution, low genetic diversity, or extremely specific habitat requirements are typically more vulnerable to extinction than their more common counterparts across taxa and geographic locations (Yang *et al.*, 2021).

Lilium ledebourii (Baker) Bioss., commonly known as Iranian lily or Susan-e-Chelcheragh, is a critically endangered, rare, and endemic ornamental plant distributed exclusively in the small and fragmented wild areas of the Hyrcanian Forest in northern Iran (Shokrollahi *et al.*, 2022). The Hyrcanian Forest spans about 1.85 million hectares in Iran, characterized by diverse topography and climate, with elevations ranging from sea level to 2,800 meters (Sagheb-Talebi *et al.*, 2016; Alavi *et al.*, 2020). This forest is a biodiversity hotspot and serves as a refuge for numerous Arcto-Tertiary relict taxa, with unique species compositions. *Lilium ledebourii* is a perennial herbaceous plant from the genus *Lilium*, part of the *Liliaceae* family, which includes around 220 genera. The genus *Lilium* includes approximately 110 species with an extensive range of more than 7,000 cultivars (Salehi *et al.*, 2019). These geophytic perennial species are found across most cold and temperate mountainous regions of the Northern Hemisphere, with a primary distribution in Asia, North America, and Europe (Gao *et al.*, 2013). A notable feature of the Iranian lily is its ability to withstand cold temperatures, as it can germinate even in snow. For rare and endangered species, habitat loss, distribution shifts, and the risk of extinction increase due to their limited geographical distribution, small population sizes, and increased vulnerability to changes in environmental status. Therefore, understanding the potential impacts of climate change on the distribution of these organisms is crucial for developing appropriate conservation and management strategies to preserve current biodiversity and prevent widespread extinctions (Qazi *et al.*, 2022).

Examining the relationship between species distribution and the interplay of climate and other environmental factors has long been a central focus in the field of ecology. The quantification of these relationships forms the fundamental basis for reveal the extent of the potential ecological risk, assess species' extinction risks and design appropriate conservation strategies for adaptive management (Buse *et al.*, 2015). Species distribution modeling (SDM) has been increasingly used as a basis for predicting species occurrence under future climate scenarios based on environmental data, for prioritizing protected areas, for predicting suitable habitats for narrowly distributed, rare and threatened plants and for inferring the risk of species extinction (da Silva *et al.*, 2019). Among the different species distribution modeling (SDM) methods, the maximum entropy model (MaxEnt) is recognized as the most accurate and widely used, and widely used model in the study of species-suitable geographical distribution prediction (Zhang *et al.*, 2023). This model is effective for studying the effects of climate change on the potential future distribution range of species, species richness, and endemism hotspots, as well as for estimating the extent of occurrence and quality of protection of rare species (Qazi *et al.*, 2022). Using presence-only data, this model can accurately forecast the distribution range of threatened species, identify appropriate habitats, prioritize conservation efforts, and predict range shifts under future climate change scenarios, even with small sample sizes. In this study, SDM was conducted to (1) Map the historical geographical distribution of *L. ledebourii* in the Hyrcanian Forest; (2) assess the current areas inhabited by this species; (3) predict the future geographical distribution of this rare species under various climate change scenarios; and (4) determine the main climatic factors associated with the distribution pattern of *L. ledebourii*.

Materials and Methods

Spatial analyses

In total, 19 spatial points (Fig. 1) were used to create models of the species' potential distributions; although this value is low, it may be sufficient to make a robust estimation (Van Proosdij *et al.*, 2016).

Bioclimatic variables were obtained from the CHELSA database (Karger et al., 2017, 2018) for present-day conditions, from the NCAR-CCSM4 model for the Last Glacial Maximum (LGM; Karger et al., 2021), and three models (IPSL-CM6A-LR, MPI-ESM1-2-HR, and UKESM1-0-LL) for two future climate scenarios (SSP370 and SSP585). For both scenarios, the outputs of the three models were averaged to calculate the consensus model. To avoid correlations between variables, Pearson's correlation between rasters was calculated using the *layerStats* function from the raster package in the R environment (Hijmans, 2023). After removing the correlated rasters, nine variables remained (Table 1).

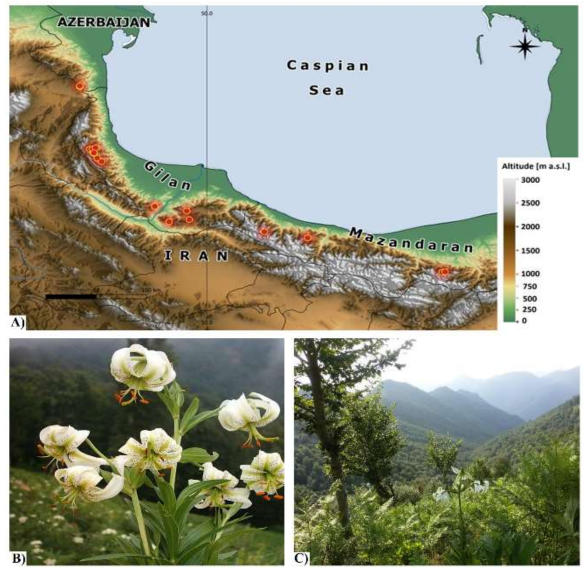

Fig. 1. Spatial points of *L. ledebourii* in this study: A) Locations of the known *Lilium ledebourii* stands (red dots) in the Hyrcanian forest; B) Natural habitats of *L. ledebourii* in western part of the Hyrcanian Forest; B) Flowering individual in natural habitat.

Table 1. Importance of all tested variables in the estimated scenarios. Values for the future climatic conditions are averaged from three different models.

	AUC	0.988	0.997	0.988	0.988
		Scenario			
		Current	**LGM**	**SSP370**	**SSP585**
Annual Mean Temperature	bio1	1.6	2.3	1.3	1.1
Mean Diurnal Range	bio2	0.8	2.3	0.5	1.1
Isothermality	bio3	0.6	0.5	0.7	0.5
Temperature Seasonality	bio4	4.5	7.1	5.6	4.6
Mean T of Wettest Quarter	bio8	1.7	1.3	1.1	2.4
Mean T of Driest Quarter	bio9	3.3	3.9	2.4	2.5
Precipitation Seasonality	bio15	20.8	15.8	16.4	17.8
Prec. of Warmest Quarter	bio18	40.6	40.0	43.2	43.3
Prec. of Coldest Quarter	bio19	26.2	26.9	28.9	26.8

The parameters of the analyses were calculated with the ENMeval package in the R environment. The model with the lowest Akaike information criterion (AIC) value was chosen (Table S1). The potential distribution of *L. ledebourii* was estimated using MaxEnt 3.4.1 software. Each scenario was tested as a bootstrap with logistic output, a 2.0 regularization multiplier, linear-quadratic-hinge features, 10^4 maximum iterations, 100 replications, 10^3 background points, and a 10^{-5} convergence threshold. The "random seed" option was used to partition the dataset into test and training sets. The accuracy of the estimated models was tested with the receiver operating characteristic (ROC) curve and area under the curve (AUC) (Wang et al., 2007). Rasters with MaxEnt suitability values exceeding 0.2 were utilized as inputs for morphological spatial pattern analysis (MSPA) using the GuidosToolbox software (Vogt and Riitters, 2017). This approach allows the species to be divided into several spatial classes, which helps to understand fragmentation and connection across the species' potential distributions. All the maps were prepared using QGIS 3.32.1 'Lima' (QGIS Development Team, 2023).

Results

Potential distribution of *L. ledebourii*

All models tested exhibited high AUC values ranging from 0.988 to 0.997 (Table 1). The most influential variable was precipitation during the warmest quarter (bio18), contributing over 40% to the model's performance, followed by precipitation in the coldest quarter (bio19) and precipitation seasonality (bio15; Table 1). The temperature variables had a minor contribution. The present potential range of the species covers 40,909.6 km^2 (Table 2), creating a long strip in the Hyrcanian area with the highest suitability (above 0.8; 4,973.09 km^2) in the mountains (Figure 2A). The potential range spread through the eastern Mazandaran to Golestan, where the analyzed species does not occur.

During the LGM, the species potential range was approximately 16% greater than the current range (Table 2), with one highly suitable area in Mazandaran and a second, smaller suitable area in Gilan (Figure 2B). Golestan was almost unsuitable for this species during this time. Under future conditions, the potential range of the species is likely to be drastically reduced, and suitability will decrease significantly (Table 2, Fig. 2C, D). Similarly, under the climate scenarios tested (SSP370 and SSP585), very highly suitable areas disappeared completely, while the potential range shifted to higher altitudes. In total, under the consensus SSP370 model, 10,957.82 km^2 remains suitable, whereas under the SSP585, only 7,535.95 km^2 remains suitable.

Table 2. Area of potential range according to the tested scenarios.

Tested scenario	Low (0.2-0.39)	Moderate (0.4-0.59)	High (0.6-0.79)	Very high (≥0.8)	Total	% of current area
Current	15 988.96	10 109.43	9 838.12	4 973.09	**40 909.60**	100%
LGM	20 850.39	9 943.31	7 119.84	9 428.38	**47 341.92**	116%
SSP370	10 110.67	813.23	33.92	0.00	**10 957.82**	27%
SSP585	7 022.25	513.70	0.00	0.00	**7 535.95**	18%

Spatial patterns of the potential range

According to the MSPA results, under the current conditions, the potential range of *L. ledebourii* forms one core area that extends from the borders of Iran and Azerbaijan to Golestan (Table 3, Fig. 3A). During the LGM, there was likely a gap between the western and eastern parts of the potential range, although some connections may have existed in the lowlands (Fig. 2B). In the future, the potential range of *L. ledebourii* will be fragmented under both tested scenarios; the main core area will remain in Gilan and in the central regions of Mazandaran (Fig. 3 C, D). The connections between these core areas will be very restricted.

Discussion

This study demonstrated a high level of accuracy for the MaxEnt model applied to *L. ledebourii* occurrence data in the Hyrcanian Forest, with AUC values ranging from 0.988 to 0.997. In general, the AUC ranged from 0.5 to 1. Model predictions infrequently occur in the real world and are no better than random expectations when the AUC is less than 0.5; failure and poor performance are indicated by values between 0.5 and 0.7, while 0.7 and 0.9 indicate reasonable or moderate performance, respectively. A value greater than 0.9 indicates high simulation accuracy and performance of the model (Zhang et al., 2022).

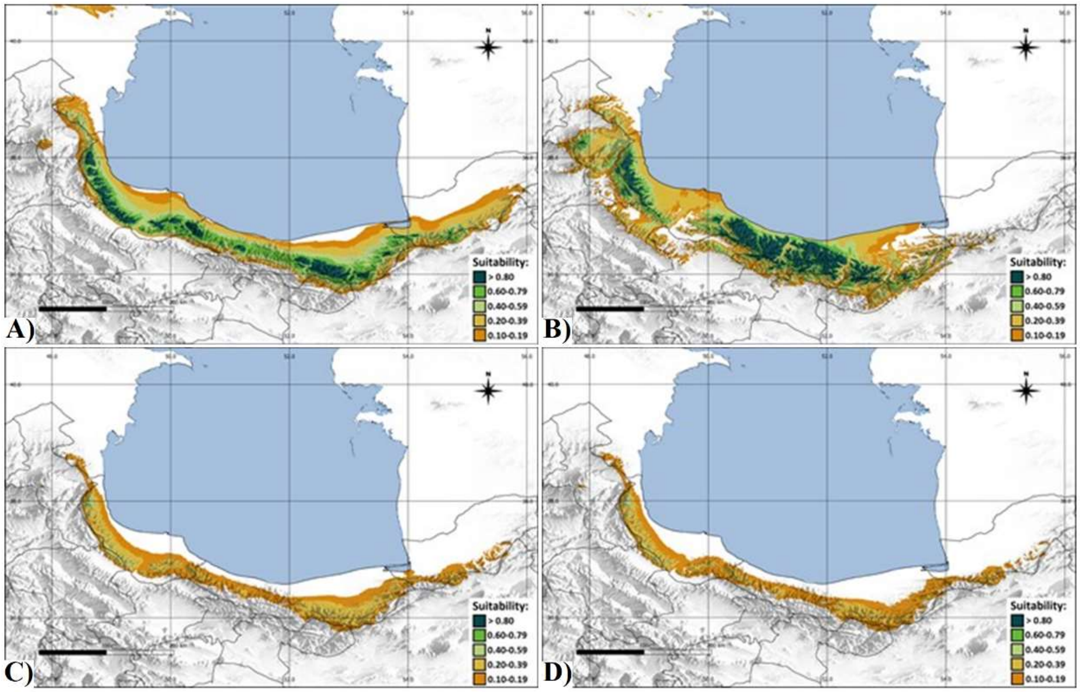

Fig. 2. The potential range of *L. ledebourii*: A) In current conditions; B) During LGM; C) In the consensus SSP370 scenario; D) In the consensus SSP585 scenario.

Table 3. Theoretical area of particular classes in MSPA analysis for the area with suitability above 0.2.

	Core	Loop	Bridge	Islet	Edge	Branch	Perforation	Total
Current	35 831.31	363.72	7.56	78.38	4 255.29	332.09	41.25	**40 909.60**
LGM	35 560.49	1 365.60	1 346.32	787.10	6 123.87	1 952.27	206.27	**47 341.92**
SSP370	6 962.92	275.94	251.91	297.90	2 435.38	689.15	44.62	**10 957.82**
SSP585	3 601.67	309.24	237.09	398.58	2 170.90	818.47	0.00	**7 535.95**

Our findings align with those of Mir et al. (2020) (AUC = 0.95) and Dhyani et al. (2021) (AUC = 0.980), who investigated the potential distribution of the endangered *Lilium polyphyllum* in the western Himalayas. However, it is important to note that a species' range is influenced not only by bioclimatic variables but also by additional factors, such as interspecies competition, and the estimation of the future range is always highly influenced by the model used. Thus, the calculated future change in the occupied area should be treated as a trend rather than as a precise estimation.

Lilium ledebourii is commonly distributed around the timberline of the Hyrcanian Forest. Ecological conditions within this zone (Kampfzone) are extreme, posing significant challenges to survival, growth, and competition (Mayor et al., 2017), and this altitudinal belt is highly sensitive to the impacts of global climate change. Numerous studies have documented climatic changes occurring at the timberline (Sakio and Masuzawa, 2020). In fact, climate change and its impact on environmental factors will lead to significant or minor changes in species geographical ranges, rapidly endangering biodiversity worldwide (Bellard et al., 2012). For instance, in Japan, climate change has been linked to increased vegetation cover and the upward shift of the alpine timberline (Sakio and Masuzawa, 2020).

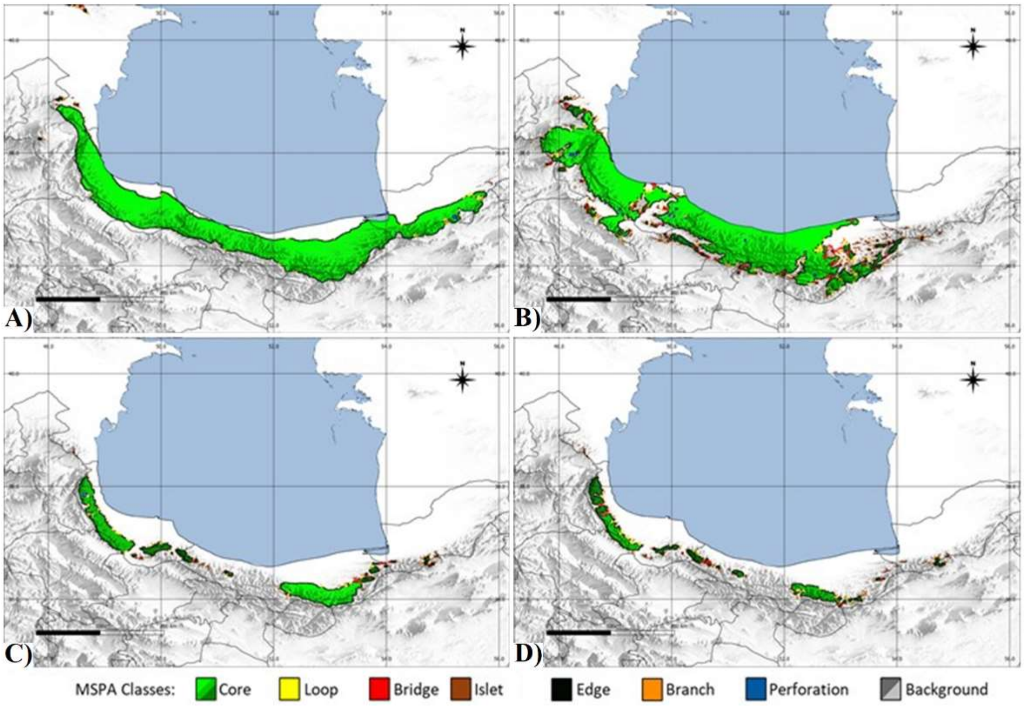

Fig. 3. The MSPA results: A) in current conditions; B) during LGM; C) in the consensus SSP370 scenario; D) in the consensus SSP585 scenario.

In this study, precipitation-related bioclimatic variables were identified as the primary predictors influencing habitat suitability, including precipitation in the warmest quarter, which accounted for more than 40% of the contribution; precipitation in the coldest quarter; and precipitation seasonality. The temperature during the growing season (Wang et al., 2016) and rainfall (Lamarche and Mooney, 2018) are two important factors that determine the characteristics of the alpine timberline and improve growing conditions. This effect has also been observed on the northeastern and northern slopes of the Himalayas.

Lilium ledebourii is commonly found in cold and temperate mountainous regions across Iran, particularly on the eastern slopes of the Alburz Mountains. This bulbous perennial herbaceous species thrives at elevations reaching up to 1,800 m above sea level. Its growth cycle begins the spring season, concomitantly with the sprouting and development stages. The flowers of this perennial species blossom during late spring and early summer. Prior investigations have demonstrated that the optimal temperature range for *Lilium* growth is approximately 18-22 °C (Yin et al., 2008). Elevated temperatures (>28 °C) have detrimental effects on *Lilium* growth, leading to the appearance of undesirable traits such as reduced flower bud count and length. Furthermore, cold stress inhibits the growth of lily bulbs; in non-hardy taxa, exposure to temperatures as low as -6 °C often leads to bulb mortality, while at -8 °C, nearly all bulbs die and fail to regenerate (Ding et al., 2021). Most lily bulbs develop dormancy to withstand unfavorable environmental conditions, meaning that seeds have immature embryos. *Lilium* seeds can germinate as soon as they experience enough rainfall and warm weather in the environment (Dhyani et al., 2021).

According to a previous study, L. ledebourii seeds begin germination during a warm period, with optimal temperatures between 17–20 °C, followed by a chilling requirement of eight to fourteen weeks (Dehkaei et al., 2005). In its natural habitat, the seed capsules of *L. ledebourii* mature in September; it is likely that some seeds begin germinating in late September or early October. After overwintering, the true leaf emerges in early spring of the following year (Dehkaei et al., 2005). This evidence confirms the prediction of the model used in this study regarding the critical role played by precipitation during the driest month. In this regard, a similar finding has been reported for *L. polyphyllum* in the Indian Western Himalayan region (Dhyani et al., 2021).

First, it should be noted that *L. ledebourii* in its native range (Hyrcanian Forest) seems to occupy a rather small climatic space and alpine timberline. To better understand how the occurrence of the species can change over time, its climatic niche should be assessed. In the present study, the potential species range during the LGM was approximately 16% greater than the current range. During the LGM, a probable gap existed between the western and eastern regions of *L. ledebourii*'s potential range in the Hyrcanian forest, while under current conditions, the potential species range forms a core area from the borders of Iran and Azerbaijan to Golestan, and the species spread into previously unsuitable areas from Mazandaran to Golestan. Under the future conditions of the two tested climate change scenarios (SSP370 and SSP585), the potential species range is likely to decrease dramatically, whereas suitability will decline significantly. Areas of very high suitability will disappear completely, and the potential range shifts to higher altitudes. Plant species cannot adapt quickly enough to the speed of observed climate change. This is a major cause of changes in their geographical ranges (Waldvogel et al., 2020), as well as the upward movement of tree lines into new habitats from lower to higher elevations and upslope (Anderson, 2016), which can lead to eventual extinction of species through changes in phenology, biological interactions, and nutrient regimes (Franklin et al., 2016).

Evidence is mounting that climate change is causing widespread shifts in species distribution worldwide, with the scale of these shifts now believed to be 2.5 times greater than previously reported (Taheri et al., 2021). Refugial areas provide the best opportunities for large-scale and long-term survival and persistence of species under climate change conditions (Wang et al., 2023). Several studies have identified declines in habitat suitability and shifts in the altitudinal distribution of endangered species as key impacts of climate change on a global scale, as well as in the Hyrcanian Forest region (Yousefzadeh et al., 2022). The climatic conditions of the Hyrcanian Forest exhibit a west-to-east gradient, marked by a decline in precipitation from 1,350 mm to 530 mm, increasing temperature (15 to 17.5 °C), and a lengthening dry season (from one to three months) across this region (Sagheb Talebi et al., 2014). The signs of climate change documented over the past 20 years include an increase in the mean temperature of 0.74 °C at numerous synoptic weather stations across northern Iran (Attarod et al., 2017).

Furthermore, projections indicate potential decreases of around 9.6% and 19.2% in precipitation during the driest month, along with increases of approximately 2.9°C and 4.3°C in mean annual temperature by 2050 and 2070, respectively (Alavi et al., 2019). *L. ledebourii* exhibits rapid growth and is resistant to conditions characterized by low light, cold temperatures, and extreme cold. One of the main eco-factors that affects *L. ledebourii* habitat suitability and distribution is elevation, which is related to its inverse relationship with temperature and the need for cold in this species for the vernalization process and proper flowering in the spring season (Saeedifard et al., 2008). According to previous studies, the distribution of *L. ledebourii* has been recorded at an altitude ranging from 1350 to 2250 m (Ghorbanalizadeh and Akhani, 2022). Deficiencies in precipitation, escalating temperatures, and heatwaves influence the susceptibility and hydrological mechanisms of the Hyrcanian Forest by increasing water consumption and desiccation in the forest, in addition to altering the composition of the species and the structure of the forest. Thus, the rise in mean temperature, as a predicted consequence of climate change, clearly promotes the tendency of *Lilium* to shift its ecological niche toward higher altitudes.

The root system of *Lilium* comprises two types of roots: basal roots and stem roots. Located beneath the soil surface, the stem roots play a crucial role in the growth and development of lily shoots (Song, 2017). *Lilium ledebourii* possesses contractile roots, which serve as the foundation for the stem and facilitate plant penetration into the soil. As a result, deep soil enhances the growth and productivity of this species (Amjad and Ahmad, 2015). Over time, many lily bulbs are gradually pulled deeper into the soil on an annual basis until they reach areas with relatively stable temperatures. The duration of this contracting process is determined by temperature fluctuations on the surface.

The negative impacts of climate change on erosion rates and the depletion of soil organic carbo; and changes in soil structure, nutrient availability, stability, and the capacity to retain water in the topsoil have already been substantiated. As a consequence, the phenomenon of soil erosion, caused by alterations in climate patterns, has the potential to induce a deterioration in the habitat suitability for the successful establishment of *Lilium* within the soil. As a result, this will lead to a decrease in the availability of suitable habitats for this species in the future.

According to biogeographic analyses, *Lilium* most likely originated in East Asia and subsequently dispersed to North America, Europe, West–Central Asia, and North Asia (Shokrollahi et al., 2022). Given that *L. ledebourii* occurs as a relict species, dispersed in small populations on cliffs above the tree line, it suggests that the current range of this species likely served as a refuge for the remnants of large preglacial populations (Shokrollahi et al., 2022). With an extent of occurrence (EOO) of 10,238 km² and an area of occupancy (AOO) of 4,900 km², the conservation status of *L. ledebourii* is classified as endangered (EN) according to IUCN categories and criteria. This species can be found in subalpine grasslands and forest margins and extends to Ardabil, Gilan, Mazandaran, and Talish in northern Iran (IUCN, 2019; Ghorbanalizadeh and Akhani, 2022). The vulnerable status of *L. ledebourii*, marked by its susceptibility to extinction due to factors such as indiscriminate grazing and inherently limited seed reproductive capacity, poses a significant obstacle in the production of high-quality reproductive material. Moreover, the risk of extinction for this rare and endangered species has grown due to its restricted geographical distribution, small population sizes, and increased susceptibility to changes in environmental conditions.

The findings of this study offer valuable insights that can help advance guidelines for the conservation of *L. ledebourii.* The model predictions in the present study indicated potential suitable habitats for the preservation of *L. ledebourii* both within and outside its natural range. Additionally, these predictions have identified regions that could serve as refuges from climate change, remaining unaffected by the redistribution of *L. ledebourii*, despite the occurrence of climatic alterations. Furthermore, the prediction of the distribution range for this lily species has highlighted the necessity of establishing protected areas and enhancing the current reserves in regions that are at high risk due to changes in climate.

Special attention to *L. ledebourii* is emphasized from several aspects:

1- Small size and isolation of populations: Because the habitats of *L. ledebourii* are very small, scattered, and generally in the steep areas of the Hyrcanian Forest, many of which are also affected by livestock grazing, they are very vulnerable and threatened with destruction. Additionally, it seems that the gene flow of individuals between different habitats has almost been cut off, and the isolation of populations started a long time ago in the Hyrcanian habitat.

2- Placement of the habitat on the upper border of the timberline: Given that most of the habitats of *L. ledebourii* are situated above the tree line, climate change, particularly global warming, could have significant implications for this species, this species has little maneuverability to move to another habitat. Thus, from this standpoint, due to the loss of habitat suitability, it is under serious threat.

3- Ex situ conservation: An in situ conservation strategy is always preferable for endangered species. However, for the several reasons mentioned above, ensuring the long-term survival of *L. ledebourii* is recommended as soon as possible, and attention should be given to the ex situ conservation of this species, especially its seeds, from all identified populations.

Acknowledgments

We would like to thank the research team at the Educational and Research Forest of Tarbiat Modares University (Iran) for their support and assistance in preparing the information.

Funding

This research was partially funded by the Iran National Science Foundation (INSF), grant number 4004488.

Conflict of interests

The authors have no conflicts of interest to declare.

Data availability

Data will be made available upon request.

Contributions

H. Y conceived and designed this study. M. B. and M. P contributed in sampling and Lab work. H. Y., L. W. and N. A. wrote the original draft. G. K. and L. W. edited the manuscript. All authors have read and agreed to the published version of the manuscript.

References

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. *Regional Environmental Change*, 19, 1495-1506.

Amjad, A., & Ahmad, I. (2015). Optimizing plant density, planting depth and postharvest preservatives for *Lilium longifolium*. *Journal of Ornamental Plants*, 2(1), 13-20.

Anderson, J. T. (2016). Plant fitness in a rapidly changing world. *New phytologist*, 210(1), 81-87.

Attarod, P., Kheirkhah, F., Khalighi Sigaroodi, S., Sadeghi, M., & Bayramzadeh, V. (2017). Trend analysis of meteorological parameters and reference evapotranspiration in the Caspian region. *Iranian journal of Forest*, 9(2), 171-185.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology letters*, 15(4), 365-377.

Birhane, E., Gidey, T., Abrha, H., Brhan, A., Zenebe, A., Gebresamuel, G., & Noulèkoun, F. (2023). Impact of land-use and climate change on the population structure and distribution range of the rare and endangered *Dracaena ombet* and *Dobera glabra* in northern Ethiopia. *Journal for Nature Conservation*, *76*, 126506.

Buse, J., Boch, S., Hilgers, J., & Griebeler, E. M. (2015). Conservation of threatened habitat types under future climate change–Lessons from plant-distribution models and current extinction trends in southern Germany. *Journal for Nature Conservation*, *27*, 18-25.

da Silva, J. M. C., Rapini, A., Barbosa, L. C. F., & Torres, R. R. (2019). Extinction risk of narrowly distributed species of seed plants in Brazil due to habitat loss and climate change. PeerJ, 7, e7333

Dehkaei, M. P., Khalighi, A., & Moosavi, R. N. A. (2005). Effect of alternating and constant temperature on seed germination of Chelcheragh liliy (*Lilium ledebourii*) in Iran. *Acta horticulturae*, (6731).

Dhyani, A., Kadaverugu, R., Nautiyal, B. P., & Nautiyal, M. C. (2021). Predicting the potential distribution of a critically endangered medicinal plant *Lilium polyphyllum* in Indian Western Himalayan Region. *Regional Environmental Change*, 21, 1-11.

Ding, L., Wu, Z., Teng, R., Xu, S., Cao, X., Yuan, G., ... & Teng, N. (2021). LlWRKY39 is involved in thermotolerance by activating LlMBF1c and interacting with LlCaM3 in lily (*Lilium longiflorum*). *Horticulture Research*, 8.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, 113(14), 3725-3734.

Garza, G., Rivera, A., Venegas Barrera, C. S., Martinez-Ávalos, J. G., Dale, J., & Feria Arroyo, T. P. (2020). Potential effects of climate change on the geographic distribution of the endangered plant species *Manihot walkerae*. *Forests*, 11(6), 689.

Ghorbanalizadeh, A., & Akhani, H. (2022). Plant diversity of Hyrcanian relict forests: An annotated checklist, chorology and threat categories of endemic and near endemic vascular plant species. *Plant Diversity*, 44(1), 39-69.

Hijmans, R. J., & Van Etten, J. (2020). Raster: geographic data analysis and modeling. R package.

IUCN, P.S. (2019). Guidelines for using the IUCN red list categories and criteria, version 14.

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. *Ecological Informatics*, 60, 101150.

Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H., & Zimmermann, N. E. (2021). CHELSA-TraCE21k v1. 0. Downscaled transient temperature and precipitation data since the last glacial maximum. *Climate of the past discussions*, 2021, 1-27.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E, Linder, H.P., Kessler, M. (2018). Data from: Climatologies at high resolution for the earth's land surface areas. Envi Dat**.**

Kumar, A., Nagar, S., & Anand, S. (2021). Climate change and existential threats. In *Global climate change*, 1, 1-31.

LaMarche Jr, V. C., & Mooney, H. A. (1972). Recent climatic change and development of the bristlecone pine (*P. longaeva* Bailey) krummholz zone, Mt. Washington, Nevada. *Arctic and Alpine Research*, 4(1), 61-72.

Liu, D., Li, Y., Hong, L., Guo, H., Xie, Y., Zhang, Z., Lei, X., & Tang, S. (2018). The suitability of potential geographic distribution of natural forest types in Jilin Province based on maximum entropy models. *Scientia Silvae Sinicae*, 54(7), 1-15.

Mayor, J. R., Sanders, N. J., Classen, A. T., Bardgett, R. D., Clement, J. C., Fajardo, A., Lavorel, S., Sundqvist, M.K., Bahn, M., Chisholm, C., Cieraad, E., & Wardle, D. A. (2017). Elevation alters ecosystem properties across temperate treelines globally. *Nature*, 542(7639), 91-95.

Mir, A. H., Tyub, S., & Kamili, A. N. (2020). Ecology, distribution mapping and conservation implications of four critically endangered endemic plants of Kashmir Himalaya. *Saudi Journal of Biological Sciences*, 27(9), 2380-2389.

Phillips, S.J., Dudík M., Schapire, R.E. (2020). [Internet] Maxent software for modelling species niches and distributions (Version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2024-1-8.

Qazi, A. W., Saqib, Z., & Zaman-ul-Haq, M. (2022). Trends in species distribution modelling in context of rare and endemic plants: a systematic review. *Ecological Processes*, 11(1), 1-11.

QGIS Development Team. (2023). QGIS Geographic Information System. *Open Source Geospatial Foundation Project* (OSGeo).

Saeedifard, M., Hosseini, M., Moradi, R., & Padasht Dehkaei, M. N. (2008). Ecological Evaluation of *Lilium ledebourii* site in Gilan in order to determine ecological needs of this species. *Environmental Sciences*, *5*(4).

Sagheb-Talebi, K.S., Sajedi, T., & Pourhashemi, M. (2016). Forests of Iran: A Treasure from the Past, a Hope for the Future; Softcover Reprint of the Original 1st ed. 2014 Edition.

Sagheb-Talebi, K.S., Sajedi, T., & Pourhashemi, M. (2014). Forests of Iran. A treasure from the past, a hope for the future. 10.

Sakio, H., & Masuzawa, T. (2020). Advancing timberline on Mt. Fuji between 1978 and 2018. *Plants*, *9*(11), 1537.

Salehi, M., Hatamzadeh, A., Jafarian, V., & Zarre, S. (2019). New molecular record and some biochemical features of the rare plant species of Iranian lily (*Lilium ledebourii* Boiss.). *Horticulture, Environment, and Biotechnology*, 60, 585-593.

Shokrollahi, S., Yousefzadeh, H., Parisod, C., Heshmati, G., Bina, H., Ali, S., Amirchakhmaghi, N. and Song, Y. (2022). Phylogenetics and Biogeography of *Lilium ledebourii* from the Hyrcanian Forest. *Diversity*, 14(2), 137.

Song, J. (2017). The relationship of root system with the growth and development of bulbs and shoots in lilies. *HortScience*, 52(2), 245-250.

Taheri, S., Naimi, B., Rahbek, C., & Araújo, M. B. (2021). Improvements in reports of species redistribution under climate change are required. *Science Advances*, 7(15), eabe1110.

van Proosdij, A. S., Sosef, M. S., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, 39(6), 542-552

Vogt, P., & Riitters, K. (2017). GuidosToolbox: universal digital image object analysis. *European Journal of Remote Sensing*, 50(1), 352-361.

Waldvogel, A.M., Feldmeyer, B., Rolshausen, G., Exposito-Alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., & Savolainen, O. (2020). Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution Letters*, 4(1), 4-18.

Wang, L., Liu, J., Liu, J., Wei, H., Fang, Y., Wang, D., Chen, R., & Gu, W. (2023). Revealing the long-term trend of the global-scale *Ginkgo biloba* distribution and the impact of future climate change based on the ensemble modeling. *Biodiversity and Conservation*, 32(6), 2077-2100.

Wang, Y., Pederson, N., Ellison, A. M., Buckley, H. L., Case, B. S., Liang, E., & Julio Camarero, J. (2016). Increased stem density and competition may diminish the positive effects of warming at alpine treeline. *Ecology*, 97(7), 1668-1679.

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(20), 2788-2794.

Yousefzadeh, H., Amirchakhmaghi, N., Naseri, B., Shafizadeh, F., Kozlowski, G., & Walas, Ł. (2022). The impact of climate change on the future geographical distribution range of the endemic relict tree *Gleditsia caspica* (Fabaceae) in Hyrcanian forests. *Ecological Informatics*, 71, 101773.

Yin, H., Chen, Q., & Yi, M. (2008). Effects of short-term heat stress on oxidative damage and responses of antioxidant system in *Lilium longiflorum*. *Plant Growth Regulation*, 54, 45-54.

Zangiabadi, S., Zaremaivan, H., Brotons, L., Mostafavi, H., & Ranjbar, H. (2021). Using climatic variables alone overestimate climate change impacts on predicting distribution of an endemic species. *Plos one*, 16(9), e0256918.

Zhang, H., Yang, S., Wei, X., Wang, L., Sun, X., Hou, Z., Zhong, Q., & Liu, W. (2023). Forecasting the favorable growth conditions and suitable regions for chicory (*Cichorium intybus* L.) on the Qinghai plateau under current climatic conditions. *Ecological Informatics*,78, 102343.

Zhang, L., Zhu, L., Li, Y., Zhu, W., & Chen, Y. (2022). Maxent modelling predicts a shift in suitable habitats of a subtropical evergreen tree (*Cyclobalanopsis glauca* (Thunberg) Oersted) under climate change scenarios in China. *Forests*, 13(1), 126.