

Predicting the habitat suitability and niche dynamics of two *Ziziphus* species in response to climate change

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Abstract

Climate change, a global threat of utmost significance, has the potential to trigger shifts in biodiversity distribution and the emergence of novel ecological communities. For species with limited dispersal abilities or geographical barriers within their range, niche conservatism can further constrain their ability to colonize and thrive in future suitable habitats, rendering them more vulnerable to the effects of global climate change. In this study, an ensemble modeling framework and climatic niche dynamics analysis were employed to forecast the impact of climate change on climatic niche dimensions and transferability of two indicator species, namely, *Ziziphus spina-christi* and *Ziziphus nummularia*, in Iran. Our analysis revealed that, under optimistic and pessimistic climate change scenarios, the habitat suitability for *Z. spina-christi* will expand during 2041-2070 and 2071-2100, predominantly towards higher latitudes. In contrast, *Z. nummularia* is anticipated to experience a general decline in habitat suitability during the same periods and climate scenarios, resulting in the loss of portions of its southern range. Our examination of climatic niche dynamics unveiled a relatively low observed niche overlap between the two species. Randomization tests further underscored the adherence of these species to their historical niches, suggesting challenges in adapting to changing climatic conditions. The integration of predictive models and niche dynamics analysis indicates that these species may encounter difficulties migrating to the tracked niches in distant habitats due to their preserved niches. Given the high sensitivity of arid ecosystems to environmental disturbances and slow recovery rates, the repercussions for arid land biodiversity are indeed profound and irrevocable. Conservation and management measures, including identifying priority areas and creating artificial habitats, are crucial to protect these species' habitats. The study's conclusions are valuable for biodiversity conservation authorities, local stakeholders, and individuals dedicated to preserving *Ziziphus* habitats within the study area.

Predicting the habitat suitability and niche dynamics of two *Ziziphus* species in response to climate change

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Keywords:

Species Distribution Models; Niche Conservatism; Niche Dynamics; Climate Warming; Arid Ecosystems

1. Introduction

The Earth's average temperature is projected to increase by 0.3–4.8 °C by the close of the twenty-first century, as reported by the Intergovernmental Panel on Climate Change (Stocker et al., 2014). Human-induced climate change represents a destructive force that directly and indirectly threatens biodiversity. The rising trend in climate change has wrought irrevocable changes in ecosystems' structure, composition, services, and stability (Thuiller, 2007; Weiskopf et al., 2020). Various species respond differently to this phenomenon, including adaptation, phenology alterations, and the pursuit of suitable climatic conditions (Robinet & Roques, 2010; Couet et al., 2022). Species failing to adapt to these altered conditions may attempt migration, but if they cannot disperse, they face the grim prospect of local or global extinction (Thuiller et al., 2008; Bellard et al., 2012). Climate change can potentially provoke shifts in species' distribution ranges at varying scales, affecting individual populations and entire ecosystems (Karl et al., 2009). Numerous studies have documented the occurrence of "uphill retreats" in various taxa as a response to climate change (Thomas et al., 2006).

Given the pervasive impact of ongoing climate change across the globe, recent research has been intensely focused on predicting its effects on species' ranges. These efforts aim to develop management strategies to mitigate adverse consequences (Huang et al., 2023; Chowdhury, 2023; Song et al., 2023). Ecologists have underscored the challenge of biodiversity forecasting over the past two decades and have called for adopting predictive ecology (Mouquet et al., 2015). Over nearly four decades, "species distribution models" (SDMs) were initially conceived as snapshots of species distribution (Stanton et al., 2012). Today, SDMs are recognized as one of the most widely employed tools for evaluating species vulnerability in response to environmental changes (Guisan & Zimmermann, 2000; Zachariah Atwater & Barney, 2021). SDMs find application in diverse areas, including the protection of endangered species, habitat management and restoration, environmental risk assessment, invasive species control, and forecasting species' range expansion or contraction under the influence of climate change (Franklin, 2010; Zurell et al., 2020). Numerous studies have explored the repercussions of climate change on species' spatial distribution (e.g., Behroozian et al., 2020; Baumbach et al., 2021; Karami et al., 2022; Naqinezhad et al., 2022; Wani et al., 2022; Shaban et al., 2023). The variability in predictions from different SDMs often presents challenges in result interpretation. To mitigate the uncertainty in SDM forecasts, a practical approach is to employ an ensemble modeling framework, enhancing projections' precision (Araujo & New, 2007; Marmion et al., 2009; Naimi et al., 2022).

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Addressing the impact of global changes on species' niche dynamics poses a significant challenge for ecologists. This challenge underscores the necessity of employing techniques for analyzing and quantifying distinctions among species' niches. Ecologists have developed various approaches and metrics for scrutinizing species' niche dynamics across spatial and temporal scales (Broennimann et al., 2012). A central question in niche theory revolves around whether species maintain or diverge from their ecological niches (Vaissi and Rezaei, 2022). Niche conservatism, a biological concept, characterizes the inclination of species to adhere to their ancestral niches (Wiens & Graham, 2005; Vaissi & Rezaei, 2022; Du et al., 2023; Han et al., 2023). Climate change has brought niche conservatism into focus as a potential concern and threat to organisms (Wiens et al., 2010; Aguirre-Gutierrez et al., 2015). Niche divergence occurs when species occupy niches distinct from their ancestral ones (Vaissi and Rezaei, 2022). While niches' distribution and speciation patterns often remain conserved over time, divergence drives species diversity along ecological gradients (Wiens & Graham, 2005; Vaissi & Rezaei, 2022). Given the rapid pace of global change, understanding whether species alter their niches over time and space has gained paramount importance. Consequently, various tests and criteria have been devised to quantify niche shifts (Guisan et al., 2014). Niche conservatism challenges the transferability of Species Distribution Models (SDMs) predictions (Zachariah Atwater and Barney, 2021). One of the most crucial applications of niche dynamic analysis is the potential to transfer ecological niches, using SDMs, to new geographical and temporal scales, thereby facilitating SDM-based management applications. Such spatial and temporal model transfers find utility in designing conservation areas, introducing new species, and predicting species responses to climate change (Zhu & Peterson, 2017; Yates et al., 2018; Sequeira et al., 2018; Liu et al., 2022).

The genus *Ziziphus* sp. (Rhamnaceae) encompasses approximately 100-170 species of deciduous and evergreen trees and shrubs, primarily distributed in tropical and subtropical regions (Saied et al., 2008; Baghazadeh-Daryai et al., 2017). Among these species, Christ's thorn jujube (*Ziziphus spina-christi*) stands out as a native and pivotal species in the Middle East, displaying remarkable resilience to drought and heat stress. Its global distribution spans North Africa, the Arabian Peninsula, India, Lebanon, Iraq, Pakistan, Afghanistan, and Iran (Saied et al., 2008; Rojas-Sandoval, 2022). In Iran, *Z. spina-christi* is nearly ubiquitous within the Sahara-Sindian (Khalijo-Omanian) region. Another noteworthy species, the Wild jujube (*Z. nummularia*), is a deciduous shrub found in India, Pakistan, Iraq, and Iran (Pandey et al., 2010). Its distribution primarily concentrates in the southwest of Iran. Both *Z. spina-christi* and *Z. nummularia* play a pivotal role in soil and water conservation, wind and water erosion control, and overall ecosystem sustainability in arid and semi-arid environments (Saied et al., 2008; Pandey et al., 2010; Rojas-Sandoval, 2022).

Data concerning the potential impacts of climate change on these invaluable species remain limited. Predicting changes in species' ranges under climate shifts is essential to guide conservation efforts effectively. In this study, Species Distribution Models (SDMs) were employed to forecast the potential consequences of climate change on the range expansion or contraction of the two *Ziziphus* species while considering their climate niche divergence or conservatism.

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Our primary objectives were to address the following questions: (1) How will the climatic niches' dimensions and spatial patterns of the two *Ziziphus* species change in response to climate warming? (2) Which evolutionary hypotheses govern these two species—conservatism or divergence? (3) Do these two species remain faithful to their established climatic niches, and what implications does this have for their transferability?

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2. Materials and Methods

2.1. Study Area

Iran, encompassing a vast area of 1,648,000 km², occupies a strategic position in southwest Asia, situated

between 25deg-40degN and 44deg-63degE. The country exhibits diverse climatic conditions, with annual temperature fluctuations from 20degC to 50degC and annual rainfall varying between 120 mm to 2000 mm (Karimi et al., 2018; Farashi & Karimian, 2021). Notably, Iran boasts an extraordinary wealth of plant species due to its unique geographical location, serving as a confluence point for three prominent phytogeographical regions: the Irano-Turanian, Saharo-Sindian, and Europe-Siberian regions. This geographical convergence has rendered Iran's plateau a cradle for evolution and a sanctuary for some of the planet's oldest biodiversity. It functions as a crucial ecological bridge, facilitating the exchange of flora and fauna between Eurasia's eastern and western regions (Noroozi et al., 2019).

The Saharo-Sindian phytogeographical region stretches across a vast expanse, encompassing the western territories of India, Pakistan, the southern periphery of Iran, including the Persian Gulf and the Oman Sea, the Arabian Peninsula, and Iraq, ultimately extending into North Africa. In Iran, this region is referred to as the Khalijo-Omanian zone, which encompasses seven provinces: Khuzestan, Kohgiluyeh-Boyer Ahmad, Fars, Bushehr, Hormozgan, Kerman, and Sistan-Baluchistan, all situated along the Persian Gulf. It is worth noting that the Khalijo-Omanian arid ecosystem experiences an average annual rainfall of less than 100 mm (Naderi Beni et al., 2021). The region's summers are characterized by their protracted duration and extreme, parched heat (Sagheb Talebi et al., 2014).

2.2. Species Occurrence Localities

The primary vegetation map of *Z. spina-christi* and *Z. nummularia* was sourced from the Iran Research Institute of Forest and Rangeland (IRIFR) from 1988 to 2016. This map served as the foundation for delineating the spatial distribution of these two species and identifying their respective presence locations. Comprehensive field surveys were conducted from October 2021 to April 2022 to gather information on the presence locations of both *Z. spina-christi* and *Z. nummularia*. The efforts acquired 419 presence locations for *Z. spina-christi* and 161 presence locations for *Z. nummularia*.

To mitigate spatial autocorrelation and prevent model overfitting, a spatial filter with a radius of 1 kilometer was applied, utilizing the SDM Toolbox as described by Mahmoodi et al. in 2022. Additionally, the global Moran's I statistic was computed, following the methodology outlined by Dormann et al. in 2007, using ArcGIS software (version 10.8.1). Subsequently, a refined dataset consisting of 348 presence locations for *Z. spina-christi* and 130 presence locations for *Z. nummularia* was used to construct the climate niche models for these species (see Fig. 1).

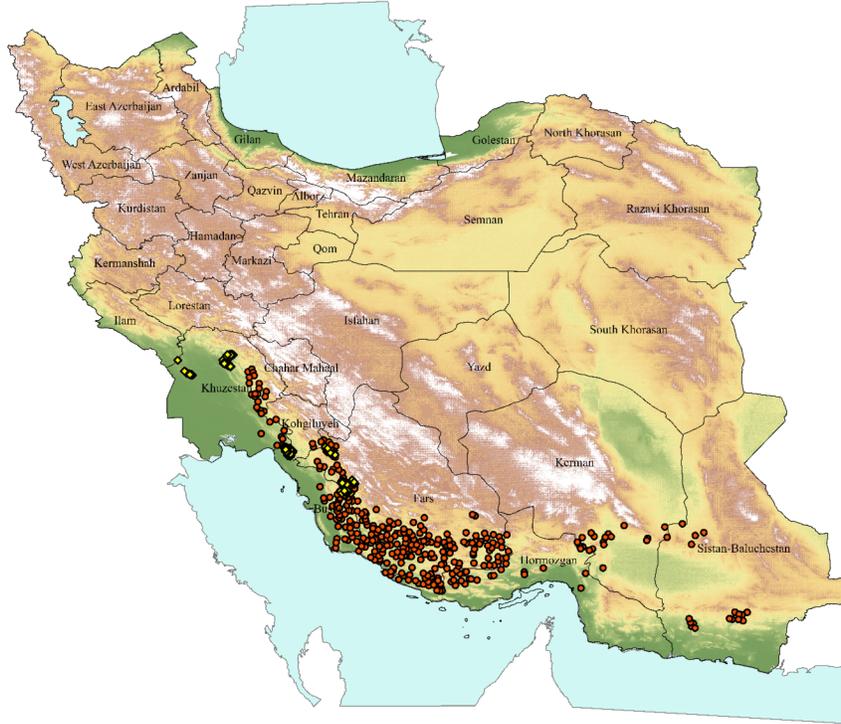


Fig 1 . Location of the study area (a), presence localities of *Z. spina-christi* (b), and *Z. nummularia* (c).

2.3. Predictor variables

A comprehensive dataset comprising 19 bioclimatic variables, with a spatial resolution of 30'' (approximately 1 km) was obtained from CHELSA ver. 2.1 (<http://chelsa-climate.org>) (Karger et al., 2017) to delineate the existing climatic niche of various species. Additionally, future climate variables were obtained from the 6th assessment report of the Intergovernmental Panel on Climate Change (IPCC AR6) for two distinct Shared Socioeconomic Pathways scenarios (SSP-126 and SSP-585). These climate projections were derived using the Global Circulation Model (GCM) of GFDL-ESM4 (Shaban et al., 2023; Mathias et al., 2023) and span two temporal scales: 2041-2070 and 2071-2100. To address collinearity issues among these variables, hierarchical cluster analysis was employed with Pearson's correlation coefficient (with a cutoff set at 0.7) (Gallego-Narbón et al., 2023). This approach was executed using the 'remove collinearity' function in the R package 'virtuallspecies' (Leroy et al., 2016; Louppe et al., 2020; Almeida et al., 2023). Ultimately, a total of seven predictors were retained in the model, encompassing isothermality (bio3), maximum temperature of warmest month (bio5), temperature annual range (bio7), mean temperature of wettest quarter (bio8), precipitation seasonality (bio15), precipitation of wettest quarter (bio17), and precipitation of coldest quarter (bio19).

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2.4. Climate niche modeling

Three distinct algorithms were employed within an ensemble modeling framework to assess the current and future climate niche of the species. These algorithms included the Generalized Linear Model (GLM) proposed by Nelder and Wedderburn in 1972, the Generalized Boosted Model (GBM) introduced by Friedman in 2001, and the Maximum Entropy (MaxEnt) method developed by Phillips and others in 2006, as outlined by Breiner et al. in 2015.

To generate pseudo-absence data, 10,000 background points were created by randomly sampling at a specific

distance from the presence points, following the methodology suggested by Naimi et al. in 2022 and Collart et al. in 2023.

The evaluation process involved splitting the occurrence data into two sets: 70% for calibration and 30% for evaluation, following the guidelines set by Ngila et al. in 2023 and Collart et al. 2023. This entire procedure was repeated ten times to ensure the creation of predictions independent of the training data, as recommended by Guisan et al. in 2017.

For all three modeling algorithms, the default parameters provided by the biomod2 R package, as detailed by Thuiller et al. in 2009, were utilized.

The performance of the models was assessed using two distinct evaluation metrics: firstly, the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve, as introduced by Jiménez-Valverde in 2012, and secondly, the True Skill Statistics (TSS) method developed by Allouche et al. in 2006.

Finally, an ensemble habitat suitability map was created using a weighted average approach for two species, following the procedure described by Ahmadi et al. in 2023. The predictions derived from the ensemble models were classified into five categories: (1) unsuitable ([?] 0.2), (2) low (0.21-0.4), (3) moderate (0.41-0.6), (4) high (0.61-8), and (5) excellent ([?] 0.81). Notably, the high and excellent categories were considered acceptable thresholds for the analysis. Top of Form

2.5. Climatic niche divergence

The study utilized the framework introduced by Broennimann et al. in 2012, which is available as part of the R package Ecospat (Di Cola et al., 2017). This framework analyzed the overlap in climatic niches between two distinct species. The analysis involved extracting data from 19 bioclimatic variables at the locations where these species were recorded. This data extraction was done using the kernel density function developed by Broennimann et al. in 2012, implemented within the modified principal component analysis (PCA-env) multivariate space.

The resulting density grids were the foundation for calculating the climatic niche overlap, assessed using Schoener's D metric, a well-established method (Schoener, 1970; Warren et al., 2008). Schoener's D metric ranges from 0 to 1, where 0 indicates no overlap between the niches of the two species, and 1 signifies complete overlap (Broennimann et al., 2012; Hemami et al., 2020; Sillero et al., 2022).

Two randomization tests were applied to determine whether there was climatic niche divergence or conservation between the two species: niche equivalency (or identity) and niche similarity (or background). The niche equivalency test aimed to assess whether the climatic niches of the two species in their respective geographic regions were similar (Broennimann et al., 2012; Hemami et al., 2020; Oboudi et al., 2021). However, since the niche equivalency test did not consider the environmental background, the niche similarity test was conducted in two directions. This test aimed to determine whether the climatic niche of one range was significantly more similar to the niche of another range than would be expected by chance (Warren et al., 2008; Broennimann et al., 2012). The null hypothesis of the niche similarity test was rejected when the observed overlap (Schoener's D) was significantly lower than the simulated values ($P < 0.05$) (Broennimann et al., 2012), indicating that the climatic niche of the two species was not more similar than what would occur randomly (DeChaine et al., 2014).

In order to provide a more comprehensive understanding of climate niche dynamics, three additional indicators were computed: "niche stability," "niche expansion," and "niche unfilling" (Datta et al., 2019; Bates & Bertelsmeier, 2021).

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3. Results

3.1. Current and future climate niche modeling

The models demonstrated outstanding predictive performance for both of the species under consideration. The ensemble predictions exhibited robustness in forecasting the potential climate niches of these species. Notably, the top-performing models for *Z. spina-christi* included GBM (AUC = 0.97, TSS = 0.89), MaxEnt (AUC = 0.97, TSS = 0.85), Ensemble (AUC = 0.97, TSS = 0.86), and GLM (AUC = 0.93, TSS = 0.77). Conversely, for *Z. nummularia*, the most effective algorithms were MaxEnt (AUC = 0.99, TSS = 0.96), GBM (AUC = 0.99, TSS = 0.98), Ensemble (AUC = 0.99, TSS = 0.97), and GLM (AUC = 0.98, TSS = 0.95).

The key factors influencing the climate niche of *Z. spina-christi*, as determined by the contribution of three algorithms, were the maximum temperature of warmest month (38.94%), precipitation of coldest quarter (14.37%), and precipitation seasonality (13.73%). In the case of *Z. nummularia*, precipitation of coldest quarter, maximum temperature of warmest month, and isothermality played the most significant roles in predicting its distribution, accounting for 32.65%, 18.70%, and 13.92% of the contribution, respectively.

The habitat potential distribution map, created using the ensemble framework, indicated that under current climatic conditions, approximately 161×10^3 km² (9.78%) of the study area (covering 1,648,195 km²) – encompassing seven southern provinces, namely Khuzestan, Kohgiluyeh-Boyer Ahmad, Fars, Bushehr, Hormozgan, Kerman, and Sistan-Baluchistan along the Persian Gulf in the Saharo-Sindian phytogeographical region – is predicted to be suitable for *Z. spina-christi*. This suitability falls within the good (0.61-0.8) and excellent (0.81-1.0) threshold classes.

For *Z. nummularia*, the suitable habitat area was estimated to be about 71,684 km² (4.34%) of the country, with 78,599 km² (4.76%) falling within the sound and excellent suitability classes. Notably, *Z. nummularia*'s distribution covers a smaller area compared to *Z. spina-christi*, spanning approximately 23,330 km² (1.41%) of the country's area under current climatic conditions, primarily concentrated in the southwestern and western regions of Iran. The acceptable suitability threshold for *Z. nummularia* was defined with an estimated 16,777 km² (1.01%) and 14,650 km² (0.88%) of the country falling into the good and excellent suitability classes, respectively (Fig. 2). Top of Form

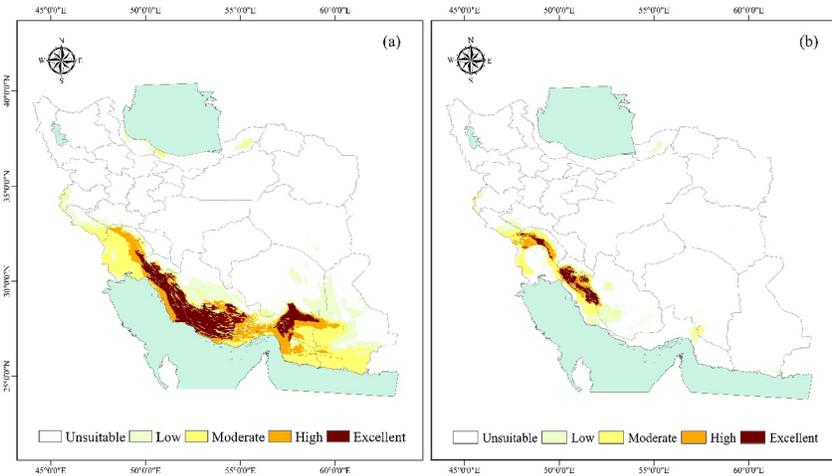


Fig 2. Habitat suitability map in the current climate conditions based on the ensemble model for (a) *Z. spina-christi* and (b) *Z. nummularia*.

The study projected the ensemble model into future climate scenarios, revealing an overall distribution pattern for habitat suitability. A decrease in unsuitable habitat classes was observed in the future potential distribution of *Z. spina-christi*, considering two climatic scenarios (SSPs) across two time periods (2041-2070 and 2071-2100). In areas with acceptable suitability, the range showed fluctuations, with both increases and

decreases. Nevertheless, the overall trend pointed towards an increase in suitable habitat. The predictions indicated that under the climate scenario SSP-585, a suitable habitat will emerge in South Khorasan province during 2071-2100 in regions with no previous records of this species. Conversely, regions likely to become unsuitable in the future encompass parts of Khuzestan, Kerman, and Southern Fars provinces. These areas will experience a decrease in the spatial integrity of the predicted habitat, resulting in fragmentation (as illustrated in Fig. 3 and detailed in Table 1 and Table 3). **Top of Form**

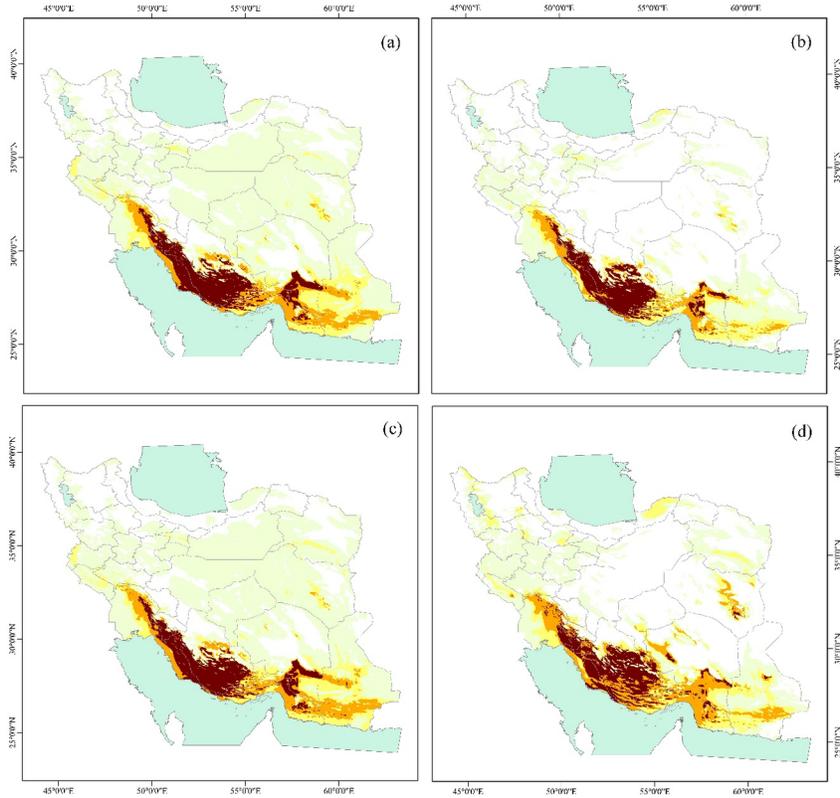


Fig 3 . Tracking the suitable habitats of *Z. spina-christi* in the face of climate change scenarios. (a) SSP-126; 2041-2070 (b) SSP-585; 2041-2070 (c) SSP-126; 2071-2100 and (d) SSP-585; 2071-2100.

Table 1. Changes in the suitable habitat area for *Z. spina-christi* under climate change scenarios.

Habitat Suitability

Acceptable Threshold GCM	Acceptable Threshold Scenario (SSP)	Acceptable Threshold Time periods	Acceptable Threshold Unsuitable km ² /percent	Acceptable Threshold Low km ² /percent	Acceptable Threshold Moderate km ² /percent	Acceptable Threshold High km ² /percent	Acceptable Threshold Excellent km ² /percent
GFDL-ESM4	SSP126	Current	1240462.92 75.26%	119560.72 7.25%	137887.53 8.36%	71684.75 4.34%	78599.06 4.76%
		2041-2070	461651.65 28%	838523.35 50.87%	141562.00 8.58%	98866.25 5.99%	107591.73 6.52%
		2071-2100	473694.79 28.74%	837523.43 50.81%	132180.92 8.01%	103249.18 6.26%	101546.66 6.16%

SSP585	2041-2070	1056198.55 64.08%	325560.59 19.75%	104995.74 6.37%	68993.32 4.18%	92446.76 5.60%
	2071-2100	847292.15 51.40%	410215.00 24.88%	159237.61 9.66%	133054.56 8.07%	98395.65 5.96%

Regarding *Z. nummularia*, habitat suitability is expected to decline under climate scenarios SSP-126 and SSP-585 across 2041-2070 and 2071-2100. The suitable areas for this species, particularly under scenario SSP-585 in 2071-2100, will be severely impacted in Fars, Bushehr, and Kohgiluyeh-Boyer Ahmad, leading to almost destruction. Conversely, a suitable habitat will emerge in the province of Ilam at a higher latitude (as illustrated in Fig. 4 and detailed in Table 2 and Table 4).

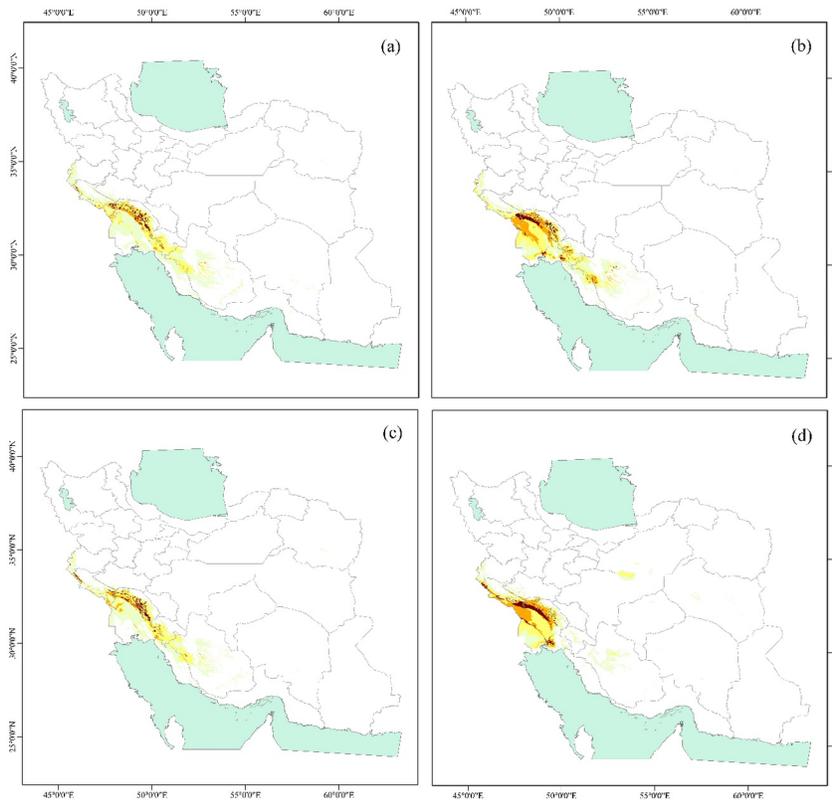


Fig 4. Tracking the suitable habitats of *Z. nummularia* in the face of climate change scenarios. (a) SSP-126; 2041-2070 (b) SSP-585; 2041-2070 (c) SSP-126; 2071-2100 and (d) SSP-585; 2071-2100.

Table 2. Changes in the suitable habitat area for *Z. nummularia* under climate change scenarios.

Habitat Suitability

Acceptable Threshold GCM	Acceptable Threshold Scenario (SSP)	Acceptable Threshold Time periods Current	Acceptable Threshold Unsuitable km ² /percent	Acceptable Threshold Low km ² /percent	Acceptable Threshold Moderate km ² /percent	Acceptable Threshold High km ² /percent	Acceptable Threshold Excellent km ² /percent
			1540626.75 93.47%	38290.06 2.32%	37850.30 2.29%	16777.73 1.01%	14650.14 0.88%

SSP126	2041-2070	1542212.54	63377.74	31289.12	8050.78	3264.80
		93.56%	3.84%	1.89%	0.48%	0.19%
SSP585	2071-2100	1557910.33	49944.83	28696.07	7914.23	3729.52
		94.52%	3.03%	1.74%	0.48%	0.22%
SSP126	2041-2070	1536874.47	44609.70	42178.90	18702.70	5829.22
		93.24%	2.70%	2.55%	1.13%	0.35%
SSP585	2071-2100	1559412.41	34875.48	28893.56	17978.08	7035.44
		94.61%	2.11%	1.75%	1.09%	0.42%

Table 3. Range changes suitable habitat for *Z. spina-christi*.

Scenarios	Unsuitable %	Low %	Moderate %	High %	Excellent %	Mean change%
SSP126 2041-2070	- 47.25	+ 43.62	+ 1.64	+ 0.22	+ 1.75	+ 37.80
SSP585 2041-2070	- 11.17	+ 12.49	- 0.16	- 1.99	+ 0.84	+ 8.94
SSP126 2071-2100	- 46.52	+ 43.56	+ 1.91	- 0.34	+ 1.39	+ 37.21
SSP585 2071-2100	- 23.85	+ 17.63	+ 3.72	+ 1.29	+ 1.20	+ 19.08

Table 4. Range changes suitable habitat for *Z. nummularia*.

Scenarios	Unsuitable %	Low %	Moderate %	High %	Excellent %	Mean change%
SSP126 2041-2070	+ 0.09	+ 1.52	- 0.39	- 0.52	- 0.69	- 0.07
SSP585 2041-2070	- 0.22	+ 0.38	+ 0.26	+ 0.11	- 0.53	+ 0.18
SSP126 2071-2100	+ 1.04	+ 0.70	- 0.55	- 0.53	- 0.66	- 0.83
SSP585 2071-2100	+ 1.13	- 0.20	- 0.54	+ 0.07	- 0.46	- 0.91

3.2. Climate niche divergence/conservatism

The initial two axes of PCA accounted for 45.44% and 23.16% of the total variance, respectively. The climate niche overlap between the two species was relatively low, with Schoener’s D value being 0.30. Notably, the outcomes of the niche equivalency test, as depicted in Fig. 5, revealed that the actual overlap value was significantly higher (Schoener’s D) compared to the simulated niche ($P < 0.009$). This suggests that the similarity in climate niches between the two species is more pronounced than what would be expected by random chance. Furthermore, as per the niche similarity test, the observed niche overlap did not exhibit a significant increase compared to what would be anticipated based on the environmental conditions available to each species in both directions ($P(1 \rightarrow 2) < 0.07$, $P(2 \rightarrow 1) < 0.06$). When calculating climatic niche dynamic indices, which indicate niche shifts in similar conditions, it becomes evident that there is a high degree of niche stability at 96%. Additionally, the degree of niche unfilling stands at a moderate 43%, while niche expansion is notably low at 3%.

A comprehensive analysis of climatic niche quantitative tests underscores that *Z. spina-christi* and *Z. nummularia* exhibit limited overlap (Schoener’s D = 30%) (Broennimann et al., 2012; Ahmad et al., 2019; Datta et al., 2019; Xian et al., 2023) (as illustrated in Fig. 5 and detailed in Table 5).

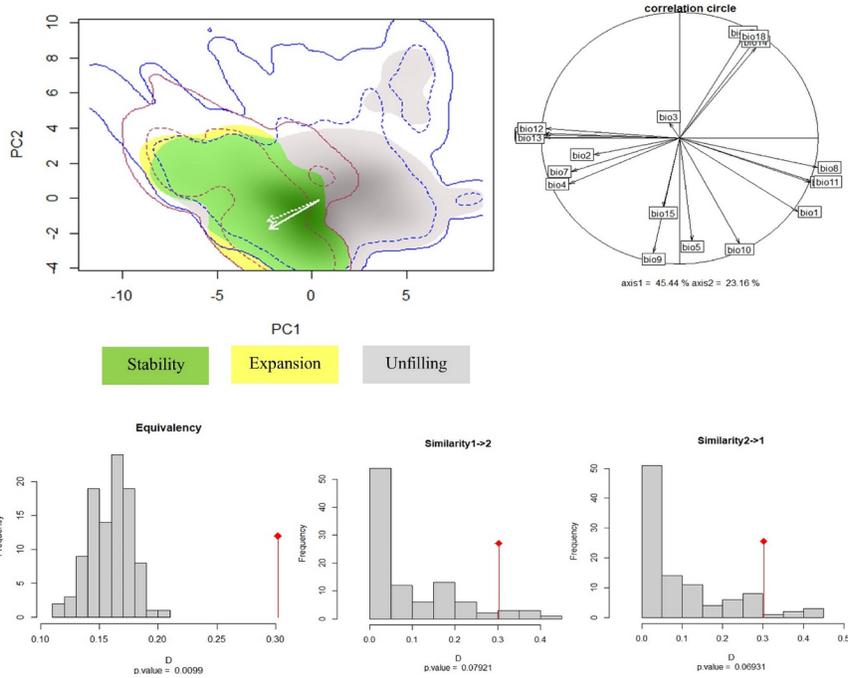


Fig 5. A visualization of realized niche dynamics, comparing the two *Ziziphus* species within the climatic space based on Principal Component Analysis (PCA-env). In this two-dimensional plot, colors signify niche characteristics, with green indicating stability, gray representing unfilling, and yellow signifying expansion. White arrows denote the shift in the center of the species’ niche (solid) and describe the background conditions (dashed). The darker shading indicates the density of species occurrences in their historical niche. The solid line delineates the full range (100%) of climatic niche breadths for pairs of compared species. Conversely, the dashed line represents 50% of the environmental density, marking the boundary climate conditions for defining the niches of *Z. spina-christi* (blue) and *Z. nummularia* (red). The results of the niche equivalency and niche similarity tests are visually presented with histograms showcasing the simulated overlap (gray bars) and the observed overlap (red diamonds). Notably, the results are non-significant ($P > 0.05$), indicating no significant difference between the simulated and observed niche overlaps.

Bottom of FormTable 5. Pairwise niche overlap indices and niche shift metrics.

Comparison	Comparison	Niche shift metrics	Niche shift metrics	Niche shift metrics	Niche shift metrics
Niche 1	Niche 2	D	Expansion	Stability	Unfilling
ZISP	ZINU	0.30	0.03	0.96	0.43

0.009*

(Significantly * indicates $P < 0.05$)

4. Discussion

Climatic factors are the paramount determinant influencing the spatial distribution of species on a broad scale (Thuiller et al., 2008). Consequently, alterations in climate conditions stemming from human activities can adversely affect species’ future distribution and survival. Among various ecosystems, arid and semi-arid regions encompass roughly one-third of the Earth’s surface and exhibit heightened vulnerability to the evolving climate. To effectively plan and execute initiatives for biodiversity conservation, it becomes imperative to forecast the potential habitat range of species and delineate their spatial patterns under future climate conditions. This is particularly crucial for the hot and arid Saharo-Sindian ecosystem, characterized

by low resilience. In the study, the task of predicting the impact of climate change on the spatial distribution of *Z. spina-christi* and *Z. nummularia* while also assessing their spatial niche segregation was undertaken. The findings carry substantial implications for the conservation of these species (Harris et al., 2006; Ghehsareh Ardestani et al., 2021).

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Our research revealed that variables linked to temperature exerted the most influence on predicting the spatial range of *Z. spina-christi*. In the case of *Z. nummularia*, the most influential factors were the precipitation during the coldest quarter, maximum temperature during the warmest month, and isothermality. Notably, Ghehsareh Ardestani et al. in (2021) conducted a study in southern Iran focusing on the distribution of *Haloxylon persicum* and highlighted the pivotal role played by temperature-related variables in determining the species' range. It is worth noting that our findings diverge from those presented by Ksiksi et al. (2019). According to their research, the three primary predictors influencing the geographical distribution of *Ziziphus spina-christi* in the United Arab Emirates encompassed precipitation during the coldest quarter, annual precipitation, and mean diurnal range, accounting for approximately 80% of the predictions.

4.1. Range shift of *Z. spina-christi* and *Z. nummularia*

The present geographical range of *Z. spina-christi* is primarily concentrated in the southern regions of Fars, parts of Bushehr, the southern and western portions of Khuzestan, as well as areas to the south of Kohgiluyeh-Boyer Ahmad and Kerman provinces. Climatically suitable habitats are limited in the country's southeastern part, specifically in Hormozgan and Sistan-Baluchistan. The Khalijo-Omanian zone, a subregion of the Saharo-Sindian region in Iran, encompasses this area. This phytogeographical region can be further divided into two distinct territories: Khalijo-Omani. These territories exhibit ecological differences, with varying climates and higher temperatures along the Omani coasts. The average temperature in this zone tends to increase from west to east (Sagheb Talebi et al., 2014).

Within the Khaliji territory, *Z. spina-christi* plays a pivotal role. In the Omani territory, the prevailing plant community consists mainly of *Acacia* genus, which are paramount in the region's woody flora (Sagheb Talebi et al., 2014). The decrease in habitat suitability for *Z. spina-christi* in southeastern Iran reflects the shifting plant communities. Our study has illuminated significant distinctions between these two ecological zones. In an optimistic scenario (i.e., SSP-126), during two periods (2041-2071 and 2071-2100), the spatial distribution of *Z. spina-christi* is expected to expand slightly into the central parts of Fars and the western regions of Khuzestan. However, under the SSP-585 scenario for the 2041-2070 period, suitable habitats are projected to fragment and diminish in southern Kerman and Khuzestan. Conversely, habitat expansion and extension are anticipated in Fars towards higher latitudes.

In light of the temperature increase projected in scenario SSP-585, the period from 2071 to 2100 may witness the contraction and reduction of local habitats in southern Kerman while new suitable habitats emerge in the northwest of Kerman. Fars province is expected to experience a shift in suitable habitats towards higher latitudes, and suitable habitat is anticipated to develop in South Khorasan province, where the presence of *Z. spina-christi* presence has not been previously documented. In summary, the overall trend for the distribution of *Z. spina-christi* is expected to increase. Several global studies have reported similar patterns of species range changes, including Ksiksi et al. (2019), Liu et al. (2021), Singh et al. (2022), and Koldasbayeva et al. (2022).

As for *Z. nummularia*, its current range is primarily located in the southwestern and western regions of the country, covering an area of approximately 23,000 square kilometers. Typically, this species is observed and recorded as a companion species within *Z. spina-christi* vegetation communities, but they do not form distinct plant communities. The habitat suitability of *Z. nummularia* in the future, under the optimistic SSP-126 scenario for the periods of 2041-2070 and 2071-2100, may result in the elimination and possible local extinction of suitable habitats for this species in Fars, Bushehr, and Kohgiluyeh-Boyer Ahmad, with a reduction in existing habitats in Khuzestan. Conversely, in the pessimistic SSP-585 scenario and the 2041-2070 periods, there is an anticipation of a slight expansion of this species' spatial distribution in Khuzestan

province, extending to higher latitudes.

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However, under the climatic scenario SSP-585 from 2071 to 2100, this species' habitat is projected to experience widespread contraction and extinction. This will destroy all suitable habitats for *Z. nummularia* in Fars, Bushehr, Kohgiluyeh-Boyer Ahmad, and southern Khuzestan, while new habitats will emerge at higher latitudes in Ilam province. Ultimately, the overall trend for the distribution of *Z. nummularia* is expected to decrease. Various studies support the observed pattern of changes in *Z. nummularia* distribution, including those conducted by Tarnian et al. (2021) and Khanal et al. (2022).Top of Form

4.2. Climate niche divergence/conservatism

The current investigation, employing niche dynamic analysis, has revealed a noteworthy phenomenon regarding the climatic niche of two species, thereby affirming the concept of niche conservatism (Xian et al., 2023). The niche equivalency test, as applied, demonstrates that the observed overlap in niche characteristics between the two species is more pronounced than expected under random assignment, thus shedding light on the transferability of their climatic niche (Sillero et al., 2022). Notably, the observed overlap in the niche similarity test, while notably more significant than that expected by random assignment or simulation, did not attain statistical significance. Gallego-Narbón et al. (2023) elucidated that a scenario where the observed overlap is relatively high and the similarity test remains non-significant indicates geographical proximity between the species pairs. This reinforces the outcomes of our study, illustrating that these species are not identical but share similarities within their environmental habitat and are indeed geographically proximate.

The presence of stringent criteria for expansion and high stability criteria point towards these species displaying non-aggressive behavior, with their native niche exhibiting stability and a limited ability to adapt to novel environmental conditions. In simpler terms, these species exhibit fidelity to their existing climatic conditions, actively seeking niches that mirror historical climates (Wang et al., 2023). Our findings align with those of Lustenhouwer & Parker (2022), where the niche conservatism hypothesis remains unchallenged, marked by low expansion criteria and a predominance of niche stability. Furthermore, niche unfilling is evident, with the species utilizing less than half of the available environmental space, contingent on their dispersal capabilities (Keppel et al., 2012). It is imperative to identify areas less susceptible to climate change, called climate macro-refugia, due to the escalating pace of climate change. Given the conserved nature of these species' climatic niche and their limited adaptability to new climatic conditions, their occurrence is confined to habitats resembling their ancestral or native ranges. Considering the regional topography, physiological and phenological traits, and the constrained seed dispersal resulting from the seeds' substantial weight, it can be reasonably concluded that these species exhibit limited spatial and temporal transfer capabilities. Consequently, they are highly vulnerable to the impacts of climate change, lacking the natural ability to migrate to habitats projected by species distribution models.

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Conservation Implications

Biodiversity within arid ecosystems is remarkable; however, these regions are highly susceptible to environmental disturbances, including climate change, drought, and fire. Unfortunately, the recovery process in such environments is notably slow, often resulting in irreversible harm and far-reaching consequences for the various components of these dry ecosystems.

The success of our endeavors to monitor the natural habitats of two specific species, *Z. spina-christi* , and *Z. nummularia* , under both current and projected climate conditions hinges on whether these species possess the capacity and inclination to migrate to the designated habitat areas. The findings from our research have revealed that both *Z. spina-christi* and *Z. nummularia* exhibit fidelity to their historical climatic niches. Regrettably, these species appear ill-equipped to adapt to the challenges posed by climate warming while maintaining their existing habitats. Consequently, their best action is to migrate to the designated habitat zones.

A strategic approach is imperative to safeguard the *Z. spina-christi* and *Z. nummularia* communities and preserve this ecosystem's distinctive plant and animal diversity. Identifying priority areas and establishing protected zones emerges as the most effective strategy. It is essential to recognize that *Z. spina-christi* and *Z. nummularia* serve a dual role as protective and nurturing entities for other species, acting as "biological refuges." Over time, these species contribute to the fortification of biodiversity, enhanced ecosystem productivity, and increased resilience—essentially providing insurance for the ecosystem.

Additionally, in light of both biotic and abiotic factors and the multifaceted threats of climate change, the concept of "artificial habitats" warrants consideration. These habitats can be conceived and restored within vacant niches or suitable areas, identified through tracking and designed protection programs to mitigate the impact of climate change on these species. Top of Form

4.4. Scope and model limitations

While the predictive models employed in the study exhibited strong performance in delineating the climate niche of the species under examination, certain constraints within the predictions should be acknowledged. It is essential to recognize that the actual niche occupied by the species tends to be more confined when compared to its potential niche.

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This discrepancy arises from the fact that climatic variables, while pivotal, do not exclusively dictate a species' ecological niche. Additional factors, notably biotic and edaphic elements, introduce constraints and exert subtle influences on the habitat distribution of a given species.

On a macro scale, it remains evident that climatic factors remain the primary drivers behind species distribution. Nevertheless, it is imperative to note that our predictive models exclusively relied on climatic variables, excluding other biotic and abiotic factors from consideration. Consequently, our models may not offer a comprehensive prediction of the potential impacts of climate change on the future range of the species in question.

To illustrate, human activities, including but not limited to land use alterations, overgrazing, and urbanization, will wield substantial influence over species distribution in the future. These activities introduce additional complexities and limitations to the future range of the species, which are not accounted for by our models. Top of Form

Furthermore, uncertainties surrounding future greenhouse gas concentrations could undermine our predictions' validity.

In summary, while the predictive models employed in this study displayed commendable accuracy in delineating the climate niche of the species, it is essential to acknowledge the inherent limitations stemming from the exclusion of crucial biotic and abiotic factors. These omissions underscore the complexity of forecasting the impact of climate change on the species' future range, especially in the face of evolving human activities and uncertain environmental variables.

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5. Conclusions

The capacity of species to locate appropriate habitats in the face of a changing climate is influenced by many factors. In the case of the species under investigation, it appears that various elements, including geographical barriers and complex topography of the region, characterized by a hot and arid Saharo-Sindian climate, as well as limitations in seed dispersal (both species have heavy seeds), competition from indigenous species and invasive species like *Prosopis juliflora*, may impose constraints on the ability of *Z. spina-christi* and *Z. nummularia* to track and inhabit climatically suitable habitats in the future. Beyond these factors, the dynamic niche analysis demonstrates the preservation of the climatic niche of both species, implying that these species might encounter difficulties migrating to anticipated climatically suitable habitats in the

future, given the projected climate scenarios. Climate change, while pivotal, does not operate in isolation when it comes to influencing species distribution. Other elements, such as land use and drought alterations, should also be viewed as interrelated variables warranting investigation in subsequent research endeavors, as they are influenced by global warming. Top of Form

In light of the historical fidelity of the species to their climatic niche and the precarious conditions characteristic of the Khalijo-Omanian hot and arid ecosystem, the proposal is to implement a comprehensive strategy and immediate conservation measures aimed at safeguarding these two invaluable species.

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Nevertheless, in order to substantiate the ability of these species to adapt to suitable habitats and to validate evolutionary hypotheses, it is imperative to take into account a range of factors, encompassing biological interactions, topographic variations, edaphic conditions, and phylogenetic considerations across diverse geographical scales. Such an approach can significantly enhance the accuracy of our predictions.

Authorship contribution statement

Saeed Behzadi: Formal analysis; Investigation; Writing - original draft . **Gholamabbas Ghanbarian:** Conceptualization; Data curation; Funding acquisition; Project administration; Writing - review & editing . **Rasool Khosravi:** Conceptualization; Formal analysis; Funding acquisition; Methodology; Software. **Roja Safaeian:** Investigation; Resources; Writing - review & editing . **Hamid Reza Pourghasemi:** Software; Validation; Writing - review & editing

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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