



RESEARCH ARTICLE

Multi-scale niche modeling of three sympatric felids of conservation importance in central Iran

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Abstract

Context Carnivores in the central Iranian plateau have experienced considerable declines in their populations during the last century. Ecological niche models can inform conservation efforts aimed at increasing the suitability of carnivore habitat by providing valuable information on the scale-dependent relationships between species and their environment.

Objectives We used a multiscale modeling framework to predict habitat suitability and investigate the influence of spatial scale on species-environment relationships for three sympatric felids, chosen as

surrogate species, including Asiatic cheetah (*Acynonix jubatus*), Persian leopard (*Panthera pardus*), and sand cat (*Felis margarita*) with the aim of informing conservation efforts for these species and other Iranian carnivores more widely.

Methods We used opportunistically collected occurrence data and a presence-only, multiscale MaxEnt approach whilst exploring the impact of spatial filtering and data partitioning on model predictions and performance.

Results Scaling optimization showed that the performance of models was associated with variables at multiple spatial scales, with relationships tending to be strongest at the largest scales (4–8 km). Our findings showed that landscape composition generally have stronger influences on occurrence of the studied species than configuration. The comparison among models showed distinct patterns of habitat selection, implying niche partitioning between species.

Conclusions Our knowledge of scale-dependent relationships between three sympatric felids and their spatial niches facilitates effective conservation of habitat connectivity for multiple carnivore species by prioritizing predicted key suitable patches inside and outside of protected areas which have significant contribution in maintaining landscape connectivity in Iran.

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Keywords Carnivores · Ecological niche models · Multiscale species distribution models · Spatial filtering · Spatial scale

Introduction

The central Iranian plateau supports a high diversity (18) of carnivore species. Despite their ecological importance, carnivores in this region have experienced considerable declines in their populations during the last century due to prey depletion and habitat destruction (Hemami and Groves 2001). Simultaneously, limitations such as budget and labour force availability have hampered management efforts to implement conservation actions for each species individually. Khosravi and Hemami (2019) identified a suite of surrogate species, which are species that are used to represent other species or aspects of the environment to obtain a conservation objective (Caro 2010), including Asiatic cheetah (*Acinonyx jubatus venaticus*), Persian leopard (*Panthera pardus saxicolor*), and sand cat (*Felis margarita*) for providing a comprehensive conservation umbrella for many other species in central Iran. They used ecological niche modeling, experts' information, and attitudes of local communities to score ten carnivore species based on the thirteen criteria in order to select a suite of ecologically and culturally suitable surrogate species.

Evidence-based, data-driven conservation of carnivores is a relatively new field in Iran and the limited research that has been conducted on the spatial distribution of carnivores has shown that prey availability, topographic roughness, vegetation cover, and distance to human-dominated areas are the main predictors affecting distribution of a range of carnivore species (Ahmadi et al. 2017; Hemami et al. 2018; Khosravi et al. 2018; Shahnasari et al. 2019). Spatial niche partitioning in coexisting carnivores is an important mechanism structuring the spatial distribution of carnivore guilds (Hearn et al. 2018). Therefore precise data on the spatial distribution and ecological niche partitioning in a guild of carnivores is essential to improve the effectiveness of management actions aimed at protecting and enhancing the suitability of carnivores' habitat.

Habitat preservation in many parts of the world is one of the most effective approaches to biological

conservation (Coetzee 2017). Therefore, the effectiveness of protected areas (PAs) to protect the most important populations and suitable habitats is essential. With increasing human populations and economic development leading to broad-scale transformation of natural landscapes, coupled with ongoing range shifts for many species in response to recent climate warming, safeguarding the present network of PAs does not guarantee the long-term survival of these species. Therefore, managing suitable habitats and biological corridors based on surrogate species requirements beyond the existing PA network can provide a cost-effective conservation strategy (Di Minin et al. 2013).

Predicting habitat patches, biological corridors and spatial niche partitioning is highly dependent on accurate distribution data (Rabinowitz and Zeller 2010). Ecological niche models (ENMs) are fundamental tools for describing the multivariate structure of a species niche and producing spatially explicit maps of probability of occurrence at the landscape scale. Developing reliable ENMs is challenging and the correlative methods used in some studies may suffer from overfitting and biased prediction due to issues relating to spatial autocorrelation and sampling bias in presence localities (Redding et al. 2017), inappropriate background data selection (Barbet-Massin et al. 2012), insufficient independent testing data (Radosavljevic and Anderson 2014), incorrect spatial scale of environmental covariates (McGarigal et al. 2016a), and improper model parameterisation (Huang et al. 2018; Gábor et al. 2019).

The effects of landscape composition and configuration on a species' distribution and abundance tend to vary with spatial scale of environmental variables (Holland et al. 2004). Although the interaction between a species and its environment usually occurs on many scales, it is only observable when the spatial extent and grain of covariates matches the spatial scale of the species' response (McGarigal et al. 2016b). Multiscale ENMs have been proposed in recent years to optimize the grain and extent of species response to landscape factors (e.g. Shirk et al. 2012; Wan et al. 2017). These approaches offer valuable insights into species' habitat requirements and produce more reliable inferences than single-scaled habitat modeling applications (Wasserman et al. 2012; Mateo Sanchez et al. 2013; Vergara et al. 2016). Despite the importance of selecting appropriate spatial scale in ENM

(e.g. McGarigal et al. 2016a; Vergara et al. 2016), little attention has been given to identify suitable scales for predicting the distribution of carnivores in Iran. The previous studies in the region (e.g. Farhadinia et al. 2015; Ahmadi et al. 2017; Hemami et al. 2018; Shahnaseri et al. 2019) have tended to focus on single spatial scales to predict the distribution of the studied species, which may limit usefulness of their results.

Calibrating ENMs with biased occurrence data is another issue that may cause overfitting and biased inference regarding the species-environment relationships (Kramer-Schadt et al. 2013). Several correction methods have been proposed to correct spatial autocorrelation and biased presence records (Syfert et al. 2013; Brown 2014). In addition to the occurrence localities, the behavior of the different ENMs vary widely depending on how, where and how many background localities are used in presence-only ENMs (Phillips et al. 2006). Dividing occurrence data into spatially independent calibration and evaluation datasets for model evaluation is another issue in ENMs, which may have large influences on overfitting or underfitting of the models (Radosavljevic and Anderson 2014).

We use opportunistically collected occurrence data and a multiscale spatial modeling framework to predict the spatial niche divergence of three sympatric felid species as biodiversity surrogates in Iran and to investigate the impacts of sampling bias in presence and absence localities, data partitioning methods, and spatial scale of environmental covariates on the predicted ecological niche of these three species.

Materials and methods

Case study landscape

The study focuses on the landscape comprising the desert ecosystems of central Iran (29–34°N, 49–56°E). The study landscape is 167,914 km² in extent, of which 54% is covered by rangelands, 42% by rocks and barelands, 1.9% by croplands, 1.5% by wetlands and water surfaces, 0.35% by woodlands and forests, and 0.25% by human settlements and infrastructure. Despite their arid environmental conditions, central Iranian ecosystems are home to a diverse guild of carnivores (see text S1 in Online Resource 1 for details). A network of conservation areas has been

established by the Department of Environment (DoE) to protect large-scale ecological processes of ecosystems (Fig. 1).

The methodological framework

We carried out a spatial modeling analysis that consists of six steps to produce, evaluate and map multiscale ENMs for the target species (i.e. Asiatic cheetah, Persian leopard, and sand cat) and to assess spatial niche differentiation among them (Fig. 2). The steps undertaken in the study are explained in detail in the following sections.

Step 1: creating multiscale predictors

A total of 37 predictors (Table S1; Online Resource 1) belonging to five categories including land cover, topography, climate, vegetation, and human-influence were selected based on existing literature on distribution modeling of carnivores in Iran (e.g. Farhadinia et al. 2015; Ahmadi et al. 2017; Khosravi et al. 2018). Eight land use and land cover (LULC) types, including urban area, agriculture, surface water, sparse rangeland with a canopy density of $\leq 20\%$, mixture of grassland–scrubland with a canopy density of $\geq 25\%$, shrubland, scrubland, and bareland, were derived from a LULC map obtained from the Iranian Forests, Rangeland and Watershed Management Organization at a scale of 1:250,000 (FRWMO 2005). We used FRAGSTATS (McGarigal et al. 2012) to calculate the spatial pattern of LULCs using five landscape-level (Aggregation index, AI; Edge density, ED; Patch density, PD; Shannon Diversity Index, SHDI; Contagion index, CONTAG) and three class-level metrics (Patch density, PD; Gyrate_{am} index, GYR; and Percentage of landscape, PLAND; Table S1 in Online Resource 1).

Three topographic indices including focal mean elevation (ELEV), compound topographic index (CTI) and roughness (ROUGH) were calculated from a 90-m resolution digital elevation model (<http://srtm.csi.cgiar.org>) using the Gradient and Geomorphometric Modeling Toolbox for ArcGIS (Evans et al. 2014). Because of the inherent high correlation among bioclimatic variables, they were limited to mean annual temperature (Bio1) and precipitation (Bio12; Hijmans et al. 2005). We used the method developed by Flint and Flint (2012) to downscale the 1-km WorldClim

data to the target resolution of 250 m (Khosravi et al. 2016).

We used 23 layers of Normalized Difference Vegetation Index (NDVI) derived from MODIS imagery (250 m resolution) at an interval of 16 days in 2013. Principal component analysis (PCA) was used to reduce the 23 NDVI values per pixel to a smaller number of components (PCs). The first component with the highest explained variance (82% of total variance) was used in the distribution models. Village and road density were extracted using a LULC map (Table S1 in Online Resource 1). All predictors were resampled to a 250 m cell size.

Due to the scarcity of data on the local movement for the studied species in Iran, we evaluated a range of spatial scales reflecting the likely uncertainty in scales of dispersal ability and habitat selection of each species. We used focal statistic in the ‘Multiscale Maxent Toolbox’ (Bellamy et al. 2013) to calculate a mean statistic on all raster layers, excepting landscape metrics, within six spatial scales (250, 500, 1000, 2000, 4000, 8000 m) around each original cell. We used the moving window option in FRAGSTATS to calculate each landscape metric at the six extent sizes (Fig. 3a).

Fig. 2 Multiscale spatial methodological framework including input files, clustering of presence localities, and the consecutive steps undertaken to build the optimized ENMs for the target species

Step 2: species occurrence data, spatial autocorrelation and sampling bias correction in presence localities

Our sampling did not follow a systematic approach; instead we collated data opportunistically collected in different strata (PAs) with different densities of carnivores. The carnivores’ occurrence points were obtained from a variety of sources including opportunistic direct observation, camera-trapping and sign identification during field surveys from 2015 to 2017 (Table S2; Online Resource 1).

We implemented spatial filtering using the SDM toolbox (Brown 2014) in ArcGIS 9.3 (ESRI, Inc., Redlands, CA, USA) to reduce spatial autocorrelation in presence records. As the studied species, especially sand cat and Asiatic cheetah, inhabit areas with relatively low topographical heterogeneity in central Iran, we used climate heterogeneity instead of topographic heterogeneity for spatial filtering of the presence points. Presence localities were spatially filtered at 1, 3 and 5-km of each other in areas of high, medium, and low climate heterogeneity respectively

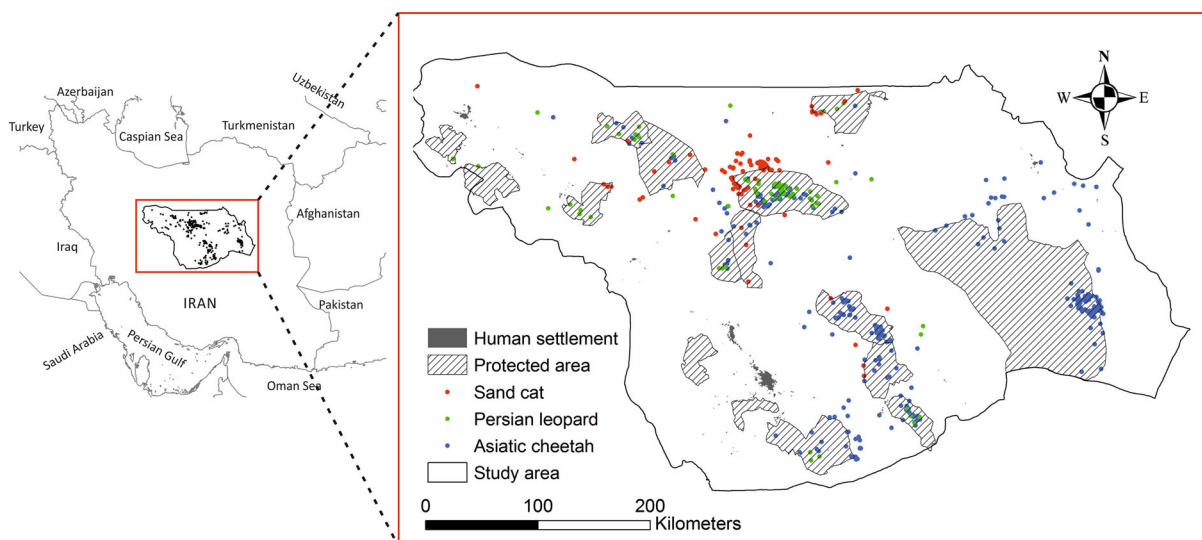
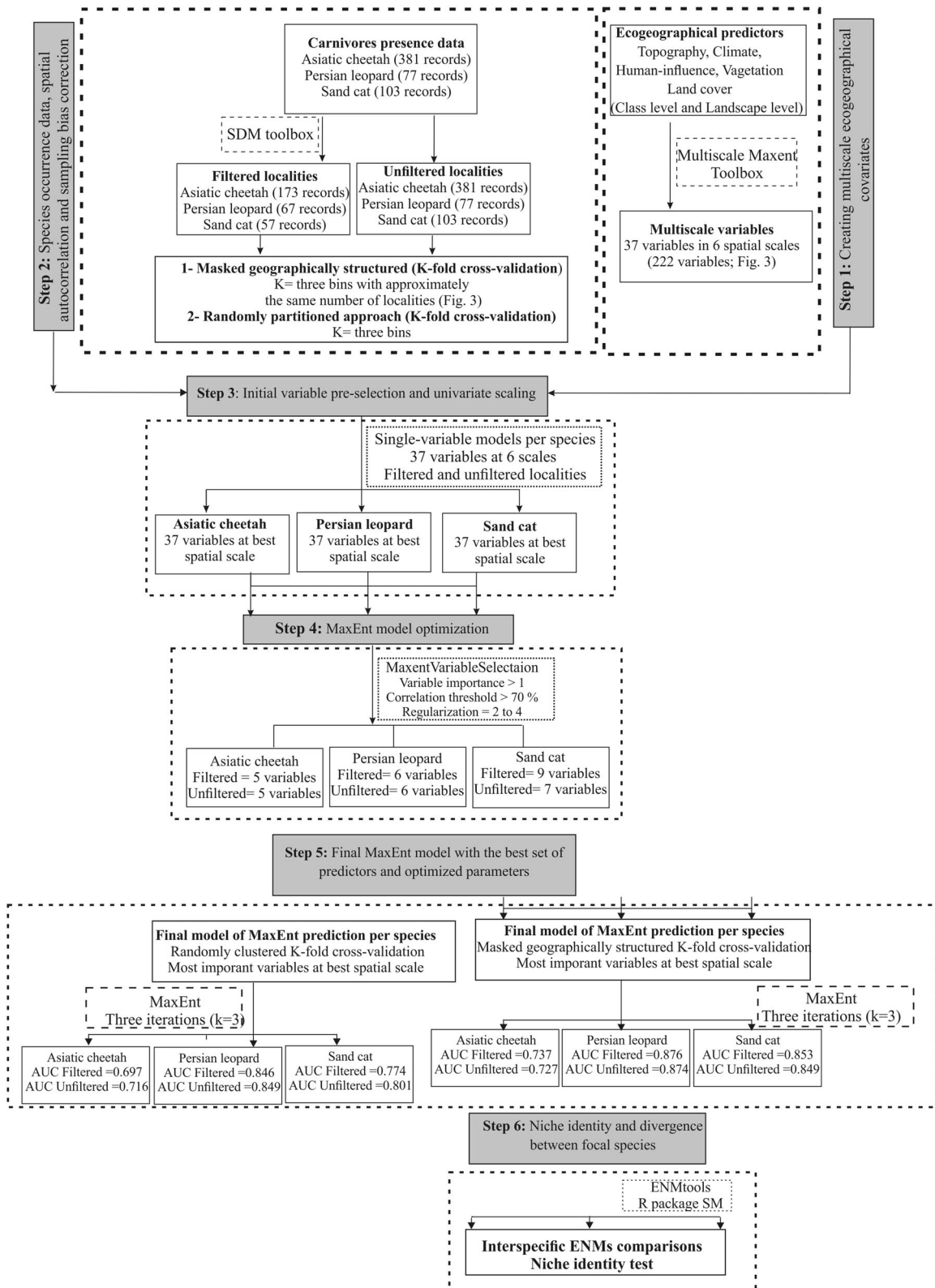


Fig. 1 Location of the study landscape in the central Iran. Dashed polygons and colored filled circles display the border of protected areas (PAs) and presence localities respectively



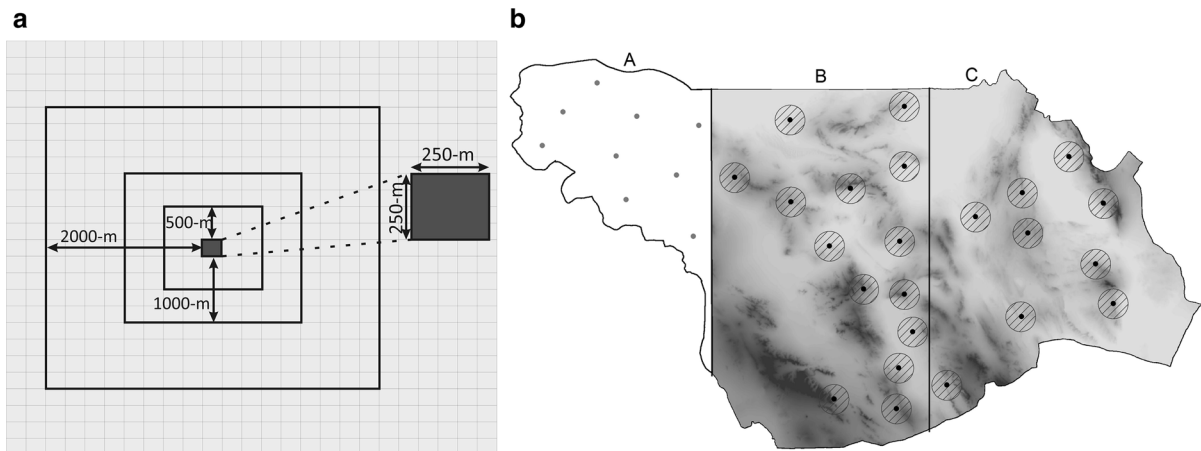


Fig. 3 The concepts of extent size (unfilled squares) and grain size (black-filled square) in this study. Grain size fixed at 250-m and extent size expanded (a). Example of spatially data-partitioning based on masked geographically structured k-fold cross-validation approach (A, B, and C) and corresponding

(see Fig. S1 and text S2 in Online Resource 1 for details).

To prevent environmental bias and selecting background data from environmental conditions outside the range of presence data, we selected 500 random background points within a maximum buffer size of 20-km from presence localities (Fig. 3b). We used these buffers as a mask in MaxEnt software (Vergara et al. 2016). Equal weights was assigned to presence and absence points.

Step 3: initial variable pre-selection and univariate scaling

To identify the extent at which each predictor shows the highest performance (i.e. AUC_{test} , the MaxEnt model performance based on the receiver operating characteristic (ROC) for the presence localities used for model evaluation), an initial MaxEnt model was run independently using each variable at each scale using the R package ‘dismo’ (Hijmans et al. 2016). We used a masked geographically structured approach for data partitioning and cross-validation. In masked geographically structured cross-validation (Fig. 3b), presence localities are segregated spatially into geographical bins with approximately the same number of points in each cluster. In each iteration, the models were trained using two bins and tested on the withheld bin (Radosavljevic and Anderson 2014). We masked

regions for background selection used in MaxEnt models. Black circles represent localities used for model calibration and grey ones denote localities employed in model evaluation. Shaded areas correspond to regions used for background sampling

out environmental data for background sampling from the area corresponding to the localities used for model evaluation (Fig. 3b). MaxEnt was run using the parameters described by Mateo Sanchez et al. (2013) and Vergara et al. (2016). A total of 222 single variable models per species were constructed. Following initial variable pre-selection, the best-performing scale of each covariate (37 covariates in total) was used subsequently to map the species’ distribution.

Step 4: MaxEnt model optimization

We used the R package ‘MaxentVariableSelection’ (Jueterbock 2015) to remove highly inter-correlated variables and to avoid multicollinearity and under or overfitting in multivariate modeling. We tested combinations of features and varied the regularization multiplier between 2 and 4 by a step of 0.5. The candidate set of variables was pruned to discard variables with an importance value of less than 1. A threshold of 0.7 was used for removing inter-correlated variables (Bellamy et al. 2017). Finally, the best combination of variables, optimal regularization value, and feature types for the MaxEnt model were identified as the model of highest AUC or lowest sample-size-adjusted Akaike information criterion (AICc) values. While the ‘MaxentVariableSelection’ package estimates AICc values from single models that include all presence localities, AUC values,

instead, are averaged over tenfold cross validation. Both methods selected the same variables as the best set of predictors (Table S3 in Online Resource 1).

Step 5: final MaxEnt model with best predictors and optimized models

Following univariate scaling, selection of important variables, and model optimization, we used the package ‘dismo’ to predict the final distribution map of each candidate species. We calculated three threshold-independent measures to evaluate the overall model performance including AUC_{test} , $AUC_{test-train}$ and kappa statistic (Cohen 1960, 1968). AUC_{train} and AUC_{test} calculate the model performance based on the ROC for the presence localities used for model calibration and evaluation respectively. $AUC_{test-train}$ is calculated by subtraction of the AUC_{test} from AUC_{train} . We calculated all measures across the three geographic folds and then averaged the values across the three geographic clusters. We applied the Maximum Training Sensitivity plus Specificity (MTSS) occupancy rule to convert the distribution map to a binary map (Liu et al. 2013).

Step 6: niche divergence between focal species

We used three methods to calculate niche overlap between species. First, we used the niche identity test in ENMtools (Warren et al. 2010) to investigate whether habitat suitability scores generated from the best distribution model for the three focal species are different from those expected by chance. We used 100 replicates to calculate a null distribution. The null hypothesis of niche identity is rejected when the observed measure of niche overlap (Schoener’s D and Hellinger’s I metrics) is significantly different from the null distribution (Warren et al. 2010). Second, we calculated the spatial niche difference between each pair of species in a gradient of the probability of occurrence obtained from the MaxEnt model. Finally, we assessed the results of single variable niche overlap among the species according to the density profile of occurrence points for the most important predictor variables using the R package “SM” (Bowman and Azzalini 2015).

Other modeling procedures for comparison

In addition to running the model using spatially filtered localities and masked geographically structured k-fold cross-validation, we used three other different datasets for comparison: (1) spatially filtered localities and randomly clustered k-fold cross-validation, (2) unfiltered localities and masked geographically structured k-fold cross-validation, and (3) unfiltered localities and randomly clustered k-fold cross-validation. We used unfiltered presence localities to test for the expected effect of reducing spatial autocorrelation in presence localities. In the randomly partitioned approach we used three-fold cross-validation in which the presence data for each bin were selected at random. For all models, MaxEnt was run using the parameters described by Mateo Sanchez et al. (2013) and Vergara et al. (2016).

Results

Species occurrence data

Out of 560 occurrence localities, we used 381 localities for Asiatic cheetah, 77 for Persian leopard and 102 for sand cat as unfiltered localities. After spatial filtering we retained 173 locations for Asiatic cheetah, 67 for Persian leopard, and 57 for sand cat.

Variable pre-selection and univariate scaling

The species habitat suitability modeling for each covariate at each spatial scale showed that the performance of the models is highly sensitive to the scale at which variables were measured. Initial variable pre-selection based on different extent sizes revealed that around half of the variables performed best at the largest scales (4–8 km) for all three species (Fig. S2 in Online Resources 1 and 2). In contrast, climate variables (Bio1 and Bio12) had highest AUC at fine scales (250–500 m). While topographic variables (ROUGH and CTI) measured at broad spatial scale (4000 m) performed best for the Persian leopard, these measures at fine to medium scales did better for the Asiatic cheetah (500 m) and sand cat (1000 and 2000 m respectively).

MaxEnt model optimization

The optimization of model parameters and selection of the most important variables in the final MaxEnt models using “MaxentVariableSelection” showed that the optimal models for all species incorporated a different set of variables. For all target species, the best-performing model consisted of 5 to 9 variables. The optimal parameter settings, especially “regularization multiplier” were different between species (Table S3; Online Resource 1).

Final MaxEnt Model distribution with the best predictors and optimized models

The final MaxEnt models had high predictive power for all species regarding the threshold-independent measures ($AUC \geq 0.74$). The ENM for each species showed high discrimination performance for sand cat and Persian leopard ($AUC_{\text{Persian leopard}} = 0.88$ and $AUC_{\text{sand cat}} = 0.85$), and moderately high for Asiatic cheetah ($AUC_{\text{Asiatic cheetah}} = 0.74$). The values of Cohen's kappa, as a more conservative performance measure, for Asiatic cheetah (0.25) and Persian leopard (0.28) was higher than sand cat (< 0.2) indicating fair and poor performance respectively. Nevertheless all models performed substantially better than random. Topographic roughness at a fine extent (ROUGH_500), compound topographic index at a broad scale (CTI_4000), and percentage of landscape covered by sparse rangeland with a density of $\leq 20\%$ at a fine scale (PLAND_Lcr_250) had the highest percentage contribution (65%, 14% and 3% respectively) of total variable contribution for Asiatic cheetah (Fig. S3, Online Resource 1). With increasing topographic roughness, Asiatic cheetah habitat suitability increased to its maximum and then leveled off. For Persian leopard, broad scale topographic roughness (ROUGH_4000), percentage of landscape covered by sparse rangeland with a density of $\leq 20\%$ at a broad scale (PLAND_Lcr_4000), village density at a fine scale (VID_250) and a measure of habitat availability and landscape connectivity of barelands at a broad scale (GYR_Bar_8000) showed the highest percentage contributions (71.5%, 5.3%, 4.3% and 4.2% respectively). The model predicts that habitat suitability for Persian leopard increases with increasing topographic roughness (Fig. S4, Online Resource 1). Finally, the density of shrubland and agriculture

patches at a broad scale (PD_Shr_8000; PD_Agr_8000), medium scale topographic roughness (ROUGH_2000) and fine scale village density (VID_250) had the largest contribution in the final sand cat distribution map (23%, 15.8% and 9.2% respectively). The density of villages and increasing topographic roughness had negative impacts on the presence of sand cat, with village density having the largest effect (Fig. S5, Online Resource 1).

Niche identity and divergence between species

Predicted suitable habitats in the final MaxEnt models were different among the species. The area of suitable habitats of Asiatic cheetah and sand cat showed the widest (11.6% of study area) and most limited (9.4%) distributions, respectively (Table 1). The suitable habitats for Asiatic cheetah and Persian leopard were predicted to be more widely distributed across the landscape than those of sand cat (Fig. 4). The areas of suitable habitats covered by protected areas were different among species (32% for Asiatic cheetah, 37% for Persian leopard, and 24% for sand cat; Table 1; Fig. 4).

Persian leopard occurrence is predicted to be concentrated in the mountainous portions of the western and central parts of the region (Fig. 5). On the other hand, Asiatic cheetah tends to select relatively high roughness in areas that at broad scales have low roughness (e.g. the plains in the east and center of the landscape). The sand cat is a relatively abundant species in the northern and central parts of the study area, and dwells in and around shrub-covered sand dunes. The identity test in ENMtools highlighted that the Asiatic cheetah, Persian leopard and sand cat niches were significantly different than those expected by chance ($p < 0.01$). The observed values of niche overlap for all pairwise comparisons revealed niche differentiation among species (Table 2). Asiatic cheetah and Persian leopard showed the most ($D = 0.62$) and Persian leopard and sand cat showed the least spatial overlap ($D = 0.27$). The results of single variable niche overlap according to the density profile of occurrence points for each species showed that the Persian leopard had different tolerance ranges compared to sand cat and Asiatic cheetah for the most important predictors (Fig. 6).

Table 1 Optimal MaxEnt model settings to predict distribution map for carnivore species

Species	Bin	Masked geographically structured cross-validation					Suitable habitat area (km ²) (% in PAs)	Randomly partitioned approach				
		Train (n)	Test (n)	AUC	Mean AUC	Kappa		Train (n)	Test (n)	AUC	Mean AUC	Kappa
Asiatic Cheetah (filtered)	Bin_1	128	45	0.76	0.74	0.25	19,261 (32%)	115	58	0.69	0.69	0.25
	Bin_2	99	74	0.76				115	58	0.68		
	Bin_3	119	54	0.69				116	57	0.71		
Asiatic Cheetah (unfiltered)	Bin_1	171	172	0.73	0.73	0.31		204	102	0.73	0.71	0.35
	Bin_2	241	96	0.70				204	102	0.72		
	Bin_3	200	113	0.75				204	102	0.69		
Persian Leopard (filtered)	Bin_1	46	21	0.89	0.88	0.28	17,138 (37)	44	23	0.77	0.84	0.31
	Bin_2	36	31	0.86				45	22	0.86		
	Bin_3	52	15	0.88				45	22	0.90		
Persian Leopard (unfiltered)	Bin_1	60	17	0.88	0.87	0.23		50	26	0.81	0.85	0.25
	Bin_2	37	39	0.86				51	25	0.87		
	Bin_3	55	21	0.88				51	25	0.85		
Sand Cat (filtered)	Bin_1	44	13	0.84	0.85	0.10	15,560 (24)	38	19	0.76	0.77	0.10
	Bin_2	26	31	0.86				38	19	0.80		
	Bin_3	44	13	0.86				38	19	0.75		
Sand Cat (unfiltered)	Bin_1	82	14	0.86	0.85	0.30		64	32	0.84	0.80	0.33
	Bin_2	29	68	0.82				64	32	0.74		
	Bin_3	81	20	0.86				64	32	0.80		

n the number of points used for calibration and evaluation of model in each bin. *AUC* the model performance based on the ROC for the presence localities used for model evaluation (i.e. *AUC_{test}*). *Kappa* Cohen's kappa (Cohen 1968). *Suitable habitat* the area of highly suitable habitats. Numbers in parenthesis show the percent of highly suitable habitats covered by PAs

Comparison between modeling procedures

The MaxEnt models for all target species made with the spatially filtered presence points and a masked geographically structured approach were slightly superior to those from the unfiltered localities and randomly clustered three-fold cross-validation (Table 1).

Discussion

We used a multiscale structured framework to quantify the niche differentiation among three sympatric felids in central Iran considering spatial autocorrelation in presence localities, sampling bias in presence and background localities and spatial scale of predictors. We showed three main results, which we summarize here and elaborate on in the sections

below. Firstly, the predictive ability of the predictors in ENMs changed notably depending on the spatial scale of predictors and performance of ecological niche models was associated with variables at multiple, and often broad spatial scales. Secondly, landscape composition generally have stronger influences on occurrence of the studied species than configuration. Thirdly, the comparison among ENMs showed distinct patterns of habitat selection, implying spatial niche partitioning between species.

Effect of spatial scale of predictors on carnivore habitat selection

A number of studies have suggested that a multiscale approach typically outperforms single scale multivariate ENMs (Shirk et al. 2012; Mateo Sanchez et al. 2013; Wan et al. 2017). Our multiscale findings confirmed that the predictive ability of the predictors

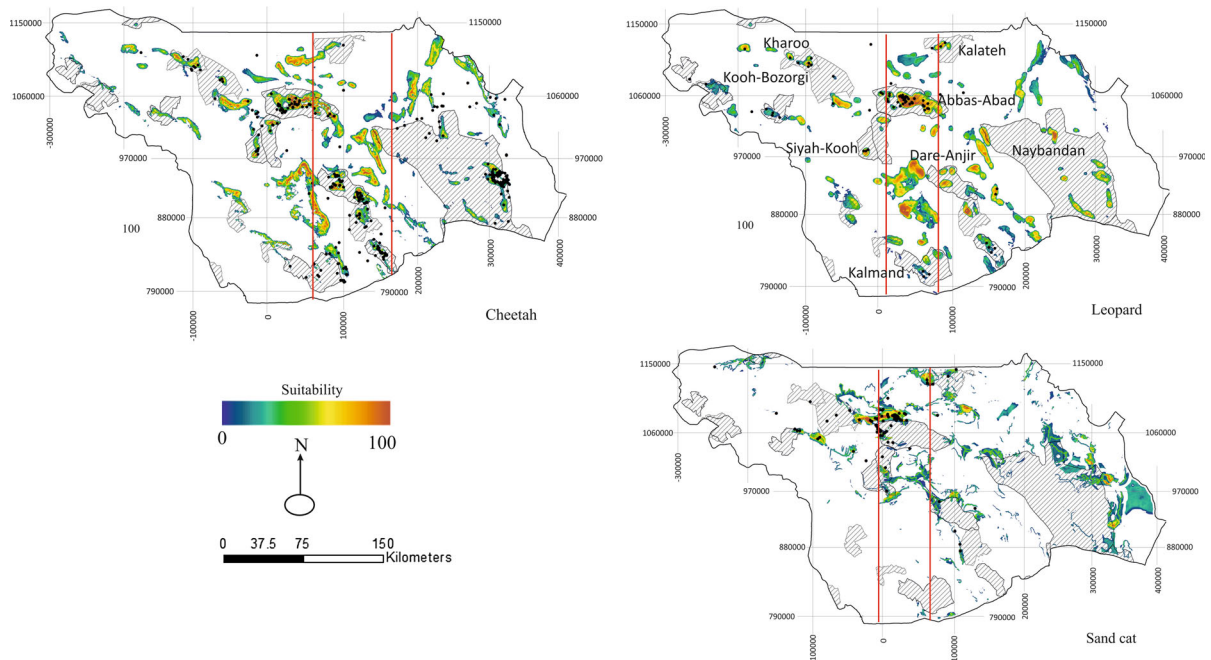


Fig. 4 The output of the optimized MaxEnt model for the three target species using spatially filtered presence points and masked geographically structured approach for model evaluation (red rectangles). The areas in white indicate pixels with

values below the suitability threshold. The dashed polygons and black filled circles show the border of protected areas (PAs) and presence localities respectively. (Color figure online)

changed notably depending on the spatial scale of variables. The studied species responded to most landscape features at relatively broad scales. This strong association of carnivores with broader scales of environmental variation has also been seen in other studies (e.g. Hearn et al. 2018).

The medium to broad scale relationships between topographic variables and occurrence of Persian leopard and sand cat may be due to their broad avoidance of human activities. The fine-scale sensitivity of sand cat and Asiatic cheetah to edge density probably reflects a tendency of these species to associate with edges and ecotones for supplementary and complementary resource use (Mateo Sanchez et al. 2013). In contrast, the importance of edge density for Persian leopard may be due to the species selection of high elevations, where the variation in land cover types is low, and broad scale avoidance of human activities. The importance of rough topography for carnivores has also been seen in tigers (Reddy et al. 2017) and clouded leopards (Hearn et al. 2018), and may generally be expected when carnivores live in remnant habitats in human dominated landscapes, where topographically rough ridge systems have the

lowest human footprint and highest remaining prey populations.

McGarigal et al. (2016a) referred to the multiscale approach we used in this study as “pseudo-optimized” because the best scale is determined univariately across a continuous range of scales and not multivariately in the context of the full multivariable model. As noted by McGarigal et al. (2016a), very few studies have compared this “pseudo-optimization” approach to a true multivariate, multi-scale optimization. Therefore, while future research should explore the development of better and more efficient technical solutions to scale optimization, the approach used here is the most commonly used and well evaluated method of evaluating scale dependency in habitat relationships.

The effect of environmental predictors on distribution of carnivores

The geographical patterns of predicted suitable habitats for all studied species was quite similar to previously published predictions in the region (Khosravi et al. 2018). We found high correlation between

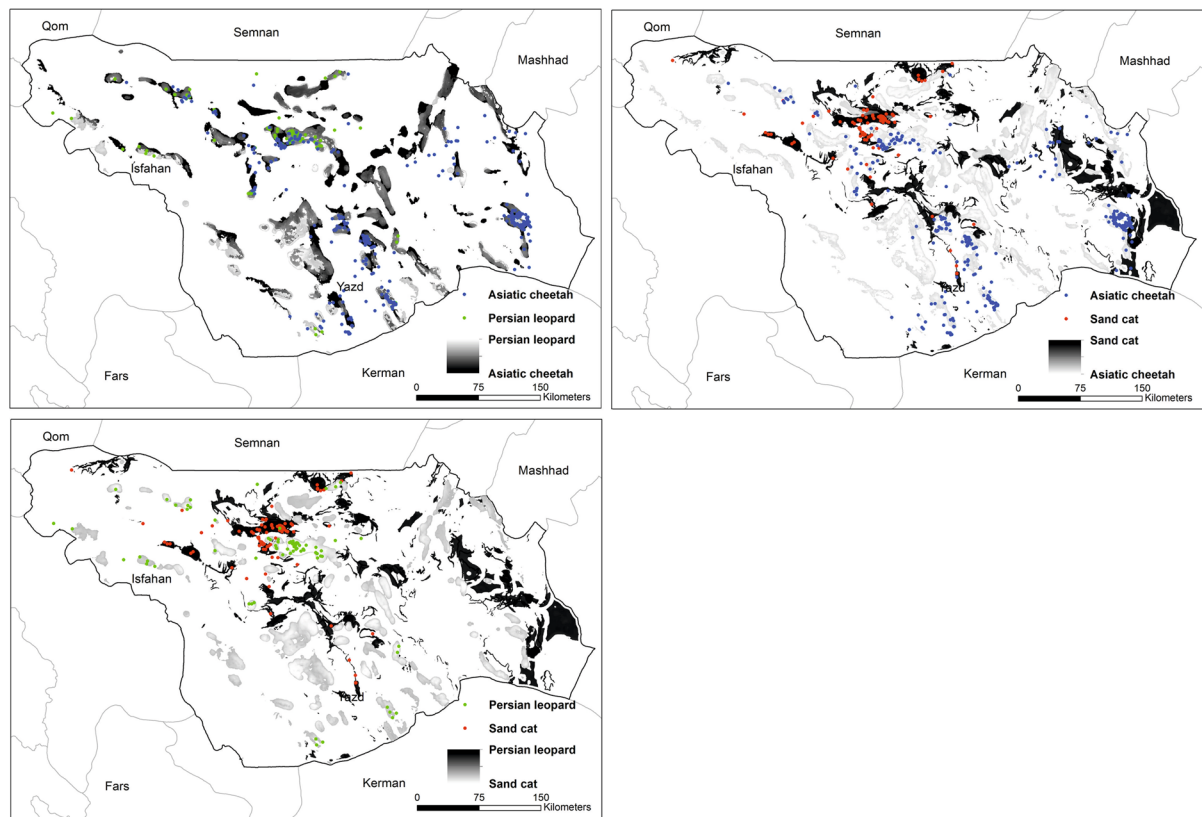


Fig. 5 The spatial niche comparisons between each pair of species in a gradient of the probability of occurrence obtaining from MaxEnt model. The maps are produced by subtraction of the occurrence probability maps of species. Each map represents the maximum probability of occurrence for sand cat (in purple)

to the maximum probability of occurrence for the Asiatic cheetah and Persian leopard (in green). The areas in white indicate pixels with values below the suitability threshold. (Color figure online)

Table 2 The niche identity result for pairwise comparisons according to the MaxEnt model

Pairwise comparison	D metric		I metric	
	Observed	Pseudoreplicates	Observed	Pseudoreplicates
Asiatic Cheetah—Persian leopard	0.62	0.71	0.67	0.74
Asiatic Cheetah—Sand cat	0.42	0.71	0.70	0.74
Persian leopard—Sand cat	0.27	0.66	0.55	0.71

D and I are Schoener's and Hellinger metrics respectively. *Observed* observed measure of niche overlap based on the habitat suitability scores generated from the best distribution models for the three focal species. *Pseudoreplicates* expected measure of niche overlap scores generated from 100 replicates

the predicted suitable values in the study conducted by Khosravi et al. (2018) and present study for Persian leopard ($r = 0.70$), Asiatic cheetah ($r = 0.65$), and sand cat ($r = 0.70$). However, the refinement of predictions through scale optimization identified

suitable habitat patches that were smaller in area and less spatial connectivity than the previous study. This difference might be due to the use of variables related to landscape composition and configuration in this study. Given that species habitat quality is related to

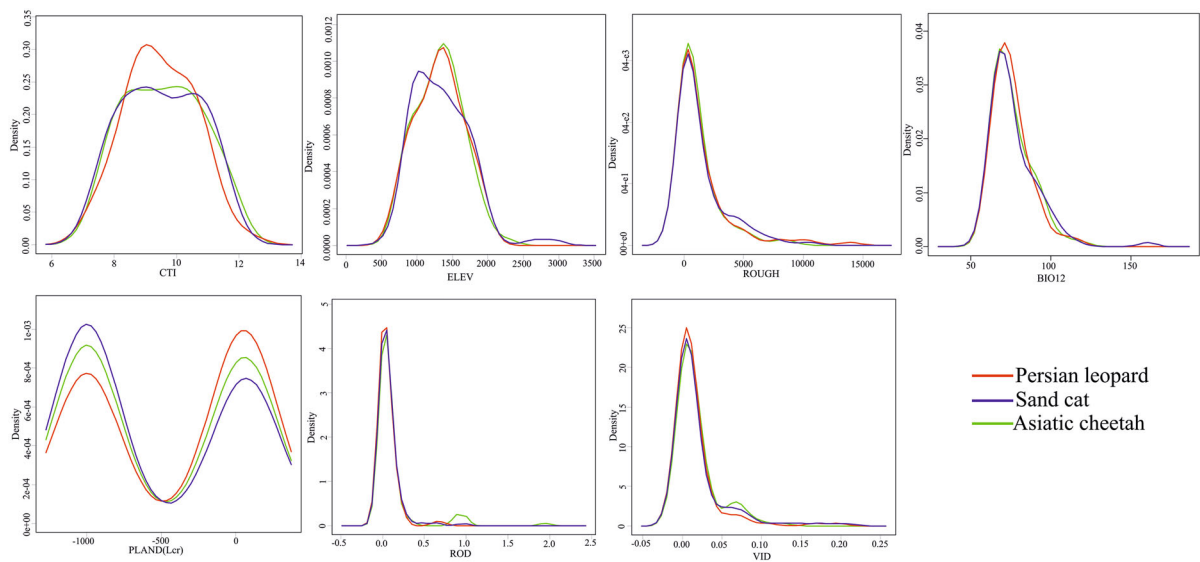


Fig. 6 The density of occurrence localities of each target species in response to gradient of most importance environmental variables recognized from the optimized MaxEnt model

both amount and pattern of environmental factors, inclusion of these predictors may provide more reliable ENMs. Another potential explanation for such contradictory results is that, as seen previously by Shirk et al. (2014) and Wasserman et al. (2012), multi-scale optimization produces predictions that have more spatial discrimination between predicted high and low quality habitat, which typically results in higher heterogeneity and patchiness of predictions. This seems to be a general pattern in which scale optimization focuses and clarifies habitat relationships leading to models with higher spatial discrimination and higher accuracy. To quote McGarigal et al. (2016a), “scale is the lens that focuses ecological relationships; Page 1161”.

Asiatic cheetah live in certain ecological regions characterized by arid and relatively flat and open conditions. The model showed a positive relationship between the probability of occurrence of Asiatic cheetah and topographic roughness at small scale, suggesting that within the relatively flat desert areas preferred by Asiatic cheetah at broad scales, the species selects areas with higher topographic roughness. The explanation of this is likely that areas with moderate vegetation cover at intermediate amounts of topographic roughness offer the best food resources and lowest impacts of human activities. The species is strictly dependent on a few ungulate species in central

Iran, including gazelles (*Gazella* spp.), wild sheep (*Ovis orientalis*), and wild goat (*Capra aegagrus*; Farhadinia and Hemami 2010). Prey availability is one of the most important factors affecting habitat suitability of carnivores (Hayward et al. 2006). Previous studies in Iran have confirmed that Asiatic cheetahs are scattered predominantly in rangelands with relatively rough terrain (Ahmadi et al. 2017). The current widespread use of rough areas by Asiatic cheetah may be also attributed to a shift in prey selection as Asiatic cheetah’s primary prey has been dramatically declined in more open, flat and low elevation areas (Durant et al. 2010).

Roughness had by far the largest influence on Persian leopard occurrence of all variables in the model, and suggests that Persian leopard is strongly associated with rough topography, which is likely related to both increased prey availability and lower human impacts in these parts of the landscape. Our results also predict that an increase in the amount of rangeland with a density of $\leq 20\%$ reduces the relative probability of Persian leopard occurrence. These results suggest that the area of rangelands with sparse vegetation might be a useful metric for evaluating habitat suitability of Persian leopard across large landscapes.

In our study, the presence of shrub and wood patches was among the best predictors of the sand cat

habitat suitability. This species is closely associated with shrublands due to higher density of rodents and higher visual cover in shrublands, and presence of stabilized soil, which improves den digging efficiency (Khosravi et al. 2018). Agriculture patches are another important food source for sand cat and hence influence the species habitat suitability as we found in our study, which increases with the density of agricultural patches. This suggests that the small size and cryptic nature of the sand cat make it more tolerant of human dominated landscapes and less vulnerable to human persecution than larger carnivores such as cheetah.

The effect of landscape composition and configuration on distribution of carnivores

There has been a long debate in the landscape ecology literature about the relative importance and influence of landscape composition versus landscape configuration (e.g., Flather and Bevers 2002; Fahrig 2003). The majority of evidence suggests that in most cases the composition of the landscape is more important to species distributions than is its spatial configuration (Mateo Sanchez et al. 2013). In this study, predicted suitable habitat for all three species covered about 12% of the study area. Our findings clearly showed that landscape configuration variables, had relatively weaker relationships with Persian leopard and Asiatic cheetah habitat suitability than landscape composition. The comparatively weak role of landscape configuration in habitat suitability for these species may be due to the high mobility of the species which allows them to integrate across landscapes of differing configurations resulting lower sensitivity to habitat fragmentation. The amount of available sparse vegetation and grassland–scrubland habitats had a strong relationship with Asiatic cheetah occurrence when measured as percentage of landscape area. These findings confirm that importance of habitat amount at the landscape scale should be the conservation priority for large carnivores.

Patch density of shrubland and agriculture had strong relationships with sand cat habitat suitability. Species with large body size, intermediate mobility, high trophic level, and high habitat specialization are thought to be most likely to be strongly influenced by changes in habitat configuration (Sauder and Rachlow 2014). Sand cat, a wide-ranging mesocarnivore meets most of these criteria. Similar results have been found

for American marten and pine marten (Shirk et al. 2014; Vergara et al. 2016). Also, a number of studies have shown that the importance of habitat configuration for a species is higher when there are relatively low amounts of habitat area in a landscape (Villard and Metzger 2014). Sand cat was the species with the lowest extent of quality habitat, which, coupled with its relatively higher specialization on particular vegetation types, likely makes it highly sensitive to both landscape composition and configuration. Our results for sand cat indicate that composition and configuration of the landscape are important, but as configuration is highly confounded with composition (correlation above 0.7) it is impossible to resolve the relative importance of the two. This species benefits from a mix of agricultural land and shrubland in the landscape. Therefore the amount of shrublands and agriculture fields, and habitat diversity of the landscape (i.e. a mix of agricultural land and shrubland) are important considerations for sand cat to mitigate the effects of habitat loss.

Niche divergence in carnivore species

Topographic conditions and well-connected sparse vegetation can be considered as limiting factors determining the distribution of the study species across the area and shaping the differences in spatial niche of the three species. Persian leopards select higher elevation and rougher terrain than Asiatic cheetah suggesting spatial niche separation between these two species. However, we observed a relatively higher spatial niche overlap between Asiatic cheetah–Persian leopard than Persian leopard–sand cat (Table 2, Fig. 5). The avoidance of Asiatic cheetah as a sub-ordinate predator from Persian leopard in their area of sympatry may have rather facilitated temporal niche partitioning than spatial niche partitioning, reducing food competition and the risk of dangerous interactions (Hemami et al. 2018). Dröge et al. (2017) found that Asiatic cheetahs made about 70% of their kills during full daylight, whereas leopards are strongly nocturnal. Persian leopards and Asiatic cheetah seem to be able to coexist in areas of open habitats in central Iran where spatial avoidance is difficult, suggesting the potential importance of temporal displacement. High spatial niche overlap between Asiatic cheetah and Persian leopard may also be due to the vegetation structure in deserts of central

Iran which is highly uniform and dominated by sparse vegetation with a density of < 20% with high visibility over long distances. These conditions enable large carnivores to detect one another relatively easily which facilitates avoidance (Dröge et al. 2017). While sand cat and Asiatic cheetah can coexist locally in some regions in Iran, the identity test showed substantial spatial niche divergence among the two species, which was further supported by the habitat suitability maps. The sand cat is strongly influenced by topography and is absent in regions with high topographic roughness. Dröge et al. (2017) suggested that open environments with a simple prey set (like desert ecosystems of Iran) constrain the options for subordinate species like sand cat, promoting competitive exclusion. However, spatial partitioning as well as dietary differences may allow for coexistence of sand cat and Asiatic cheetah. Hemami et al. (2018) suggested that exclusive selection of sand dunes by sand cat facilitate spatial niche partitioning between sand cat and other felid species.

Spatial filtering

Spatial filtering has been identified as a straightforward and effective method to limit residual spatial autocorrelation in ENMs (Fourcade et al. 2014; Kittle et al. 2018). Fourcade et al. (2014) suggested that systematic sampling of presence localities is one of the best methods to account for sampling bias. Kramer-Schadt et al. (2013) and Boria et al. (2014) named systematic sampling as ‘spatial filtering’. Our findings were consistent with the previously studies and showed that spatially filtering the dataset tended to slightly improve the model performance. The masked geographically structured approach showed slightly higher AUC values than randomly partitioned cross-validation. This difference emphasizes the importance of selecting calibration regions that match modeling assumptions and also the importance of parameterization of MaxEnt models to identify optimal model complexity for a given species and dataset.

Conclusion and management implications

This was one of the first multiscale niche modeling studies to investigate niche divergence among three sympatric carnivore species. In a somewhat similar

study, Hearn et al. (2018) used multi-scale optimization with generalized linear modeling to compare niche structure for clouded leopard, leopard cat, bay cat and marbled cat in Borneo and found, similarly to this study, high scale-dependence of habitat relationships. Our results also support the findings of Hemami et al. (2018) and reinforce the role of montane areas and desert shrublands/woodlands in low relief plains of central Iran as important habitats providing food and cover for threatened carnivores. Our multiscale framework emphasized the importance of optimizing the spatial scale of environment predictors, and the evaluation data and background localities for predicting species niches and investigating spatial niche divergence. The scaled models revealed that predicted habitat suitability for the Asiatic cheetah and Persian leopard is more strongly associated with landscape composition than landscape configuration, but most strongly to topography. Hence, to maximize the viability of these carnivore populations, conservation efforts should focus on maintaining large extents and well-connected areas of natural vegetation in areas of relatively rough topography with a low density of human settlements. The predicted suitable habitats should be evaluated and verified in future monitoring programs to obtain more accurate estimates of population size and distributions of these species across the study region. This is particularly important for species with dispersed distributions and very few records such as Asiatic cheetah, which is at the edge of extinction (less than 50 individuals remain in Iran; Khalatbari et al. 2018).

Using the results of multi-scale models for the surrogate species, conservation managers can develop a multi-species conservation program for overall biodiversity conservation in central Iran by prioritizing key suitable patches predicted for the selected surrogate species. For example, the patches in Abbas-Abad and Dare-Anjir wildlife refuges, Kalate and Kharoo no-hunting areas can be considered as key habitat patches that managers can give high priority to them in the future conservation programs (Figs. 4 and S6; Online Resource 1). Also, the results suggest that there are some key habitat patches outside of protected areas which have significant contribution, especially as stepping stones, in maintaining landscape connectivity in central Iran (e.g. the key patches between Dare-Anjir, Siyah-Kooh and Kalmand protected areas).

The obtaining information is clearly useful for conservation and can make a case for increasing the size of existing PAs or areas adjacent to PAs. Our outputs also could be used to guide location of new large-scale ecological corridors that are big enough to provide habitat for species and as such act as large scale corridors for these focal species. Furthermore, given the high fragmentation of predicted habitats, we recommend implementing habitat restoration to create stepping stones and movement corridors (e.g. Cushman et al. 2018; Khosravi et al. 2018) among the suitable habitat patches. More attention should be paid in the designation process of PAs to improve connectivity among them.

We would like to note that, given relatively rapid land-use change in the study area, species occurrence patterns may be in disequilibrium with the environment. If this is the case then the species-environment associations developed will reflect the disequilibrium relationship rather than any equilibrium outcome, and thus not ideally represent the “suitability”. However they will represent the current “probability of detection or occurrence”, which does reflect the disequilibrium state. To clarify the current relationship between species and the environment to account for time lags in occurrence, future research should focus on studies that assess performance measures, such as fecundity, survivorship and fitness, rather than mere occurrence or presence and absence.

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References

Ahmadi M, Nezami Balouchi B, Jowkar H, Hemami MR, Fadakar D, Malakouti-Khah S, Ostrowski S (2017) Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia. *Divers Distrib* 23(6):592–603

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol Evol* 3(2):327–338

Bellamy C, Scott C, Altringham J (2013) Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *J Appl Ecol* 50(4):892–901

Bellamy CC, van der Jagt AP, Barbour S, Smith M, Moseley D (2017) A spatial framework for targeting urban planning for pollinators and people with local stakeholders: a route to healthy, blossoming communities? *Environ Res* 158:255–268

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Model* 275:73–77

Bowman A, Azzalini A (2015) package ‘sm’: nonparametric smoothing methods (version 2.2-5.4). 2014

Brown JL (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol* 5(7):694–700

Caro T (2010) Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press

Coetsee BW (2017) Evaluating the ecological performance of protected areas. *Biodivers Conserv* 26(1):231–236

Cohen J (1960) A coefficient of agreement for nominal scales. *Educ Psychol Measur* 20(1):37–46

Cohen J (1968) Weighted kappa: nominal scale agreement provision for scaled disagreement or partial credit. *Psychol Bull* 70(4):213

Cushman SA, Elliot NB, Bauer D, Kesch K, Bothwell H, Flyman M, Mtare G, Macdonald DW, Loveridge AJ (2018) Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one* 13(7):e0196213

Di Minin E, Hunter LT, Balme GA, Smith RJ, Goodman PS, Slotow R (2013) Creating larger and better connected protected areas enhances the persistence of big game species in the Maputland-Pondoland-Albany biodiversity hotspot. *PLoS ONE* 8(8):e71788

Dröge E, Creel S, Becker MS, M’soka J (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecol Evol* 7(1):189–199

Durant SM, Craft ME, Foley C, Hampson K, Lobora AL, Msuha M, Eblate E, Bukombe J, Mchetto J, Pettorelli N (2010) Does size matter? An investigation of habitat use across a carnivore assemblage in the Serengeti, Tanzania. *J Anim Ecol* 79(5):1012–1022

Evans J, Oakleaf J, Cushman S, Theobald D (2014) An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0-0. Laramie, WY. <http://evansmurphy.wix.com/evansspatial>

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34(1):487–515

Farhadinia MS, Ahmadi M, Sharbafi E, Khosravi S, Alinezhad H, Macdonald DW (2015) Leveraging trans-boundary conservation partnerships: persistence of Persian leopard (*Panthera pardus saxicolor*) in the Iranian Caucasus. *Biol Conserv* 191:770–778

Farhadinia M, Hemami M-R (2010) Prey selection by the critically endangered Asiatic cheetah in central Iran. *J Nat Hist* 44(19–20):1239–1249

Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am Nat* 159(1):40–56

Flint LE, Flint AL (2012) Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. *Ecol Process* 1(1):2

- Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE* 9(5):e97122
- Gábor L, Moudrý V, Barták V, Lecours V (2019) How do species and data characteristics affect species distribution models and when to use environmental filtering? *Int J Geogr Inf Sci*. <https://doi.org/10.1080/13658816.2019.1615070>
- Hayward M, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley G (2006) Prey preferences of the leopard (*Panthera pardus*). *J Zool* 270(2):298–313
- Hearn AJ, Cushman SA, Ross J, Goossens B, Hunter LT, Macdonald DW (2018) Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? *PLoS ONE* 13(7):e0200828
- Hemami M-R, Esmaili S, Brito JC, Ahmadi M, Omid M, Martínez-Freiría F (2018) Using ecological models to explore niche partitioning within a guild of desert felids. *Hystrix Ital J Mammal* 29(2):216–222
- Hemami M, Groves C (2001) Global antelope survey and regional action plans: Iran. In: Mallon D, Kingswood S (eds) *Antelopes: Part 4 North Africa. The Middle East and Asia. Switzerland and Cambridge: IUCN*, pp 114–118
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25(15):1965–1978
- Hijmans RJ, Phillips S, Leathwick J, Elith J, Hijmans MRJ (2016) Package 'dismo'. Circles, 1
- Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *AIBS Bull* 54(3):227–233
- Huang Q, Fleming CH, Robb B, Lothspeich A, Songer M (2018) How different are species distribution model predictions?—Application of a new measure of dissimilarity and level of significance to giant panda *Ailuropoda melanoleuca*. *Ecol Inform* 46:114–124
- Jueterbock A (2015) 'MaxentVariableSelection' vignette
- Khalatbari L, Yusefi GH, Martínez-Freiría F, Jowkar H, Brito JC (2018) Availability of prey and natural habitats are related with temporal dynamics in range and habitat suitability for Asiatic Cheetah. *Hystrix Ital J Mammal* 29(1):145–151
- Khosravi R, Hemami M-R (2019) Identifying landscape species for ecological planning. *Ecol Ind* 99:140–148
- Khosravi R, Hemami MR, Cushman SA (2018) Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. *Divers Distrib* 24(2):193–207
- Khosravi R, Hemami MR, Malekian M, Flint A, Flint L (2016) Maxent modeling for predicting potential distribution of goitered gazelle in central Iran: the effect of extent and grain size on performance of the model. *Turk J Zool* 40(4):574–585
- Kittle AM, Watson AC, Cushman SA, Macdonald DW (2018) Forest cover and level of protection influence the island-wide distribution of an apex carnivore and umbrella species, the Sri Lankan leopard (*Panthera pardus kotiya*). *Biodivers Conserv* 27(1):235–263
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers Distrib* 19(11):1366–1379
- Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *J Biogeogr* 40(4):778–789
- Mateo Sanchez MC, Cushman SA, Saura S (2013) Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *Int J Geogr Inf Sci* 28(8):1531–1546
- McGarigal K, Cushman S, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, Massachusetts, USA. www.goo.gl/aAEbMk
- McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016a) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol* 31(6):1161–1175
- McGarigal K, Zeller KA, Cushman SA (2016b) Multi-scale habitat selection modeling: introduction to the special issue. *Landscape Ecol* 31(6):1157–1160
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190(3–4):231–259
- Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biol Conserv* 143(4):939–945
- Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J Biogeogr* 41(4):629–643
- Redding DW, Lucas TC, Blackburn TM, Jones KE (2017) Evaluating Bayesian spatial methods for modelling species distributions with clumped and restricted occurrence data. *PLoS ONE* 12(11):e0187602
- Reddy PA, Cushman SA, Srivastava A, Sarkar MS, Shivaji S (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. *Divers Distrib* 23(8):863–874
- Sauder JD, Rachlow JL (2014) Both forest composition and configuration influence landscape-scale habitat selection by fishers (*Pekania pennanti*) in mixed coniferous forests of the Northern Rocky Mountains. *For Ecol Manage* 314:75–84
- Shahnaseri G, Hemami M-R, Khosravi R, Malakoutikhah S, Omid M, Cushman SA (2019) Contrasting use of habitat, landscape elements, and corridors by grey wolf and golden jackal in central Iran. *Landscape Ecol* 34:1263–1277
- Shirk AJ, Raphael MG, Cushman SA (2014) Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). *Ecol Appl* 24(6):1434–1444
- Shirk AJ, Wasserman TN, Cushman SA, Raphael MG (2012) Scale dependency of American marten (*Martes americana*) habitat relations [Chapter 12]. In: Aubry KB, Zielinski WJ, Raphael MG, Proulx G, Buskirk SW (eds) *Biology and conservation of martens, sables, and fishers: a new synthesis*. Cornell University Press, Ithaca, pp 269–283
- Syfert MM, Smith MJ, Coomes DA (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE* 8(2):e55158
- Vergara M, Cushman SA, Urra F, Ruiz-González A (2016) Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and

- Martes foina) in the northern Iberian Peninsula. Landscape Ecol 31(6):1241–1260
- Villard MA, Metzger JP (2014) Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. J Appl Ecol 51(2):309–318
- Wan JZ, Wang CJ, Tan JF, Yu FH (2017) Climatic niche divergence and habitat suitability of eight alien invasive weeds in China under climate change. Ecol Evol 7(5):1541–1552
- Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33(3):607–611
- Wasserman TN, Cushman SA, Wallin DO (2012) Multi scale habitat relationships of Martes americana in northern Idaho, USA. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, p 21

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