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Climate change drives the retreat of *Aethionema spinosum* (Brassicaceae) to high-elevation refugia

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Global climate change poses an increasing threat to biodiversity, prompting scientists to utilize ecological and evolutionary knowledge to address this challenge. Understanding these fields and their interconnections is crucial for improving conservation strategies. Accordingly, we conducted a study to assess the potential repercussions of climate change on *Aethionema spinosum*, a plant species endemic to the mountains of the Irano-Turanian floristic region. Employing ecological niche modeling (ENM), we projected the potential geographic distribution of *A. spinosum* under current conditions and two future climate scenarios (SSP2–4.5 and SSP5–8.5) for the period 2041–2060. Key climatic factors, including annual mean temperature (bio1), isothermality (bio3), and precipitation of the wettest quarter (bio16), exhibited the highest percentage contribution rates influencing the distribution of *A. spinosum*. The current model predicted the distribution of *A. spinosum* in montane areas, while under future-climatic conditions, a reduction and shift toward higher elevations were anticipated. Notably, substantial losses were observed in areas proximate to existing habitats. These findings are useful for the management and conservation of *A. spinosum* and provide insights into the potential future impacts of climate change on its distribution in the Irano-Turanian region.

Keywords Conservation, Climate change, Ecological niche modeling, Endemic species, Irano-Turanian

Climate change has profound affects on plants, affecting their growth, production, survival, development, and species distribution area[1–4]. A growing area of research focuses on how species respond to these changes, particularly in terms of shifts in their geographic ranges[5–7]. To survive, species employ three primary strategies: shifting their range to match their ecological niche, adapting phenotypically to new conditions, or evolving genetically to suit local environments[8]. Understanding the strategies chosen by a given species requires detailed studies using ecological data and molecular tools at various scales[8]. In this context, Brassicaceae family has played a pivotal role in enhancing our understanding of plant genomes, largely due to the presence of the model species *Arabidopsis thaliana* (L.) Heynh[9]. Recently, attention has also turned to *Aethionema W.T.Aiton*, which represents the sister group to the crown clade of the Brassicaceae[1011]. Studies aim to enhance our understanding of genome evolution within the Brassicaceae family[101112]However, relatively few studies have explored the interplay between climate change and genomic response, and methodologies are still being developed to address these gaps[8]., which represents the sister group to the crown clade of the Brassicaceae[10,11]. Studies aim to enhance our understanding of genome evolution within the Brassicaceae family[10–12] However, relatively few studies have explored the interplay between climate change and genomic response, and methodologies are still being developed to address these gaps[8].

Expanding the availability of both ecological and genomic data on *Aethionema*, the earliest diverging lineage in the Brassicaceae family, could provide valuable insights into the relationships between ecology and species' response to global changes. Unlike the members of the crown group of the Brassicaceae, *Aethionema* has evolved at a slower rate and has not expanded its distribution range as much[13]. While the rate of climate change exceeds

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that of almost any other species' evolution, *Aethionema* will lag even further behind due to its slow evolutionary rate.

Although many *Aethionema* species are not currently endangered in terms of population numbers within their distribution areas[14], they may be especially vulnerable to climate change due to their adaptation to narrow geographical zones. For instance, of the 18 *Aethionema* species found in Iran, eight are endemic[14]. Moreover, many *Aethionema* species are native to mountainous regions[14,15]. These areas are of heightened concern due to their limited geographic ranges and relatively narrow environmental tolerances. With global warming exerting its influence, montane regions are undergoing rapid transformations in the 21st century. Consequently, comprehending the effects of climate change on individual endemic species in these areas is essential for holistic biodiversity conservation planning[16,17].

In recent years, ecological niche models (ENMs) have evolved into essential tools for assessing the potential impacts of climate change on plant distributions[7,18,19]. These models provide a rough estimate of a species' current or future niche dimensions related to climate traits. They overlook within-species variation, local adaptation, and the genetic potential for rapid evolutionary change. Despite these limitations, they are highly useful and widely applied for diverse purposes, such as predicting species distributions, exploring diversity patterns, understanding historical biogeography, conducting conservation assessments, and assessing the impacts of global change[20–23]. Among various ENM algorithms, MaxEnt stands out for its robust performance, particularly when dealing with limited occurrence data[19,24,25].

Aethionema spinosum (Boiss.) Prantl, as the earliest diverging lineage within the Brassicaceae family, represents a key taxon for understanding evolutionary patterns and responses to environmental change in this economically and ecologically important plant group. Unlike the more derived members of the Brassicaceae crown group, such as *Arabidopsis Heyhn.*, *Brassica* L., and *Thellungiella* O.E.Schulz, which have undergone extensive diversification and adaptation to a wide range of habitats, *A. spinosum* has retained several ancestral traits and exhibits a relatively slow rate of molecular evolution[11,13]. This species is particularly vulnerable to climate change due to its restricted geographic distribution and narrow ecological niche. It is endemic to mountainous regions of Iran and southern Turkmenistan, where it occupies an altitudinal range of 1000–2500 m and thrives in harsh, low-moisture environments such as scree slopes and rocky outcrops[14,15]. These montane ecosystems are experiencing rapid transformation due to global warming, making *A. spinosum* an ideal model for studying the impacts of climate change on endemic flora with limited dispersal abilities. Moreover, *A. spinosum* forms small, fragmented populations that are unevenly distributed and highly susceptible to habitat loss and extreme climatic conditions[14]. Despite not being currently classified as endangered based on population size alone, its geographic isolation, specialized habitat requirements, and limited genetic diversity suggest a high degree of vulnerability under future climate scenarios. Additionally, compared to other *Aethionema* species, *A. spinosum* has a relatively clear taxonomic delimitation (Moazzeni, unpublished data) and reliable occurrence records from field collections and herbarium specimens—factors that enhance its suitability for modeling studies. Its phylogenetic position, conservation status, and ecological specificity together provide a solid rationale for selecting *A. spinosum* as a representative species for assessing the potential impacts of climate change on Irano-Turanian endemics.

Aethionema spinosum is a perennial subshrub with hard spiny branches, white to pink flowers, and regularly broadly winged and indehiscent fruit (Fig. 1). It is an endemic species to the Irano-Turanian floristic region[14,26]. It mainly inhabits the mountainous areas throughout Iran, and a small area of southern Turkmenistan with a restricted altitudinal range of 1000–2500 m. *Aethionema spinosum* grows in stressful low-moisture habitats on screes, rocky slopes, and sub-alpine limestones. It forms small, isolated, and dispersed populations that are unevenly distributed[14]. However, their likelihood of extinction is increasing due to extreme environmental conditions, small geographic ranges, and badly fragmented habitats. Therefore, understanding the ecology and factors that limit the distribution of *A. spinosum* and predicting how climate change will affect its geographic range is of utmost importance for its future conservation.

This study aims to investigate how climatic variables influence the current and potential future distribution of *A. spinosum*. Specifically, the objectives of the study are to: (1) model the current suitable habitat of *A. spinosum*. (2) identify the key climatic variables that determine its distribution. (3) project how its habitat might change under future climate change scenarios.

Materials and methods

Study area

This study focused on the Irano-Turanian (IT) region in southwestern Asia, including sub-regions IT1, IT2, IT3, IT4[27], among which IT2, housing the Iranian Plateau, is particularly remarkable[28]. This distinction arises from its unique climate and the remarkable diversity of physiognomic types, encompassing forest, scrub, alpine, sub-alpine grassland, steppe, montane steppe, desert steppe, and diverse halophytic communities[27,29–32]. Moreover, the Iranian plateau serves as a significant hotspot for evolutionary and biological diversity within the Old World, facilitates the migration of numerous plant species, and bridges the gap between the eastern and western floras of Eurasia (Fig. 2)[33]. The Alborz and Zagros Mountains are the two main mountain ranges in the Iranian plateau, which may have had a profound impact on the history of the IT floristic region[33]. Climatically, IT2 is broadly characterized by an arid to semi-arid, highly continental regime with low annual precipitation. However, its complex topography generates a wide variety of habitats. Isolated mountain ranges, often above 1,500 m a.s.l., create striking environmental contrasts with surrounding basins. These montane zones are distinguished by lower temperatures, frequent seasonal snow cover, intense solar radiation, and predominantly shallow, stony soils or rocky substrates that are poorly developed and low in organic matter. Such harsh edaphic and climatic conditions favor specialized plant assemblages, including lithophytes and chasmophytes, which are adapted to drought, cold stress, and physical disturbance[34,35].

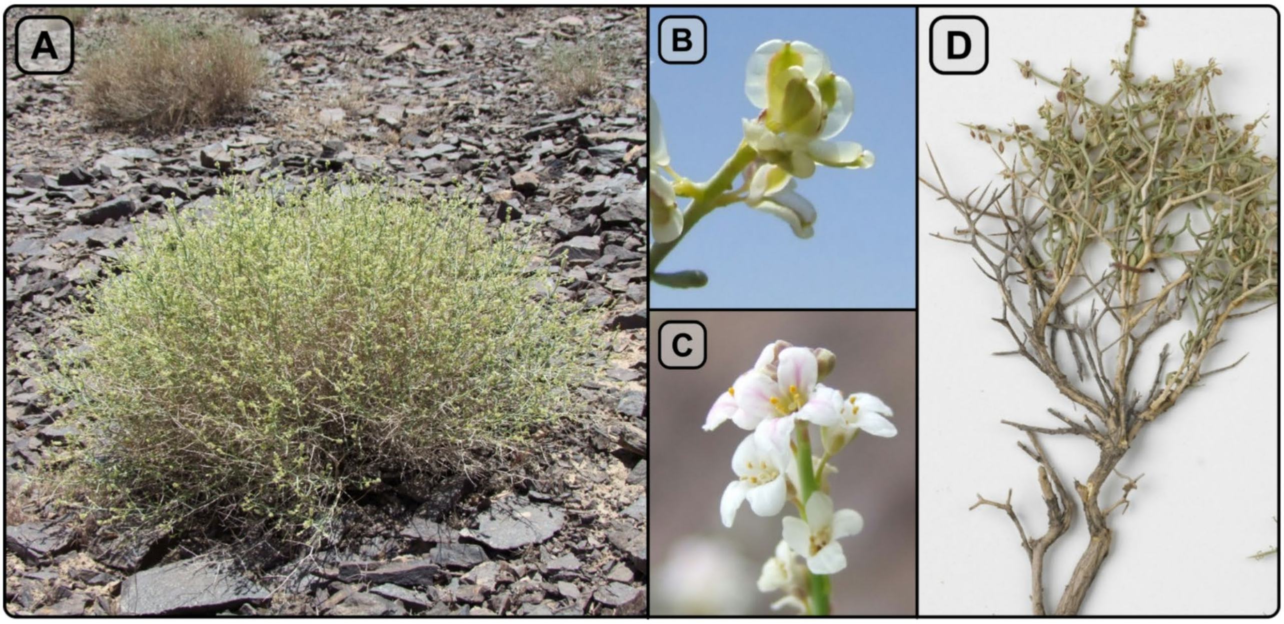

Fig. 1. *Aethionema spinosum*: (**A**) plants in their native environment; (**B**) a detailed view of the fruits; (**C**) a close-up of the flowers; (**D**) spines arranged in a zigzag pattern on the stems from the growth of the previous year (Photos **A–C** from Hamid Moazzeni, photo **D** from: https://data.rbge.org.uk/herb/E00061157).

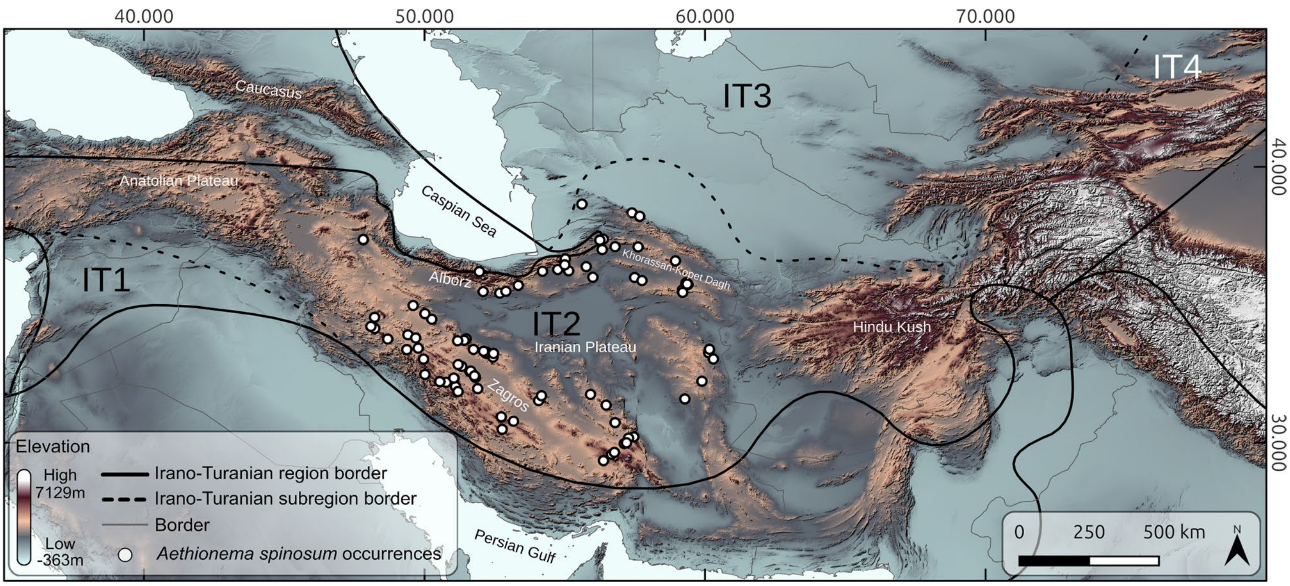

Fig. 2. Study area and distribution of *Aethionema spinosum* in the Irano-Turanian region. Phytogeographical map of the Irano-Turanian (IT) region, with numbers 1 to 4 indicating the four subregions proposed by White and Léonard[28]. The map illustration was generated in QGIS (version 3.28, Long Term Release, https://qgis.org/).

Phytogeographically, the high mountains of IT2 act as critical zones of biotic interchange as well as ecological "islands," where endemic Irano-Turanian elements coexist with taxa from adjacent floristic regions. Steep ecological gradients promote high species turnover and localized speciation, reinforcing the region's exceptional rates of endemism[30,34]. Vegetation in these high-altitude habitats is typically sparse and dominated by cushion-forming perennials and low shrubs, morphologically adapted to conserve water and withstand strong winds, frost, and temperature extremes. These specialized habitats represent the ecological setting for narrow endemics such as *Aethionema spinosum*, underlining the unique biogeographic and evolutionary importance of the IT2 subregion[36,37].

Data collection

The occurrence data were primarily gathered by Moazzeni et al., (unpublished data). Additionally, we utilized other sources such as the Global Biodiversity Information Facility (GBIF)[38] and online herbaria to supplement the dataset, as well as Iranian herbaria, including FUMH, TARI, and TUH. To reduce geolocation uncertainty, we cross-referenced all occurrence points with online maps. We excluded occurrences out of the known range for *A. spinosum* and those with vague descriptions. Records with imprecise locality descriptions, those lacking geographic coordinates, or those falling outside the known distribution range of *A. spinosum* were excluded. In total, we compiled 90 records.

Sample selection bias poses a significant challenge to species distribution models based on presence-only data such as occurrence records found on the web and in herbaria[39]. The presence of different biases between occurrence and generated background data can lead to inaccurate models[39]. To address this concern, we utilized the "raster" package[40] in R version 4.1.2 to eliminate samples that occupied the same cell in the environmental factor grid.

Environmental data

In order to provide an overview of both current and future climate conditions, two climate datasets were utilized. The first data set, obtained from WorldClim version 2.1 www.worldclim.org[41], represented the current environmental conditions. The second dataset, also downloaded from WorldClim, was used to represent the future environmental conditions under various climate change scenarios. Both data sets comprised 19 bioclimatic variables with a resolution of 30 arc-seconds (1 km). We selected the SSP2-4.5 (moderate stabilization pathway) and SSP5-8.5 (high-emission trajectory) scenarios for the 2041–2060 period. These Shared Socioeconomic Pathways were chosen to capture a broad yet distinct range of plausible future climate conditions, representing both intermediate mitigation efforts and a fossil fuel-intensive future. Specifically, SSP2-4.5 represents a "middle-of-the-road" pathway with moderate socio-economic development and intermediate emissions, while SSP5-8.5 describes a high-emission scenario driven by rapid economic growth and intensive fossil fuel use[42,43]. Using these two contrasting scenarios allows us to evaluate species responses across a wide spectrum of potential future climates, from moderate to extreme warming. We opted for this mid-century projection period to balance the immediate relevance for conservation planning with enough temporal scope to reveal ecologically significant distributional changes. This timeframe (2041–2060) also reduces the higher uncertainties inherent in long-term forecasts, which are highly sensitive to socio-economic assumptions, emission pathways, and technological or policy shifts. Moreover, it aligns with regional and global biodiversity conservation planning horizons, making the results directly applicable to management and policy decisions[44]. This timeframe also helps minimize the increasing uncertainty associated with longer-term forecasts (e.g., extending to 2100), where projections become highly sensitive to assumptions about future greenhouse gas emissions and socio-economic developments[45]. While this approach allows for a focused comparison of species responses under clear climatic futures, we recognize that incorporating additional scenarios or extended timeframes could offer a more comprehensive understanding of long-term habitat shifts and conservation risks.

To forecast the future potential distribution of *A. spinosum*, five general circulation models (GCMs) were chosen: BCC-CSM2-MR, CCESS-CM2, CMCC-ESM2, MRI-ESM2.0, and MIROC6, across both climate scenarios (Supplementary Table S1).

The selection of variables significantly influences model accuracy, and the presence of multicollinearity among bioclimatic variables can lead to artifacts in the models[46]. To mitigate the impact of multicollinearity and dimensionality on model accuracy, we processed the bioclimatic variables in two steps: (1) Four layers (bio 8, bio 9, bio 18, and bio 19) were omitted from the analysis because of their known spatial distortions[47]. (2) To determine the importance of environmental variables for *A. spinosum*, we conducted PCA analysis with the remaining 15 variables, identifying the significant variables in two axes (Supplementary Fig. S1). Then, using the "USDM" package[48] in R, we performed a step-wise variance inflation factor (VIF) procedure with a threshold of less than 10 (Supplementary Table S1). Based on the PCA results, we selected the most important variables while minimizing multicollinearity between them.

Ecological niche models

We employed the Maximum Entropy algorithm (MaxEnt)[49] to conduct the Ecological Niche Modeling (ENM), using the "ENMeval" package (version 2.0)[50] within R, and utilized Java Maxent (version 3.4.4)[51]. The MaxEnt approach demonstrates a strong capacity to handle models with limited sample sizes and has exhibited robust performance in comparison to alternative algorithms[52,53]. This has led to its increased adoption for modeling species distributions. However, recent research has highlighted that relying solely on default settings might not always be optimal, particularly when working with small sample sizes[54,55].

Within our geographical scope, we drew pseudo-absences tailored to the *A. spinosum*, employing the approach outlined by VanDerWal, et al.[56]. Evaluation models were executed at intervals of 100 km (ranging from 100 to 500 km from the occurrence points) using the "sf" package[57] in R with Maxent.jar. This was done to determine the optimal maximum distance for selecting pseudo-absences, considering both model assessment metrics and the number of influential variables (the presence of 1–2 dominant variables indicated an excessive distance). Consequently, our selection of pseudo-absences was confined to a maximum distance of 500 km from the recorded occurrences of *A. spinosum* as M area (Supplementary Fig. S2).

In pursuit of the optimal model, we assessed a comprehensive set of possibilities. This involved evaluating a total of 651 models, which comprised a combination of 21 regularization parameter values ranging from 0.1 to 1.0 in increments of 0.1, values from 1 to 5 in increments of 0.5, and values from 6 to 9 in increments of 1. Additionally, 31 distinct combinations of model response types, encompassing linear, quadratic, product, threshold, and hinge responses, were examined using ENMeval. The model exhibiting the lowest Akaike information criterion (AICc) value was selected as the best model.

We generated final models using determined parameters as the best model in ENMeval with 10 bootstrap replicates. This model was extended across the broader region under current and future environmental conditions. To gauge suitability for current conditions within the region, we relied on the median values derived from the replicate analyses. Furthermore, for future conditions, we computed the median values of all 5 GCMs for each RCP.

In order to facilitate map comparison and interpretation, we converted them into binary representations, where scores are categorized as either suitable or unsuitable. This transformation was achieved by applying a calculated minimum training presence threshold to each map. The visualization and computation of expected changes in distributional patterns under future conditions were conducted using QGIS version 3.22.

To assess our model's performance, we utilized several metrics: AUC_{TEST} (calculated on evaluation data) to measure discriminatory ability, OR10 (omission rate with a threshold causing 10% of calibration records to be omitted), and $AUC_{DIFF,}$ which is the difference between AUC_{TRAIN} (calculated on training data) and AUC_{TEST}, offering a threshold-independent overfitting evaluation. These metrics were also applied to 100 null models created with random data, allowing comparisons with our model[58,59]. High AUC_{TEST} and AUC_{TRAIN} values and positive effect sizes indicate high performance, while low values and negative effect sizes signify strong AUC_{DIFF} and OR10 performance.

Results

Occurrence data and variables selection

Initially, we compiled 102 occurrence records for A. spinosum. We then excluded 22 records due to insufficient precision and other data-quality considerations, such as a 1 km filtering distance. Ultimately, 90 unique occurrences were retained for ecological niche model calibration and evaluation (Fig. 2).

Following step-wise variance inflation factor (VIF) and PCA analysis results (Fig. S1, Supplementary Table S2), eight predictor variables were eliminated from the analysis. Six variables, including annual mean temperature (bio1), isothermality (bio3), temperature annual range (bio7), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), and precipitation of the driest quarter (bio17), were selected for developing ecological niche models.

Variables significance and model performance

The importance of explanatory variables in the prediction models was assessed using the jackknife test (Supplementary Fig. S3). The explanatory variables that contributed most to the regularization training gains were annual mean temperature (bio1), precipitation seasonality (bio15), temperature annual range (bio7), isothermality (bio3), wettest quarter precipitation (bio16), and driest quarter precipitation (bio17), in that order. The percentage contribution rates of environmental variables to MaxEnt modeling are detailed in Supplementary Table S3. The three most important variables were bio1 (45.6%), bio3 (19.3%), and bio16 (11%), which together accounted for 75.9% (Supplementary Table S3).

Based on the response curves, the habitat suitability of *Aethionema spinosum* showed clear relationships with the selected bioclimatic variables. Response curves indicated that the distribution of *A.* s*pinosum* is strongly associated with narrow ranges of three climatic predictors. Suitability peaked for annual mean temperature (bio1) at around 15–17 °C, with sharp declines at both lower and higher values. For isothermality (bio3), habitat suitability reached its maximum around 32–35%, while falling rapidly outside this interval. Similarly, precipitation of the wettest quarter (bio16) showed the highest suitability at approximately 200–250 mm, beyond which suitability decreased abruptly. These patterns highlight the relatively narrow ecological tolerances of the species to both temperature and precipitation gradient.

Throughout the model selection process, 651 models were generated. However, only one model, characterized by a blend of Linear and Quadratic features, coupled with a regularization multiplier (RM) set at 0.2, emerged as the most fitting model based on AICc. This selected model exhibited exceptional performance, boasting an average AUC_{TEST} value of 0.95 under the current climate conditions, indicating a robust fit, optimal performance, and high reliability. Similarly high average AUC_{TEST} values were consistent across all investigated future climate change scenarios. The average $AUCT_{RAIN}$, AUC_{DIFF}, and OR10 values were 0.94, 0.01, and 0.14, respectively. Comparative analysis with indices derived from null models (AUC_{TRAIN} $P<0.001$, AUC_{TEST} $P<0.001$, and AUC_{DIFF} $P<0.001$) provided strong evidence that the optimal model outperformed the null models, except for the average OR10 (OR10 $p \simeq 0.67$) (Supplementary Fig. S4).

Current and future potential distribution

The best model's median highlighted varying degrees of suitability for *A. spinosum* in montane regions, covering parts of Iran, Afghanistan, Pakistan, Syria, Central Asia, and Turkey. High-suitability areas were expected in Zagros, Alborz, Khorassan-Kopet Dagh mountains in Iran, the northern highlands of Afghanistan and Pakistan, and the eastern mountains of Uzbekistan, along with a small part of montane areas in Syria (Fig. 3A). According to the binary map, only 11.57% of the entire Irano-Turanian region is considered suitable habitat, while the remaining 88.43% is categorized as unsuitable (Fig. 3B).

The potential distribution of *A. spinosum* under the scenarios SSP2-4.5 and SSP5-8.5 is shown in Fig. 4. In these scenarios, the species' habitats were relatively fragmented, with areas of high suitability mainly concentrated in the mountainous regions of Iran, Afghanistan, and Central Asia. Notably, these areas of high suitability expanded and shifted to higher elevations in Iran and Afghanistan (see Fig. 4A and B). Compared to the suitable habitats under current conditions, the projected future ranges show a slight decline across both

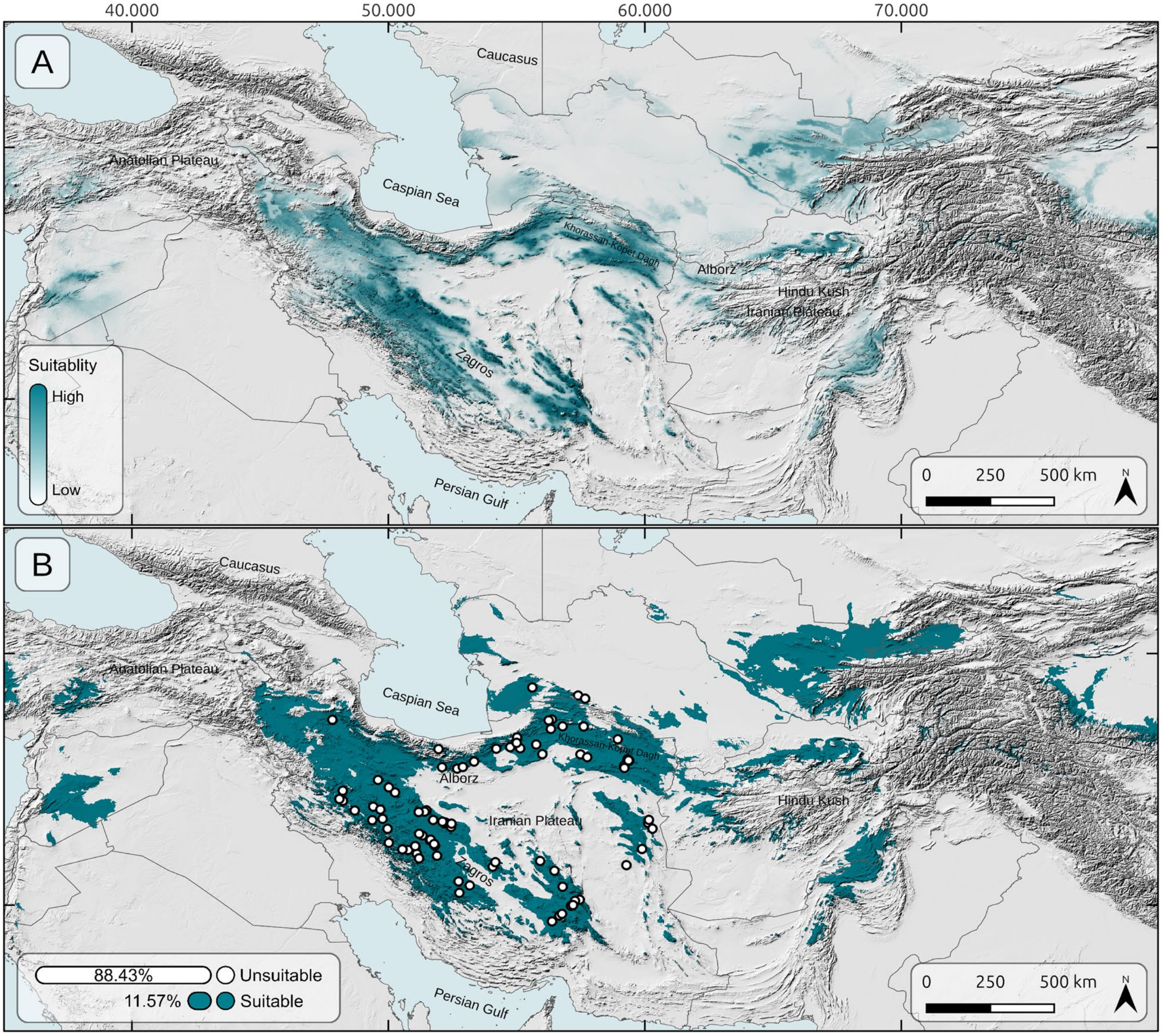

Fig. 3. Current suitable areas for the distribution of *Aethionema spinosum* based on the results of the Maxent model across the Irano-Turanian region. (**A**) Predicted areas of high suitability for current conditions (median prediction). (**B**) Binary map based on a threshold approach for the lowest training presence. All map calculations and illustrations were generated in QGIS (version 3.28, Long Term Release, https://qgis.org/).

climate scenarios. Specifically, the area of suitable habitat for the species decreased by 4.33% and 6.71% from the current conditions to the conditions of SSP2-4.5 and SSP5-8.5, respectively (see Fig. 4A and B).

Considering changes in habitat suitability from current to future conditions under two climate scenarios (SSP2-4.5 and SSP5-8.5), suitability is predicted to decline at mountain slopes, while suitable habitats are expected to increase at higher altitudes. Under the SSP2-4.5 scenario, 5.36% of the area is predicted to remain suitable, 6.21% will undergo contraction (losing suitability mainly along the slopes), and 1.88% will see expansion (newly suitable at higher altitudes), resulting in a net decrease of 4.33%; 86.56% will remain unsuitable. In the more severe SSP5-8.5 scenario, the suitable area decreases further, with only 3.53% remaining suitable, 8.05% contracting, and 1.33% expanding, resulting in a net decrease of 6.71%. Consequently, 87.11% will remain unsuitable. These results indicate that higher emission pathways lead to greater habitat loss and reduced opportunities for range expansion (Figs. 5A, B).

Spatially, the most prominent contractions of suitable habitat are observed across the Zagros Mountains, much of the Alborz Mountains, and parts of the Kopet Dag, where currently suitable areas are projected to become unsuitable under both scenarios—especially under SSP5-8.5. On the other hand, areas of expansion are mostly concentrated in the Hindu Kush, eastern Alborz, and the Himalayan foothills in northern Pakistan and western India, where regions currently unsuitable are projected to become climatically favorable, particularly under SSP2-4.5. These patterns suggest a potential eastward and upward shift in suitable habitats in response to climate change, with montane regions playing a critical role in providing future refugia (Figs. 5A, B).

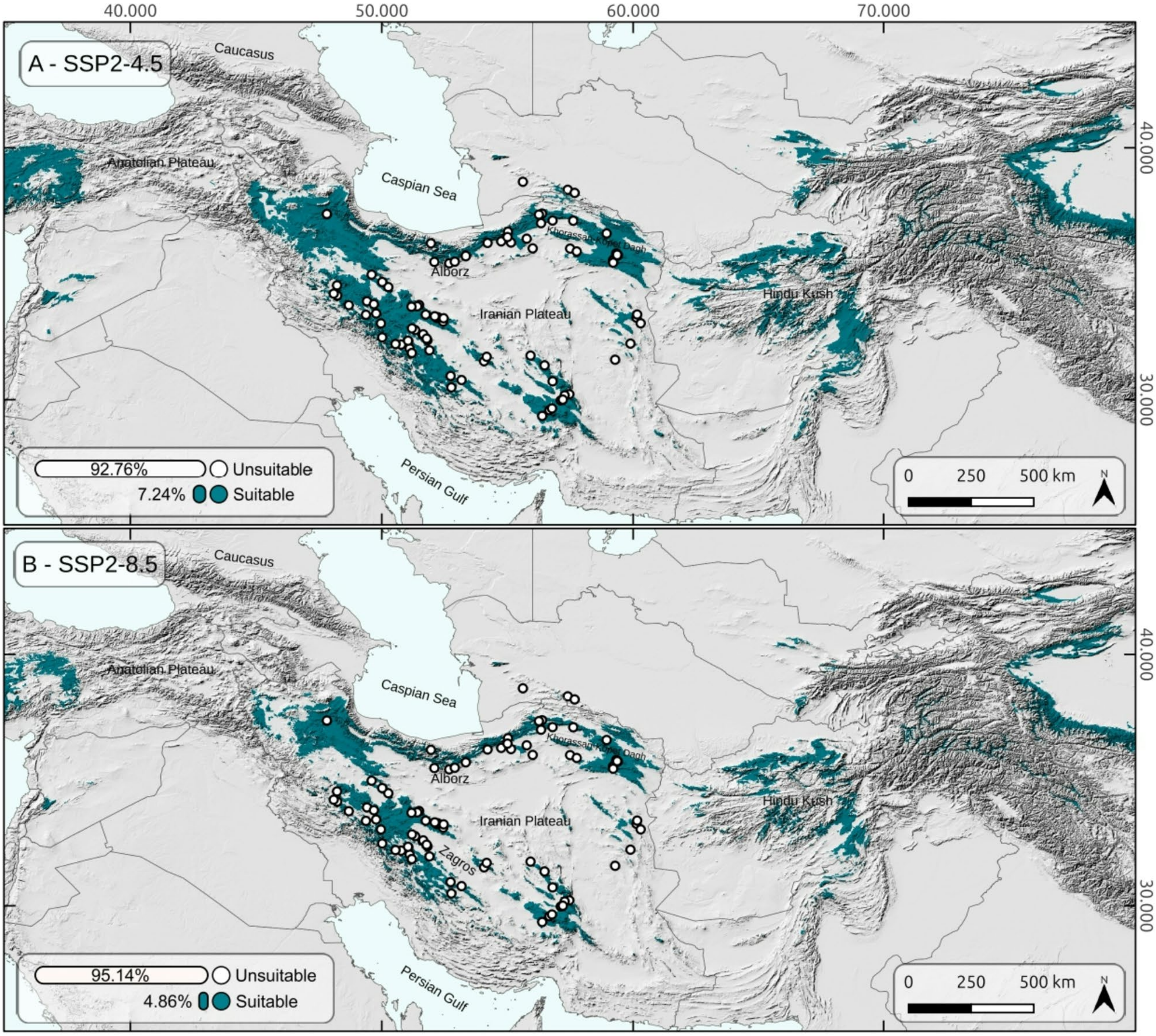

Fig. 4. Future suitable areas for the distribution of *Aethionema spinosum* based on Maxent model outputs under Shared Socioeconomic Pathways across the Irano-Turanian region. Binary predicted suitable areas based on the least training presence threshold: (**A**) SSP2-4.5 scenario; (**B**) SSP5-8.5 scenario. All map calculations and illustrations were generated in QGIS (version 3.28, Long Term Release, https://qgis.org/).

Discussion

The present findings underscore the significant influence of bioclimatic factors on the geographical distribution of *A. spinosum* in our study area. Predominantly, three temperature-related bioclimatic variables (bio1: annual mean temperature; bio3: isothermality; bio7: temperature annual range) and two precipitation-related bioclimatic variables (bio16: precipitation of the wettest quarter; bio17: precipitation of the driest quarter) exerted the most considerable influence based on the model output under current climate conditions. Changes in temperature patterns, a consequence of climate change, can directly impact plant growth and distribution by regulating crucial physiological and biochemical activities such as photosynthesis, respiration, and material transfer[60,61]. Besides temperature, precipitation, influencing plant physiology, soil moisture, and nutrient availability, stands as another pivotal environmental variable[62–64]. Thus, variations in temperature and humidity in environments are likely crucial in constraining the distribution of *A. spinosum*. The strong dependence of *A. spinosum* on a narrow thermal range (15–17 °C; bio1) suggests that its physiological processes, such as photosynthesis and respiration, are optimized within this interval[65]. Temperatures below this threshold may restrict metabolic activity and growth, while higher values could increase evapotranspiration and water stress, limiting survival[66]. Likewise, the species' preference for intermediate isothermality values (32–35%; bio3) reflects a sensitivity to diurnal and seasonal temperature fluctuations[67]. Too much variability may impose stress on reproductive and vegetative phases, whereas very low variability may constrain the adaptive plasticity of the species[68]. Finally,

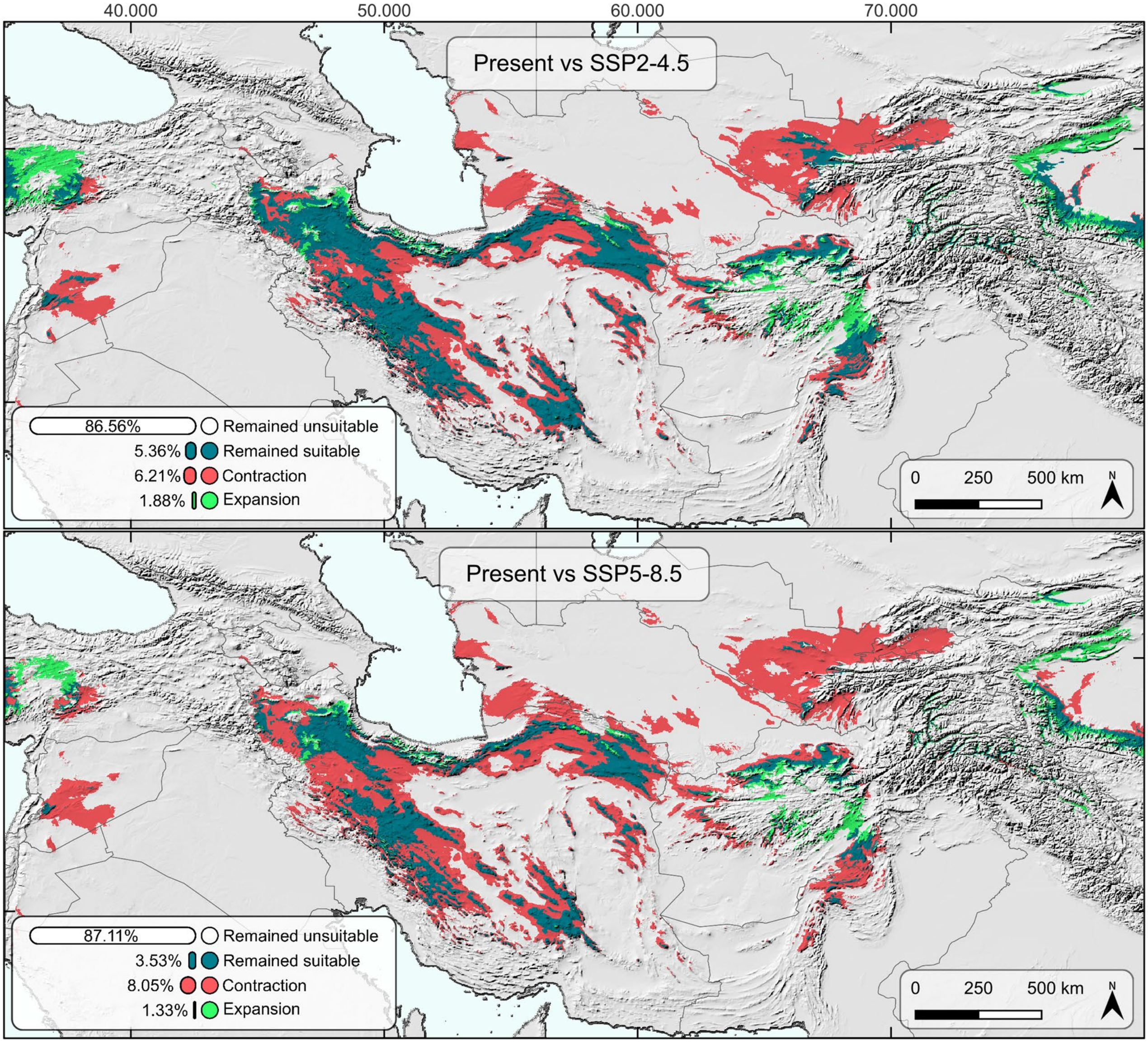

Fig. 5. Predicted suitable areas and changes in suitability of *Aethionema spinosum* based on Maxent model outputs under climate change scenarios SSP2-4.5 and SSP5-8.5. All map calculations and illustrations were generated in QGIS (version 3.28, Long Term Release, https://qgis.org/).

the reliance on precipitation of the wettest quarter (bio16) around 200–250 mm underscores the importance of adequate soil moisture during the main growing or flowering season[69]. This precipitation likely ensures successful germination, flowering, and seed production, while either deficit or excess rainfall outside this optimum reduces habitat suitability[70]. Together, these relationships indicate that *A. spinosum* occupies a specialized climatic niche, tightly constrained by combined temperature and moisture regimes.

These findings align with prior research on plant species distribution in the Irano-Turanian region, emphasizing precipitation and temperature as fundamental climatic factors shaping species distribution[71,72].

While *Aethionema spinosum* is known for its specific edaphic and microhabitat preferences, our modeling focused exclusively on bioclimatic variables to ensure consistency across current and future climate scenarios. Although high-resolution soil data, such as from SoilGrids[73], are available for the region, their accuracy in complex mountainous environments remains uncertain, particularly at the microhabitat scale relevant to *A. spinosum*. Furthermore, soil and topographic variables are largely static and not easily projected under dynamic climate change scenarios, unlike bioclimatic variables, which are directly linked to future climate projections. Including such static variables can also unnecessarily increase model complexity and introduce risks of multicollinearity or overfitting, especially when working with limited occurrence records[74,75]. Therefore, we prioritized ecologically relevant and temporally responsive predictors. Nonetheless, we acknowledge that incorporating fine-scale soil or terrain data could enhance model performance in future studies focused on local-scale ecological processes.

Based on current climatic variables, we have delineated expansive potential distributions for *A. spinosum* in the Irano-Turanian region. Our models highlight that nearly all suitable habitats for this species are located in montane areas ranging from mid to high altitudes. While certain mountainous regions in northern Afghanistan, Pakistan, and Central Asia could prove to be favorable for certain species, the interplay of climate change, dispersal opportunities, and capacities will be crucial in determining whether these species will actually spread to the predicted locations.

While several *Aethionema* species exhibit antitelechorous (retention of seeds near the parent plant) or telechorous (long-distance dispersal) strategies, *A. spinosum* possesses winged fruits, which suggest a greater potential for wind-assisted dispersal compared to some of its congeners. However, despite this morphological adaptation for wider dispersal, our findings indicate that *A. spinosum* still exhibits limited range expansion, particularly into newly emerging suitable habitats under future climate scenarios. Despite having winged fruits that facilitate the dispersal of *A. spinosum* seeds over considerable distances, its ability to colonize uninhabited, suitable areas depends on factors such as hardiness, germination capacity, and viability. Moreover, specific environmental requirements (such as humidity and shade) for germination, as noted in some studies e.g., Kalimuthu and Lakshmanan[76] and Venkataramaiah, et al.[77], further restrict the establishment of *A. spinosum*. Previous research has also indicated a low germination rate for some *Aethionema* species in natural habitats[78]. Moreover, it is shown that the dispersal of species is linked to local events, such as the uplift of the Anatolian and Iranian plateaus, the formation of major mountain ranges, and probably a climatic change in seasonality towards summer aridity[78]. These factors create formidable barriers that impede dispersal and limit the establishment of the species even under suitable conditions. Thus, while *A. spinosum* may possess morphological traits that favor dispersal, its ecological constraints appear to align with those of its congeners, ultimately limiting its capacity to shift its range in response to climate change.

Our model outcomes under future scenarios (SSP2-4.5 and SSP5-8.5) also forecasted a consistent distributional pattern akin to current conditions. The most noteworthy difference was how climate change has turned middle-elevation regions that were once thought to be suitable for the species under the current circumstances into unfavorable habitats. These models predicted a potentially large geographic shift of high-suitability areas toward higher elevations, especially in the mountainous regions of Turkey, Iran, Afghanistan, and Central Asia (Fig. 5).

The predicted results also indicated a general reduction in the suitable area for *A. spinosum* in the study region under the two future scenarios. This reduction was projected to primarily impact lower elevations within mountainous regions spanning Iran, Afghanistan, Pakistan, Turkmenistan, Uzbekistan, Turkey, and Syria (refer to Fig. 5). The losses in geographic range were not expected within the current habitats of the species, which are anticipated to remain suitable under future climate scenarios. Nevertheless, significant losses were observed in neighboring habitats, compelling the species to migrate toward new suitable regions at higher elevations. This suggests that these losses could be attributed to the limited adaptability of *A. spinosum* to climate changes in these areas[79]. Conversely, environmental factors such as wind speed, UV radiation, daily temperature fluctuations, and minimum temperature may adversely impact the growth and survival of the species in montane areas[80,81]. While our findings suggest that these abiotic factors may negatively influence the survival and distribution of *A. spinosum*, they were not incorporated into our final species distribution models. Their exclusion was primarily due to limitations in data availability, as high-resolution and spatially consistent datasets for these variables are either lacking or incomplete for the Irano-Turanian region[82]. Additionally, to maintain model robustness and reduce the risk of overfitting, we limited the number of predictors and avoided multicollinearity among environmental variables[74]. Nevertheless, these factors are ecologically significant, particularly in high-altitude ecosystems where microclimatic conditions can impose strong local constraints on species persistence and dispersal[83,84]. Future studies employing fine-scale climatic data or mechanistic models could offer deeper insights into potential range shifts and the vulnerability of *A. spinosum* under changing environmental conditions. This limitation is acknowledged here to better contextualize the scope and interpretation of our projections.

These findings anticipate the detrimental impacts of climate change, leading to a reduction in environmentally suitable areas for species, significant shifts in potential distributions, and, ultimately, the risk of species loss, whether locally or globally. This scenario can be exacerbated by the species' limitations in establishing and colonizing new suitable regions. These results align with prior studies indicating that climate change contributes to the upward and northward shift of two endemic species in the Irano-Turanian region[71,72]. Similar upward and poleward shifts in suitable habitats have been reported for *Dianthus polylepis*[71] and *Nepeta glomerulosa*[72], both of which, like *A. spinosum*, are adapted to high-altitude environments with narrow ecological niches. These studies also reported habitat contractions at lower elevations and increased suitability in higher altitudinal zones under future climate scenarios, supporting our projection of *A. spinosum* retreating to high-elevation refugia. However, unlike some widespread Irano-Turanian species that show greater potential for range expansion (e.g., *Nepeta glomerulosa*), *A. spinosum* exhibited limited colonization of newly suitable areas. This difference may be linked to its more restricted dispersal ability, small and fragmented populations, and specific microhabitat requirements. Furthermore, while some high-altitude species in Central Asia and the Mediterranean have demonstrated resilience through broader climatic tolerance[85], our results indicate that *A. spinosum*'s specialized adaptation to rocky, low-moisture habitats may constrain such resilience. These contrasts underscore the significance of species-specific traits in shaping distributional responses to climate change, even among species inhabiting similar ecological zones.

However, the Irano-Turanian region boasts a diverse topography owing to a complex tectonic history. While this intricate topography has created a favorable physiographic context for the region's flora, it concurrently constitutes formidable barriers that restrict the dispersal of species within this area[86,87]. The challenge is aggravated by the prevalent W-E and NW-SE orientation of the Irano-Anatolian plateaus and the Central Asian Mountain ranges, rendering adaptation to a warmer environment more arduous[35,88].

Limitations

Our ecological niche modeling provides valuable insights into the potential impacts of climate change on *Aethionema spinosum*, but several limitations should be acknowledged. First, occurrence data may still harbor sampling biases, particularly in remote or inaccessible parts of the Irano-Turanian region, despite spatial filtering. Second, our models relied exclusively on bioclimatic variables to ensure comparability across current and future climate scenarios, while omitting key edaphic, topographic, and microclimatic factors (e.g., soil properties, wind exposure, UV radiation, frost) due to limited spatial data availability and their static nature, which hinders realistic future projections. Third, MaxEnt's presence-only modeling and assumption of unlimited dispersal may overestimate suitable habitat and colonization potential, as it cannot account for real-world constraints such as population dynamics, establishment success, or genetic and phenotypic variability. Finally, projections carry inherent uncertainty from multiple sources, including variability among General Circulation Models (GCMs), differences in emission scenarios (SSP2-4.5 and SSP5-8.5), and methodological assumptions of ENM, which our ensemble approach mitigates but cannot fully eliminate. These factors collectively suggest that modeled potential distributions should be interpreted as broad-scale estimates rather than precise predictions of future occurrence.

Conclusion and conservation implications

In the present study, we have illuminated the potential impact of current and future climatic conditions on the distribution of *A. spinosum*, a constituent of the Irano-Turanian region. The predominant climatic variables, namely mean annual temperature, isothermality, and precipitation of the wettest quarter, had the greatest impact on the distribution of *A. spinosum*, and contributed the most in percentage terms. Our results indicate a foreseeable reduction in potentially suitable areas for the species, coupled with a shift to higher elevations. This predicts the vulnerability of the species to climate change, particularly if it is unable to migrate to new regions. While no geographical losses were expected in the species' current habitats, significant losses occurred in nearby areas, forcing the species to relocate to new suitable zones at higher elevations. The study emphasizes the vulnerability of *A. spinosum* and its potential habitats to the impending impacts of climate change, highlighting the urgency of regional conservation initiatives for *A. spinosum* in its natural habitats. These findings underscore the urgent conservation needs of *A. spinosum*, an endemic and evolutionarily distinct species threatened by climate change. Projected habitat losses in the Zagros and central Alborz Mountains necessitate immediate in situ protection through safeguarding critical habitats from land-use pressures, including overgrazing and infrastructure development, along with monitoring programs to track population trends and detect early signs of habitat loss. High-elevation montane regions in Iran, Turkey, Afghanistan, Central Asia, the eastern Alborz, Hindu Kush, and northern Pakistan are identified as current and future climatic refugia and should be prioritized for conservation. Proactive measures, including biodiversity surveys, seed collection, habitat restoration, and assisted migration trials, are essential to facilitate range shifts despite limited natural dispersal and topographic barriers. Given its fragmented populations and narrow niche, ex situ conservation, such as seed banking, is also crucial for safeguarding genetic diversity. Integrating these strategies into national biodiversity action plans (NBSAPs) across Iran, Afghanistan, and neighboring countries could foster transboundary collaboration. Finally, due to its unique phylogenetic position as the earliest diverging lineage within the Brassicaceae, *A. spinosum* warrants inclusion in red-list assessments and expanded protection efforts within the Irano-Turanian biodiversity hotspot. Although this study highlights the potential impacts of climate change on *A. spinosum*, future studies could incorporate fine-scale environmental data such as soil type, microtopography, and microclimatic conditions, while also investigating dispersal capacity, genetic diversity, phenotypic plasticity, and adaptive potential. Field-based validation of predicted refugia and the application of mechanistic models will be crucial for strengthening confidence in distribution projections and guiding evidence-based conservation strategies, including climate-adaptive measures such as assisted migration.

Data availability

The supporting information associated with this article is available via the following link: https://github.com/Jafarighm/Climate-Change-Impacts-Aethionema-spinosum-Brassicaceae-Retreating-to-High-Elevation-Refugia.

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Declarations

Competing interests
The authors declare no competing interests.

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