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ORIGINAL RESEARCH

Spatially heterogeneous habitat use across distinct biogeographic regions in a wide-ranging predator, the Persian leopard

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Abstract

Large carnivores, despite being sensitive to specific habitat conditions, are able to distribute in a wide range of natural habitats. Such pattern of distribution raises the question of whether ecoregional differences should be considered when developing habitat suitability models. We assessed habitat suitability of the Persian leopard (*Panthera pardus tulliana*) as an example of a wide-ranging predator across four different biogeographic zones of Iran. We used the maximum entropy model (MaxEnt) to perform a general and ecoregion-specific habitat suitability model and projections of the future distribution of the species for the year 2050. The results showed that the habitat use of leopards in each ecoregion differed depending on the habitat conditions and that, due to smoothing response curves of the explanatory variables, the ecoregion-specific distribution models were suppressed in the general model. Topographic ruggedness, access to prey, NDVI, and human presence affect species' habitat suitability in different orders and gradients across the four ecoregions. We also found that the leopard's response to future climate change varies depending on ecoregions and climate change scenarios. While habitat loss is greater than habitat gain in Hyrcanian and Saharo-Sindian regions, this pattern reversed in Irano-Turanian and Zagros ecoregions. We argued that zoning across wide geographical ranges in niche modelling of widespread species, while may underestimate their environmental tolerance, allows for proper judgments on the required conservation measures in different ecoregions.

Keywords *Panthera pardus* · Species distribution models · Climate change · Conservation planning · Ecoregion

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Introduction

Species Distribution Models (SDMs) are practical tools that explore the variables governing species distribution and habitat use through multivariate analysis of ecological niches and production of landscape-level habitat suitability maps. They have extensively been used to identify suitable habitats under the influence of environmental variables (Guisan et al. 2013), model habitat connectivity and gene-flow corridors (Ahmadi et al. 2017; DeMatteo et al. 2017), investigate conservation gaps and spatial conservation prioritisation (Khosravi et al. 2019; Ahmadi et al. 2020), compare patterns of habitat use and niche partitioning among sympatric species (Hemami et al. 2018; Ashrafzadeh et al. 2020), and evaluate the climate change effect on species distribution (Sheppard et al. 2014; Ahmadi et al. 2019).

Although SDMs play a pivotal role in habitat prediction and conservation, they present significant limitations and uncertainties whose understanding in conservation planning is required (Guisan et al. 2013; Sequeira et al. 2018). For example, ignoring the importance of algorithm features and input parameters leads to model ambiguity and misinterpretation of the outcomes (Warren et al. 2014). SDMs are highly sensitive to the type (Sheppard et al. 2014; Huang et al. 2018) and scale of input variables (Levin 1992; McGarigal et al. 2016). Equally important, the ecological diversity of the study area and the possibility of distinct ecological structures are of essential importance (Zimmermann et al. 2010; Pottier et al. 2013). Due to the possible adaptability of populations to local conditions, species may follow a different ecological niche occupation in habitats with different ecological characteristics (Asharafzadeh et al. 2020; Lorestani et al. 2022). With such divergent within-taxon structures provoking potential ecological niche differences, lumping occurrence points may cause general models that predict an inflated niche width (Pearman et al. 2010).

We addressed this challenge in a wide-ranging large carnivore, the Persian leopard (*Panthera pardus tulliana*). As the most widespread large felid from Africa through the Middle East to Southeast Asia (Jacobson et al. 2016), the leopard can live in a wide range of habitat and climate conditions (Jacobsen et al. 2016). Also, having the widest trophic niche among the obligate carnivores (Hayward et al. 2006) and the remarkable persistence of the species even in urban areas (Athreya et al. 2013; Powell et al. 2021) highlight the species as a generalist predator. Among the nine sub-species, the Persian leopard, distributed in West Asia, occupies the highest diversity of its natural habitats (Sanei and Zakaria 2009, Kiabi et al. 2002). Within this range, Iran is known as the primary source of Persian leopard marginal populations in neighboring countries such as eastern Turkey, the Caucasus, Turkmenistan, and Iraq (Bleyhl et al. 2022). Iran is also a unique representative of the global distribution of the species, where the country encompasses a broad spectrum of habitats from semi-desert areas and cold steppes to temperate forests and high mountains. However, despite the high diversity in habitat types, our understanding of the species range is at the scale of the region (Ebrahimi et al. 2017; Mohammadi et al. 2022). Whereas leopards may differ in habitat use based on environmental conditions, such as biomes, which can be associated with biome-specific conservation concerns.

Recent studies on the Persian leopard habitat suitability were either local (Hemami et al. 2018; Khosravi et al. 2021; Farhadinia et al. 2015) or relied on the combination of species presence points across the entire study regions (Asharafzadeh et al. 2020; Ahmadi et al. 2020). However, bias adjustment and model parameterisation depending on the target species' prevalence and the study area's extent result in varying spatial predictions (Pottier et al. 2013). This variation is most noticeable for widespread species, which, due to their general habitat selection, are very sensitive to spatially-biased occurrence data (Stolar and Nielsen 2015). In this case, performing an SDM with a pooled dataset of presence points from diverse habitat structures increases the possibility of niche breadth inflation caused by smoothing response curves of the input variables (Pearman et al. 2010). As such, niche inflation is more challenging for widespread species with abundant data (Randin et al. 2006). Further, different climatic responses of distinct within-taxon niche structures highlight the necessity of within-species investigation of the effect of climate change on species distributions (Pearman et al. 2010).

In the current research, we used the leopard as a model species to predict its habitat requirements across diverse ecoregions of Iran, which harbours the majority of leopard range in west Asia (Bleyhl et al. 2022). We first compared the species' general and ecoregion-based distribution models to specify whether local conditions of different ecoregions influence predicting the habitat suitability of a generalist and large-bodied predator. We further adopted our SDM procedure for future climate change projections. By doing so, we aimed to examine how our approach helps identify ecoregions that are more sensitive to future negative impacts of climate change. This can benefit reduce uncertainty in species distribution modelling of a generalist species and more efficiently identify its climate refugia in the future.

Material and methods

Study area

The present study was carried out in the entire Iranian territory of 1,648,000 km^2. Iran has a broad spectrum of habitat types and topographic heterogeneity with four major floristic ecoregions of Irano-Turanian, Hyrcanian, Saharo-Sindian, and Zagros (Fig. 1, Sagheb-Talebi et al. 2014). With an area of 966,576 km^2 (58% of Iran), the Irano-Turanian ecoregion covers the largest part of the Iranian plateau with two altitudinally distinct regions of cold mountainous and hot and dry steppes and deserts. Local climate differences have contributed to the diversity of vegetation forms in this ecoregion, with the dominance of the *Zygophyllum*, *Pteropyrum*, *Astragalus*, and *Amygdalus* genera. The Hyrcanian ecoregion, with an approximate area of 55,100 km^2 (3% of Iran), comprises a diversity of fertile agricultural plains, deciduous forests, and ecotone areas extended along the southern shore of the Caspian Sea in the northern Alborz mountain range. This ecoregion contains a rich native tree diversity such as *Parrotia persica*, *Quercus castaneifolia*, *Gleditsia caspica*, *Buxus hyrcana* owing to suitable temperature (annual mean range of 15 to 18 °C) and precipitation (annual mean range of 600 to 2000 mm) ranges (Sagheb-Talebi et al. 2014). The southwestern part of the country, including all Iranian coasts of the Persian Gulf and Oman Sea, with an area of 355,044 km^2 (22% of Iran), constitutes the Saharo-Sindian ecoregion. The region is characterised by a dry, tropical, and subtropical climate, which is affected by the Sahara-Arabian vegetation in the west and the Nubo-Sindic realm in the east. This ecoregion's most common plant genera are *Ziziphus*, *Acacia*, *Prosopis*, *Rhizophora*, and *Avicennia* (Sagheb-Talebi et al. 2014). The Zagros ecoregion, with an area of 228,435 km^2 (14% of Iran), extends from northwest to south of Iran. The Zagros climate is influenced by the Mediterranean rainfall system and includes various tree and shrub species of the genera *Quercus*, *Prunus*, *Crataegus*, and *Pistacia*. In most parts, however, the oak species of *Q.*

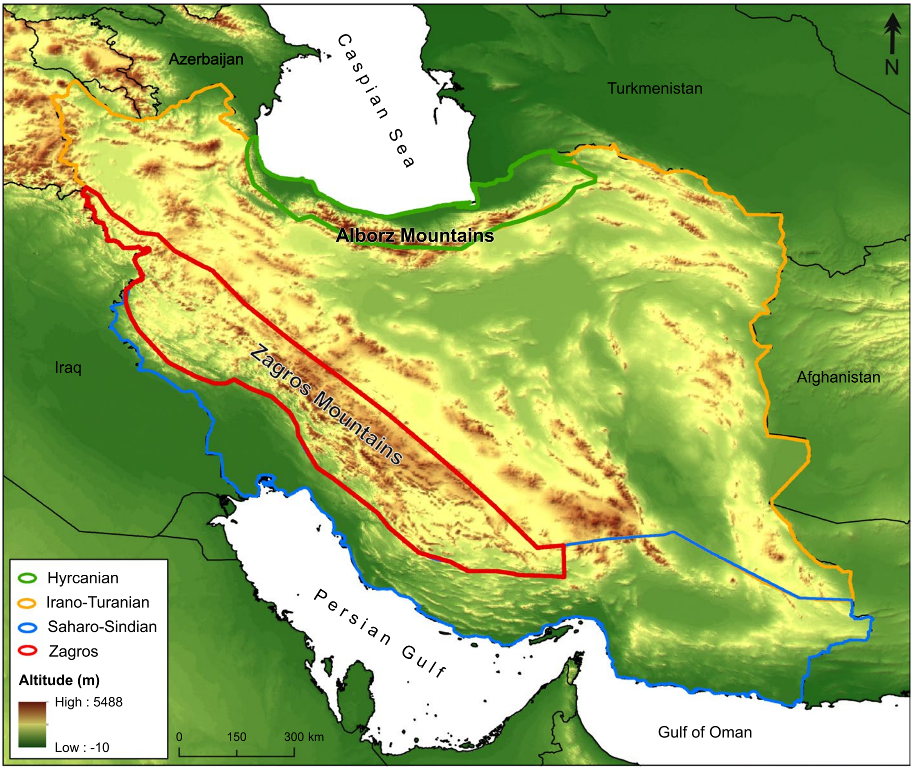

Fig. 1 Geographic position of the study area and the ecoregions used to predict general and ecoregion-based habitat suitability model of the Persian leopard

macranthera and *Q. brantii* shapes the ecoregion's vegetation landscape (Sagheb-Talebi et al. 2014).

Occurrence data

In total, we obtained 632 Persian leopard presence points from three major sources: direct field surveys by the authors across central Iran, collected data by game guards of the Department of Environment, and camera trapping surveys implemented by one of the authors (MSF) during 2010–2017. Using a spatially continuous sampling program, the obtained observations cover whole the possible natural habitats of the Persian leopard in all Iranian ecoregions. We checked the probability of spatial autocorrelation (SAC) between occurrence points using the Global Moran's I test. To do so, we extracted value of the variables at the occurrence points and based on the resulting data frame we used the function 'Spatial Autocorrelation' in ArcGIS to calculate MC for all variables independently. Due to the clumpiness of the occurrence points in some parts and to reduce the negative impacts of SAC, duplicated points within a radius of 5 km (Farhadinia et al. 2015) were removed by considering a spatial filtering approach (Kramer-Schadt et al. 2013). This process reduced occurrence points to 424.

Predicting variables

Input variables were prepared to perform two modelling approaches: an SDM for predicting the current Persian leopard habitat suitability and an SDM for evaluating the effects of climate change on the species distribution. Five categories of variables, including vegetation, prey availability, human pressure, topography, and climate, were considered to model the species' habitat suitability. The monthly NDVI vegetation index was obtained from the MODIS 2019 time series, downloaded from Earthexplorer dataset (https://earthexplorer.usgs.gov). We then used the GEOMATICA software (Geomatics 2005) to extract NDVI bands. Given the high correlation between monthly NDVI layers, they were analysed using the principal component analysis (PCA). The results of PCA indicated that the first component explained 80% of the vegetation variance; hence, the raster layer of this component was used as vegetation heterogeneity in the SDM analysis.

Wild goat (*Capra aegagrus*), mouflon (*Ovis gmelini*), urial (*O. vignei*), and wild boar (*Sus scrofa*) are the main prey items for the Persian leopard (Farhadinia et al. 2018). The contribution of each prey to the leopard diet was calculated as the frequency of each prey among leopard faeces sampled in multiple sites covering different biogeographical realms of leopards in Iran (Taghdisi et al. 2013; Sharbafi et al. 2016). In these studies, a total of 406 leopard faeces were investigated, of which 32% (n = 131) and 26% (n = 104) samples belonged to wild goat and urial, respectively. Wild boar, rodents, domestic dogs, and livestock were secondary items, but we did not consider them in our study due to the lack of reliable data on their distribution. To account for prey availability in our SDM analysis, we generated a prey availability map by multiplying the prey habitat suitability maps by the leopard trophic preference (Shahnaseri et al. 2019). In doing so, the habitat suitability of wild goat and wild sheep (including mouflon and urial) were modeled using 225 and 324 presence points, respectively, across the entire country (Figs. S1 and S2). We used raster layers of the explanatory variables that were prepared to model the habitat suitability of the Persian leopard (modelling details are described in the species distribution modelling section).

The human footprint model, as a combination of population density data and human infrastructure (road network, land change, and human access) (Venter et al. 2016), was included to include human presence effects in the Persian leopard habitat suitability model. The digital elevation model (DEM) was acquired from the CGIAR-CSI GeoPortal (https://srtm.csi.cgiar.org/) to include two topographic variables in the SDM analysis: elevation and topographic ruggedness. Topographic ruggedness was calculated as the standard deviation (SD) of the elevation of all raster cells in a 2.5 km radius (Farhadinia et al. 2015). Climatic variables consisted of mean annual temperature, temperature seasonality, maximum temperature of the warmest month, annual precipitation, precipitation seasonality, and precipitation of the wettest month. We considered these climatic variables to account for general climatic condition including annual mean temperature (bio1) and annual precipitation (bio12), seasonal variability including temperature seasonality (bio4) and precipitation seasonality (bio15), and extremes of temperature and precipitation including maximum temperature of the warmest month (bio5) and precipitation of the wettest month (bio13) in the habitat suitability modeling of the species. By reflecting adaptation to extreme climatic conditions, these variables represent important environmental constraints on species distributions, niche evolution, and adaptability (Saladin et al. 2019). All climatic variables were obtained from the WorldClim database v. 2.1 (https://www.worldclim.org/) with a cell size of 30 arc-second (approximately 1 km).

In order to evaluate the effect of climate change on the leopard distribution by 2050, we used four global public circulation (GCM) models, including MIROC5, CCSM4, HadGEM2, CM5-CNRM for two mild (RCP 2.6) and severe (RCP 8.5) scenarios. Emission scenarios are a specific standard for assessing the effects of greenhouse gas emissions on future climate change and are published by the Intergovernmental Panel on Climate Change (IPCC) (Moss et al. 2010). Most previous predictions of the effects of climate change on species distribution have ignored biological connections and only relied on climatic variables. There are complex and important interactions between climate change and other environmental constraints, e.g., the presence of prey has a significant effect on the Persian leopard habitat in the face of climate change in Iran (Khosravi et al. 2021). Consequently, the climatic suitability models of wild goat and wild sheep were constructed under the two scenarios of RCP 2.6 and RCP 8.5, employing the six climatic variables. The prey climatic suitability maps (Fig. S3) were then multiplied by their respective contribution to the leopard's diet and, along with climatic variables, were used to project leopard's habitat suitability to year 2050. Before the SDM analysis we checked the multicollinearity between input variables based on variance inflation factor (VIF) using the package usdm (Naimi 2015). We found no VIF > 10, hence, all variables were used for the SDM analysis.

Species distribution modelling

For both habitat suitability modelling and future climate change projections, modelling was performed in two schemes; national level (hereafter general model) and regional level (hereafter ecoregion model). The maximum entropy (MaxEnt) model, version 3.4.4., was used as the species distribution modelling algorithm and the Cloglog format was selected to generate habitat suitability maps. One of the key advantages of the Maxent model is that it only requires presence data and has the potential to unveil simple and complex relationships between presence points and independent variables (Phillips et al. 2006). Modelling was performed using the Maxent function of the dismo package (Hijmans et al. 2017) in the R environment v. 4.1.2. The Maxent model requires background data; hence, we used 10,000 randomly-selected background points for the entire study area and each ecoregion. We used the area under the curve (AUC) of the Receiver Operator Characteristic (ROC) curve to evaluate the performance and overall fit of the model. True Statistical Skill (TSS) was also computed to assess the model classification accuracy. Most studies use a random iteration technique for cross-validation and data partitioning (Hao et al. 2019). This method ignores the spatial structuring of the input data and thus might underestimate prediction errors. For better use of occurrence and background data, we used a spatial cross-validation strategy using the blockCV (Valavi et al. 2018) package in the R environment. This technique divides the data into K spatial blocks. One block is used in each iteration to test the model performance, while the remaining blocks are used to fit the model. We performed the modelling based on the repetition of 5 spatial blocks, and ultimately, the final model was built by averaging the maps produced in 5 replications. We then converted the continuous map of the suitability model into a binary presence and absence map using the 10-percentile threshold of training data (Ahmadi et al. 2020). There are two advantages to using this classification: first, it allows removing marginal points that are located in areas of low or no suitability, and second, it considers biased errors or uncertainties resulting from out-of-reach occurrence points. We also conducted a paired t-test to determine whether the mean area of the suitable habitat patches in the current and future scenarios is significantly different.

Results

Species distribution modelling

The predicted leopard suitable habitats were produced for Iran (general model; Fig. 2a) as well as four ecoregions (ecoregion models; Fig. 2b). The performance of the habitat suitability and climate suitability models was satisfactory based on AUC and TSS criteria (Table 1). The highest prediction performance of the Maxent model was calculated for Irano-Turanian and Saharo-Sindian ecoregion. In general, the AUC and TSS values calculated for the model of the ecoregions were similar to those of the general model (Table 1). The geographical distribution of suitable habitats was of two prominent interconnected habitat patches along the Alborz Mountains in the north and the Zagros Mountains in western Iran. In other areas, suitable habitats were relatively patchily distributed (Fig. 2).

The area of suitable habitats in the general model (392,308 km^2, equal to 24% of Iran) was greater than the total area of suitable habitats in four ecoregions (313,226 km^2, equal to 19% of Iran). The extent of suitable habitats in the general model was 28%, 5%, and 22% larger than that of ecoregion-based models for Hyrcanian, Irano-Turanian, and Zagros, respectively. Contrarily, for Saharo-Sindian, the extent of suitable habitats in its ecoregion-based model was 10% larger than that of the general model (Table 2).

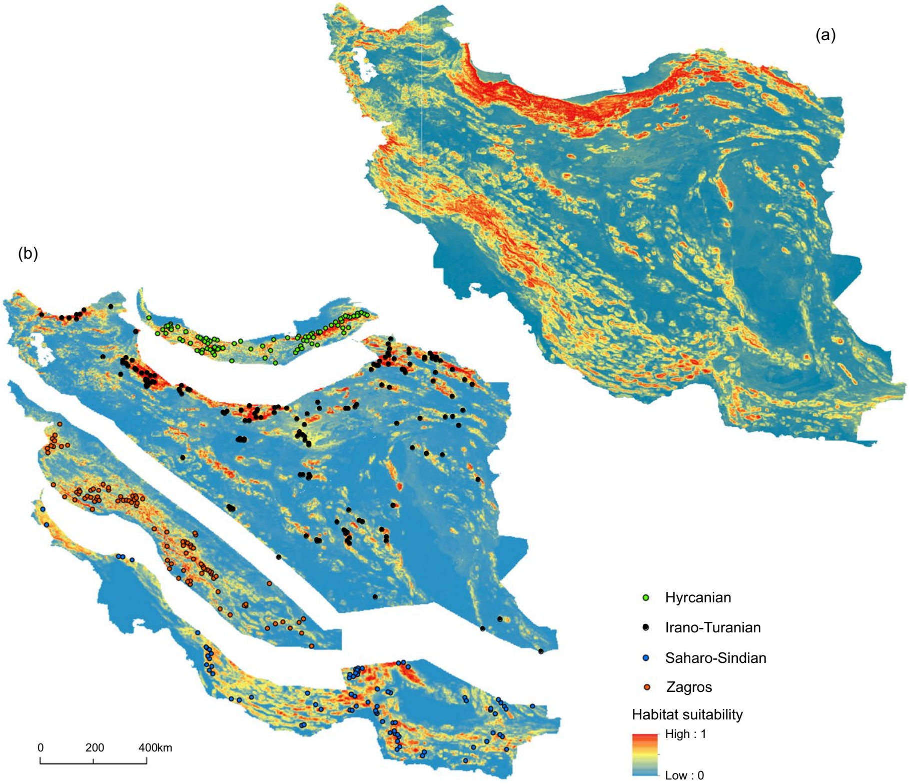

Fig. 2 Predicted habitat suitability model of the Persian leopard based on a general (**a**) and pooled dataset (**b**) of occurrence points obtained based on the MaxEnt model

Table 1 Predictive performance of Maxent habitat suitability and climatic suitability models of the Persian leopard based on a pooled dataset of the occurrence points (general) and an ecoregion-based scheme

Ecoregion	Habitat suitability model		Climatic suitability model	
	AUC	TSS	AUC	TSS
Hyrcanian	0.89	0.52	0.85	0.43
Irano-Turanian	0.91	0.55	0.89	0.44
Zagros	0.87	0.57	0.82	0.55
Saharo-Sindian	0.91	0.57	0.9	0.56
General	0.90	0.55	0.90	0.57

Table 2 Area of the predicted suitable habitats of the Persian leopard in different ecoregions

Ecoregion	Total area (Km^2)	Area of suitable habitat (Km^2)		Percent of suitable habitat	
		Ecoregion	General	Ecoregion	General
Hyrcanian	80,341	22,862	45,352	28	56
Irano-Turanian	965,441	119,678	160,766	12	17
Zagros	237,584	46,621	98,395	20	42
Saharo-Sindian	361,384	124,065	87,795	34	24
General	1,644,750				

Although the importance order of the variables differed between the ecoregion-based models, topographic ruggedness was the most important variable in the species distribution across all ecoregions (Table 3). Elevation, followed by vegetation and prey availability, were the most important variables affecting leopards' suitable habitats based on the general model. Except for the Irano-Turanian ecoregion, prey availability ranked among the four most important variables. NDVI was identified as the second most important variable in the Hyrcanian and Zagros models. The human footprint was classified as an important variable in the Irano-Turanian and Saharo-Sindian models.

Comparing the density plots of the variables showed that all variables in the general model had smoother changing curves than the ecoregion-based models encompassing a wider range of changes with reduced density peaks (Fig. 3). The maximum difference in occupying variables' gradients was observed for the temperature seasonality in the Zagros region, annual mean temperature in the Saharo-Sindian, and maximum precipitation of the warmest month and NDVI in the Hyrcanian ecoregion. Results also showed different distribution patterns in response to precipitation seasonality and prey density across all regions.

Climate change projections

The climate change projections showed that the Persian leopard habitat varies differently under GCM scenarios and among the ecoregions (Fig. 4). In the Hyrcanian region, under RCP 2.6 and RCP 8.5 the area of leopard's suitable habitats reduce by 34% and 67%, respectively (Table 4). The current leopard habitat is dispersed throughout the Hyrcanian region and would shrink to the west in the future (Fig. 4). Similarly, habitat loss due to climate change in the Saharo-Sindian was projected to be 16% and 54% for RCP 2.6 and RCP

Table 3 Mean and standard deviation of the contribution of environmental variables in the habitat suitability model of Persian leopards based on the general and ecoregion-based modelling approach

Ecoregion	variable	Mean	SD
Hyrcanian	Topographic ruggedness	0.43	0.03
	NDVI	0.15	0.04
	Precipitation seasonality	0.12	0.02
	Prey	0.09	0.02
Irano-Turanian	Topographic ruggedness	0.50	0.04
	Precipitation seasonality	0.15	0.03
	Temperature Seasonality	0.12	0.02
	Human footprint	0.10	0.06
Zagros	Topographic ruggedness	0.5	0.13
	NDVI	0.17	0.07
	Annual mean temperature	0.15	0.01
	Prey	0.11	0.01
Saharo-Sindian	Topographic ruggedness	0.61	0.10
	Prey	0.17	0.07
	Max temperature of warmest month	0.09	0.07
	Human footprint	0.07	0.05
General	Topographic ruggedness	0.73	0.03
	NDVI	0.06	0.01
	Prey	0.04	0.01
	Precipitation seasonality	0.04	0.01

8.5, respectively (Table 4). Contrarily, suitable habitats were projected to be increased by 43% and 82% in the Irano-Turanian and 61% and 99% in the Zagros ecoregions under RCP scenarios of 2.6 and 8.5, respectively (Table 4). North and northwest of the Irano-Turanian and highlands of the Zagros ecoregion will provide new habitats for the leopard (Fig. 4). Based on the general model, we envisaged the total leopard habitat to increase by 9 and 22% under RCP 2.6 and 8.5 scenarios, respectively (Table 4). The leopard habitat range shift towards higher altitudes was highest in the Saharo-Sindian (26 and 454 m under RCP 2.6 and RCP 8.5, respectively), followed by Zagros (203 and 215 m under RCPs of 6.2 and 8.5, respectively)(Table 5). In contrast, no considerable altitudinal range change was expected for the Hyrcanian and Irano-Turanian ecoregions (Table 5).

Discussion

Our study showed that the extent of suitable habitats in the general model was 5% (79,082 km^2) larger than the sum of those yielded under ecoregion-based models. The general model deals with a very flexible species that can use contrasting habitats, from mountains and deserts to Hyrcanian broadleaved forests. Therefore, the model predicts vast regions of Iran as suitable habitats. However, in a specific ecoregion, the modelling approach illustrates a more limited niche, which yields an output with a comparatively less suitable habitat. This approach can effectively balance the issue arising from imbalanced-biased data sampling, i.e. different numbers of presence points by ecoregion (El–Gabbas and Dormann, 2018). For example, a larger number of presence points were

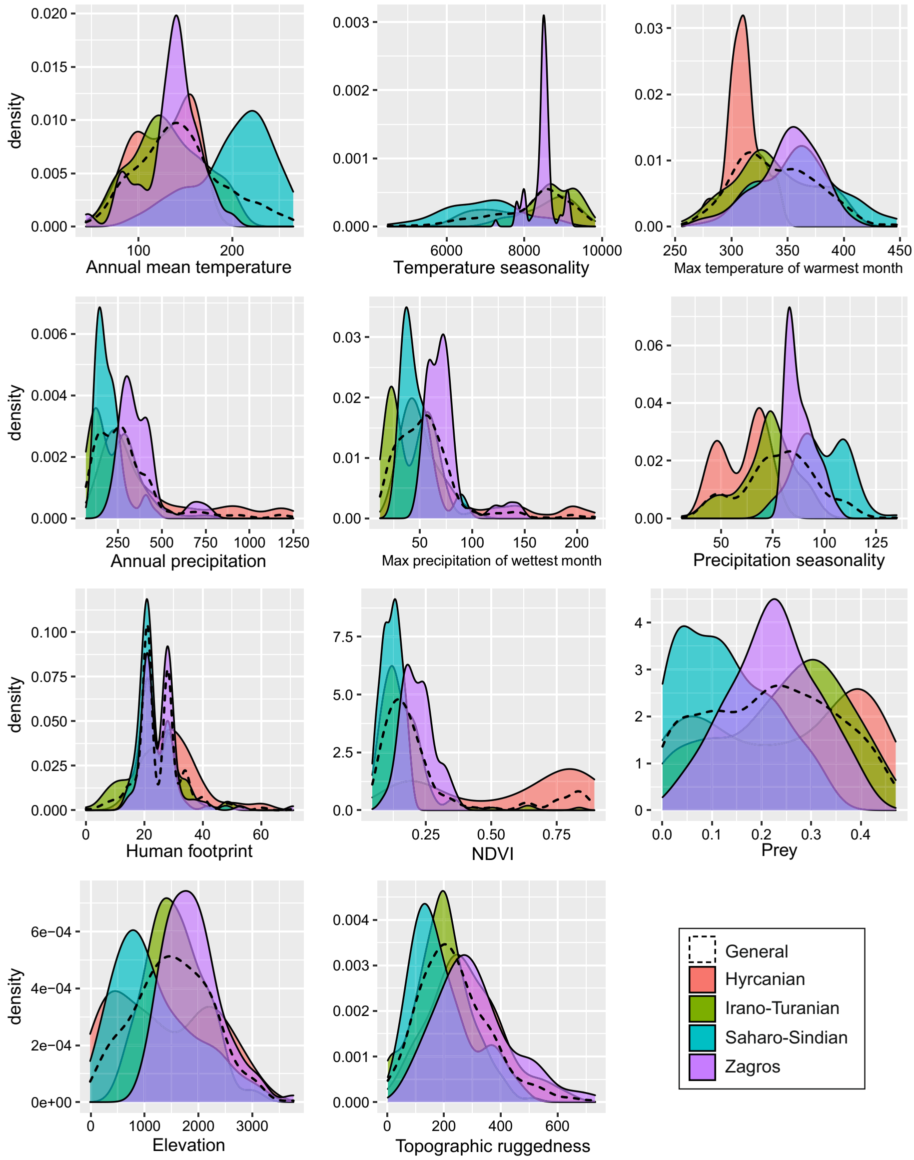

Fig. 3 Density plots of the environmental variables affecting habitat suitability of leopards based on general (pooled dataset of the occurrences) and ecoregion-based models

available in the Hyrcanian ecoregion due to better accessibility, higher habitat suitability, and proliferation of similar studies, causing the general model to over-representing habitat suitability in favor of this ecoregion. On the contrary, areas having relatively few presence points experienced a buried ecological niche in the general model. This eventually leads to smoothing variables' response curves fitted under the general model (Pearman et al. 2010; Lorestani et al. 2022).

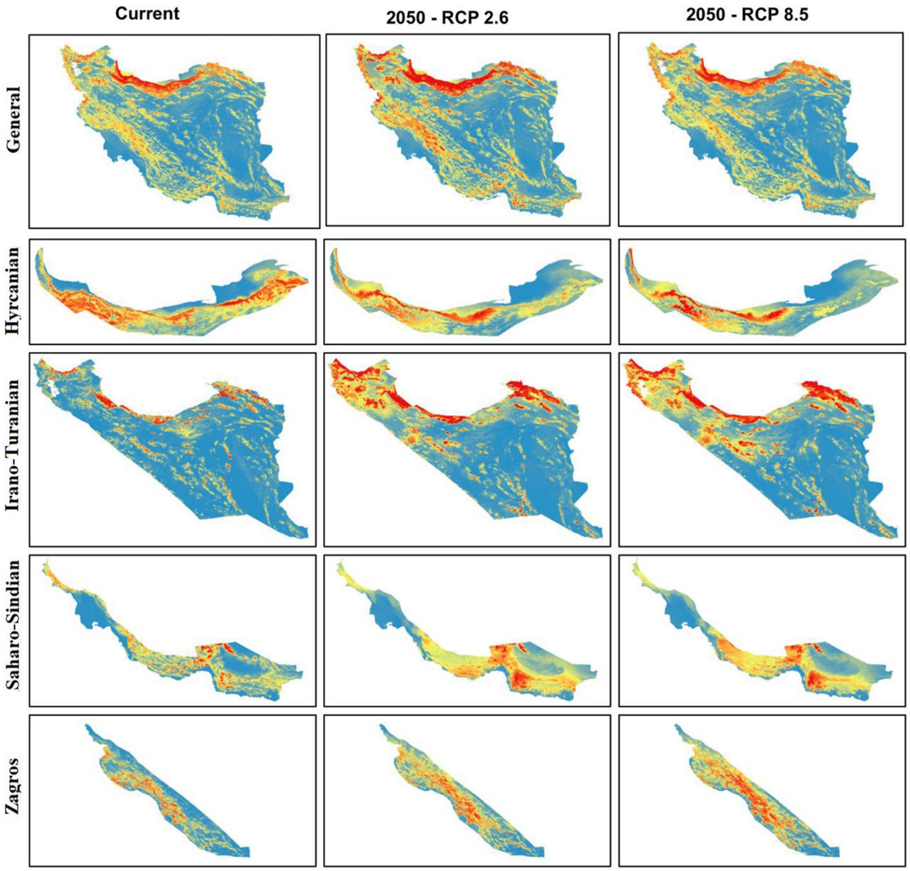

Fig. 4 Predicted climatically suitable habitats for leopards based on the general and ecoregion-based models for the current and 2050 climates projected under RCP scenarios 2.6 and 8.5. Future climatic projections are derived based on an average of four GCMs

Habitat suitability comparison

Although general and ecoregion-based models performed similarly in predictive performance, they showed two main differences in response curves and suitable habitat areas. First, the predicted suitable habitats of leopards are more discontinuous in the ecoregion-based models compared to the general model, particularly across Hyrcanian and Saharo-Sindian ecoregions. Second, topography outperformed other variables in all modelling regions, which is in accordance with previous studies (Farhadinia et al. 2015; Khosravi et al. 2021). Topography helps the leopard to avoid possible conflicts with humans and provides more untouched habitats with abundant prey (Farhadinia et al. 2015; Khosravi et al. 2021). Similarly, the NDVI, as a proxy for prey availability, ranked among the main factors determining the leopard distribution in the general, Hyrcanian, and Zagros models while it scored lower in drier ecoregions,i.e. Saharo-Sindian and Iran-Turanian ecoregions. This differentiated response between dryer and temperate ecoregions can be explained by the leopard's dependence on vegetation to secure prey

Table 4 Results of the paired t-test to determine whether mean areas of suitable habitat patches in the current and future climate change scenarios are significantly different

Ecoregion	RCP	Current (km^2)	Future(km^2)	Change (%)	*t*	P
Hyrcanian	RCP 2.6	37,447	24,590.21	34.32↓	2.7	0.07
	RCP 8.5		12,433.26	66.71↓	4.3	0.02
Irano-Turanian	RCP 2.6	145,132	206,997	42.64↑	4.3	0.02
	RCP 8.5		264,145.5	82.0↑	– 2.9	0.02
Zagros	RCP 2.6	68,383	110,110.74	61.13↑	– 5.24	0.01
	RCP 8.5		136,395.25	99.40↑	– 16.34	<0.01
Saharo-Sindian	RCP 2.6	128,026.1	107,542	16.15↓	1.13	0.35
	RCP 8.5		58,892	54.26↓	2.41	0.09
General	RCP 2.6	430,087	468,047.71	8.81↑	– 3.02	0.05
	RCP 8.5		523,802	21.73↑	– 3.51	0.37

Values for future climatic scenarios are based on an average of four GCMs. Statistical analysis used for intergroup comparison

Table 5 Altitudinal change (meter) of the suitable habitats of the Persian leopard projected based on the general and ecoregion-based models

Ecoregion	Current	RCP 2.6	RCP 8.5
General	1564 (754)	1588 (775)	1563 (780)
Hyrcanian	1314 (442)	1337 (426)	1340 (415)
Irano-Turanian	1646 (684)	1716 (758)	1666 (775)
Zagros	1856 (458)	2059 (625)	2071 (654)
Saharo-Sindian	1150 (395)	1376 (485)	1604 (490)

Values in the parenthesis represent the standard deviation of the altitude. Values for future climatic scenarios are based on an average of four GCMs

and cover in Hyrcanian and Zagros ecoregions (Hemami et al. 2018). In contrast, the hot and dry climatic conditions of the Saharo-Sindian has caused poor vegetation cover of the region compared to other ecoregions, especially Zagros and Hyrcanian ecoregions, which in turn, has limited the distribution of the leopard's prey in this ecoregion.

The Hyrcanian ecoregion is characterised by higher vegetation cover and rainfall, and lower annual temperature and rainfall fluctuations compared to other ecoregions. The higher rate of vegetation productivity under these climatic conditions provides higher prey availability for leopards. Multiple authors have underscored the importance of seasonal rainfall in the leopard distribution (Ebrahimi et al. 2017; Ashrafzadeh et al. 2020; Khosravi et al. 2021). Conversely, the higher seasonal temperature was found as an influential condition affecting leopard distribution in the Irano-Turanian ecoregion. High temperature fluctuations and low rainfall are two major characteristics determining continentality in the Irano-Turanian ecoregion (Djamali et al. 2013). The importance of this variable in the leopard distribution was demonstrated in the study of Khosravi et al. (2021) in a smaller area within the Irano-Turanian ecoregion. The effect of the maximum temperature of the warmest month on the leopard distribution in the Saharo-Sindian ecoregion indicates the importance of climatic extremes on the distribution of leopard species in harsh regions.

The species' vulnerability to climate change

We found that the ecoregions differed in their future projections towards climate change. Although the Hyrcanian and Saharo-Sindian ecoregions are expected to experience habitat loss, the leopard suitable habitats in Irano-Turanian and Zagros ecoregions would increase by 2050. The large extent of habitat loss in the Hyrcanian ecoregion, exacerbated by the extensive deforestation and human-leopard conflicts (Soofi et al. 2019), can jeopardise the persistence of leopards across the ecoregion. Moreover, the feasibility of an upward range-shift in the Hyrcanian forests was estimated to be up to 20 m. Considering that the leopard's current suitable habitats in the Hyrcanian forests already include high-altitude ranges, the species has to experience range contraction in the future.

Given the arid climate of the Saharo-Sindian and Irano-Turanian ecoregions, water resources act as a vital limiting factor to wildlife species that are predominantly available in mountainous areas (Ahmadi et al. 2017). These ecoregions will become warmer and drier in the future, forcing the leopard to shift to higher altitudes in search of water resources. Accordingly, our results showed that the leopard's future distribution range in the Irano-Turanian ecoregion would be shifted towards more elevated northern and northwestern parts of the region. The northern parts of the Irano-Turanian ecoregion, especially along the Alborz mountain range, are bordered by the Hyrcanian ecoregion, which plays a key role in the long-term survival of the leopard. This region acts as a source population for other Iranian ecoregions and adjacent sink populations. Zagros was projected to be the least affected ecoregion by climate change compared to other ecoregions. Due to its high altitudes (more than 3000 m a.s.l.), permanent snow covers, and sub-zero temperatures in cold seasons, more suitable habitats are expected to be available under future climate change scenarios. This ecoregion is more underdeveloped than the Hyrcanian region and displays a relatively high altitudinal range of about 200 m a.s.l, enabling the leopard to better undertake elevational movements. Nevertheless, human disturbances in highlands and excessive vegetation degradation at the expense of livestock overgrazing threaten the species' long-term survival (Ashrafzadeh et al. 2020).

Our study had three limitations. First, although the leopard can respond to climate change through altitudinal shifts since it is able to live across wide range of altitudes (Farhadinia et al. 2020) and latitudes (Cheraghi et al. 2019; Bleyhl et al. 2022), land-use change can interrupt the gene flow and threaten the species' long-term survival (Khosravi et al. 2021). Combining the impacts of climate change and land use changes helps prioritise critical habitats for conservation (Gouveia et al. 2016). Second, the prey availability was incorporated in our modelling based on a simplified scenario, implying that the prey populations would not be exposed to limiting factors such as poaching and disease. Also, we did not include livestock, such as sheep and goat, in the prey availability whereas it is a supplementary source of food for leopards in many parts of its range (Farhadinia et al. 2018; Sharbafi et al. 2016; Soofi et al. 2019). Finally, as with leopards, generalist species can resist in a broad range of habitats, thus, they can potentially adapt to considerable environmental changes (Lavergne et al. 2013). The amplitude of environmental changes in a certain ecoregion, for example, the Hyrcanian ecoregion in our case, is much more limited than the entire distribution of the target species. As a result, when modelling climate change effects on the distribution of a generalist species within a subregion with comparatively limited environmental extremes, the model may be prone to overestimate the impacts of climate change. Conformally, for regions with broader environmental variability, for instance, the Irano-Touranian ecoregion, the impact of climate change may be projected to be less prominent. Nevertheless, overestimating the impacts of climate change in a limited sub-region compared to a general model can results in more conservation-oriented outlooks for threatened species that, as a protection buffer, can assist in expediting conservation measures in the future.

Conclusion

Our findings showed that habitat suitability analysis and identification of influential variables affecting wide-ranging species require considering the regionalisation across large geographical ranges. Habitat suitability modelling in distinct ecoregions provides invaluable judgment of the region-specific habitat requirements and associated conservation measures across different temporal scales. In contrast, general modelling, yielded from an inflated niche prediction, can mislead conservation prioritisation of areas required to secure the long-term persistence of the target species. The suitable habitats predicted in this research can be considered as the species climate refugia and be used in prioritising further conservation implications. Future suitable habitats can also be considered in designating new protected areas to reduce the species' climatic vulnerability. Improving the protection level of the current habitat network concerning future intact habitats can alleviate the impacts of climate change on the Persian leopard's long-term persistence in the region.

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