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Multispecies assessment of core areas and connectivity of desert carnivores in central Iran

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Abstract

Aim: Central Iran is a priority area for biodiversity conservation, which is threatened by encroachment on core habitats and fragmentation by roads. The goal of this study was to identify core areas and connectivity corridors for a set of desert carnivores by predicting habitat suitability and calculating resistant kernel, factorial least-cost path modelling and graph network indices.

Location: Iran.

Methods: We used an ensemble model (EM) of habitat suitability methods to predict the potential habitats of leopard, cheetah, caracal, wild cat, sand cat and grey wolf and used resistant kernel and factorial least-cost path modelling to identify important core habitats and corridors between patches. We also used a graph network analysis to quantify the importance of each core patch to landscape connectivity.

Results: Potential habitats of the studied carnivores appeared to be strongly influenced by prey density, annual precipitation, topographical roughness, shrubland density and anthropogenic factors. Most of the core patches were covered by protected areas and no-hunting areas. This may be attributed to the relatively high resistance outside protected areas leading to isolated occupied patches. Patch importance to connectivity was significantly correlated with patch extent, density of dispersing individuals and probability of occurrence in the core patch.

Main conclusions: Our findings revealed that prey abundance in core habitat is critically important, and has higher influence than habitat area per se. In addition, our analysis provided the first map of landscape connectivity for multiple species in Iran and revealed that conserving these species requires integrated landscape-level management to reduce mortality risk and protect core areas and linkages among them. These results will assist the development of multispecies conservation strategies to protect core areas for carnivores.

KEYWORDS
carnivores, core habitat, corridor, ensemble model, landscape connectivity, potential habitat, probability of connectivity, resistant kernel, UNICOR

1 | INTRODUCTION

Human-induced habitat fragmentation (HIHF), one of the major global threats to biodiversity, can increase patch isolation and reduce the ecological suitability of the remnant fragments (Fahrig, 2003). These changes may affect negatively impact gene flow, demographic exchange and local extinction risk. In a fragmented landscape, species with extensive area requirements (e.g., large carnivores) often persist in a metapopulation pattern in which dispersal among subpopulations is essential for regional viability (Wiens, 2001). Therefore, maintaining landscape connectivity through the conservation of migration paths is a primary solution for effective conservation in human-dominated landscapes (Di Minin et al., 2013).

Landscape connectivity (Kindlmann & Burel, 2008; Taylor, Fahrig, Henein, & Merriam, 1993) is species-specific and determined by the interactions between landscape structure and species' behaviour (Goodwin, 2003). Quantifying functional connectivity is challenging due to uncertainty about the effects of landscape features on movement, and limited understanding of species dispersal ability (Cushman, Landguth, & Flather, 2013; Cushman, McRae, et al., 2013). Most connectivity modelling approaches are based on predicting connectivity across a resistance surface (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). The usefulness of resistance surfaces depends on how well they reflect biological responses of the focal species. Ideally, connectivity models should be parameterized based on empirical movement data of dispersing individuals (e.g., Elliot, Cushman, Macdonald, & Loveridge, 2014; Spear et al., 2010) or genetic data (Braunisch, Segelbacher, & Hirzel, 2010; Castillo, Epps, Davis, & Cushman, 2014; Cushman, McKelvey, Hayden, & Schwartz, 2006). However, quantitative data on animal movement or genetic structure across landscapes are often unavailable. As a result, a large portion of connectivity analyses uses either expert opinion (e.g., Puyravaud, Cushman, Davidar, & Madappa, 2016; Zeller, McGarigal, & Whiteley, 2012) or habitat suitability models (e.g., Ahmadi et al., 2017; Mateo-Sánchez et al., 2016) as surrogates to estimate landscape resistance. In this context, Mateo-Sánchez et al. (2016) found that a lower exponential transformation of habitat suitability is often a close proxy for estimates of resistance.

Predicting population connectivity across a landscape is also highly dependent on accurate distribution data of the taxon. Specifically, connectivity is a function primarily of three things: the pattern of landscape resistance in the landscape, the dispersal ability of the focal organisms and the distribution and abundance of the focal species (Cushman, Landguth, & Flather, 2012). Habitat suitability algorithms, such as MaxEnt (Phillips, Anderson, & Schapire, 2006), can be effectively used to estimate the distribution and relative density of the focal species for use in estimating source points for connectivity modelling.

Once a landscape resistance model and origin source points have been specified, the next critical step of connectivity analysis is to choose a method to predict connectivity across the resistance surface (Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013). A wide variety of methods have been proposed for this task, including least-cost path modelling (Adriaensen et al., 2003), current flow (McRae, 2006), factorial least-cost path density (Cushman, McKelvey, & Schwartz, 2009), resistant kernels (Compton, McGarigal, Cushman, & Gamble, 2007) and randomized shortest path algorithm (RSP; Panzacchi et al., 2016). The cumulative resistant kernel approach is a particularly useful method to identify core habitats, fracture zones and corridors across a landscape (Cushman, Lewis, & Landguth, 2014; Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013). This method estimates the expected number of dispersing individuals traversing each cell of a grid-based landscape based on landscape resistance, and the species dispersal ability using a specific dispersal function (Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013). Importantly, the method is spatially synoptic (Cushman et al., 2014), producing spatially explicit predictions of movement rates for every location across the landscape, rather than for a few source or destination patches. In addition, factorial least-cost path analysis provides useful information to complement results of resistant kernel modelling and provides localization of the highest importance and usage corridors between source points (e.g., Cushman et al., 2014).

There is a growing interest in the use of network-based modelling approaches for quantifying the contribution of core patches to landscape connectivity. Recently, indices such as probability of connectivity (Saura & Pascual-Hortal, 2007) and integral index of connectivity (Pascual-Hortal & Saura, 2006) have been developed to assess the contribution of individual habitat patches to different aspects of landscape connectivity (Estrada & Bodin, 2008). Graph indices are adaptable to different degrees of available information and are operational with sparse data (Saura & Rubio, 2010).

Large carnivores are apex predators that play an important role in the regulation of ecological interactions and ecosystem health. Despite their ecological importance, most carnivores have experienced major declines in both population size and geographic range over the past century (Ripple et al., 2014). Identifying core areas and potential biological corridors that link them is crucial for the long-term survival of carnivore populations (Zeller et al., 2012). The central Iranian plateau supports a variety of carnivore species. Recent decisions on selecting protected areas (PAs) and no-hunting areas (NHAs) in Iran have been more strongly based on "structural connectivity" than "functional connectivity." Most of the PAs in Iran is surrounded by dense human infrastructure, which limits animal movements among them. It is therefore vital to assess connectivity among reserves and identify key linkage areas to conserve and enhance to ensure long-term survival of multiple carnivore species.

The aim of this study was to evaluate landscape connectivity for six key carnivore species, including Persian leopard (*Panthera pardus saxicolor*; Pocock, 1927), Asiatic cheetah (*Acinonyx jubatus venaticus;* Griffith, 1821), caracal (*Caracal caracal;* Schreber, 1776), wild cat (*Felis silvestris;* Schreber, 1777), sand cat (*Feils margarita;* Loche, 1858) and grey wolf (*Canis lupus;* Linnaeus, 1758) in central Iran based upon a combination of ensemble habitat suitability modelling to predict potential habitats and source locations, resistant kernel modelling to predict and map core areas, factorial least-cost path modelling to map corridors and network-modelling algorithms to quantify the relative importance of habitat core areas and biological corridors. We had four objectives: (1) to determine the most significant environmental and anthropogenic factors influencing habitat suitability for these carnivore species; (2) to identify core habitats for these species based on the resistant kernel approach; (3) to identify corridors among core areas using factorial least-cost path modelling; (4) to evaluate the relative importance of core patches and corridors to landscape connectivity for species of conservation concern using graph network analysis.

2 | METHODS

2.1 | Study landscape and focal species

The study areas are on the central Iranian plateau, centred at 32–34° N, 51–55° E (59,625 km^2) with an elevation ranging from 697 to 3814 m. The Alborz and Zagros mountain ranges prevent moisture bearing systems to pass through to the south and the east, respectively. As a result, the climate of the region is arid and semi-arid. Most precipitation occurs during winter, with an average annual precipitation of 90 mm. Mean annual temperature ranges from 11 to 27°C. Human activity within the study area includes small-scale farming and livestock herding. Large towns exist only on the western and central part of the study area. Paved roads are one of the most impactful fragmenting features in this landscape (Moqanaki & Cushman, 2016).

Despite the arid environmental conditions, this part of Iran is rich in biological diversity. Dwarf scrub vegetation is common in large areas and is very diverse and rich in species, including *Artemisia siberi*, *Astragalus gossypius*, *Zegophyllum* and *Amygdalus*. The region also supports a diverse guild of large and medium-sized carnivores, including five species of felids (*Acinonyx jubatus*, *Panthera pardus*, *Caracal caracal*, *Feils margarita*, *Felis silvestris*), five species of canids (*Canis lupus*, *Canis aureus*, *Vulpes vulpes*, *Vulpes cana*, *Vulpes rueppellii*, 1825) and striped hyaena (*Hyaena hyaena*). The region also supports five ungulate species, including wild sheep (*Ovis orientalis*), goitered gazelle (*Gazella subguturosa*), wild goat (*Capra aegagrus*), jebeer gazelle (*Gazella bennetti*) and wild boar (*Sus scrofa*). Poaching, competition from livestock and habitat destruction are the main factors that threaten wildlife in this landscape. Starting in the early 1970s, the Department of Environment (DoE) of Iran established a network of conservation areas to protect and manage the faunal, floral and geological diversity of Iran. Currently, almost all existing wildlife populations are confined to protected areas, which are often surrounded by dense human settlement and road networks. Five PAs (one national park, Siyah-kooh; one wildlife refuge (WR), Abbasabad; and three protected areas, Kahyaz, Ghamsar and Karkas) and four NHAs have been designed to protect large-scale ecological processes that would disappear from small protected areas (Figure 1).

2.2 | Species occurrence data and ecogeographical variables

The occurrence data for the target species were obtained from a variety of sources including opportunistic direct observation, camera-trap detections, scat identification and environmental guards' direct sightings from 2010 to 2016. Our sampling did not follow a systematic approach, but we tried to collect data across different strata (protected areas) with different densities of carnivores. The camera-trapping data were derived from surveys carried out in the study landscape during 2015–2016 and were used to evaluate the model. A global Moran's I test was used to investigate the distribution pattern of the presence points and to avoid pseudoreplication (Dormann et al., 2007). To ensure that all the records were independent, only presence points separated by a distance of five km or more were included in the analysis. For wild cat, sand cat and caracal, no spatial filtering of point selection was necessary due to low spatial autocorrelation among points based on global Moran's I test.

Thirteen ecological and ecogeographical variables (EGVs) including bioclimatic, topographic, land cover, anthropogenic and prey information were selected for modelling the potential habitats of the target species based on their relevance to the species' ecology. To avoid multicollinearity among variables, we dropped predictors with a Pearson's correlation >0.80 (Elith et al., 2006). Topographic position index (TPI) with threshold value ±1 (*SD*) in a 3,000-m search radius was calculated from a 90-m resolution digital elevation model (DEM) (Tagil & Jenness, 2008). Average surface roughness

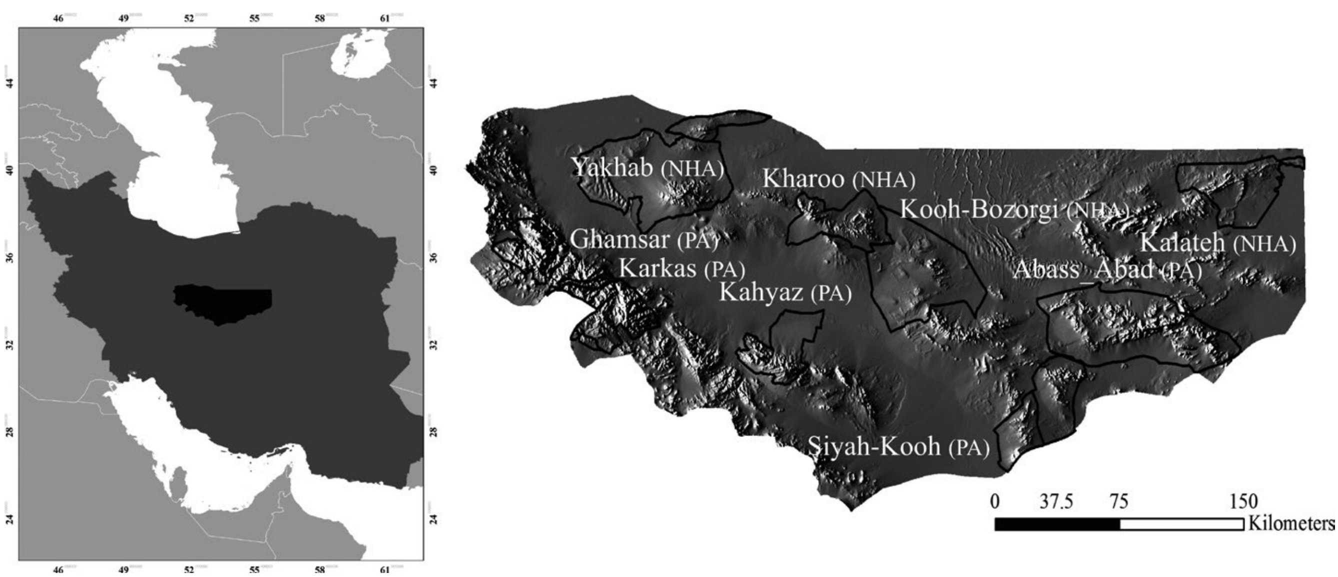

FIGURE 1 Location of the study landscape in Iran for modelling landscape connectivity and biological corridors. Black lines display the border of the PAs and NHAs

was calculated at the 250-m cell size using the method specified by Hobson (1972). The mean annual precipitation was downloaded from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 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. Normalized difference vegetation index (NDVI) values were calculated from 26 MODIS satellite images in 2012 at 250-m resolution using MODIS Vegetation Indices (MOD13) C5 User's Guide (Solano, Didan, Jacobson, & Huete, 2010). We used principal component analysis (PCA) to reduce the bi-weekly NDVI variables into a smaller number of uncorrelated linear combinations (PCs). We obtained a digital map of vegetation cover from the DoE and reclassified it into four cover classes, including (1) poor range (sparse vegetation with density ≤25%), (2) moderate canopy rangeland (mixture of grassland–scrubland with density ≥25%), (3) shrubland (patches covered by scrubs–shrubs with canopy cover ≥10%) and (4) bareland (uncovered areas including sand dunes and salty lands). The proportional extent of each vegetation cover type was calculated within a 2 × 2 km grid network. Croplands, human settlements, villages and roads density were extracted using a land use map developed by the Iranian Department of Environment. We considered the home range size of each target species as the search radius in calculating anthropogenic density maps. To account for the density of the main prey species of the target carnivores, we used occurrence data of four ungulate species including wild sheep (*Ovis orientalis;* Gmelin, 1774), goitered gazelle (*Gazella subguturosa*; Güldenstädt, 1780), wild goat (*Capra aegagrus;* Erxleben, 1777) and jebeer gazelle (*Gazella bennetti;* Sykes, 1831) in a 2 × 2 km grid network. Due to the scarcity of data on the local distribution of wild prey for small cats (caracal, wild cat and sand cat), NDVI was used as a proxy for increased density of small mammal prey species (Abade, Macdonald, & Dickman, 2014; Loe et al., 2005). The raster files were converted in habitat-grid cells of 250 × 250 m resolution according to their original resolution size.

2.3 | Building the predictive ensemble model

We assessed the robustness of the habitat suitability predictions by comparing the results of three modelling methods including MaxEnt, generalized linear model (GLM) and generalized boosted model (GBM). The algorithms were selected based on their high predictive power. First, we used all uncorrelated variables to build the full model using MaxEnt. Next, we used important variables recognized from jackknife analysis in MaxEnt to produce a final ensemble model (EM; Araujo & New, 2007) using all three algorithms. We used only about six to nine predictors in the final model for each species (Table S1 and S2). Algorithms were implemented in the "biomod2" Package in R using all the default parameters (Thuiller, Georges, Engler, & Breiner, 2016). We generated a randomly drawn sample of 5,000 background points (e.g., pseudo-absence points) from the extent of study area excepting occurrence cells. The predicted probabilities of occurrence for 5,000 points randomly distributed throughout the study landscape were compared between the algorithms using the Pearson correlation coefficient (Zheng & Agresti, 2000). We calibrated models using the 75% of occurrence points as training data, and remaining 25% of data for evaluation models predictions. The performance of each model was evaluated by the area under the curve (AUC) of the receiver operating characteristic plots (ROC; Deleo, 1993) and Kappa statistic (Landis & Koch, 1997). An ensemble model was calculated using the weighted average of the resulting AUC values of each model as described in Marmion, Parviainen, Luoto, Heikkinen, and Thuiller (2009) and Rodrıguez-Soto et al. (2011). The ensemble model outputs depict a gradient of suitability across the landscape and therefore probability of species occurrence varying from 0 to 100.

2.4 | Identifying the core habitat patches and corridor network

The resistant kernel approach (Compton et al., 2007) was used to identify and map core habitats, and the factorial least-cost path approach (Cushman et al., 2009) was used to predict corridors among these core habitats for each target species. Resistant kernels and factorial least-cost paths were run in universal corridor network simulator (UNICOR; Landguth, Hand, Glassy, & Cushman, 2012). The UNICOR uses Dijkstra's algorithm (Dijkstra, 1959) to solve the single shortest path problem from each species occurrence point to every other occurrence point (Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013). We converted the ensemble habitat suitability maps for each species to resistance maps describing the cost of crossing each pixel relative to the least-cost condition using a negative exponential function (e.g., Mateo-Sánchez et al., 2016). The use of an exponential transformation means that larger portions of the studied landscape offer low resistance, allowing more flexibility in where a corridor is located, than would be expected if resistance were a linear function of habitat suitability, as has often been assumed (e.g., Keeley, Beier, & Gagnon, 2016; Mateo-Sánchez et al., 2016).

These costs were used as weights in the dispersal function in the UNICOR model. We used occurrence records as source points to predict core areas. The initial expected density for our target species was set to 1 in each cell containing an occurrence record, and the kernel density buffering for each short path was calculated using Gaussian function (as in Li & Racine, 2010). We also used factorial least-cost paths to map corridors (e.g., Cushman et al., 2012). The buffered least-cost paths were then combined through summation (as in Cushman et al., 2009) to produce maps of connectivity among all pairs of presence points. The core habitats were defined as contiguous units with resistant kernel values >10% of the highest resistant kernel for the species (as in Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013).

Because of lack of data about dispersal movements of carnivores in Iran, we ran a sensitivity analysis to evaluate how robust our predicted core patches are to this uncertainty (e.g., Puyravaud et al., 2016). Hence, we used a range of dispersal thresholds in UNICOR (i.e., edge distance: 5,000, 10,000, 15,000, 20,000 and 25,000) reflecting dispersal abilities ranging from 5 to 25 km in optimal habitat for each species. Core habitats identified by UNICOR resistant kernel analysis are predicted based on cumulative resistance from the source point;

the resistant kernel will extend to a distance of 20,000 cost units from the source point, which will be different in all directions, weighted by the cumulative resistance. We calculated largest patch index (LPI), number of predicted patches (NP) and correlation length (CL) for areas predicted to be connected by dispersal (core habitat) at each dispersal threshold is correct using FRAGSTATS (McGarigal, Cushman, Neel, & Ene, 2002). Correlation length is the expected distance a species can move in a random direction from a random starting point within a patch before encountering the patch boundary, and largest patch index is the size of the largest patch of core connected habitat as a proportion of the full extent of the study area.

2.5 | Contribution of core habitats to network connectivity

Graph network algorithms have been shown to be a powerful tool for connectivity analysis (Pascual-Hortal & Saura, 2008). The relative importance of each identified core patch to total landscape connectivity was assessed using Conefor 2.2 (CS22; Saura & Torné, 2009). Core extent, the mean of expected relative density of dispersing individuals in each core habitat predicted by resistant kernels and the mean probability of species occurrence predicted by the EM maps were used as node characteristics in the graph analysis. To incorporate uncertainties in carnivores' movement behaviour, we used Euclidean distance between each pair of core habitats considering different maximum movement abilities for each species including 50, 100, 200 and 300 km (Ahmadi et al., 2017). To quantify the relative importance of each habitat patch to total landscape connectivity, we calculated the probability of connectivity (dPC; Saura & Pascual-Hortal, 2007). As we aimed to evaluate the importance of the core habitats for connectivity, we assessed the three fractions of the dPC (intra, flux and connector) separately. These metrics are important in assessing the different ways a core habitat can contribute to landscape connectivity (Bodin & Saura, 2010; Saura & Rubio, 2010). We changed the movement abilities (D) for all species to estimate at which dispersal distances the intermediate connecting patches are most important for overall habitat connectivity as measured using dPC-connector.

In addition, we calculated an overall index value of landscape connectivity EC (PC) for the mosaic of core patches for each carnivore species in the study landscape using Conefor. EC (PC) corresponds to the equivalent connected area (ECA) index (Saura, Estreguil, Mouton, & Rodríguez-Freire, 2011) and is defined as the size of a single habitat patch (maximally connected) that would provide the same value of PC metric as the actual habitat pattern in the landscape. This index provides an idea of the current status of the connectivity and patches distribution.

3 | RESULTS

3.1 | Observation points, potential habitats and model performance

We surveyed all possible habitats of the species in the protected areas which cover about 25% of the landscape. We recorded 479 locations for all target species over the temporal extent of the research (2010–2016; Table 1). Few location points were collected outside the PAs and NHAs. We incorporated these points to provide a better representation of species distribution patterns. The number of predictors used in the final ensemble model (EM) varied from 6 to 9 across species (Table S2).

Comparison of the algorithms revealed fairly high correlation and similarity of the predicted potential habitats (Table 2). All three modelling approaches performed reasonably well at predicting occurrence points (AUC above 0.7), indicating that the ecogeographical variables were good predictors of the potential habitats of the species (Table 3). The GBM algorithm outperformed the other algorithms in terms of predictive power (Table 3). However, based on the spatial agreement between predictions of the different algorithms and the robustness of ensemble modelling, we consider the results from the EM.

The areas of highly suitable habitats in the final EMs were different among species (Table 4). Highly suitable habitats of wolf and leopard showed the widest (2%) and most limited (0.3%) distributions, respectively. No areas with high habitat suitability for leopard were identified outside the PAs and NHAs. Nevertheless, using the mean value of habitat suitability for presence points as a threshold, 4% of study landscape was mapped as suitable for the species with a few patches scattered outside of the PAs and NAHs (Figure 2). In contrast, the highly suitable habitats for wolf, caracal and wild cat were more widely distributed across the study area (Figure 2). Overall, the most suitable areas for the majority of the

TABLE 1 The source of species presence points used for habitat suitability modelling of six carnivore species in central Iran

		Occurrence data source		
Species	Total	Direct observation	Sign identification	Camera trapping
Leopard	52	40	9	3
Cheetah	66	46	17	2
Caracal	124	102	12	10
Wild cat	59	48	8	3
Sand cat	93	74	18	2
Wolf	85	48	34	3

TABLE 2 Spatial correlation between habitat suitability maps obtained from three modelling methods (GLM, MaxEnt, GBM) for the six studied carnivore species. Numbers in each cell of the table show correlation among the modelling methods for leopard, cheetah, caracal, wild cat, sand cat and wolf, respectively

	GLM	MaxEnt	GBM
GLM		0.32, 0.76, 0.50, 0.74, 0.54, 0.82	0.61, 0.68, 0.60, 0.59, 0.64, 0.76
MaxEnt	0.32, 0.76, 0.50, 0.74, 0.54, 0.82		0.22, 0.82, 0.71, 0.74, 0.68, 0.85
GBM	0.61, 0.68, 0.60, 0.59, 0.64, 0.76	0.22, 0.82, 0.71, 0.74, 0.68, 0.85	

Species	Important variables in Ensemble model	Model performance (AUC, Kappa) GLM	MaxEnt	GBM
Leopard	Prey density, Roughness, shrubland density, road density	0.95, 0.71	0.88, 0.85	0.89, 0.94
Cheetah	Prey density, Roughness, annual precipitation, village density, Shrubland density	0.95, 0.80	0.96, 0.83	0.98, 0.94
Caracal	Annual precipitation, Roughness, settlement density, village density, road density,	0.84, 0.53	0.89, 0.63	0.96, 0.85
Wild Cat	Annual precipitation, roughness, road density, village density, shrubland density	0.82, 0.54	0.85, 0.56	0.97, 0.89
Sand Cat	Shrubland density, annual precipitation, poor range density, road density	0.94, 0.76	0.94, 0.75	0.99, 0.93
Wolf	Prey density, midrange density, roughness, village and bareland density	0.86, 0.58	0.91, 0.67	0.96, 0.84

TABLE 3 The most important variables in the development of ensemble model of potential habitats for carnivore species in central Iran. The performance of each modelling method was predicted using area under the curve (AUC) and Kappa statistic, respectively

	Suitable habitat-km^2 (% of study area)					
	(%) prob. occurrence of presence points					
Species	h.s. > 25%	h.s. > 50%	h.s. > median	Number of core habitats	Area (km^2)	(%) in PAs and NHAs
Leopard	5,423 (9)	2,451 (4)	192 (0.3)	12	4,392	79
Cheetah	7,019 (12)	3,431 (6)	314 (0.5)	8	5,539	69
Caracal	16,676 (28)	7127 (12)	747 (1)	18	4,839	64
Wild Cat	18,629 (31)	7221 (12)	434 (1)	16	3,171	53
Sand Cat	6137 (10)	2271 (4)	344 (0.5)	8	3,296	34
Wolf	18,950 (32)	9255 (15.5)	848 (2)	15	6,068	54

TABLE 4 The total area of suitable habitats for carnivore species according to the ensemble model output and different thresholds for highly suitable habitats (h.s) including 25% and 50% of the mean value of habitat suitability for presence points and median value of habitat suitability for presence points

studied species were located predominantly in the south-east and central sections of the landscape, mainly in Abbasabad wildlife refuge, Kharoo and Kooh-Bozorgi no-hunting areas (Figure 2). In total, 8.1% of the study area was predicted to be highly suitable for all six carnivore species.

The average importance of the variables among the models revealed that each species shows selectivity for specific habitat types within the study area (Table 3; Tables S2 and S3). Overall, prey density, annual precipitation, roughness, density of shrubland, human population and road density were the most important predictors of the carnivores' potential habitats.

3.2 | Identifying the core habitat patches and biological corridors

We mapped five different alternative models for each species based on different dispersal abilities. The correlation length of connected habitat was predicted to increase greatly, and the number of patches was predicted to decrease with increasing dispersal distance for all species. But, the largest patch index shows a unimodal behaviour for all species and the peak of LPI was different for each species (Table 5). The increase in LPI and CL indices was greater for large carnivores such as leopard and cheetah than small cats (sand cat and wild cat), which reflected the limited dispersal ability in small cats and concentration of core habitats in limited areas.

Results for 10,000 cost unit cumulative resistant kernels are shown in Figure 3. The predicted core habitats for cheetah, leopard, grey wolf and caracal were relatively widespread across the landscape (Figure 3). We predicted a relatively large area of core habitats with high internal movement rates for these species (Table 4). The predicted core habitats for wild cat were concentrated in the central and south-east regions. We also observed an extensive network of strong corridors connecting core habitats of wild cat in this part of the landscape (Figure 3). There was also a network of corridors of lesser predicted strength connecting the full network of the species occurrence records. The core habitats of cheetah in Abbasabad, Kooh-Bozorgi and Kharoo are interconnected with corridors.

We found relatively little overlap between the core habitats of the carnivore species (Figure 4). Less than 3% of the total extent of the landscape in Abbasabad and the three NHAs (Kalateh, Kooh-Bozorgi and Kharoo) is predicted core habitat for all six species. Patches of relatively high habitat quality for the six species are small in isolation.

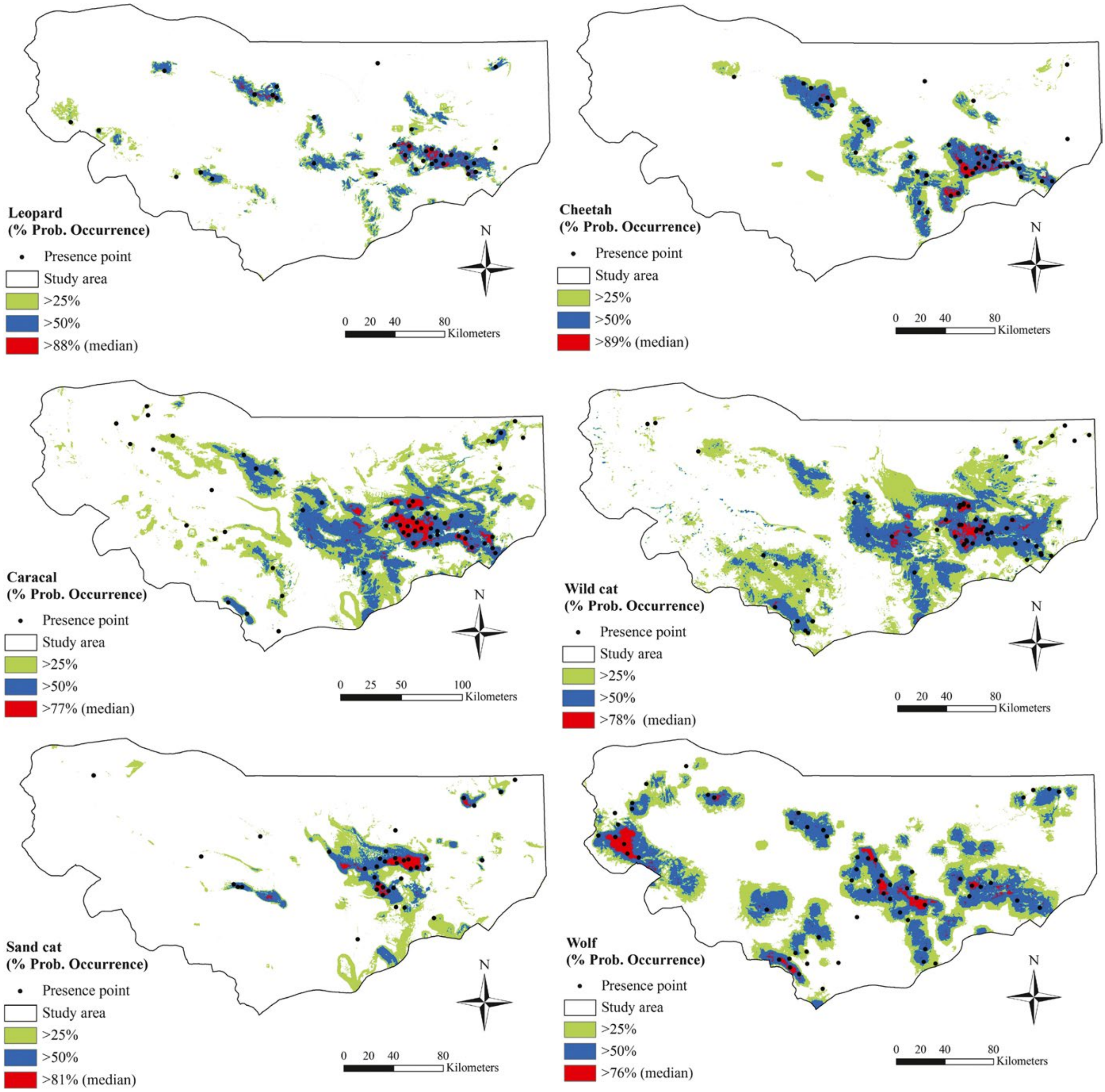

FIGURE 2 Potential habitats of carnivores in the central landscape of Iran according to the EM for each species. The colour gradient indicates the probability of species occurrence. [Colour figure can be viewed at wileyonlinelibrary.com]

These results suggest that Abbasabad wildlife refuge has a significant role in maintaining landscape connectivity of carnivores in central Iran. There was a high density of predicted corridors among all PAs and NHAs except those located in the western and south-western parts of the landscape. We identified locations where major roads cross the predicted corridor routes (Figure 5). These intersections are potential barriers and locations of potentially high mortality risk due to traffic collisions. Protected areas in western part of the landscape are more isolated, probably because of extensive highways in this region (Figure 5 and Fig. S1).

3.3 | Relative contribution of core habitats to network connectivity

The contribution of core habitats to landscape connectivity based on the PC index revealed a different pattern of patch importance depending on which patch characteristic was used for ranking (Table S4). Based on the core extent and expected density of dispersing individuals in each core habitat, the patches 11, 5, 13, 16, 7 and 10 were most important for sustaining connectivity for leopard, cheetah, caracal, wild cat, sand cat and wolf, respectively (Table S4 and Figure 3). Similar

TABLE 5 FRAGSTATS results for largest patch index (LPI), correlation length of core habitats (CL) and number of individual core patches (NP) for each carnivore species across five levels of dispersal ability (50,000, 10,000, 15,000, 20,000 and 25,000). The core habitats were defined as contiguous units with resistant kernel values >10% of the highest resistance kernel for the species

	Dispersal ability (cost units)									
	Leopard					Cheetah				
	50,000	10,000	15,000	20,000	25,000	50,000	10,000	150,000	200,000	250,000
NP	13	12	8	6	6	9	8	7	4	3
LPI	49.08	43.62	41.41	67.18	68.93	72.08	64.52	56.67	90.56	92.03
CL	14,424.12	16,290.98	22,094.51	47,100.21	47,709.33	25,474.55	26,582.39	30,900.01	57,866.94	60,540.84
	Caracal					Wild cat				
NP	19	18	11	6	2	16	7	5	4	3
LPI	56.97	47.31	44.41	60.29	89.01	47.22	66.97	61.64	72.13	69.82
CL	18,587.45	18,935.32	24,675.34	43,963.29	76,221.18	17,883.65	36,426.94	39,040.41	49,423.40	51,507.69
	Sand cat					Wolf				
NP	12	10	8	8	4	15	12	6	3	3
LPI	68.25	59.98	56.10	52.24	73.89	26.40	30.59	50.18	68.28	66.85
CL	16,586.00	18,257.84	23,438.44	25,387.18	43,300.56	16,985.19	21,162.24	40,406.67	59,402.77	60,607.58

results were obtained for patch importance when it was calculated based on the mean probability of occurrence, but patches 8 and 10 were ranked first for leopard and caracal, respectively. The importance of core habitats was significantly correlated with core area, mean relative density of dispersing individuals and mean probability of occurrence (Fig. S2). The dPC values tended to increase slightly as modelled dispersal capabilities increased. For leopard, wild cat and caracal, with core extent and the mean of kernel density as patch characteristics, core habitats 11, 16 and 13 were the most important patches at all dispersal distances, respectively. However, when considering mean probability of occurrence, core habitats 8, 11 and 10 were the most important patches, respectively (Table S4). For cheetah and sand cat, core habitats 8 and 7 were the most important patches at all dispersal scenarios and different patch characteristics, respectively.

The correlation coefficient between patch characteristics and fractions of the dPC was higher for the intrafraction and lower for the connector fraction than for the total dPC (see Figs S3–S5). The connector fraction evaluates a patch's contribution to landscape connectivity between other patches by acting as a stepping stone patch (Saura & Rubio, 2010). The maximum contribution of dPC-connector, considering patch area, was considerably higher for wolf, cheetah and leopard than other species for large dispersal distances (peaks at about 22%, 13.5% and 6.5% for the wolf, cheetah and leopard, respectively; Figure 6). At a threshold distance of 200 km, dPC-connector was at its maximum for cheetah, leopard and wolf and did not increase further for longer geographic distance among core patches. The contribution of dPC-connector is almost zero for large distances (Bodin & Saura, 2010). It seems that this threshold is close to the estimated dispersal distance for the large carnivores. Hence, the species having dispersal distance near or more than 200 km can move directly from one patch to another without needing intermediate stepping stones patches. But, species having dispersal distance of lower than 200 km require intermediate stepping stone patches (Saura & Rubio, 2010). For sand cat and caracal, dPC-connector reaches a plateau and does not increase further for longer dispersal distances. These results confirm that geographic distance higher than 200 km between core habitats in the studied landscape leads to decrease in connectivity between protected areas. These findings highlight the importance of intermediate stepping stone patches for improving landscape connectivity between core patches for species with <200-km dispersal abilities. Given a threshold dispersal distance of 200 km, the patches with the most dPC-connector were patch number 10 for caracal, 7 for cheetah, 6 for leopard, 7 for sand cat, 11 for wild cat and 10 for wolf. As shown in Figure 3, all these patches are located in Kooh-Bozorgi NAH and Abbasabad WF. Hence, these habitat patches have a significant role as acting as an intermediate stepping stone patches to facilitate dispersal and landscape connectivity.

4 | DISCUSSION

4.1 | Influence of ecogeographical variables on species potential habitats

We mapped potential habitats, core population areas and landscape connectivity for the major carnivore species in central Iran using the most reliable data set available on species occurrences, ensemble habitat modelling and advanced connectivity modelling methods. All carnivore species showed intermediate to high levels of specialization; for example, wolf showed a low level of tolerance of habitat disturbances, although their spatial niche breadth was relatively wide. In contrast, sand cat showed a high level of niche specialization. The EM model showed that most highly suitable habitats for leopard, caracal and wolf are located in PAs and NHAs, while suitable habitats for sand cat are mainly distributed outside of protected areas. We also found some core patches outside of protected areas for cheetah, a species with high

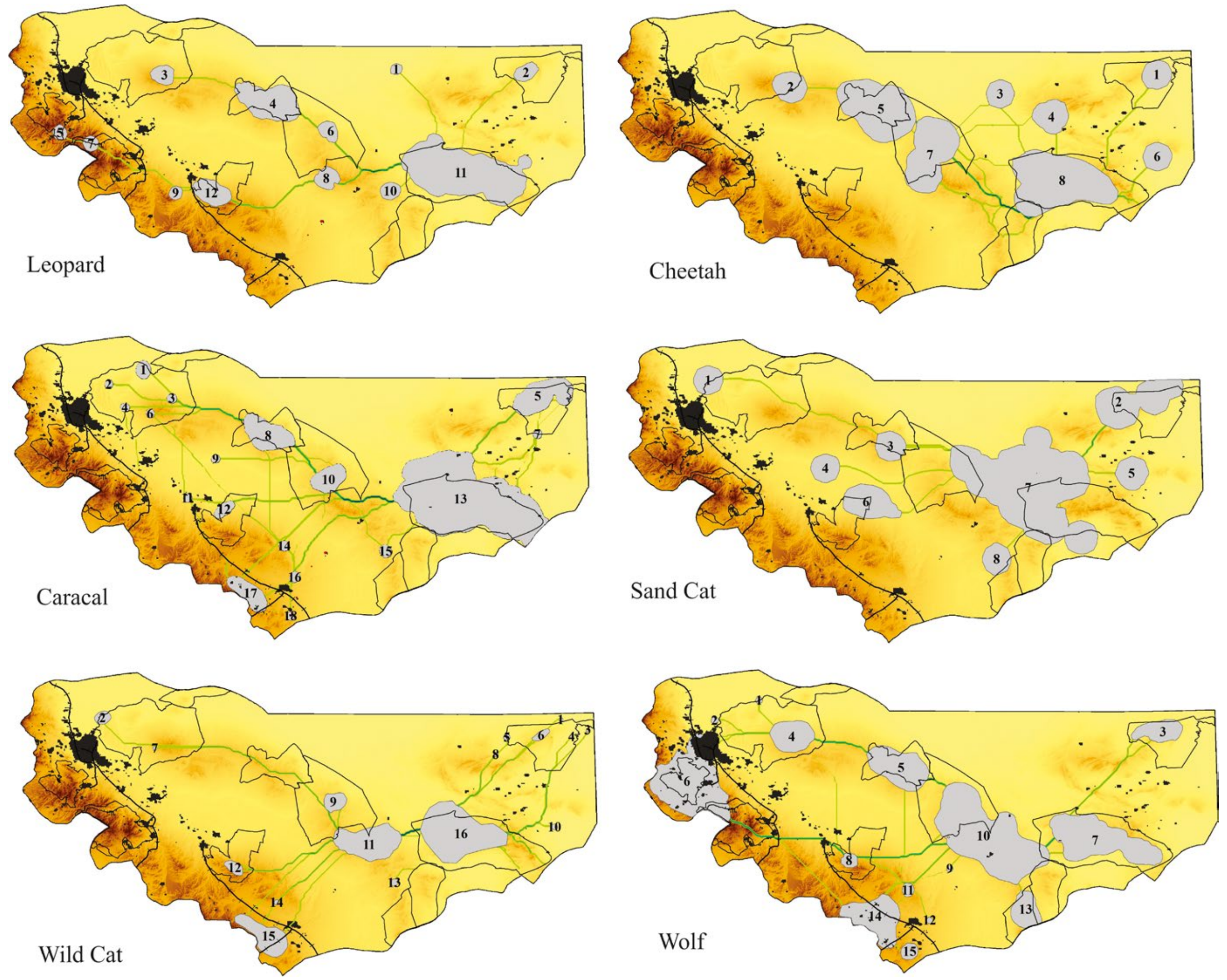

FIGURE 3 Resistant kernel core habitat areas (grey polygons) and the UNICOR corridor pathways for six carnivores in central Iran. The colour gradient for corridors represents predicted connectivity between core patches from weak (light green) to strong (dark green). The border of the PAs and NHAs is shown with black polygons, and human settlements are shown with dark patches. Highways are shown with black lines. The numbers in the patches show core patch's number (name of PAs and NHAs are shown in Figure 1). [Colour figure can be viewed at wileyonlinelibrary.com]

dispersal ability and large home range size. Potential habitats of caracal and wild cat appeared to be strongly influenced by similar variables, implying comparable resource use patterns. Overall, the most important factors influencing the probability of occurrence of the studied carnivores in the landscape were prey density, annual precipitation, topographical roughness, shrubland density, roads and human settlements.

The species response to environmental predictors supports habitat associations known from past literature for cheetah (Ahmadi et al., 2017), leopard (Erfanian, Mirkarimi, Salman Mahini, & Rezaei, 2013; Farhadinia et al., 2015; Mondal, Sankar, & Qureshi, 2013), caracal (Adibi, Karimi, & Kaboli, 2014) and wolf (Bassi, Willis, Passilongo, Mattioli, & Apollonio, 2015). In many studies, carnivore habitat suitability has been linked to prey distribution (e.g., Carbone & Gittleman, 2002; Rostro-García, Kamler, & Hunter, 2015). This study corroborated the importance of prey availability to habitat suitability for carnivore species. Unfortunately, ungulate species populations in Iran have dramatically declined because of overhunting (Ziaei, 2009). Hence, currently, almost all existing ungulate populations are confined to PAs and are surrounded by areas of dense human settlement, roads and agricultural fields. The density of ungulate species in PAs is comparatively higher than the peripheral areas. Low habitat suitability of regions outside of PAs for the studied species confirms the high dependence of carnivores on prey abundance. As prey abundance was the key factor affecting large carnivores, we recommend that conservation efforts focus on protecting and expanding ungulate populations in the core areas identified as most important. There are few villages located inside the PAs and NHAs. Our findings showed that habitat suitability of the carnivores was influenced negatively by the presence of villages. Some carnivores, such as leopard and wolf, are relatively frequently found in proximity to human settlements, where they prey upon livestock (Odden & Wegge, 2005). In contrast, other species, such as cheetah, more strongly avoid areas near human settlements. These results are consistent with the previously reported data on carnivore species (Erfanian et al., 2013; Omidi, 2008).

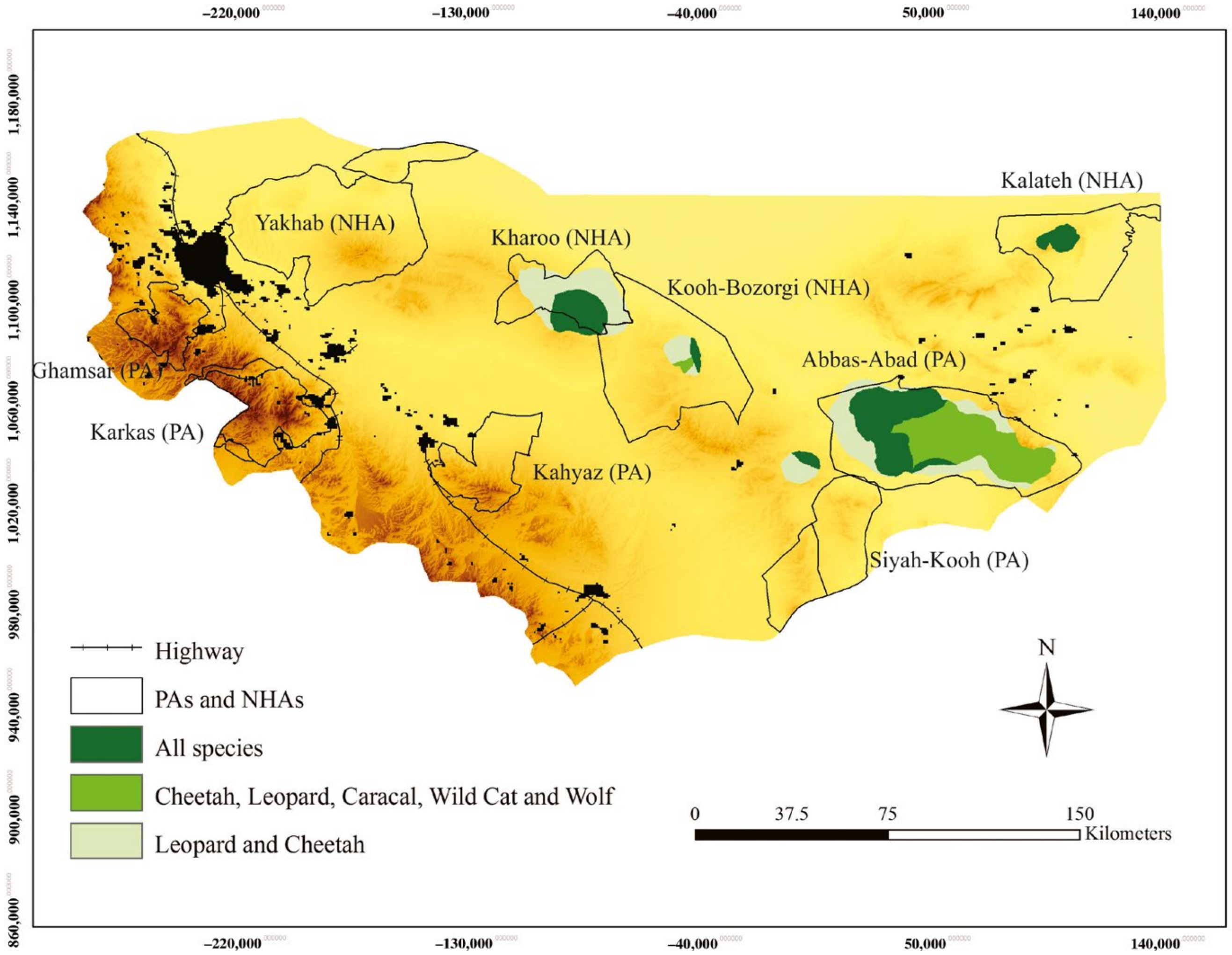

FIGURE 4 Intersection map for predicted core habitats. The colours depict different species combinations. [Colour figure can be viewed at wileyonlinelibrary.com]

Topographical roughness was another important factor influencing habitat suitability of the three larger carnivores. For leopard, selection of high elevation and high roughness is probably due to the distribution of wild goat, human avoidance, protection against high summer temperature and competition avoidance with other large carnivores, especially cheetah. The low overlap between potential habitat for leopard and cheetah supports this conclusion. Precipitation can significantly affect habitat suitability and population dynamics. The positive influence of annual precipitation on predicted habitat suitability of carnivores, especially small carnivores, is not surprising as precipitation increases net primary productivity affecting the distribution of prey species.

Distance to shrubland was another significant factor affecting habitat suitability, particularly of sand cat. Dependence of this species on shrubland can be attributed to higher density of rodents in this vegetation type, presence of good cover and stabilized soil, which provides the possibility of digging den.

The distribution of suitable habitats showed that most PAs and NHAs have a higher suitability for the carnivore species compared to unprotected areas. This pattern is potentially due to the higher density of wild prey in PAs. In addition, PAs and NHAs provide protection from direct persecution and other human disturbances. The areas of highest suitability for the carnivore species were located in the eastern parts of the landscape in Abbasabad WR, and Kharoo and Kooh-Bozorgi NHAs. According to our findings, the Abbasabad is the biggest and probably the most important area of potential carnivore habitat in the study area. Camera-trapping pictures from Abbasabad suggest that this refuge might have the potential to protect the carnivore species especially cheetah, leopard, wild cat and caracal.

4.2 | Landscape connectivity and distribution of core patches and corridors

Our resistant kernel analysis provided predictions of core habitats that can potentially be used to maintain landscape connectivity and prioritize areas for conservation. Our results show that currently between 34% (sand cat) and 79% (leopard) of core habitat patches are classified as completely protected by PAs and NHAs (Table 4). These findings could be due to relatively high resistance outside protected areas leading to isolated occupied patches and large areas where carnivore populations are likely to only occur at very low densities or are absent. Owing to the high proportion of suitable areas in protected habitats, it is clear that currently designated PAs and NHAs

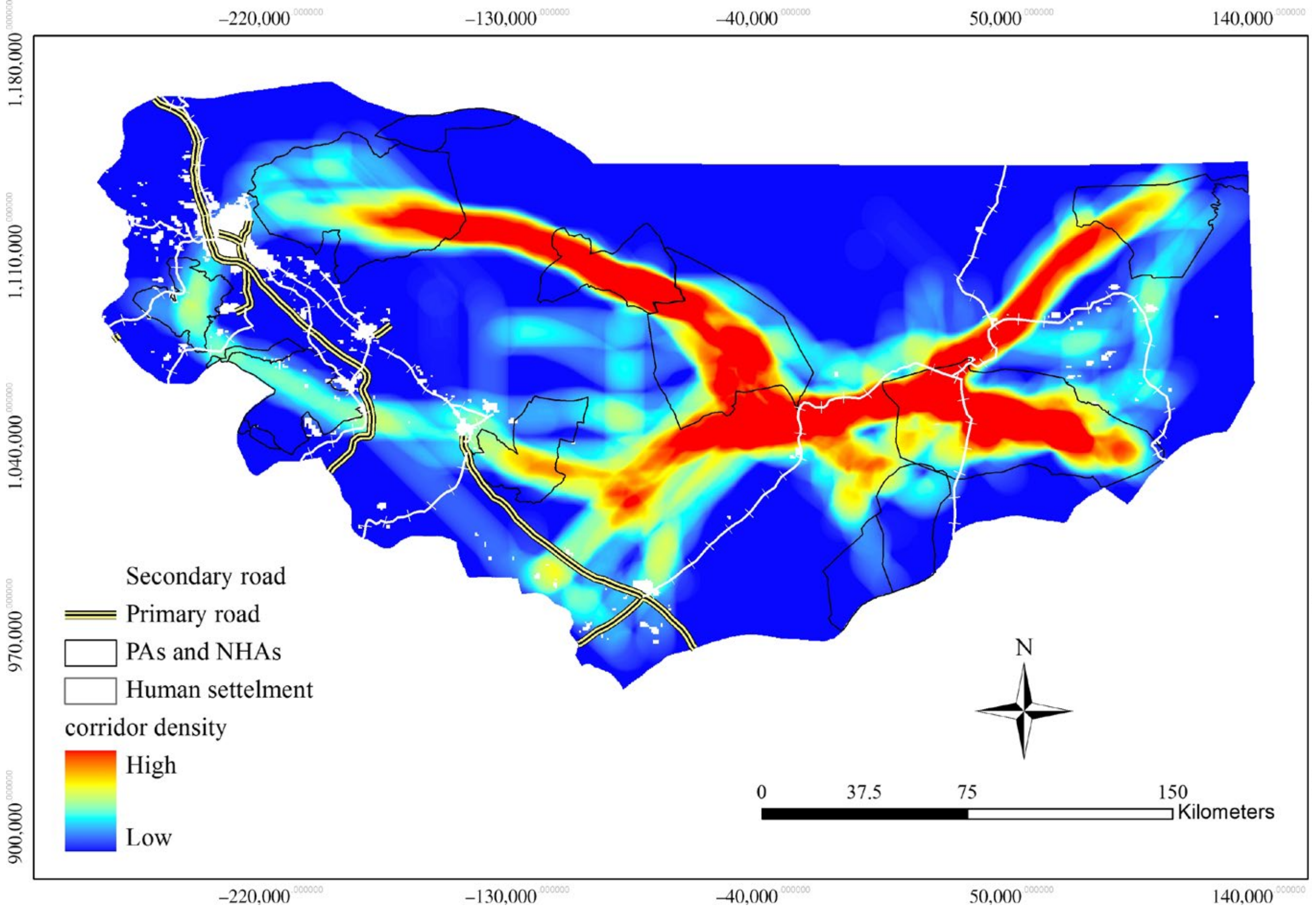

FIGURE 5 Intersection map for predicted corridors for six studied carnivores. The colour gradient represents the density of predicted corridors among PAs and NHAs from low density (blue) to high (red) for all six species. [Colour figure can be viewed at wileyonlinelibrary.com]

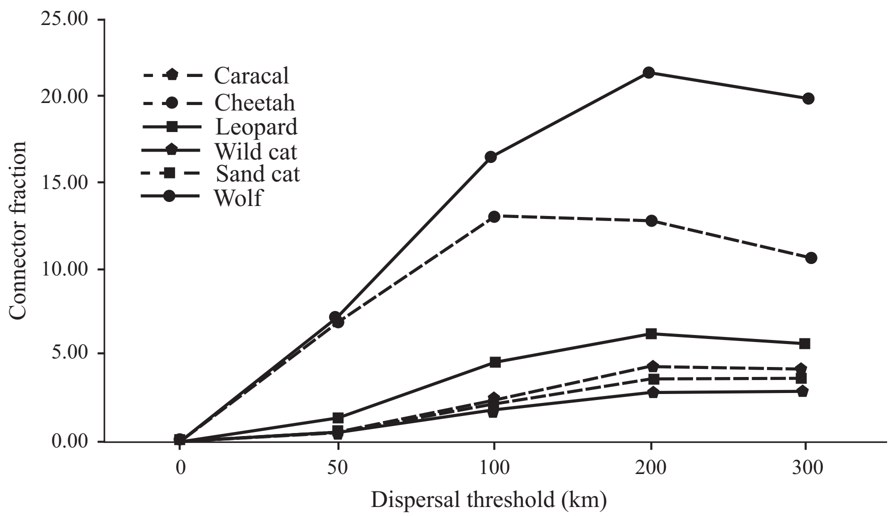

FIGURE 6 Sum of dPC-connector values for all core patches, expressed as their proportion of the total sum of all dPC-connector values for increasing threshold distances

play a critical role in carnivore conservation in the desert landscape of Central Iran.

As Saura, Bastin, Battistella, Mandrici, and Dubois (2017) suggested, protected area with less strict management objectives such as NHAs may play a fundamental role in upholding the connectivity of the PA systems. For example, Kooh-Bozorgi and Kharoo can potentially facilitate the connection between the east and west of the desert landscape. However, these areas are no-hunting areas and have lower protection level. Hence, we strongly recommend increasing their extents and protection level and giving them the highest priority for conservation. Also, as some NHAs were located within core patches of the distribution of the species, the proportion of these protected areas should be increased. A similar result was seen in Elliot et al. (2014) and Moqanaki and Cushman (2016), who found that protected area status is the most important predictor of the occurrence and dispersal of African lions and Asiatic cheetah, respectively. Moqanaki and Cushman (2016) also found corridors with high predicted connectivity rate between Abbasabad, Siyah-Kooh and Kooh-Bozorgi for cheetah, which are consistent with our results.

Saura et al. (2017) showed that most protected areas in Asia show low structural connectivity (protected connected land value <8%). However, central parts of Iran show more connectivity than other parts of the country (see Saura et al., 2017 for details). Therefore, the coverage of a protected area network should be accompanied by comparable levels of protected connected land to increase functional landscape connectivity for terrestrial species especially carnivores. Small, highly suitable patches in unprotected areas (e.g., the area between Abbasabad WR, Kharoo and Kooh-Bozorgi NHAs) may still play an important role, especially as stepping stones, to enhance protected connected land values and functional connectivity in a carnivore-oriented ecological network (Boitani, Maiorano, Falcucci, & Rondinini, 2007). For example, the core patches 8 and 10 for leopard, 6 for cheetah and 11 for wild cat lie along the main corridor connecting Abbasabad, Kooh-Bozorgi, Kalate and Kahyaz. These patches have a significant role as stepping stones for maintaining connectivity between these protected areas. For caracal, we also found a high number of small core patches among unprotected areas with high potential for enhancing dispersal between PAs.

The factorial least-cost path network identified optimal routes among habitat patches for the carnivore species in the study landscape. These corridors are the lowest cost routes to connect core patches and maintain connectivity. Carnivore species have relatively large dispersal abilities, which enable them to maintain population connectivity even in the face of habitat fragmentation. The low density of ungulate populations in some PAs can be one of the drivers for long-distance movements in carnivores (Farhadinia et al., 2015). For most species, the main core areas were separated by small gaps that were less than the predicted dispersal abilities of the species.

Our findings suggest that the role of PAs in maintaining functional connectivity should not be undervalued. Most protected areas in Iran are surrounded by roads, and road mortalities are a serious threat for carnivores (Farhadinia et al., 2015). As suggested by Kramer-Schadt, Revilla, Wiegand, and Breitenmoser (2004) and Moqanaki and Cushman (2016), although most core patches may be potentially interconnected by dispersal (such as present study), when realistic mortality risks due to road accident and other sources of mortality are considered, most patches become functionally isolated. We identified locations where primary and secondary roads cross the predicted corridor paths between the core patches. These locations are regions of potentially elevated mortality risk because of traffic collisions and higher exposure to hunting and poaching. For example, although we found corridors with high connectivity rate between Kalateh, Abbasabad and Kooh-Bozorgi, these PAs become rather isolated when we consider negative effects of roads between them. Thus, it appears that landscape connectivity for carnivores is probably more limited by mortality of dispersing individuals and illegal hunting than the distribution of dispersal habitats. Therefore, effective conservation must focus on reducing mortality to increase functional connectivity rather than solely investing in patch restoration or increasing the number of PAs.

In the present study, we used predictive models based on species occurrence, habitat suitability and landscape resistance to predict structural and functional connectivity of the populations of focal carnivore species. We modelled individual core patches as nodes in the landscape and the links between the nodes can act as a proxy for functional connectivity. Preserving linkages for dispersing individuals across a landscape by protecting corridors and stepping stones is an important strategy to increase functional connectivity, and the results presented here show likely corridors and stepping stones for a set of threatened carnivores across the landscape.

It is important to empirically validate the predicted linkages and assess the uncertainty in species responses to environmental predictors (Cushman, Landguth, et al., 2013; Cushman, McRae, et al., 2013). There are new ways to empirically validate the predicted corridors, including monitoring movements of a large number of individuals using camera-trapping and satellite tacking (e.g., Cushman & Lewis, 2010; Elliot et al., 2014), using genetic mark–recapture and landscape genetic analyses (e.g., Shirk, Wallin, Cushman, Rice, & Warheit, 2010). We recommend the implementation of telemetry studies in the study area to validate and optimize predictions of functional connectivity between the protected areas (e.g., Elliot et al., 2014; Krishnamurthy et al., 2016). In recent years, radio tracking of carnivores has been started in Iran and used for leopard and Persian Wild Ass.

Science-based conservation of biodiversity is a relatively new field in Iran, and we have limited data as well as limited resources for collecting new data. For instance, tracking of any form (radiotelemetry or satellite tracking) as a basis for validating the results of modelling studies has just been started for a few individuals across the country (four leopards, two wolves, nine onagers). We hope wildlife tracking will become more feasible in Iran in the near future, but until then, we have to rely on the results of other study approaches, such as expert opinion-based (Moqanaki & Cushman, 2016) and habitat suitability-based (this study) estimates of landscape resistance. Also, landscape genetics for a number of species have recently been studied in Iran (e.g., Khosravi et al., 2017, for Goitered gazelle). It is expected that such studies will be increased in near future.

4.3 | Core habitat importance

Patch prioritization analysis provided slightly different results depending on whether patch quantity (patch extent) or patch quality (density of expected dispersing individuals or mean probability of occurrence in each core patch) was used. Patch importance was positively correlated with the extent of core habitats regardless of the dispersal ability of the species when considering patch area as a core characteristic. These results are consistent with the results obtained by Zhao et al. (2014) and Ahmadi et al. (2017) for Tibetan antelope and Asiatic cheetah, respectively.

Dispersal ability often has a larger impact on connectivity than relative landscape resistance (e.g., Hand, Cushman, Landguth, & Lucotch, 2014; Moqanaki & Cushman, 2016). Our findings revealed that using patch quality can better show the effect of dispersal ability of the species on the importance of patches for maintaining landscape connectivity. Also, we found that dispersal threshold had significant effects on a patch's importance to landscape connectivity. For example, while core habitats 4 and 10 in low dispersal distance scenarios have low dPC value, they will have greater importance for leopard when dispersal distances become larger, and accordingly, the increment of the importance of these patches for maintaining connectivity will be higher. Most of the core patches receive greater value of PC with increasing dispersal distances. The core habitat in Abbasabad and Kooh-Bozorgi regions was the most important patches for all species across dispersal and node characteristics.

4.4 | Management implications

Conservation actions may be most effective if they focus on protecting core habitat areas in unprotected lands and along significant corridors among patches, with priority given to those core areas and corridors found to be most important in this analysis. The combination of analytical tools used here could help enable managers to evaluate the optimality of different landscape conservation strategies for these potentially focal species. Specifically, these results provide guidance for managers to provide linkages between core habitats and optimal places to position stepping stones (i.e., new protected areas) across the study area. Also, our results suggest that more attention should be paid in the PAs and NHAs designation process to improve the connecting role of protected areas or to increase the likelihood of species movements and functional connectivity (Saura et al., 2017).

Patches of relatively high habitat quality for the six species are small when taken in isolation. Therefore, the conservation of these species requires an integrated landscape management approach implemented on a regional scale to allow for the interchange of individuals between those patches along corridors. Considering patch suitability and extent, protection of core habitats and connectivity between core patches is a necessity for conservation of carnivores in Iran. To maximize the viability of these carnivore populations, we suggest several conservation efforts: (1) maintaining healthy ungulate populations, especially in PAs, to guarantee long-term survival of carnivores; (2) mitigating livestock–carnivore conflicts, particularly in areas with low density of wild ungulates, to decrease carnivore–human conflict; (3) incorporating new linkage core areas to the PAs network strategically located along the routes of highest predicted connectivity to facilitate exchange of individuals between habitats; (4) mitigating areas of limited connectivity among core habitat patches and enhancing potential corridors for species with low dispersal ability; and (5) developing land use restrictions into main movement corridors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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