scientific reports

OPEN

Endemic cushions of the Khorassan-Kopet Dagh floristic province show differential responses to future climate change

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Climate change negatively affects mountainous plants and leads to their range contraction or extinction. Cushion plants are the essential components of mountainous ecosystems. Although cushions represent the dominant vegetation form of the mountains of the Irano-Anatolian Biodiversity Hotspot, the impacts of climate change on these plants have been merely studied. The present study investigates the effects of climate change on the distribution of endemic cushion species in the Khorassan-Kopet Dagh (KK) floristic province, the eastern-most part of the Irano-Anatolian Biodiversity Hotspot. We predicted the current and future range of 19 cushions in 2040 and 2100, using 19 bioclimatic layers along with two different SSPs and an ensemble of 12 modeling algorithms. These species belong to *Acantholimon*, *Acanthophyllum*, *Astragalus*, *Jurinea*, and *Thymus* genera. Our findings revealed that approximately all studied species will face range contraction. On the other hand, *Jurinea antunowi*, *Acantholimon restiaceum*, and *Acanthophyllum speciosum* will show negligible responses to climate change effects. Moreover, all analyzed species would shift upward in their altitudinal distribution range. The predicted range size contraction of the surveyed genera will vary between 36 to 91 percent, where *Acanthophyllum* and *Thymus* will show the least and the most contraction, respectively. Based on our findings, we have provided recommendations for conservation of vulnerable species and sustainable mountainous habitats restorations.

Keywords Climate change, Cushion plants, Irano-Turanian, Khorassan-Kopet Dagh floristic province

Cushions (pulvinate plant forms) with "tightly packed foliage held close to the soil surface, and a relatively even and rounded canopy form"[1] are significant ecosystem engineers that can alter the local soil temperature and moisture[2,3]. These nurse plants are facilitators for the other species[4–7]. Cushions increase and maintain local species diversity, especially in the stressful conditions of mountainous habitats[6,8]. Furthermore, by reducing environmental fluctuations, these plants positively affect the reproduction and establishment of herbaceous plants and the formation of the soil seed bank[9].

Cushion plants are a critical part of mountainous vegetation, and their distribution or abundance changes can significantly affect plant communities[10]. Climate change can alter temperature regimes, precipitation and water availability, snow cover, and biotic interactions[11]. These factors have a negative impact on cushion plant distribution and abundance[12,13]. Thus, examining cushion plants' response to climate change is a crucial step towards sustainable management of mountainous habitats to maintain their services for the future.

The Khorassan-Kopet Dagh (KK) floristic province is in the eastern part of the Irano-Anatolian Biodiversity hotspot[14,15]. It is a mountainous region that acts as a transitional zone between the different phytogeographical units of the Middle East[15]. The KK has large mountain ranges, namely the Kopet Dagh, Hezar Masjed, Binalood, and Aladagh Mountains (Fig. 1)[15–17]. Cushion plants, especially thorn-cushion species, constitute the dominant mountainous vegetation form of the KK[15,18]. The cushion species of the KK belong to different genera, i.e., *Acantholimon*, *Acanthophyllum*, *Anabasis, Astragalus*, *Dionysia, Jurinea*, *Onobrychis*, and *Thymus*[15,18,19]. These plants occur in various communities in the region (Fig. 1)[16,19–21]. These species have different ecological roles that lead to the preservation of the biodiversity of KK's mountains[8,22,23].

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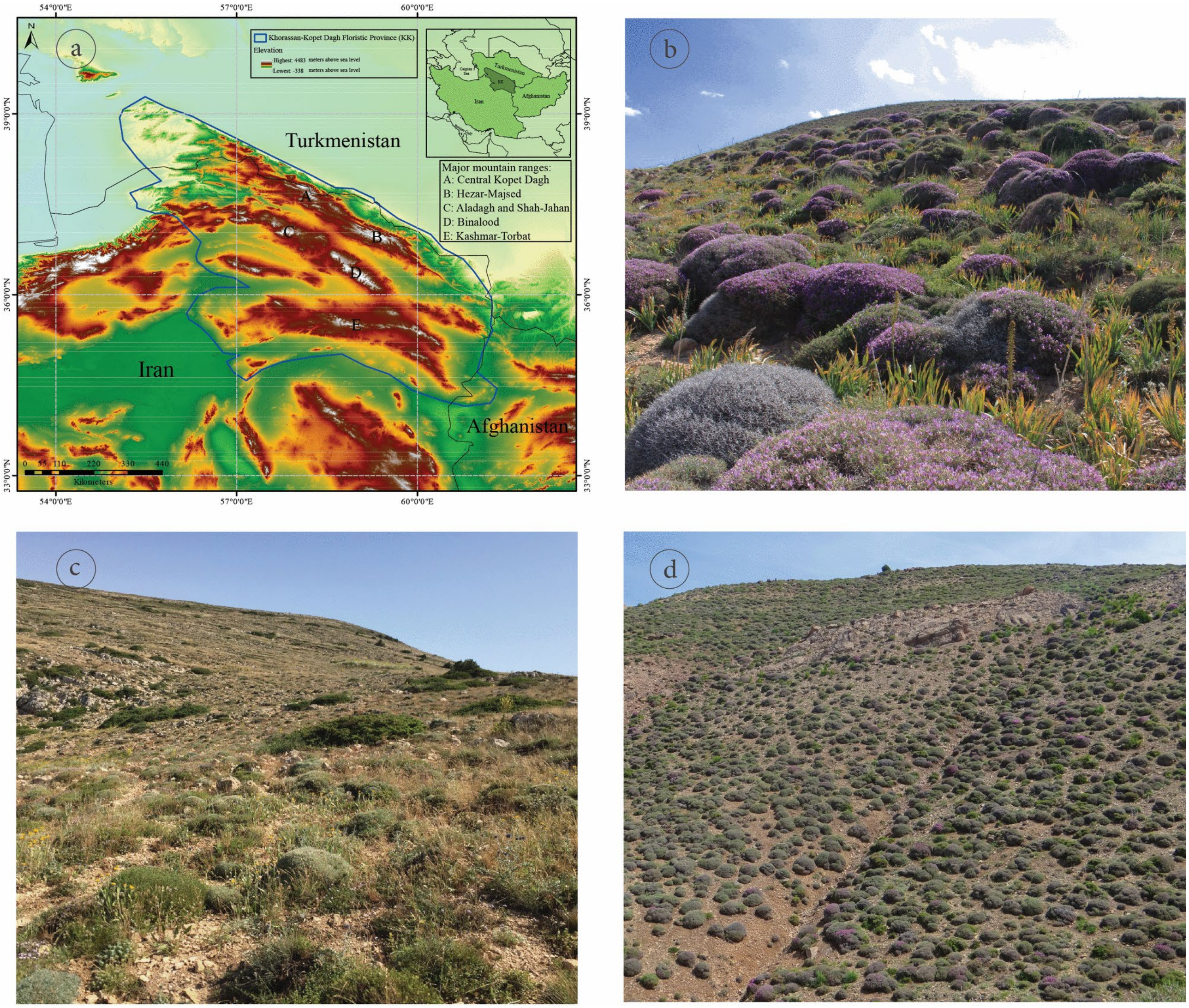

Fig. 1. **a**: Study area, the Khorassan-Kopet Dagh floristic province (KK). The original figure was adopted from Erfanian et al. ([17]). b-d: cushion vegetation type on elevations of the main ranges of KK (by Zohreh Atashgahi), (**b**) *Onobrychis*, *Acanthophyllum*, and *Acantholimon* in Binalood, (**c**) *Acanthophyllum* and *Acantholimon* in Aladagh, (**d**) and *Onobrychis cornuta* and *Acantholimon* spp. in Hezar Masjed.

Habitat suitability modeling (HSM) is used to predict species' climate niches and project potential future range shifts to evaluate the vulnerability of plant species to changing climate conditions[24–26]. The results of HSM can inform the development of adaptive management strategies, such as assisted migration, to mitigate the effects of climate change[24,27]. Although KK hosts a considerable number of 356 endemic plant species, the response of these endemic species to climate change has remained understudied. Two previous studies have evaluated the impacts of climate change on endemic (non-cushion forming) plants in KK (i.e., Behroozian et al.[28] and Erfanian et al.[17]). However, the impacts of climate change on KK's endemic cushion species have not been investigated. Few studies assessed the impacts of climate change on cushion plants of the Irano-Anatolian Biodiversity hotspot (e.g., Karimian et al.[29], Mahmoudi Shamsabad et al.[30], and Sheikhzadeh Ghahnaviyeh et al.[31]). However, they have focused on non-endemic taxa.

Mountainous habitats of KK are generally subjected to different disturbances, such as grazing[16,23,32] and land use changes[8,33]. Predicting the response of cushion plants to climate change will enable managers to preserve endangered species and plan appropriate restoration practices based on cushion species whose distribution range remains unaffected by climate change. The present study aimed to assess the impact of climate change on the distribution range of endemic cushions in the KK. This is the first study investigating the response of KK's endemic cushions to climate change. We hypothesize that (a) climate change, particularly in a pessimistic scenario, can significantly reduce the distribution of these plants; (b) the species within the same genus have similar responses to climate change due to their shared evolutionary histories. We also test whether species within a similar elevation range respond similarly to climate change. Our findings will enable us to identify the most-vulnerable and indifferent species to climate change. Management strategies for vulnerable species will be presented. The indifferent species can be used in long-term restoration practices in the region.

Materials and methods
Study area
The KK floristic province is a transitional zone that connects different phytogeographical units of the Irano-Turanian region[15]. The KK, with an area of 165,000 km^2, encompasses a complex topography ranging from approximately 250 to elevations higher than 3000 m a.s.l.[15] (Fig. 1). The dominant climatic condition of the region is the continental climate. Mountain ranges in the KK have a Mediterranean or Irano-Turanian xeric-continental bioclimate with an average annual precipitation of 300–380 mm. The mean annual temperature ranges between 12–19 °C[34]. The KK is home to diverse vegetation types, among which the montane steppes and grasslands are the most abundant[15] (Fig. 1). The region hosts 2576 vascular plants, of which 356 (13.8 percent of the total species pool) are endemic[35]. Most of the KK's endemic species are range-restricted and rare[17,36]. Various disturbances, such as overgrazing, land use change, and recreation activities, threaten the mountainous habitats in the KK[14,16,32,33,37,38]. Approximately eight percent of the KK habitats are protected and managed under different protection guidelines[18].

Species data
The definition of cushion plants in Pérez-Harguindeguy et al. ([1]) was followed to determine the cushion species of the study region. The list of the endemic plants of the KK[35], as well as the updated literature on the region's flora, was reviewed to list the cushion species of the region. Then, we collected the occurrence points through (a) the field surveys conducted in KK during the past ten years (2013–2023) (for all of the field surveys permissions for plant collection have been obtained); (b) specimens evaluation, mainly those that were deposited at Herbarium of Ferdowsi University of Mashhad, FUMH (mainly focused on the collection of plant species of the KK); (c) review of literature including Atashgahi et al.[19], Atashgahi et al.[39], Arjmandi et al.[37], Assadi et al. (Flora of Iran[40]), Maleki Sadabadi et al.[41], Parishani et al.[42], Pirani et al.[43], and Rechinger (Flora Iranica[44]). We tried to collect occurrence records from all climatic conditions where species were present. Three sets of pseudoabsence points were generated for each species using the biomod2 package[45] for the modeling. The number of random pseudoabsence points was set to 3 × number of occurrence records.

Environmental data
We used 19 bioclimatic layers (Supplementary 1), with a 1 km^2 resolution, that are reliable in defining the physio-ecological tolerances of species[46]. These layers were downloaded from Worldclim[47]. To download future layers, we selected the Hadley Centre Global Environmental Model version 2-Earth System (HadGEM2-ES), general circulation model (GCM), and two Shared Socioeconomic Pathways (SSPs) scenarios, including SSP126 (most optimistic) and SSP585 (most pessimistic). We chose the HadGEM2-ES model because it showed appropriate temperature forecasting compared to the data from different synoptic stations in Iran[17]. We chose the years to use the HSM in the near future (2021–2040, which is called 2040 hereafter) and the far future (2080–2100, which is called 2100 hereafter).

We performed a pre-run to select the most suitable layers. The pre-run had a set of pseudoabsence data and a Maxent algorithm with ten replications. We used the Maxent algorithm because it showed good performance when there was a lack of resources to use multiple algorithms[48] to make our results reproducible even using low-resource computations. Then, the first layers that account for 80 percent of variable importance were selected. We calculated the variance inflation factor (VIF) for the selected layers to remove collinear layers. VIFs were calculated by performing a step-by-step process using the usdm package (Naimi et al. 2014). We selected variables with a VIF below five. The selected variables for each species are presented in Table 1.

Modeling settings
Twelve modeling algorithms, including the Generalized Linear Model (GLM), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Classification Tree Analysis (CTA), Artificial Neural Network (ANN), Surface Range Envelop (SRE), Multiple Adaptive Regression Splines (MARS), Random Forest (RF), Maximum Entropy (MAXENT), Maximum Entropy (MAXNET), Flexible Discriminant Analysis (FDA) and eXtreme Gradient Boosting Training (XGBOOST) were used to construct the models in the current study.

The occurrence data were randomly split into two subsets, with 70 percent of the data used for model calibration and the remaining 30 percent used for model evaluation. The data was split because we had no independent data for model evaluation. The number of replications was set to 2. Therefore, we constructed 72 models for each species. We employed the True Skill Statistic (TSS) along with the Area Under Curve (AUC) of the Receiver Operation Curves to measure HSM performance. To project the final maps, we used binary transformation. For binary transformation, we employed the threshold that maximizes TSS to convert occurrence probability values into presence/absence predictions. These calculations were performed using the biomod2 package.

Ensemble forecasting
To obtain the final models, we employed the ensemble forecasting procedure. We selected those with a TSS and AUC above 0.6 to combine models. Ensemble models were projected for current and future conditions at a 1 km^2 resolution. The ensemble models were transformed into binary presence-absence predictions using the threshold that maximizes TSS[46]. The ensemble forecasting was performed using the biomod2 package.

Family	Species	AUC	TSS	Variables and their contribution to ensemble model	Number of occurrence records	Current range size (km^2)	Future change			
							2040–126	2040–585	2100–126	2100–585
Plumbaginaceae	*Acantholimon alavae* Rech.f. & Schiman-Czeika	1.000	1.000	Bio 03 (0.498), Bio 19 (0.113), Bio 08 (0.031), Bio 07 (0.0134)	5	5,704	-100.000	-100.000	-100.000	-100.000
	Acantholimon avenaceum Bunge	0.926	0.749	Bio 11 (87.329), Bio 4 (6.140), Bio 2 (5.524), Bio 14 (1.007)	19	51,296	-65.958	-73.875	-82.923	-99.848
	Acantholimon blandum Czerniak.	0.998	0.978	Bio 9 (42.675), Bio 18 (27.495), Bio 2 (15.709), Bio 19 (14.121)	10	26,600	-82.684	-87.940	-91.789	-93.778
	Acantholimon gorganense Mobayen	0.971	0.929	Bio 3 (27.039), Bio 5 (72.960)	11	12,575	-44.996	-63.471	-79.325	-100.000
	Acantholimon pterostegium Bunge	0.802	0.622	Bio 19 (0.401), Bio 02 (0.315), Bio 04 (0.275), Bio 11 (0.167), Bio 17 (0.036)	79	61,183	-35.794	-52.103	-32.249	-98.130
	Acantholimon raddeanum Czerniak.	0.971	0.853	Bio 11 (0.626), Bio 19 (0.084), Bio 12 (0.051), Bio 03(0.012)	147	22,459	-49.138	-54.624	-74.847	-97.115
	Acantholimon restiaceum Bunge	0.986	0.926	Bio 16 (0.990), Bio 19 (0.324)	9	21,361	+78.231	-30.261	+49.300	-89.415
	Acantholimon spinicalyx Köie & Rech.f.	0.969	0.852	Bio 15 (0.718), Bio 08 (0.173), Bio 09 (0.074), Bio 19 (0.052)	27	19,677	-62.078	-4.797	-47.157	-94.079
Caryophyllaceae	*Acanthophyllum adenophorum* Freyn	0.918	0.680	Bio 11 (0.413), Bio 14 (0.386), Bio 13 (0.104), Bio 08 (0.030)	54	65,173	-52.431	-51.583	-70.609	-96.397
	Acanthophyllum speciosum Rech.f. & Schiman-Czeika	0.985	0.905	Bio 12 (0.574), Bio 02 (0.062), Bio 08 (0.036), Bio 04 (0.027), Bio 06 (0.021)	14	22,076	-5.993	-0.290	+9.830	-19.714
Fabaceae	*Astragalus cystosus* Zarre & Podlech	0.994	0.963	Bio 08 (0.666), Bio 12 (0.194), Bio 02 (0.145)	6	2,486	-81.979	-35.921	-82.743	-100.000
	Astragalus hypsogeton Bunge	0.987	0.970	Bio 10 (0.850), Bio12 (0.041)	8	7,509	-80.037	-86.070	-93.355	-100.000
	Astragalus raddei Basil.	0.949	0.736	Bio 06 (0.355), Bio 16 (0.142), Bio 14 (0.100), Bio 07 (0.030), Bio 03 (0.022), Bio 08 (0.010)	75	28,383	-52.623	-62.752	-68.263	-99.915
	Astragalus turkmenorum (Boriss.) Širj.	0.998	0.978	Bio 14 (0.385), Bio 03 (0.212), Bio 08 (0.210), Bio 09 (0.158)	10	15,380	+73.257	-95.130	-46.008	-95.813
Asteraceae	*Jurinea antunowi* C.Winkl.	0.938	0.778	Bio 15 (0.957)	7	38,317	+8.946	+4.617	+1.545	+9.607
	Jurinea catharinae Iljin	0.930	0.778	Bio 16 (0.738), Bio 19 (0.633), Bio 12 (0.078)	18	59,744	+18.250	-52.996	-20.528	-86.112
	Jurinea kopetensis Rech.f.	0.994	0.968	Bio 9 (0.790), Bio 7 (0.056)	7	10,574	-95.769	-89.539	-94.672	-100.000
	Jurinea sintenisii Bornm.	0.967	0.805	Bio 11 (0.544), Bio 02 (0.166), Bio 19 (0.061), Bio 14 (0.017)	74	37,607	-45.226	-27.668	-53.046	-44.702
Lamiaceae	*Thymus transcaspicus* Klokov	0.959	0.825	Bio 14 (0.338), Bio 09 (0.220), Bio 02 (0.121), Bio 19 (0.025), Bio 07 (0.010)	47	30,274	-79.989	-89.397	-94.153	-99.990

Table 1. The AUC and TSS of the ensemble model, variable contribution, number of occurrence records, current range size and future range size changes of the endemic cushions of KK.

Range and elevation shifts

To assess the effects of climate change on the range size of the studied species, we compared each species' future distribution to its current distribution. For each species, four distinct habitat types were categorized: (a) stable habitats – habitats that are suitable in current and future climatic conditions; (b) lost habitats – currently suitable habitats that will not remain suitable in the future; (c) gained habitats – currently unsuitable habitats that will become suitable in the future; and (d) unsuitable habitats – habitats that are unsuitable for species both in current and future climatic conditions. We predicted range size changes using the biomod2 package.

The current elevation and future elevation range of each species was determined using the terra package[49]. The reported elevation range includes the midspread (quartile 1 and 3 values) of extracted elevation using the ensemble binary maps. For future elevation ranges, we concentrate on SSP 585 of 2100. For those species that would become completely extinct in this scenario, we used the value of SSP 585 of 2040.

Results

We identified 34 endemic cushion species for KK, of which only 19 had an adequate number of occurrence records suitable for the HSM (SM 2–7). The modeled species are the members of the genera *Acantholimon*, *Acanthophyllum*, *Astragalus*, *Jurinea,* and *Thymus*. The information regarding the number of occurrence records, variable contributions, and the performance metrics AUC and TSS for the ensemble model are detailed in Table 1.

The results of HSM for the five modeled genera are summarized below. The current range size and future range size changes and the current and future distribution of the modeled species are presented in Tale 3 and

Figs. 2, 3, 4, 5, respectively. The details of range size changes under SSP126 and SSP585 scenarios for each species are presented in Table 1. Current and future elevational range of the modeled species are presented in Fig. 6.

Acantholimon

The future range size changes for eight *Acantholimon* species were modeled. The average range size change for endemic species of *Acantholimon* is -64 percent (Table 1).

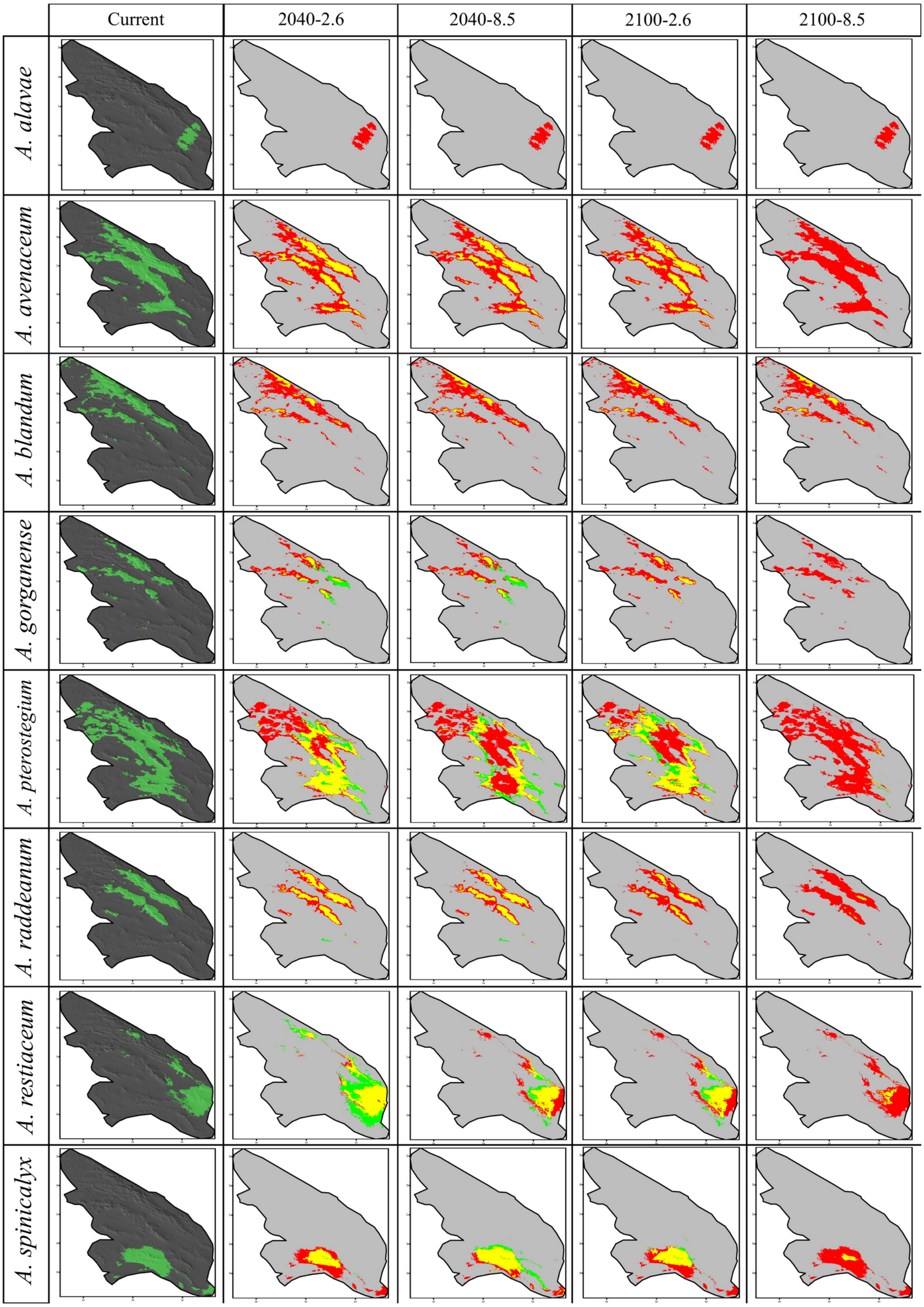

Fig. 2. Current and future distribution of endemic *Acantholimon* species of KK. The red areas represent lost habitat, the yellow stable, and the green gained habitats.

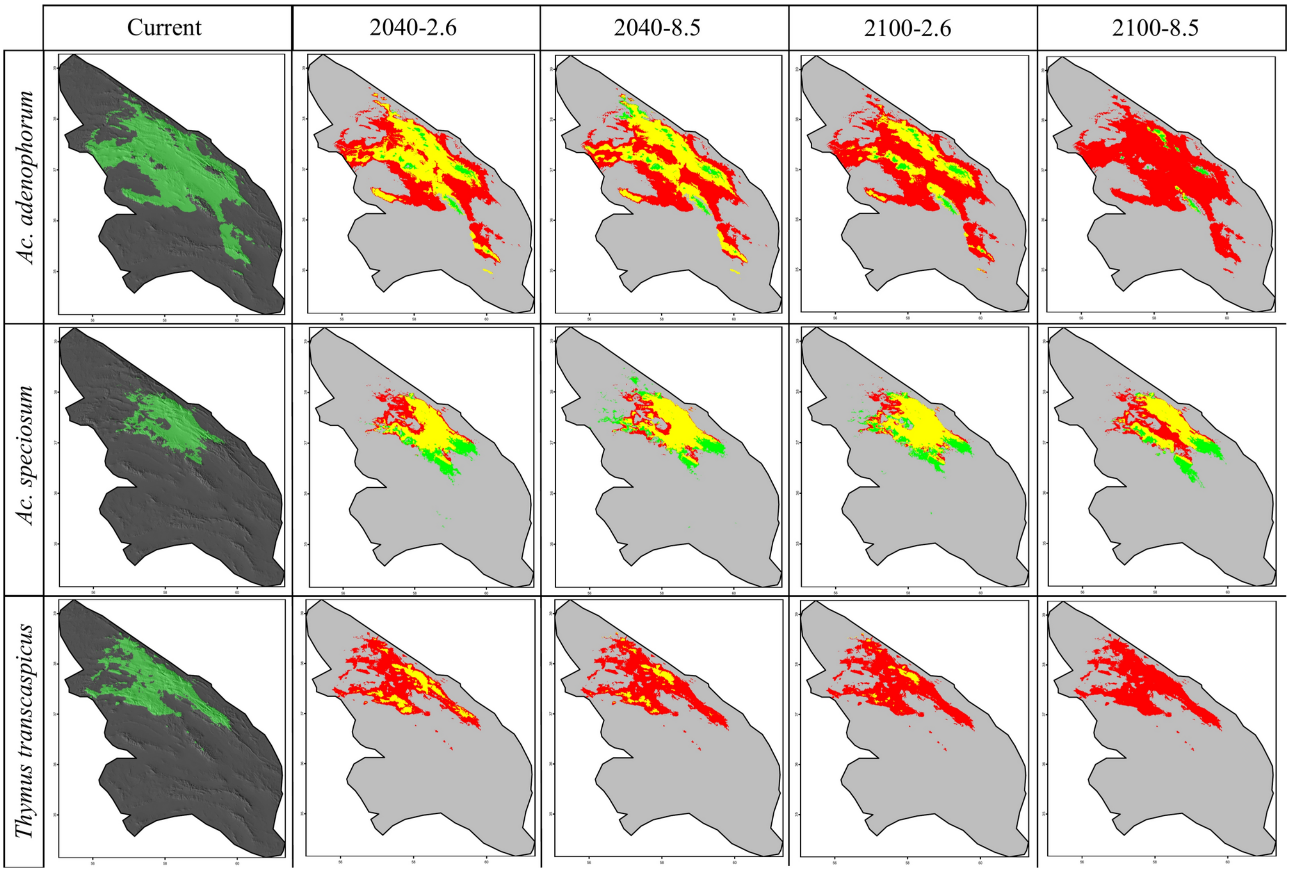

Fig. 3. Current and future distribution of endemic *Acantophyllum* spp. along with *Thymus transcaspicus* of KK. The red areas represent lost habitat, the yellow stable, and the green gained habitats.

Acantholimon alavae
The ensemble habitat suitability map indicates that the area of currently suitable habitats for *A. alavae* is 5704 km^2, delimited within 818–1235 m above sea level (m a.s.l.) (Fig. 2; Table 1; Fig. 6). This plant's limited potential suitable habitat is restricted to the mountains located east of the KK. The range size analysis shows that this species will be lost in future (Table 1).

Acantholimon avenaceum
The ensemble habitat suitability map indicated that the current range size for *A. avenaceum* is 51,296 km^2, within the elevation range of 1628–2066 m a.s.l. (Fig. 2; Table 1; Fig. 6). The distribution range of this species encompasses the Kopet Dagh mountains of Turkmenistan and extends to the Kopet Dagh-Hezar Masjed mountains in Iran, as well as the Aladagh-Binalood range, and ends in Kashmar-Torbat ranges. The potential distribution range of *A. avenaceum* is predicted to shift upward (2082–2409 m a.s.l.) in the elevations under climate change. The average range size changes for this species will be -80.7 percent.

Acantholimon blandum
The habitat suitability map demonstrated that the current range size of *A. blandum* is 26,600 km^2, within the elevation range of 1144–1996 m a.s.l. (Fig. 2; Table 1; Fig. 6). The distribution range of this species is mainly restricted to the high mountains of Turkmenistan and Iran on the Kopet Dagh-Hezar Masjed, Aladagh-Binalood, and Kashmar-Torbat ranges. It is predicted that *A. blandum* will face elevation range contraction (930–1485 m a.s.l.) and remain in its current eastern habitats. The average range size changes for this species will be -89.0 percent.

Acantholimon gorganense
The current range size of *A. gorganense* is 12,575 km^2, within the elevation range of 1762–2216 m a.s.l. (Fig. 2; Table 1; Fig. 6). Currently, suitable habitats for this plant are restricted to the high elevations of the Kopet Dagh-Hezar Masjed, Ghorkhod, Salook, and Aladagh ranges to the eastern extension of the Alborz mountain range in Almeh. It is predicted that *A. gorganense* will experience an eastward shift, as well as an upward migration in the elevations (2259–2522 m a.s.l.) under the climate change. The average range size changes for this species will be -72.0 percent.

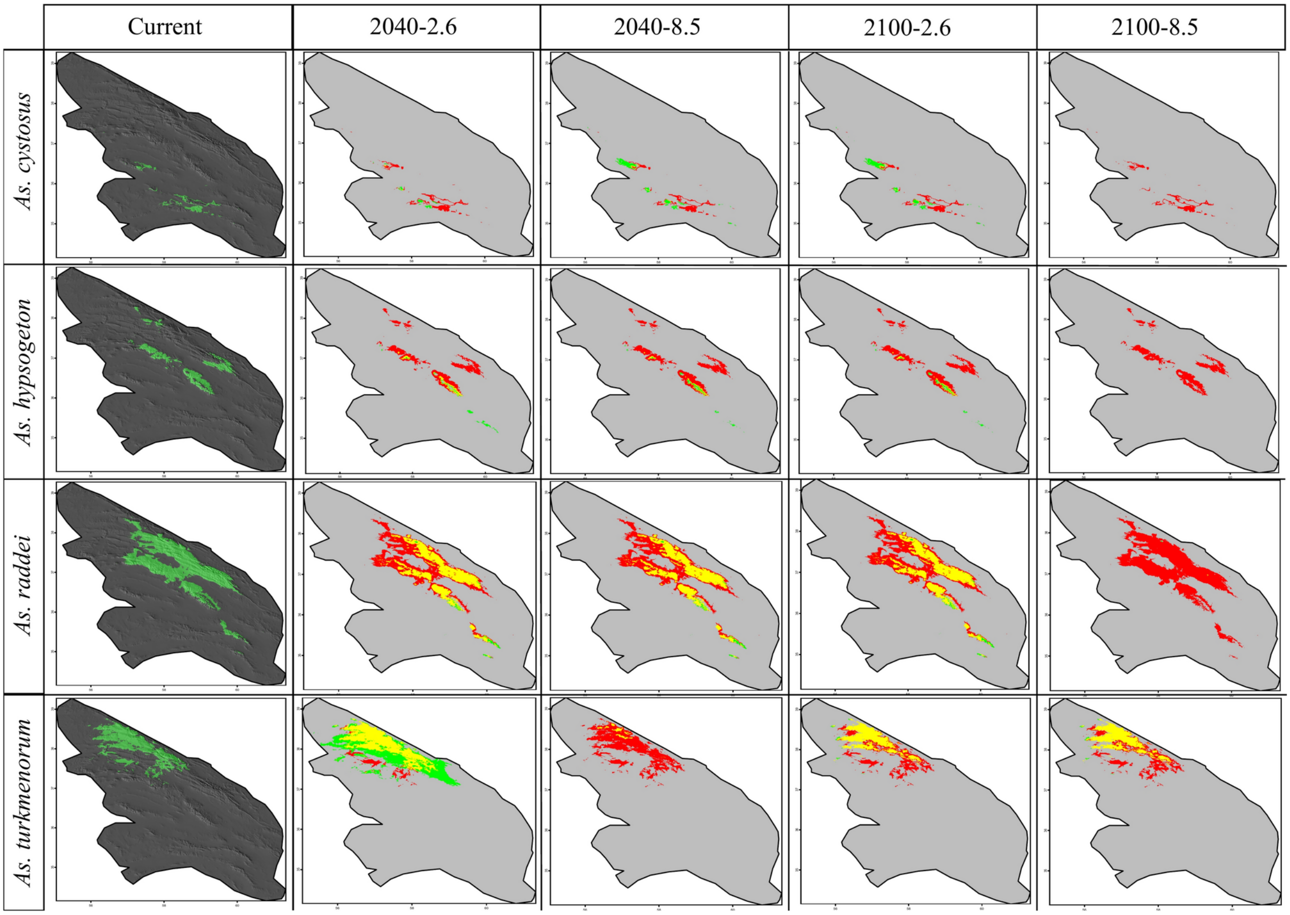

Fig. 4. Current and future distribution of endemics *Astragalus* of KK. The red areas represent lost habitat, the yellow stable, and the green gained habitats.

Acantholimon pterostegium
The ensemble habitat suitability map demonstrated that the current range size of *A. pterostegium* is 61,183 km^2, within the elevation range of 1303–1704 m a.s.l. (Fig. 2; Table 1; Fig. 6). The current suitable habitats of this species are limited to the low and mid-range elevations of central KK. It is expected that *A. pterostegium* will migrate eastward and shift upward to higher elevations (1495–1904 m a.s.l.) under climate change. The average range size changes for this species will be -54.6 percent.

Acantholimon raddeanum
The ensemble habitat suitability map demonstrated that the current range size of *A. raddeanum* is 22,459 km^2, within the elevation range of 1757–2179 m a.s.l. (Fig. 2; Table 1; Fig. 6). The currently suitable habitats of this species are delimited to mid and high-elevation ranges of the Hezar Masjed and Binalood Mountains. It is predicted that *A. raddeanum* will shift upward in the elevations (2619–2846 m a.s.l.) under climate change. The average range size changes for this species will be -68.9 percent.

Acantholimon restiaceum
The ensemble habitat suitability map indicated that the current range size for *A. restiaceum* is 21,361 km^2, within the elevation range of 994–1582 m a.s.l. (Fig. 2; Table 1). The distribution range of this species is mainly limited to the southeastern parts of KK, on the Torbat-e-Jam and Sarakhs mountains. It is expected that *A. restiaceum* will experience both eastward and upward (1155–1457 m a.s.l.) shifts under climate change. The average range size changes for this species will be + 2.0 percent.

Acantholimon spinicalyx
The ensemble habitat suitability map demonstrated that the current range size of *A. spinicalyx* is 19,677 km^2, within the elevation range of 1244–1698 m a.s.l. (Fig. 2; Table 1; Fig. 6). The current suitable habitats of this species are limited to the south of KK and the south-facing slopes of the Kashmar-Torbat range. The potential distribution range of *A. spinicalyx* is expected to shift upward in the elevations (2458–2526 m a.s.l.) under climate change. The average range size changes for this species will be -52.0 percent.

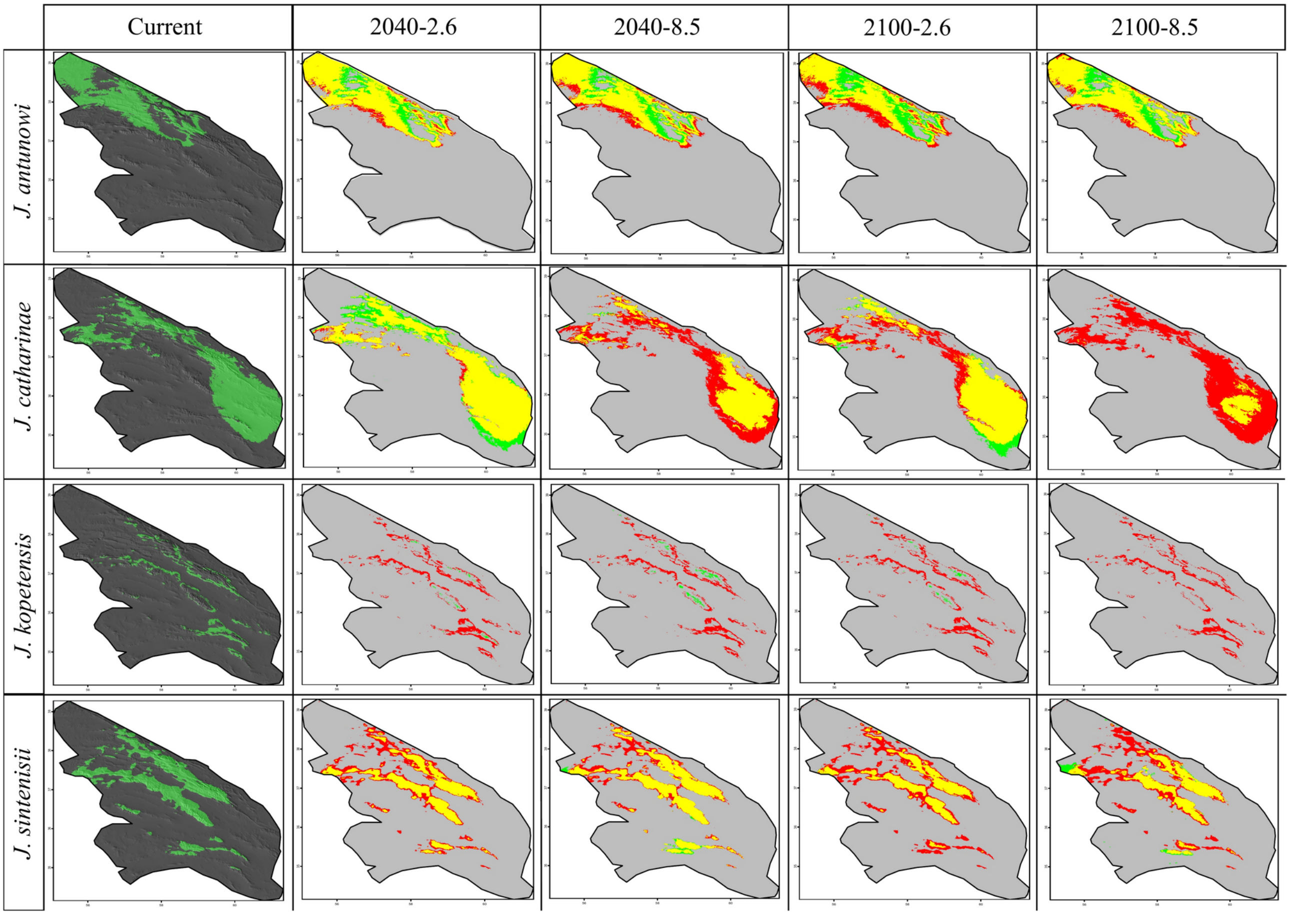

Fig. 5. Current and future distribution of endemics *Jurinea* of KK. The red areas represent lost habitat, the yellow stable, and the green gained habitats.

Acanthophyllum

The future range size changes for two *Acanthophyllum* species were modeled. The average range size change for *Acanthophyllum* is -36 percent (Table 1).

Acanthophyllum adenophorum

The habitat suitability map indicated that the current range size for *Ac. adenophorum*, is 65,173 km^2, within the elevation range of 1242–1762 m a.s.l. (Fig. 3; Table 1; Fig. 6). This species has a wide distribution in the lowlands of central KK, especially within the Kopet Dagh-Hezar Masjed and Aladagh-Binalood Mountains. Based on our results, *Ac. adenophorum* will shift upward under the climate change (2297–2678 m a.s.l.). The average range size changes for this species will be -67.8 percent.

Acanthophyllum speciosum

The ensemble habitat suitability map indicated that the current range size for *Ac. speciosum* is 22,076 km^2, within the elevation range of 1366–1892 m a.s.l. (Fig. 3; Table 1; Fig. 6). The suitable habitat is limited to the lowland ranges between the Binalood and Hezar Masjed Mountains. It is predicted that *Ac. speciosum* will experience an eastward shift as well as an upward migration (1743–2186 m a.s.l.) under climate change. The average range size changes for this species will be -4.0 percent.

Astragalus

The future range size changes for four *Astragalus* species was modeled. The average range size change for endemic cushion species of the genus *Astragalus* in the KK is -69.2 percent.

Astragalus cystosus

The ensemble habitat suitability map demonstrated that the current range size of *As. cystosus* is 2486 km^2, within the elevation range of 1656–1958 m a.s.l. (Fig. 4; Table 1; Fig. 6). The current suitable habitats of this narrowly distributed species are limited to the mid-range elevations of the Kashmar-Torbat Mountains. It is predicted that all of the current habitats of *As. cystosus* will be lost. The survival of this species would potentially rely only on the new habitats that would be gained upward (1842–2140 m a.s.l.) and westward. The average range size changes for this species will be -75.1 percent.

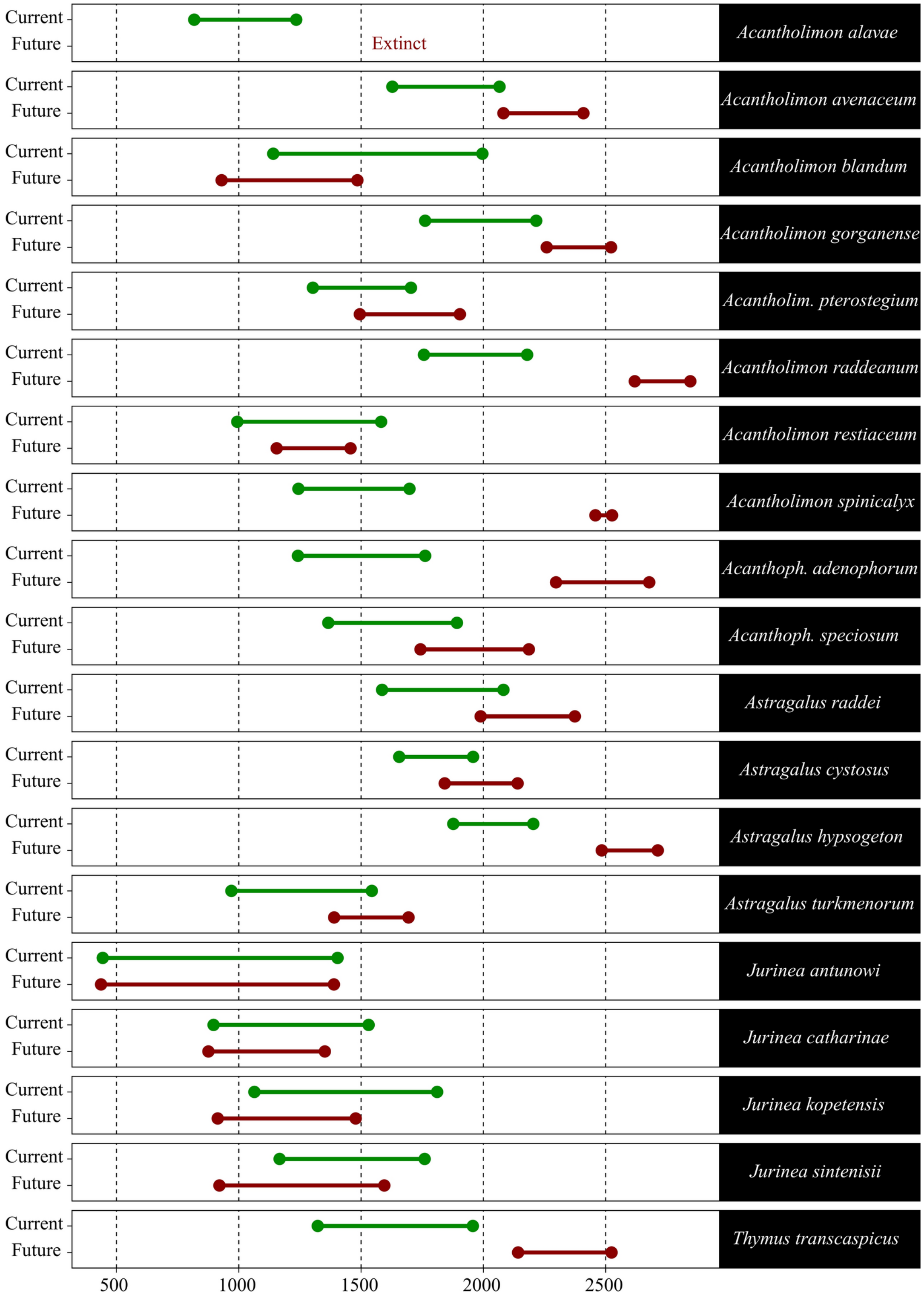

Fig. 6. Current and future elevational range of the modeled species. The data is the midspread of the retrieved from binary ensemble habitat suitability maps.

Astragalus hypsogeton

The ensemble habitat suitability map indicates that the area of currently suitable habitats for *As. hypsogeton* is 7509 km^2, within the elevation range of 1877–2204 m a.s.l. (Fig. 4; Table 1; Fig. 6). Although the existing documentation of this species is from the Aladagh and Binalood mountain ranges, this species has potential suitable habitats in Hezar Masjed, too. It is expected that *As. hypsogeton* will migrate eastward and shift upward (1989–2374 m a.s.l.) under climate change. The average range size changes for this species would be -89.9 percent.

Astragalus raddei
The ensemble habitat suitability map indicates that the area of currently suitable habitats for *As. raddei* is 28,383 km^2, within the elevation range of 1586–2082 m a.s.l. (Fig. 4; Table 1; Fig. 6). The species has a wide distribution and is found in most of the mountains and foothills of the KK, including the Kopet Dagh in Turkmenistan and Iran, Hezar Masjed, Aladagh, and Binalood mountain ranges. It is expected that *As. raddei* will shift eastward and experience an upward migration (1989–2374 m a.s.l.) under climate change. The average range size changes for this species will be -70.9 percent.

Astragalus turkmenorum
The ensemble habitat suitability map demonstrated that the current range size of *As. turkmenorum* is 15,380 km^2, within the elevation range of 970–1544 m a.s.l. (Fig. 4; Table 1; Fig. 6). The currently suitable habitats of this species are limited to the northern parts of the KK within the Kopet Dagh elevations. It is expected that *As. raddei* will shift westward and undergo an upward migration (1390–1694 m a.s.l.) along the altitudinal range under climate change. The average range size changes for this species will be -40.9 percent.

Jurinea
The future range size changes for four *Jurinea* species was modeled. The average range size change for endemic species of *Jurinea* is -42 percent (Table 1).

Jurinea antunowi
The ensemble habitat suitability map demonstrated that the current range size of *J. antunowi* is 38,317 km^2, within the elevation range of 444–1404 m a.s.l. (Fig. 5; Table 1; Fig. 6). The currently suitable habitats of this species are the Kopet Dagh in Turkmenistan and Iran, Hezar Masjed, Aladagh, and parts of the Binalood Mountains. It is predicted that *J. antunowi* will have no elevational responses to climate change (437–1389 m a.s.l.) and gain new habitats under climate change. The average range size changes for this species will be + 6.2 percent.

Jurinea catharinae
The ensemble habitat suitability map demonstrated that the current range size of *J. catharinae* is 59,744 km^2, within the elevation range of 897–1531 m a.s.l. (Fig. 5; Table 1; Fig. 6). The currently suitable habitats for this species are the eastern parts of the KK in the Hezar Masjed and Kopet Dagh, Binalood and kashmar-Torbat Mountains. It is expected that *J. catharinae* will experience an eastward shift as well as elevational range contraction (876–1352 m a.s.l.) under climate change. The average range size changes for this species will be -35.3 percent.

Jurinea kopetensis
The ensemble habitat suitability map demonstrated that the current range size of *J. kopetensis* is 10,574 km^2, within the elevation range of 1064–1811 m a.s.l. (Fig. 5; Table 1; Fig. 6). The currently suitable habitats of this species are limited to a low elevation of the western slopes of Hezar Masjed and the eastern slopes of Binalood Mountains. It is predicted that all of the current habitats of *J. kopetensis* will be lost. The survival of this species would potentially rely only on the new habitats that would be gained with an elevational range contraction (914–1478 m a.s.l.). The average range size changes for this species will be -95 percent.

Jurinea sintenisii
The ensemble habitat suitability map demonstrated that the current range size of *J. sintenisii* is 37,607 km^2, within the elevation range of 1167–1760 m a.s.l. (Fig. 5; Table 1; Fig. 6). This species has a relatively wide distribution range and has a suitable habitat in most of the KK's mountains in Turkmenistan and Iran. It is predicted that *J. sintenisii* will face elevational range contraction (921–1595 m a.s.l.) under climate change. The average range size changes for this species will be -42.7 percent.

Thymus
The single investigated species of *Thymus* will face a range size reduction (Fig. 3; Table 1).

Thymus transcaspicus
The ensemble habitat suitability map demonstrated that the current range size of *T. transcaspicus* is 30,274 km^2, within the elevation range of 1323–1957 m a.s.l. (Fig. 3; Table 1; Fig. 6). The currently suitable habitats of this species are delimited to the northern mountains of KK, including Aladagh, Kopet Dagh, and Hezar Masjed. It is expected that *T. transcaspicus* will move upward (2142–2524 m a.s.l.) under climate change. The average range size changes for this species will be -90.9 percent.

Discussion
Cushion plants are key species of the mountainous habitats[9,50]. The Irano-Anatolian biodiversity hotspot has vast mountain ranges[36]. However, there is no comprehensive study on the effects of climate change on cushion species of the region. We examined the impact of climate change on endemic cushions of KK, the eastern part of the Irano-Anatolian Biodiversity Hotspot.

How climate change affects the distribution of cushions in KK
Here, we observed that many cushions would experience range contraction due to climate change, with *A. alavae*, *J. kopetensis*, and *T. transcaspicus* facing more than 90 percent average range loss (most-vulnerable). On

the other hand, *A. restiaceum*, *Ac. speciosum*, and *J. antunowi* are species with negligible (-10 to + 10 percent average range size change) responses to climate change.

Change in habitats due to climate change is reported for all endemic species of the Irano-Anatolian Biodiversity Hotspot[51]. The majority of the species studied by the present study will shift upward along their elevational range, considering their spatial movement. The upward shift includes gaining new habitats for only six species (Figs. 2, 3, 4, 5); the remaining will lose their lower-elevation habitats and retain in their higher-elevation habitats. It should be noted that none of the modeled species can migrate to elevations above 3000 m a.s.l., revealing the upward boundary for these taxa and suggesting an increased competition in elevations below this limit. The upward migration is consistent with the results of several previous studies in different regions, e.g., Australia and Switzerland[52], China[53], the Zagros Mountains in Iran[54], and Iraq[55]. There are species that face elevational range contraction (i.e., those of *Jurinea* along with *Acantholimon restiaceum*), an extreme response was that of the *Acantholimon blandum* that will lose more than half of its current elevational range going downward. Species lose their upper elevation suitable habitats primarily because warming temperatures reduce the cool, stable environments they need, and other climate-related changes (e.g., reduced snow cover and altered precipitation) along with genetic erosion exacerbate this loss[56,57]. As well as experiencing the upward shift, seven species will move eastward, and two will move westward.

Comparing range shifts of the surveyed genera

Here, we modeled the response of 19 cushion species, arranged in five genera, to climate change. Although these plants share similar life forms[58], they inhabit various habitat types. *Acantholimon* comprises cushion-forming subshrubs possessing linear acuminate leaves that grow in poor stony and gravelly soils or on exposed rocks[59]. *Acanthophyllum* represents perennial subshrubs that predominantly form cushions with spiny leaves that grow in steppe and mountain habitats on stony or sandy hills and rocky slopes[43,60,61]. The species of these two are mostly growing together in higher elevation ranges of KK indicating their similar ecological needs. The different features of these genera lie in their phenological periods and microhabitat preferences that might be the potential influencing elements leading to their various responses to climate change. *Astragalus* exhibits high morphological variation, including short-living annual herbs to perennial herbs forming spiny cushions that grow in semi-arid and arid areas[62]. *Jurinea* comprises a genus of herbs and subshrubs most of which are steppe elements that grow in dry habitats at higher elevations[63]. *Thymus* is a genus of perennial herbs or subshrubs that mainly inhabit mountainous steppes and meadows growing in stony or gravelly soil and on rocks[64]. Our findings highlight that all modeled genera will face habitat loss. The average range size change for the studied genera is -64.04 percent (*Acantholimon*), -35.90 percent (*Acanthophyllum*), -69.21 percent (*Astragalus*), -41.71 percent (*Jurinea*), and -90.88 percent (*Thymus*). Here, we observed that genera whose species have a wide distribution across the elevational ranges have the lowest risk of range contraction. While those who inhabit a narrower elevational range would experience greater range contraction risk. This pattern is observed in monitoring, modeling, and experimental studies[17,65–68].

The majority of the endemic cushion species of the KK (22 out of 34) belong to the genera *Acantholimon* and *Acanthophyllum* (Supplementary 2). Members of these genera constitute essential cushions of the mountainous habitats of the KK. We modeled the response of eight *Acantholimon* and two *Acanthophyllum* species to climate change. Thus, further studies need to be conducted to examine how climate change will affect those species of *Acantholimon* and *Acanthophyllum* in the region that failed to be modeled by the present study.

A closer look at endemic cushions

Acantholimon

We modeled the response of eight endemic species of *Acantholimon* to climate change. The narrow-ranged *A. alavae*, is predicted to face extinction in the future (Fig. 2; Table 1). For this species, preserving genetic diversity through seed banks and botanical gardens is necessary. Additionally, planning assisted migration programs for *A. gorganense*, *A. raddeanum*, *A. blandum* in their gained habitats is recommended.

Acanthophyllum

Among the two endemic *Acanthophyllum* species modeled in our study, *Ac. adenophorum* will experience range contraction, while *Ac. speciosum* will show a negligible response in the future. A previous survey on *Ac. squarrosum* (an Irano-Turanian element) predicts that this species would experience a northward shift and gain new habitats in the coming decades[30].

Astragalus

All of the four surveyed species will experience range contraction. (Table 1). For *As. cystosus*, *As. hypsogeton*, and *As. raddei* assisted migration to higher elevation or newly-gained habitats is necessary. Range contraction was also predicted for cushion-forming *As. adscendens*[69], *As. verus*[31], *As. gossypinus*[70], *As. nuratensis*[71], and *As. variabilis*[72].

Jurinea

Seedling preservation and assisted migration is necessary to ensure the survival of *J. kopetensis.* Climate change has not yet been studied on other species of this genus in the Irano-Turanian region. Volis and Beshko[71] reported that the climate space for *J. zakirovii* will be potentially suitable and translocation to predicted suitable habitats can conserve this endemic plant of Uzbekistan.

Thymus

Thymus transcaspicus is one of the highly sensitive species to climate change. Habitat preservation, along with botanical garden preservation, is necessary to ensure the survival of this cushion plant.

Conclusions

Cushions are ecosystem engineers in mountainous ecosystems, and altering their suitable habitats will completely modify the ecosystems. Our study provides insights into the possible responses of endemic cushions of the KK to climate change. All of the 19 cushions studied by the present research, will shift upward along their elevational range. Except for three, the rest of the examined species will face range contraction. We urge reinforcing the existing populations and implement fencing in various parts of these relatively disturbed mountain ranges. Effective conservation of the three highly vulnerable endemic cushions *A. alavae*, *J. kopetensis* and *T. transcaspicus*, is crucial. In the context of climate change, certain cushion species, i.e., *A. restiaceum*, *Ac. speciosum* and *J. antunowi*, appear to be minimally affected. To expedite the sustainable recovery of degraded mountainous landscapes in the KK region, we recommend the introduction of these climate-change-resilient species in their potentially suitable habitats. Future studies should include additional sampling of the endemic cushion species that we could not model their responses to climate change.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on request.

Received: 23 June 2024; Accepted: 28 April 2025
Published online: 08 May 2025

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Acknowledgements
This work was funded by the Research Council of Ferdowsi University of Mashhad as a postdoctoral research project of the first author. We acknowledge the help of the botanists from the Herbarium of Ferdowsi University of Mashhad (FUMH).

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Z. Atashgahi: Writing – original draft, Methodology, Formal analysis; M.B. Erfanian: Methodology, Formal analysis, Writing – review & editing; H. Moazzeni: Methodology, Writing – review & editing; G. Shemirani: Formal analysis; A. Pirani: Methodology, Writing – review & editing, Project administration.

Funding
Ferdowsi University of Mashhad.

Declarations

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-00453-0.

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