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RESEARCH ARTICLE

# Comparison of habitat suitability and connectivity modelling for three carnivores of conservation concern in an Iranian montane landscape

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**Abstract**
*Context* Habitat loss and fragmentation are main drivers of biodiversity loss and are occurring at an accelerating rate globally. Carnivores are often subject to persecution and conflict with humans, typically reside in low densities and require large areas for core habitat and dispersal, which makes them especially vulnerable to habitat loss and fragmentation.

*Objectives* This paper identifies, maps and analyses habitat core areas and connectivity linkages for three mountain-residing carnivore species of high conservation importance in Iran: Persian leopard (*Panthera pardus saxicolor*), Eurasian lynx (*Lynx lynx*) and Pallas's cat (*Otocolobus manul*).

*Methods* We used ensemble habitat suitability modeling, and compared the accuracy of ensemble models with seven separate models based on AUC and TSS. We applied resistant kernel and factorial least-cost path analyses to identify population core areas and corridors across the full distributions of the three species in Iran.

*Results* Mean annual temperature, vegetation greenness (NDVI), and slope were among the most important predictor variables for all three species. We found ensemble modeling outcompeted all single-method models in terms of AUC. We found low overlap between predicted corridor locations of our modeled species with Protected Areas.

*Conclusions* Given the fragmented populations of our studied species in Iran, conserving them will require integrated landscape-level management to protect corridors and enhance connectivity, especially outside of Protected Areas. Optimized landscape

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management to conserve these species will likely promote conservation of montane landscapes and their inhabitants in Iran.

**Keywords** Connectivity · Carnivores · Protected area · Resistant kernel · Habitat suitability · UNICOR

## Introduction

Habitat fragmentation is a landscape-scale process which is characterized by the division of habitat into separate patches (Fahrig 2003; Bennett and Saunders 2011). It reduces the structural connectivity of habitat by increasing the number of patches, decreasing their size and increasing their isolation (Fahrig 2003). Connectivity is critical for long-term species conservation, and plays a major role in maintaining genetic and demographic processes that ensure long-term viability (Bennett and Saunders 2011; Kaszta et al. 2020a). Connectivity of populations is of paramount importance to both conserve species locally and to secure their range shifts in response to future hazards such as land use change (Cushman et al. 2013; Kaszta et al. 2019), and climate change (Wasserman et al. 2013). Enhancing connectivity in conservation networks may reduce the negative impacts of habitat loss and fragmentation (Wiens 2006).

Large carnivores are particularly vulnerable to human persecution and extirpation (Broekhuis et al. 2017; Mohammadi et al. 2019). They live in low densities and typically have large home ranges (Hilty et al. 2006; Carrol 2006). Carnivores' large area requirements demand vast and connected habitat areas where they are protected from human persecution. Increasing land use change and habitat fragmentation have threatened carnivore populations by reducing habitat areas and increasing their isolation, leading to a synergy of increasing direct human-caused mortality, reduced local carrying capacity, and reduced ability for populations to be integrated by dispersal or nomadism (e.g., Cushman et al. 2016; Farhadinia et al. 2016).

Given that most carnivore populations must now integrate across networks of multiple protected areas through dispersal (e.g., Cushman et al. 2018), it is increasingly inevitable that many dispersing carnivores must move between habitat patches through often dangerous unprotected and developed lands (Hilty et al. 2006; Elliot et al. 2014; Almasieh et al. 2016). Therefore, for many carnivores in many parts of the world, protected areas by themselves are not sufficient to support viable populations (Hilty et al. 2006; Cushman et al. 2016; Macdonald et al. 2019; Mohammadi et al. 2021c). Regional viability often requires large core habitat patches which are connected through a network of linkages among them to ensure long-term viability (Kaszta et al. 2019, 2020a). Thus, networks of structurally or functionally connected protected areas, rather than isolated protected areas, are the proper focus of comprehensive conservation planning (Beier et al. 2008; Romportl et al. 2013; Cushman et al. 2016, 2018).

Several methods have been used for connectivity assessment (Cushman et al. 2013), including least-cost path modelling (Adriaensen et al. 2003), current flow (McRae 2006), factorial least-cost path density (Cushman et al. 2009), resistant kernels (Compton et al. 2007) and randomized shortest path algorithms (Panzacchi et al. 2016). The factorial least-cost path and cumulative resistant kernel approaches have proved to be particularly effective methods if used in combination across a broad landscape (Moqanaki and Cushman 2016; Shahnaseri et al. 2019; Kaboodvandpour et al. 2021; Mohammadi et al., 2021a,b). These approaches, coupled with landscape pattern analysis (McGarigal and Cushman 2002), provide a framework to predict the location of core areas, fracture zones (where connectivity is attenuated by barriers or cumulative dispersal cost), and movement corridors across a range of dispersal abilities (Cushman et al. 2013).

Understanding the different factors that affect species distribution and habitat selection is important for carnivore conservation (McClure et al. 2017; Khosravi et al. 2017; Shahnaseri et al. 2019; Mohammadi et al., 2021a). Many different habitat suitability modeling algorithms are available. Among these, regression-based models such as the Generalized Linear Model (GLM) (Farashi et al. 2017; Shahnaseri et al. 2019), Generalized Additive Model (GAM) (Spencer et al. 2011; Farashi et al. 2017), Multivariate Adaptive Regression Splines (MARS) (Farashi et al. 2017), and machine-learning models such as Maximum Entropy (MaxEnt) (Farashi et al. 2017; Mohammadi et al. 2021b ), Random Forest (RF) (Ashrafzadeh et al. 2020), Generalized Boosting Model (GBM)

(Khosravi et al. 2017; Shahnaseri et al. 2019) and Artificial Neural Network (ANN) (Farashi et al. 2017) have been widely used.

Recent research has shown that machine-learning models such as RF may perform better than the regression-based algorithms (Rodriguez-Galiano et al. 2012; Mi et al. 2017; Cushman et al. 2017). Furthermore, ensemble modeling, in which several species distribution models (SDMs) are combined to quantify a range of predictions across more than one set of uncertainty sources, has been found to often increase the accuracy of model predictions (Araújo and New 2007; Shahnaseri et al. 2019) and decrease the uncertainty associated with using a single SDM (Shirk et al. 2018). However, there is not an extensive literature about the performance of ensemble modeling as compared with single machine learning techniques, especially when it comes to multi-species and connectivity studies.

In this paper we used a guild of multiple carnivore species to compare the performance of different modeling techniques across species, and test whether ensemble learning provides improvement over individual modeling algorithms. This study also focuses on habitat prioritization for three montane felid species that can be considered as a proxy for mountainous ecosystem and mountain-dependent conservation with limited resources in Iran.

Pallas's cat, Eurasian lynx, and Persian leopard share similarities in their general ecology as they all are highly dependent on high altitudes in their Iranian range. Pallas's cat and Eurasian lynx are distributed in a highly patchy and fragmented pattern across Iran, while Persian leopard is more widely distributed and well connected. Diet, habitat selection, and home range sizes are substantially different among these species (Moqanaki et al. 2010; Farhadinia et al. 2016; Mousavi et al. 2016).

These species reside in rugged and remote montane regions that are increasingly influenced by humans, thus there is an urgent need to identify and prioritize their habitats for management and conservation (Farhadinia et al. 2019a). All three species are threatened by anthropogenic landscape change and human-induced mortalities, particularly habitat loss and fragmentation and prey depletion (Moqanaki et al. 2010; Mousavi et al. 2016; Farhadinia et al. 2016, Stein et al., 2016). Persian leopard is also threatened by poaching, poisoning, and road kill in Iran (Parchizadeh and Adibi, 2019). Persian leopard is categorized as endangered (EN) by IUCN (Khorozyan 2008), and Pallas's cat and Eurasian lynx are listed as least concern (LC) globally (Breitenmoser et al. 2015; Ross et al. 2020), although both are rare in Iran.

The aims of this research were to: (1) compare several modelling methods to predict habitat suitability for multiple carnivore species [Persian leopard (*Panthera pardus saxicolor*), Eurasian lynx (*Lynx lynx*) and Pallas's cat (*Octolobus manul*)]; (2) investigate whether ensemble learning models provide improvement over single modeling methods, and if there are significant dissimilarities in the performance of these methods among different species; (3) determine the most significant environmental and anthropogenic factors influencing habitat suitability for the species; (4) define core areas for each species using resistant kernel modeling and to identify corridor routes among these core areas using factorial least-cost path modeling. (5) prioritize the predicted core habitats according to the probability of connectivity. The results provide clarity on the drivers of habitat quality for multiple carnivore species, and the patterns of habitat extent and connectivity for these species across Iran. This information will be helpful for building a conservation strategy and management plan for conservation of threatened species in Iran.

## Materials and methods

### Study area and data collection

The study area is the full extent of Iran, which covers 1,648,195 km$^2$ of southwestern Asia. Iran has two distinct topographic contexts: (1) mountainous areas, consisting principally of the Alborz and Zagros Mountains in the north west and extending southeast through the country, and (2) vast arid plains, mainly in the central and southern parts of Iran (Fig. 1).

Occurrence points for these species were collected from different parts of Iran by game wardens of the Department of Environment and multiple wildlife researchers during 2000–2019. This produced a total database of 240, 95 and 113 presence points of the Persian leopard, Eurasian lynx and Pallas's cat, respectively. To reduce spatial-autocorrelation, we placed circles with two radii (2.5 and 5 km) around each presence point to exclude proximal points using the Spatially Rarify Occurrence Data tool in the SDMtoolbox (Brown 2014). Because of two distinct topographic contexts in Iran (mountains, and plains), topographic heterogeneity was used to set two values (2.5 km for mountainous areas and 5 km for plains) based on the mean maximum distance moved by the Persian leopard per day (Farhadinia et al. 2020). In addition, we used these values for the two other study species given that the maximum dispersal ability of the Eurasian lynx and Pallas's cat was lower than the Persian leopard, and therefore they do not require a larger spatial filter distance. After spatial filtering, we retained 232, 92 and 102 presence points of the Persian leopard, Eurasian lynx and Pallas's cat, respectively, for habitat modeling. Additionally, we created 1,000 pseudo-absence points for each species for the habitat modeling. These points were randomly placed across the study area, excluding the 2.5 km radius circle around presences to reflect available resources for each species.

## Habitat modeling

Environmental variables including topography, climatic, water, land cover and human disturbance variables were used as predictor variables. We acquired a digital elevation model (DEM) from the 30 m Shuttle Radar Topography Mission (SRTM, downloaded from http://earthexplorer.usgs.gov), and calculated slope (using Surface Tool) and surface roughness variables (standard deviation of elevation of DEM's cells in the 2.5 km neighborhood using Neighborhood Tool) using Spatial Analyst Tools in ArcGIS 10.3. Out of 19 bioclimatic variables (Fick and Hijmans 2017), we selected six variables that we believed to be most relevant to predicting the distributions of the focal species: annual mean temperature (Bio1), max temperature of the warmest month (Bio5), min temperature of the coldest month (Bio6), annual precipitation (Bio 12), precipitation of warmest month (Bio 13) and precipitation of driest month (Bio14) (http://worldclim.org).

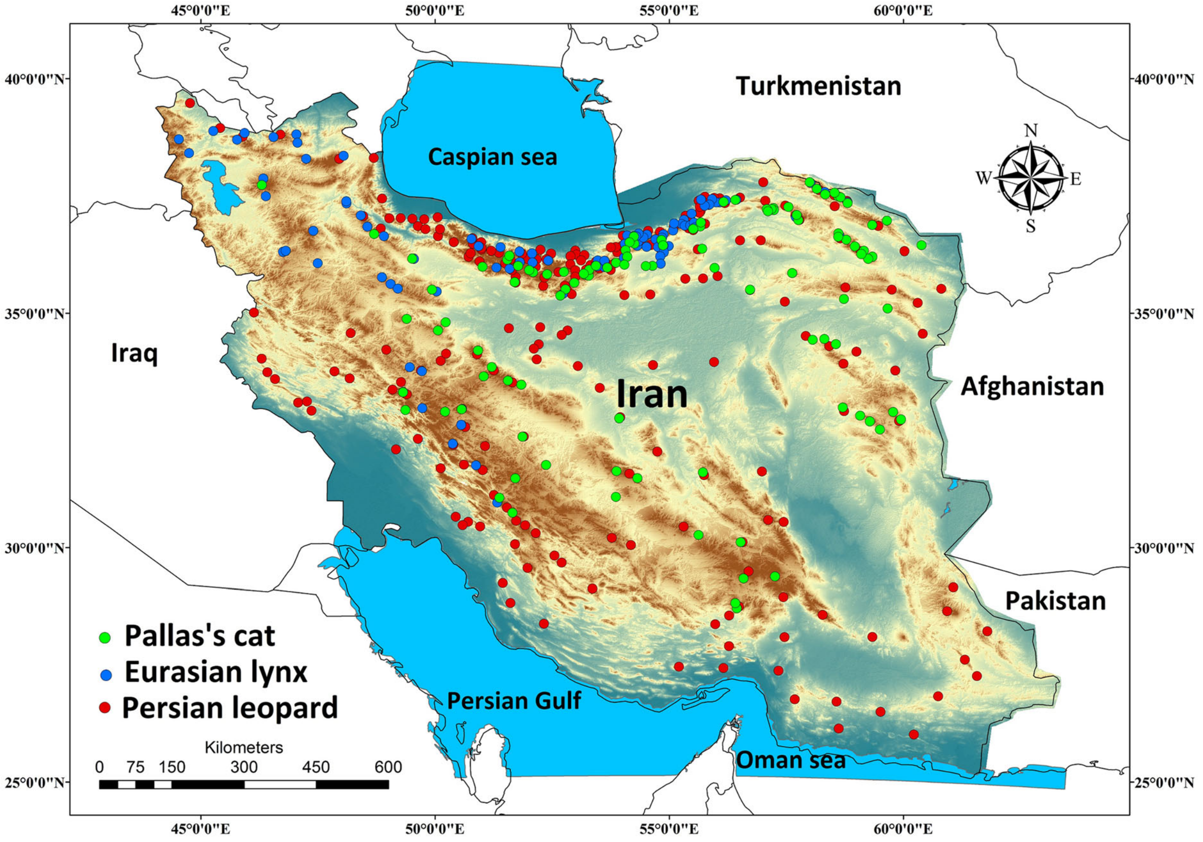

**Fig. 1** Study area including Iran and presence points of the Persian leopard, Eurasian lynx and Pallas's cat in Iran

The national land-cover map of Iran (FRWMO 2010) was used to create variables for distance from agricultural lands, distance from rangelands, distance from forests and distance from rocks using the Arc GIS Euclidian Distance Tool. We extracted these distances to cover class variables for each species observation and background point for analysis. The 16-day composite MODIS data (MOD13A1 V6 map at 500-meter cell size; http://earthexplorer.usgs.gov) was used to calculate the mean normalized difference vegetation index (NDVI) values of the year 2019. Due to the importance of water resources for wildlife (Almasieh et al. 2019a, 2019b), distance from rivers was also included. Human footprint (to provide a map of cumulative human pressure on the environment), as an indicator of population density, human access and infrastructure (Sanderson et al. 2002) was also used. Although human footprint includes roads, due to the important adverse effects of roads on cats (Mohammadi et al. 2018; Khosravi et al. 2017), distance to roads (Department of Environment, 2019) was also considered separately.

We used two methods to reduce multicollinearity among variables: (1) the Maxent Variable Selection package (Jueterbock 2015) in R (R Core Team 2018) was used to exclude variables by setting a contribution threshold of 1%, regularization multiplier of 1 to 5 with increments of 0.5 and inter-correlation of 0.7. Variables with the highest area under the curve (AUC) of receiver operating characteristic (ROC) and the lowest Akaike Information Criterion (AIC) were chosen (Table S1) and (2) the Variance Inflation Factor (VIF) of the dataset was checked using r-package usdm (Naimi et al. 2014) to exclude variables (selected in step 1) with VIF > 3 (threshold suggested by Zuur et al. 2010).

We used an ensemble modeling approach to predict habitat suitability for each study species. Our ensemble models were created by weight averaging seven different models using the biomod2 R package (Thuiller et al. 2014). These models included three regression-based models (GLM, GAM and MARS) and four machine-learning models (MaxEnt, RF, GBM and ANN).

### Model performance comparison

We evaluated and compared the performances of individual habitat suitability models and the ensemble model for each species using AUC and True Skill Statistic (TSS). We considered a model with AUC > 0.9 as excellent, 0.8–0.9 as good, 0.7–0.8 as moderate and 0.6–0.7 as poor. We considered a model with TSS > 0.75 as excellent, 0.4–0.75 as good and < 0.4 as poor (Eskildsen et al. 2013). Variable contributions to each model of each cat species were calculated in Biomod2 (Thuiller et al. 2014). In addition, response curves of presence points to the most significant variables in each model were produced and interpreted for each cat species.

### Resistance surface for connectivity analysis

To estimate landscape resistance, we converted the habitat suitability maps (ensemble model) to resistance maps using a negative exponential function (Wan et al. 2019) (Eq. 1):

$$R = 1000^{(-1 \times \mathrm{HS})}, \tag{1}$$

where R represents the cost resistance value assigned to each pixel and HS represents the predicted habitat suitability derived from the suitability models described above (Wan et al. 2019). We rescaled the resistance values to between 1 and 100 by linear interpolation, such that minimum resistance (Rmin) was 1 when HS was 1, and maximum resistance (Rmax) was 100 when HS was 0 (Wan et al. 2019).

### Connectivity analyses

We employed the universal corridor network simulator (UNICOR; Landguth et al. 2012) to create two sets of connectivity predictions including (1) resistant kernels (Compton et al. 2007) and (2) factorial least-cost paths (Cushman et al. 2009). The factorial least-cost path analysis in the UNICOR simulator applies Dijkstra's algorithm to resolve the single-source shortest path issue from every mapped species occurrence location on a landscape to every other occurrence location (Landguth et al. 2012). The analysis produces the sum of predicted least-cost paths from each source point to each destination point. The resistant kernel algorithm calculates the cumulative resistance cost-weighted dispersal kernel around each source point up to a user-defined dispersal threshold, providing an incidence function of the rate of organism movement through every pixel in the landscape as a function of the density and number of source points, the dispersal ability of the species, and the resistance of the landscape (Compton et al. 2007), and produces a map of the expected rate of movement of each species through each pixel in the landscape (Cushman et al. 2013).

To account for uncertainties regarding movement behavior of these species, we used three distance thresholds for Pallas's cat in the resistant kernel analyses: 20,000, 40,000, and 60,000 cost units, which represent movement abilities of 20, 40, and 60 km, respectively, through optimum low resistance habitat (Ross et al. 2012). For Eurasian lynx, we used dispersal threshold of 50, 100 and 150 km. For Persian leopard, we used thresholds of 60, 90 and 120 km. These dispersal distances are comparable to dispersal distances from previous research, (e.g. Farhadinia et al. (2018) reported maximum movement distances were 82 km for Persian leopards and Samelius et al. (2012) reported 148 km for Eurasian lynx). For Pallas's cat 52 km maximum movement distance was reported in Mongolia (S. Ross Personal Communication).

We calculated the factorial least-cost path network without a dispersal threshold (Cushman et al. 2017) to provide a broad-scale assessment of the regional pattern of potential linkage and to map potential long-distance corridors. The buffered least-cost paths were then combined through summation (Cushman et al. 2009) to produce maps of connectivity among all pairs of presence points.

We used the connectivity maps to identify core areas for each species. We defined core habitat patches as contiguous patches with resistant kernel values > 10% of the highest recorded for the species (as in Cushman et al. 2013; Ashrafzadeh et al. 2020). We ranked these key patches based on their strength (sum of kernel values) and size (e.g. Cushman et al. 2018). The final ranking value for the core areas prioritization represented the averaged values of these sub-rankings. To evaluate the effectiveness of the current conservation network in providing connectivity for these species in Iran, we quantified the extent and percentage of protected areas and corridors for each species that were within the current conservation network.

### Conservation prioritization of core habitats of three montane felids

We prioritized core habitat patches for three mountain dwelling felids based on the probability of connectivity (dPC) (Saura and Pascual-Hortal 2007) for all identified core habitats across the dispersal distance scenarios (Persian leopard: i.e. 60, 90 and 120 km; Eurasian lynx: 50, 100 and 150 km; Pallas's cat: 20, 40 and 60 km) in Conefor 2.6 (Avon and Bergès 2016). dPC takes into account habitat amount and habitat reachability, and the probability of dispersal between patches, and can be decomposed into dPCflux (dPCf), dPCconnector (dPCc) and dPCintra (dPCi) (Saura and Torné 2009; Ahmadi et al. 2020). dPCintra measures intra patch connectivity, while flux fraction of a specific node (dPCflux) reflects both patch attributes (e.g., area of suitable habitats) and its position within the landscape, and connector fraction (dPCconnector) depends only on the topological position of a patch in the landscape (Mateo Sanchez et al. 2014). Connector fraction quantifies the importance of the node as a stepping-stone for dispersal, i.e. facilitating dispersal between distant nodes (Ahmadi et al. 2020). We used a distance-probability value of 0.5 and 0.05 for minimum and maximum dispersal distances, respectively, as recommended by Saura and Torné 2009.

### Spatial pattern and configuration analysis

To evaluate the differences in the spatial pattern and configuration of habitat, we calculated a suite of fragmentation metrics with FRAGSTATS (McGarigal and Cushman 2002). To conduct the FRAGSTATS analysis, we first converted the UNICOR resistant kernel outputs into patches by applying a cutoff value (e.g., Wasserman et al. 2012). For each species, any values above 25th percentile of the highest dispersal scenario were reclassified as 1, representing habitat patches of high connectivity. Everything else was reclassified as 0. Then, we calculated four class level metrics using FRAGSTATS v4.2.1 (McGarigal and Cushman 2002) including: (1) the percentage of the landscape (PLAND), which quantifies the habitat patches of high connectivity as a percentage of the study area; (2) area-weighted radius of gyration (GYRATE_AM) or correlation length, which provides a measurement of the extensiveness of habitat patches of high connectivity; (3) largest patch index (LPI), which represents the percentage of the landscape comprised by the largest habitat patch of high connectivity; (4) number of isolated patches (NP), which provides a measure of the degree of fragmentation. These metrics have been used frequently in past connectivity research (e.g. Wasserman et al. 2012; Cushman et al. 2016; Macdonald et al. 2019; Moqanaki and Cushman 2016; Khosravi et al. 2017). We calculated these metrics for UNICOR resistant kernel outputs from all habitat suitability models (i.e., Ensemble, GLM, GAM, MARS, RF, MaxEnt, GBM and ANN) for each species.

## Results

### Model evaluation

Based on the maximum of AUC and the minimum of AIC in MaxentVariableSelection, 8, 9 and 9 variables were chosen for habitat modeling of the Persian leopard, Eurasian lynx and Pallas's cat, respectively (Supplementary Materials, Table S1). As VIF for these variables were $< 3$, all of these variables were included in habitat modeling (Table S2). AUC and TSS for all models were $> 0.8$ and $> 0.7$, respectively, indicating strong performance of all models (Table 1).

Overall, the ensemble learning model outcompeted all single-method models in terms of AUC and had the highest TSS for the Eurasian lynx and Pallas's cat (Table 1). The ensemble learning model ranked 4th (behind MaxEnt, MARS, and GBM) for the Persian leopard. Among the single-method models, MARS, GBM and RF had the highest AUC for the Persian leopard. For the Eurasian lynx, ANN, MaxEnt and RF had the highest AUC. For the Pallas's cat, RF, MaxEnt and GBM had the highest AUC (Table 1). MaxEnt, MARS and GBM had the highest TSS for the Persian leopard. For the Eurasian lynx, MARS, GLM and MaxEnt, had the highest TSS. Finally, for the Pallas's cat, RF, GLM and, MARS had the highest TSS.

### Environmental variables

We found topographical ruggedness highly correlated ($> 0.8$) with other variables thus we did not incorporate it in our models. Bio1 (Mean annual temperature), vegetation greenness (NDVI), and slope were among the most important variables based on variable contribution for all three species. Slope, Bio1, NDVI and distance from forests were the most important variables predicting occurrence of Persian leopard. Bio1, Bio12 (annual precipitation), NDVI and slope were the most important variables for the Eurasian lynx. Bio1, slope, Bio12 and NDVI were the most important variables for the Pallas's cat (Table 2).

Persian leopard showed positive association with increasing slope (Fig. 2). In addition, it showed a decrease in occurrence with increasing temperatures, with rapid decline in occurrence above a mean annual temperature of 10–15 °C (Fig. 2). In contrast, its occurrence increased with increasing NDVI. Eurasian lynx had a strong non-linear relationship with mean annual temperature, with dramatic decline in suitability when mean annual temperature is above 10–15 °C (Fig. 2). In addition, lynx seemed to show a unimodal relationship with mean annual precipitation, with maximum occurrence rate between 200 and 400 mm (Fig. 2). Like leopard, lynx showed positive associations with NDVI and slope, with particularly strong response to increasing NDVI. Pallas's cat was also related to mean annual temperature and precipitation. Like the other species it declined in occurrence rate at

**Table 1** AUC and TSS for all models used for habitat modeling of the Persian leopard, Eurasian lynx and Pallas's cat in Iran (Bold numbers are the highest amounts among different models for each species)

| | GLM | GAM | MARS | MaxEnt | RF | GBM | ANN | Ensemble |
|---|---|---|---|---|---|---|---|---|
| AUC | | | | | | | | |
| Persian leopard | 0.898 | 0.867 | 0.906 | 0.875 | 0.891 | 0.905 | 0.889 | **0.936** |
| Eurasian lynx | 0.929 | 0.833 | 0.930 | 0.936 | 0.935 | 0.933 | 0.938 | **0.978** |
| Pallas's cat | 0.922 | 0.871 | 0.920 | 0.930 | 0.948 | 0.927 | 0.917 | **0.969** |
| TSS | | | | | | | | |
| Persian leopard | 0.711 | 0.701 | 0.752 | **0.753** | 0.721 | 0.732 | 0.717 | 0.727 |
| Eurasian lynx | 0.801 | 0.705 | 0.802 | 0.792 | 0.738 | 0.781 | 0.778 | **0.871** |
| Pallas's cat | 0.747 | 0.720 | 0.742 | 0.722 | 0.771 | 0.724 | 0.721 | **0.832** |

**Table 2** Variable contribution (measured by Biomod by applying different environmental variables and occurrence points) in the habitat modeling of the Persian leopard, Eurasian lynx and Pallas's cat in Iran

| Variable | Species | | |
|---|---|---|---|
| | Persian leopard | Eurasian lynx | Pallas's cat |
| Slope (degree) | 26.8 | 9.2 | 23.5 |
| Bio1 (C°) | 20.8 | 44.5 | 37.5 |
| Bio12 (MM) | 6.2 | 12.4 | 11.9 |
| Distance from agriculture lands (Degree) | 8.9 | 2.6 | 3.4 |
| Distance from forests (Degree) | 11.9 | 3.2 | 3.1 |
| Distance from rocks (Degree) | – | 5.1 | 6.1 |
| NDVI (Range from −1 to +1) | 15.3 | 11.1 | 6.8 |
| Distance from rivers (Degree) | 5.7 | 7.3 | 3.6 |
| Human footprint (Range from 0 to 1) | – | 4.6 | – |
| Distance from roads (Degree) | 4.4 | – | 4.1 |

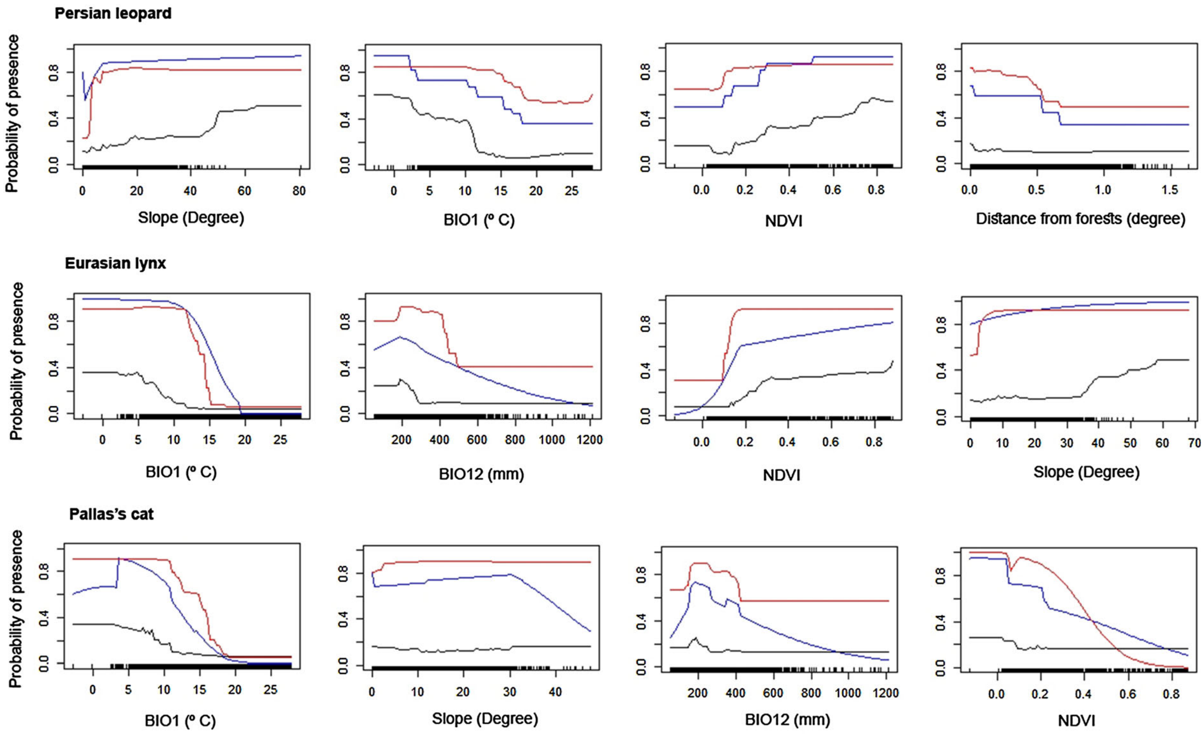

**Fig. 2** Response curves of presence points of the most important variables in habitat modeling of the Persian leopard, Eurasian lynx and Pallas's cat in Iran. For a better illustration, only models of MARS (blue), RF (black) and GBM (red) were considered

high temperatures, but was less associated with the coldest conditions, with occurrences remaining high until 12–17 C. It showed a similar optimal precipitation level as lynx (200-400 mm), and in contrast to the other species was strongly associated with low NDVI values (Fig. 2).

We mapped habitat suitability based on the ensemble of seven models for each cat species (Figs. S1, S2 and S3). Ensemble habitat suitability for the Persian leopard revealed that suitable habitat for this species concentrated in the Alborz and Zagros Mountains as well as other mountainous areas in the northern, western to southern parts of Iran (Fig. 3). Habitat suitability maps of the Eurasian lynx and Pallas's cat had the general same pattern (Fig. 3), but for Eurasian lynx, there was more suitable habitat in the northwestern and more non-suitable habitat in the southern, southwestern and southeastern parts of Iran. In addition, there was more suitable habitat for Pallas's cat in the eastern parts of Iran, reflecting its tolerance for warmer temperatures and less vegetated ecosystems (Fig. 3).

## Core habitat

Our connectivity simulation modeling for Persian leopard revealed that core habitats and connectivity areas are extensive, and are concentrated in the northern, and northeastern (Alborz mountains), western and central parts of Iran. We identified 145 core areas (Fig. 4), of which eight are more extensive than 2000 km$^2$. The largest and most important core area has an area of 48,271 km$^2$ and spans from northeastern to northwestern Iran (Golestan National Park, Khoshyeilagh Wildlife Refuge, Central Alborz Protected Area, Jahannama Protected Area) (Fig. 4 and Table 3). The second largest and most important core area, based on size (4265 km$^2$) and strength (sum of kernel value), occurred in southwestern Iran (Dena National Park and Tange Bostanak Protected Area). The average size of predicted core habitat patches for this species was 783.41 km$^2$, and 26.50% of the identified core habitats for the Persian leopard are covered by protected areas.

We identified 40 core areas for the Eurasian lynx. The largest and most important core area, according to size (10165.23 km$^2$) and strength, is in the Parvar, Jahan Nama and Hezar Jarib Protected Areas, Dodangeh and Khoshyeylagh Wildlife Refuges (Fig. 4; Table 3). The second largest and most important predicted core lynx habitat area has an area of 10204.44 km$^2$ and is located in northern Iran (Alam Kooh, Alborz and Lar Protected Areas) (Fig. 4; Table 3). The average extent of predicted core habitat areas for this species is 896.11 km$^2$. Among the predicted core habitats of Eurasian lynx, 30.07% are covered by protected areas.

For Pallas's cat, we identified 82 core areas. The largest core habitat based on size (854.53 km$^2$) and strength in occurred northern Iran (Fig. 4; Table 3). The second largest core habitat (940.21 km$^2$) occurred in northeastern Iran ( Binalood Protected Area) (Fig. 4; Table 3). Among the predicted core habitats for this species, 35.50% are covered by protected areas.

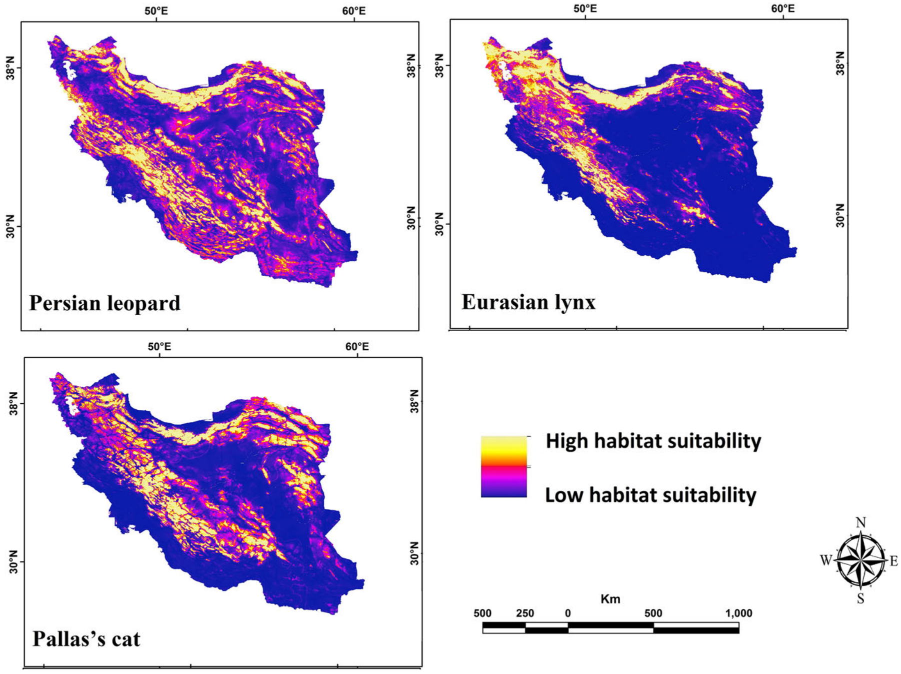

**Fig. 3** Ensemble models for habitat suitability of the Persian leopard, Eurasian lynx and Pallas's cat in Iran

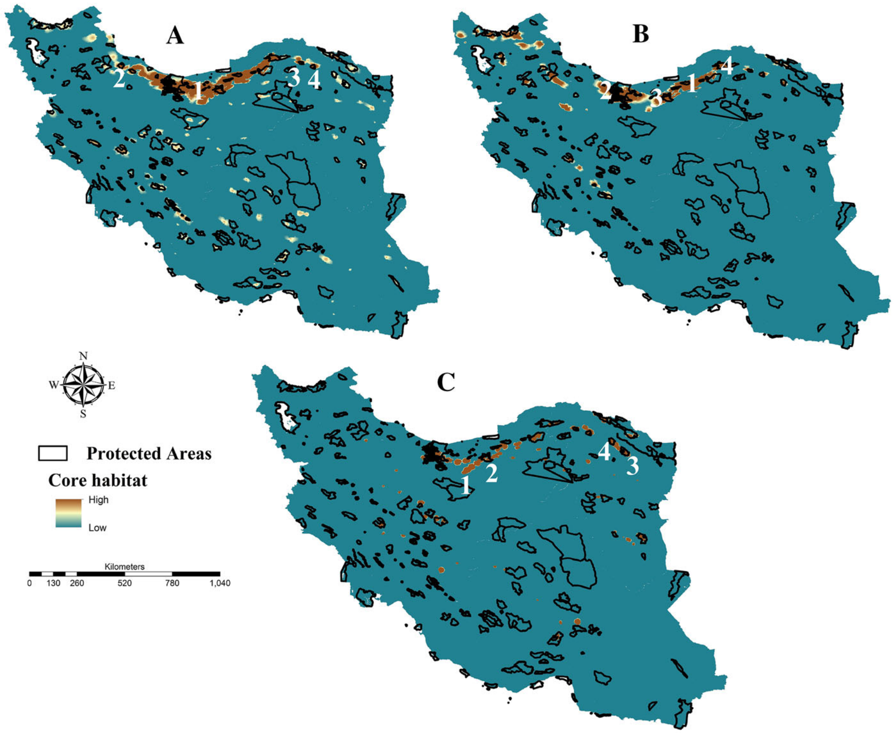

**Fig. 4** Persian leopard (**A**), Eurasian lynx (**B**) and Pallas's cat (**C**) core areas at dispersal ability 60, 50 and 20 km respectively and network of Iranian protected areas. Mean values of dPC used for prioritizing core habitats. Each number represent the prioritized core areas for each felid species

**Table 3** Number of core habitat, the extent and percent of core habitats covered by current conservation networks for three felids in Iran

| Species | Dispersal ability (km) | Number of core area | Extent of core habitats ($km^2$) | Extent of protected core habitats ($km^2$) | % of protected core habitats |
|---|---|---|---|---|---|
| Persian Leopard | 60 | 145 | 110180.71 | 33263.59 | 30.19 |
| | 90 | 85 | 149064.22 | 38952.28 | 26.13 |
| | 120 | 53 | 184440.12 | 42741.00 | 23.17 |
| Eurasian Lynx | 50 | 40 | 39429.24 | 13825.99 | 35.06 |
| | 100 | 30 | 57082.40 | 16751.29 | 29.34 |
| | 150 | 25 | 72229.08 | 18660.56 | 25.83 |
| Pallas's cat | 20 | 82 | 14701.10 | 5697.22 | 38.75 |
| | 40 | 65 | 22077.15 | 7777.27 | 35.22 |
| | 60 | 45 | 28954.57 | 9425.24 | 32.55 |

The median value of habitat suitability for presence points was used as threshold to define the highly suitable habitats

## Connectivity network

Our connectivity simulation modeling for Persian leopard revealed high connectivity areas in the northern, northeastern, central and southern parts of Iran. A total of 21.71% of the extent of this corridor network falls within protected areas (Fig. 5; Table 4). Most of the identified corridor network for Eurasian

Lynx occurred in northern, northeastern, northwestern and western Iran. Of the predicted corridor paths of Eurasian lynx, 29.94% are covered by protected areas (Fig. 5; Table 4). Only 23.10% of Pallas's cat corridors are covered by protected areas (Fig. 5 and Table 4). Our analysis showed that most predicted corridor paths for all three species are bisected multiple times by roads (Fig. 5; Table 4).

## Landscape connectivity across different models and dispersal abilities

For all three species, the percentage of the landscape, correlation length and largest patch index of connected habitat were predicted to increase significantly, and the number of patches was predicted to decrease, with increasing dispersal ability (Tables 5, 6 and 7). Among the models, RF predicted the highest number of isolated patches for the three species, especially for Eurasian lynx at dispersal ability of 50 km (Table 6). At all levels of dispersal ability, there was change in the FRAGSTATS metrics between analysis of ensemble models and other models. At the three dispersal thresholds and based on different models, 0.3 to 2.4% of the landscape is occupied by connected habitat patches for Pallas's cat. For Eurasian lynx 0.3 to 1.9% of the landscape is occupied by connected habitat patches and for Persian leopard 1.2 to 4.1% of the landscape is occupied by connected habitat patches. We predicted that the number of isolated patches for Persian leopard, Eurasian lynx and Pallas's cat were 1–2, 2–10 and 52–73 respectively (Tables 5, 6 and 7).

## Identification of top-ranked core habitats

### *Persian leopard*

Our analysis revealed that with increasing dispersal distance, there were large changes in the relative importance of different cores and an overall increase in connectivity importance across cores. Based on dPCc, Core 3 was the chief stepping stone among other cores at dispersal ability 60 km (Fig. 4, Fig. S4, Table S3). At dispersal ability of 60 km, Core 1 had the next largest contribution as a stepping stone (Fig. 4, Fig. S4, Table S3). Over dispersal distances of

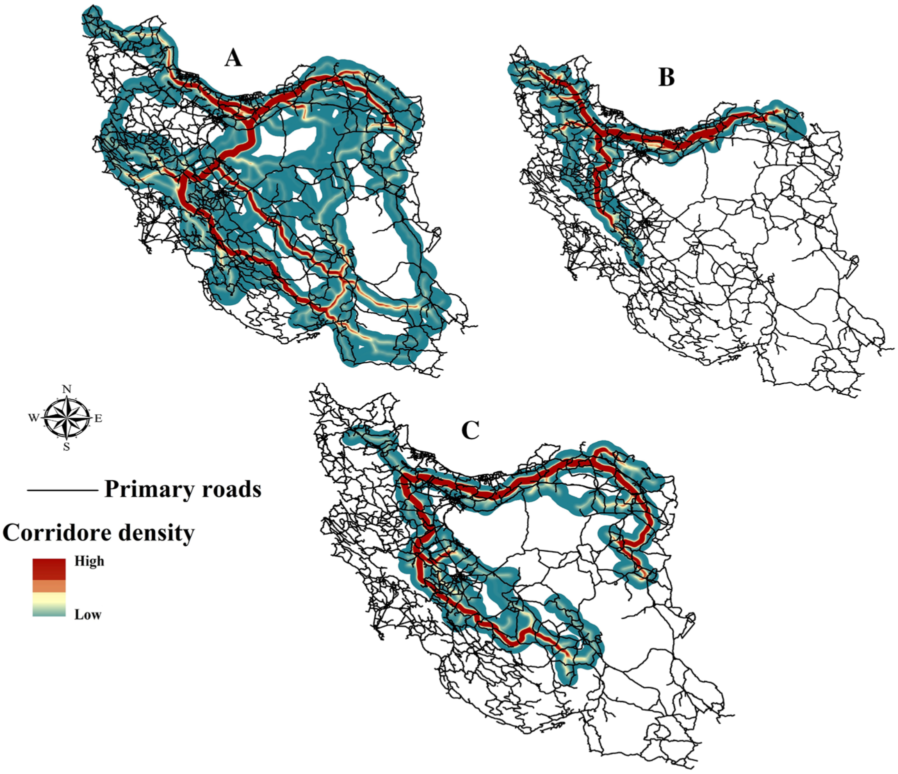

**Fig. 5** UNICOR corridor pathways for the Persian leopard (**A**), Eurasian lynx (**B**) and Pallas's cat (**C**) in Iran

**Table 4** The extent and percent of corridors covered by current conservation networks for three felids in Iran

| Species | Extent of corridors (km$^2$) | Extent of protected corridors (km$^2$) | % of protected corridors | Length of paved road cross the corridor path (km) |
|---|---|---|---|---|
| Persian leopard | 273197.67 | 59321.55 | 21.71 | 10773.72 |
| Eurasian lynx | 182485.59 | 24696.60 | 29.94 | 6733.6 |
| Pallas's cat | 125442.05 | 28977.31 | 23.10 | 14219.58 |

The median value of habitat suitability for presence points was used as threshold to define the highly suitable habitats

**Table 5** FRAGSTATS results for Persian leopard

| Metrics | Dispersal ability (km) | GLM | GAM | MARS | MaxEnt | RF | GBM | ANN | Ensemble |
|---|---|---|---|---|---|---|---|---|---|
| NP | 60 | 8 | 21 | 21 | 16 | 30 | 13 | 16 | 2 |
| | 90 | 6 | 13 | 12 | 11 | 15 | 10 | 8 | 2 |
| | 120 | 5 | 9 | 9 | 7 | 9 | 5 | 5 | 1 |
| LPI | 60 | 2.697 | 2.392 | 2.392 | 2.223 | 1.208 | 2.741 | 2.776 | 2.665 |
| | 90 | 3.497 | 3.307 | 3.307 | 2.848 | 1.662 | 3.595 | 3.648 | 3.402 |
| | 120 | 4.084 | 3.719 | 3.719 | 3.408 | 2.222 | 4.198 | 4.206 | 3.916 |
| PLAND | 60 | 2.7909 | 2.662 | 2.662 | 2.362 | 1.222 | 2.822 | 2.865 | 2.665 |
| | 90 | 3.606 | 3.387 | 3.387 | 2.848 | 1.671 | 3.683 | 3.750 | 3.402 |
| | 120 | 4.085 | 3.754 | 3.754 | 3.409 | 2.267 | 4.199 | 4.207 | 3.916 |
| CL | 60 | 27290.84 | 8854.87 | 8854.87 | 9838.49 | 4793.09 | 12973.20 | 10616.67 | 79904.74 |
| | 90 | 35186.81 | 13404.98 | 13404.98 | 20310.38 | 8842.59 | 17816.39 | 30020.90 | 84146.53 |
| | 120 | 21639.43 | 19444.04 | 19444.04 | 13776.44 | 15449.13 | 34443.11 | 25125.35 | 162542.187 |

The metrics include: *NP* number of individual core patches, *LPI* largest patch index, *PLAND* percentage of landscape in connected habitat, *CL* correlation length of core habitats. For Persian leopard in three levels of dispersal ability (60, 90, 120 km). The core habitats were defined as contiguous units with resistant kernel values >25% of the highest resistance kernel for the species

60 to 120 km, there was a decreasing trend in importance of core habitats (Core 5 to 8) as stepping stones in the connectivity network of the Persian leopard (Table S3). Based on the dPC index, the cores 1 and 2 were the most important for maintaining habitat connectivity at dispersal distance 60 to 120 km (Fig. 4, Table S3). Also, the cores 4–8 were the most important cores at dispersal distance 60 km (Fig. 4, Fig. S4, Table S3). Core 1 was the most important for the dPCi index at 90 and 120 km dispersal distance (Table S3). Based on dPCf, core 1 was the most important core but at 90 and 120 km core 2 was the next important (Table S3). Core 3 was the most important core at 60 km. At all distances, from core 4 to 8 there was a remarkable decrease in dPCf value (Table S3).

### *Eurasian lynx*

Based on dPCc, Core 3 was the chief stepping-stone among other cores at dispersal ability 50 km for Eurasian lynx (Fig. 4, Fig. S4, Table S4). At dispersal ability of 50 and 100 km, core 1 had the next largest contribution as a stepping stone (Table S4, Fig. S4, Fig. 4). Over dispersal distances of 50 to 120 km, there was a decreasing trend in importance of core habitats (Core 5 to 16) as stepping stones in the connectivity network (Fig. 4, Table S4). Based on the dPC index, the cores 1 and 2 were the most important for maintaining habitat connectivity at dispersal distance 50 to 150 km. After core 5, dPC index was reduced markedly in the remaining cores (Fig. 4, Table S4). Core 1 was the most important for the dPCi index at 150 km dispersal distance (Table S4). Also,

**Table 6** FRAGSTATS results for Eurasian lynx

| Metrics | Dispersal ability (km) | GLM | GAM | MARS | MaxEnt | RF | GBM | ANN | Ensemble |
|---|---|---|---|---|---|---|---|---|---|
| NP | 50 | 22 | 19 | 21 | 16 | 74 | 27 | 29 | 10 |
| | 100 | 5 | 14 | 12 | 8 | 16 | 13 | 16 | 3 |
| | 150 | 5 | 10 | 5 | 8 | 11 | 9 | 14 | 2 |
| LPI | 50 | 0.672 | 0.538 | 0.655 | 0.390 | 0.221 | 0.390 | 0.405 | 0.577 |
| | 100 | 1.064 | 0.859 | 0.983 | 0.738 | 0.288 | 0.857 | 0.858 | 0.908 |
| | 150 | 1.248 | 1.114 | 1.158 | 0.941 | 0.348 | 1.072 | 1.089 | 1.858 |
| PLAND | 50 | 1.267 | 0.956 | 1.234 | 1.00 | 0.385 | 0.926 | 1.052 | 1.166 |
| | 100 | 1.385 | 1.098 | 1.292 | 1.00 | 0.483 | 1.209 | 1.322 | 1.232 |
| | 150 | 1.645 | 1.641 | 1.545 | 1.371 | 0.624 | 1.716 | 1.952 | 1.904 |
| CL | 50 | 7745.05 | 7613.06 | 8029.32 | 9907.52 | 2134.03 | 5762.98 | 5800.91 | 16214.34 |
| | 100 | 23958.34 | 20935.93 | 9968.02 | 13713.71 | 8335.20 | 10103.81 | 10186.76 | 38411.75 |
| | 150 | 23993.04 | 11804.11 | 22901.18 | 14989.41 | 6763.42 | 17644.18 | 11122.30 | 57294.51 |

The metrics include: *NP* number of individual core patches, *LPI* largest patch index, *PLAND* percentage of landscape in connected habitat, *CL* correlation length of core habitats. For Eurasian lynx in three levels of dispersal ability (50, 100, 150 km). The core habitats were defined as contiguous units with resistant kernel values >25% of the highest resistance kernel for the species

**Table 7** FRAGSTATS results for Pallas's cat

| Metrics | Dispersal ability (km) | GLM | GAM | MARS | MaxEnt | RF | GBM | ANN | Ensemble |
|---|---|---|---|---|---|---|---|---|---|
| NP | 20 | 96 | 88 | 94 | 93 | 105 | 86 | 96 | 73 |
| | 40 | 86 | 84 | 84 | 85 | 101 | 85 | 81 | 62 |
| | 60 | 76 | 81 | 81 | 74 | 101 | 76 | 76 | 52 |
| LPI | 20 | 0.094 | 0.084 | 0.093 | 0.042 | 0.021 | 0.089 | 0.099 | 0.093 |
| | 40 | 0.184 | 0.161 | 0.185 | 0.150 | 0.031 | 0.185 | 0.187 | 0.186 |
| | 60 | 0.337 | 0.302 | 0.337 | 0.277 | 0.042 | 0.335 | 0.337 | 0.543 |
| PLAND | 20 | 0.982 | 0.783 | 0.932 | 0.706 | 0.346 | 0.853 | 0.958 | 0.927 |
| | 40 | 1.400 | 1.099 | 0.131 | 0.937 | 0.450 | 1.207 | 1.362 | 1.360 |
| | 60 | 2.046 | 1.536 | 1.916 | 1.347 | 0.595 | 1.738 | 1.989 | 1.933 |
| CL | 20 | 4429.86 | 4327.19 | 4403.67 | 3796.88 | 2513.62 | 4555.69 | 4351.01 | 5459.39 |
| | 40 | 5568.19 | 4290.06 | 5468.10 | 4443.19 | 2877.47 | 5176.53 | 5727.72 | 7297.83 |
| | 60 | 7000.01 | 5726.86 | 5995.87 | 5684.04 | 3245.54 | 6387.98 | 5713.12 | 9444.52 |

The metrics include: *NP* number of individual core patches, *LPI* largest patch index, *PLAND* percentage of landscape in connected habitat, *CL* correlation length of core habitats. For Pallas's cat in three levels of dispersal ability (20, 40, 60 km). The core habitats were defined as contiguous units with resistant kernel values >25% of the highest resistance kernel for the species

based on dPCf, core 1 and 2 was the most important core at 150 and 100 km respectively (Fig. 4, Fig. S4, Table S4). Core 3 to 5 was the most important core at 50 km. At all distances, from core 6 to 16 there was a remarkable decrease in dPCf value (Fig. 4, Fig. S4, Table S4).

### *Pallas's cat*

For Pallas's cat, the dPCc showed that Core 1 and 3 were the chief stepping stones among other cores at dispersal ability 60 km (Fig. 4, Fig. S4, Table S5). Our result showed that the dPC connector of core 1 was higher for this species at all distances, indicating a more important role of core 1 as stepping stones in facilitating movement of this species. Over distances of 20 and 60 km, there was a decreasing trend in importance of core habitats (especially core 5 to 18) as stepping stones in the connectivity network. Based on the dPC index, the cores 1 to 7 were the most important cores for maintaining habitat connectivity at dispersal distance 20 to 60 km (Fig. 4, Fig. S4, Table S5). In addition, based on dPCf, core areas 1 and 2 were the most important at 60 and 20 km respectively (Fig. 4, Table S5). Core 3 to core 5 were the most important cores at 40 and 60 km (Fig. 4, Table S5). Core 6 to core 14 were the most important cores at dispersal ability 20 km. From core 6 to 16, there was a large decrease in dPCf values compared to the most connected cores (Fig. 4, Table S5).

## Discussion

Predicting and understanding habitat is a central theme ecology. Researchers have developed many methods to model habitat, and ensemble learning is emerging as a particularly powerful analytical paradigm. Because ensemble learning is still a relatively new to method to many ecologists, the application of this method to study species habitat remains relatively rare. Among these studies, few have tested the potential improvement in performance that ensemble learning offers over single modeling methods, and whether and how these performances might differ among different species. In this study, we compared the performances of seven statistical methods, including an ensemble learning method, for modeling habitat of three sympatric mountainous carnivore species in Iran.

Overall, our study demonstrated that ensemble models typically perform better than any single modelling method. Garzon et al. (2006) previously reported that Random Forest was the most accurate algorithm in comparison with Tree-based Classification and Neural Networks. Mi et al. (2017) reported similar performances of RF and ensemble model for three bird species in the East of Asia. In contrast, Shahnaseri et al. (2019) showed that ensemble learning had the second highest accuracy after RF for predicting habitat suitability for grey wolf and golden jackal in central Iran. In this study, we found that ensemble model was almost always slightly better for all three carnivore species in Iran. This is consistent with Shabani et al. (2016), who showed that ensemble models outcompeted single-method models for eight species in Australia. Similarly, Araújo and New (2007) reported ensemble models outperformed single approach models. Moreover, in previous studies that had compared ensemble and single modeling methods, few had investigated whether there would be differences between different model performance metrics. By comparing both AUC and TSS across all our models, we found that the two metrics were mostly in agreement, but had some notable differences. This has potential implications for future studies in terms of choosing performance metrics for model comparisons.

### Factors influencing habitat suitability

Habitat suitability modeling for Persian leopard, Eurasian lynx and Pallas's cat revealed that their primary suitable habitat is concentrated in the Alborz and Zagros Mountains. Mean annual temperature (Bio1), NDVI and slope were the most critical variables determining habitat quality for all three of our studied species. Our results clearly show that all three species are influenced and limited by climate and topography, with all three associated with relatively cooler mountain conditions, with lynx most associated with cool temperatures, followed by leopard, and with Pallas's cat showing the greatest tolerance for warmer conditions. The results also show strong association of lynx and leopard with areas of higher vegetation density, while Pallas's cat is associated with areas with relatively sparser and more open vegetation. Distance from forests for the Persian leopard and mean annual precipitation (BIO12) for the Eurasian lynx and Pallas's cat were other vital variables in habitat modeling. This shows that lynx and Pallas's cat are likely more limited by climate (both temperature and precipitation), while leopard, as seen elsewhere (Stein et al. 2016; Rather et al. 2020) has a broader habitat niche, but relatively high vulnerability to human-wildlife conflict (Rostro-Garcia et al. 2016).

Relevant to our study, Farhadinia et al. (2015) reported that mean annual temperature, vegetation cover, and forest-shrub density were the most important variables for predicting occurrence of the Persian leopard in the Caucasus region (northwest) of Iran. Ashrafzadeh et al. (2019) further identified prey presence, slope and distance to villages as the major drivers of Persian leopard habitat suitability in western

Iran. Also, NDVI, distance from agricultural areas, and aspect are other important variables in Persian leopard habitat suitability (Erfanian et al. 2013). Barashkova et al. (2017) suggested that vertical migrations could be important for Pallas's cat to avoid deep snowy regions in winter. Additionally, a combined method of expert and habitat models revealed the significance of land cover, open forests, and aspect for Eurasian lynx (Doswald et al. 2007). Our results generalize and refine these relationships across the full extent of Iran, showing that leopard occurrence is driven both by vegetation, temperature and forest proximity (as a proxy for security from human persecution; Kittle et al. 2018).

Our study identifies potential critical thresholds in temperature that seem to control the distribution of these three species across Iran, with lynx in particular highly associated with the coldest conditions, and therefore likely most vulnerable to climate driven changes in habitat suitability (Mahdavi et al. 2020). A similar result was seen for American marten (*Martes americana*) by Wasserman et al. (2012). This suggests it may be important to project future climate change scenarios on the potential habitat and connectivity of these species (e.g., Wasserman et al. 2012; Shirk et al. 2018; Dar et al. 2021).

## Core areas, connectivity and protected areas

Our study identified northern and northeastern Iran as a critical core habitat and connectivity areas for all the three species. This is consistent with Ashrafzadeh et al. (2020) in terms of predicted core and connectivity areas for these three species. Our analysis of the relative importance of core habitats as network stepping-stones, in particular, provides a quantitative ranking of conservation importance of different land units which can guide nation-wide conservation prioritization and planning. Our result revealed that northern parts of Iran (i.e., Alborz mountains and Hyrcanian forest) were the key areas for prioritizing conservation efforts for the three felids in Iran.

Systematic conservation planning is the science of developing optimal management scenarios to enhance the preservation of biodiversity (Scott et al. 1993, Margules and Pressey, 2000, Groves et al. 2002), thus minimizing the biases in protected area selection (Watson et al. 2011). While, establishing protected areas is a critical component of conservation strategies (Chape et al. 2005, Naughton-Treves et al. 2005), for protected areas to be effective in promoting conservation objectives they need to be carefully and explicitly selected to provide sufficient conditions, extent and connectivity to sustain the biodiversity that depend on them (Nicholson and Possingham 2006, Cushman et al. 2018). In that context, it is critical to also address management problems and conflicts along the edges of protected areas, along the corridors that connect them and in the multiple-use matrix in which they are embedded (Cushman et al. 2018, Hansen and DeFries 2007). Carnivores are suitable proxies for regional conservation planning, and therefore, identifying their core habitats and connectivity can serve as an umbrella for other sympatric species (Carrol et al. 2001; Macdonald et al. 2020).

One approach for prioritizing conservation actions is based on analyzing core areas and corridors for a selection of focal species, which has recently emerged as a commonly applied approach for broad-scale conservation prioritization. For example, Cushman et al. (2013) evaluated the sufficiency of several categories of protected areas in protecting connectivity for 105 focal species with a broad range of ecological relationships and dispersal abilities. They found that protected lands in the region are primarily higher elevation forest and mountain habitats, which leave species associated with lower elevations and non-forested habitats more unprotected. A focal species approach was also employed by Cushman et al. (2016, 2018), using analysis of habitat core and connectivity areas for African lions to evaluate alternative landscape change scenarios (Cushman et al., 2016) and prioritize areas of the current landscape for designation as protected areas or biological corridors. Those studies showed unequivocally that strictly protected areas are essential as the foundation of conservation strategies for lions, but are insufficient in their current network, requiring both expansion of existing protected areas and strategic protection of critical linkage corridors among them. Similarly, Kaszta et al. (2019, 2020a, b), using the clouded leopard as a focal species for conservation planning, found that less than 25% of clouded leopard core habitat was protected across its range, and almost none of the major predicted corridors across the population received protection (Kaszta et al. 2020b). Furthermore, Swanepoel et al. (2013) revealed that most suitable habitats of leopard are located outside of

Protected Areas. By evaluating a range of alternative future scenarios, they demonstrated that likely future land use changes will have large negative impacts on the species, and were able to quantify the particular impacts of particular proposed development projects and propose alternative plans to minimize those impacts.

In our study, we also mapped and prioritized core areas and corridors for multiple focal species. We found that several regions provide core areas and corridors for several of our focal species, which is encouraging and suggests that, unlike Cushman et al. (2013), for several large carnivores in Iran it may be efficient and effective to develop landscape-based, multiple-species conservation strategies. However, unlike similar studies conducted recently in Iran (Khosravi et al. 2017, Shahnaseri et al. 2019), our study revealed relatively little overlap of corridors and core areas with Protected Areas (like Kaszta et al. 2020b). Additionally, Ashrafzadeh et al. (2020) showed a lesser extent of core overlap with protected areas of Persian leopard, Eurasian lynx and Pallas's cat, as well as a poor corridor protection. The extent of the study and studied species were different between our study and these past studies, which may explain their different results. The emergence of a collection of landscape core and connectivity assessments and prioritizations in Iran suggests future work should attempt to synthesize the results of these studies to find the common and universal implications. In addition, some of the differences in predictions appear to be fundamental, suggesting additional work, in particular using more robust methods to assess connectivity, such as landscape genetics (e.g., Wasserman et al. 2010) and movement modeling (e.g., Elliot et al. 2014) should be conducted on multiple focal species to clarify relationships between occurrence, dispersal, gene flow and landscape structure.

### Core area prioritization

The relative importance of predicted habitat core areas changed with simulated dispersal ability. Our results showed that generally the most important patches for three mountainous felids were those occupying the largest extents (e.g. Core 1) (Fig. 4). For Persian leopard, Eurasian lynx and Pallas's cat core 1, core 1–2 and core 1–6 were the most important core habitats respectively. Our result was consistent with Shahnaseri et al. (2019) and Mohammadi et al. (2021a). For the majority of core patches, we found remarkable change in rank of a given core habitat in connectivity importance when changing the dispersal distance scenario, which suggests very strong influence of scale and dispersal ability on conservation prioritization.

### Implications for conservation

Our analysis identified and quantified the strength and importance of the corridor network connecting the identified core areas across Iran for the three study species. We found that all three study species express strong habitat relationships and that climate and vegetation cover variables are highly important to all of them. We found that the most important core areas were concentrated in the main mountain areas of northern and western Iran, and that these three species have highly overlapping core habitats and somewhat coincident corridor networks. This enables efficient conservation of all three species through integrated multi-species conservation planning. However, the core areas and corridors of all three species are poorly protected by existing protected areas. Our results, therefore, provide critical guidance to expanding existing protected areas and establishing new protected areas in locations that will have the maximum benefit for conserving core habitat and connectivity for multiple species. Importantly, our results suggest that most identified corridor paths are bisected multiple times by roads, and therefore indicate areas that should be prioritized for mitigating road-mortality risk and increasing road permeability (such as overpass structure placement). Most protected areas in Iran are surrounded by roads, and road mortalities are a serious threat for carnivores (Moqanaki and Cushman 2016; Mohammadi and Kaboli 2016; Mohammadi et al. 2018). For instance, Parchizadeh and Adibi (2019) showed that road kills are one of the most important human-caused mortality factors of Persian leopard in Iran. Ongoing development in Iran is rapidly altering habitats across the country, leading to accelerating habitat loss and fragmentation. For example, The Belt and Road initiative includes several major ongoing and planned projects in Iran, including pipeline and transportation networks, which likely would lead to habitat loss, fragmentation, increased human-wildlife conflict and potentially promote illegal carnivore trade (Farhadinia et al. 2019b; Kaszta et al. 2020b).

## Conclusions

In this study, we combined ensemble habitat suitability modeling, landscape pattern analysis and connectivity simulation for a large carnivore and two mesocarnivores across their ranges in Iran. We found all three species to be associated with temperature, topography and vegetation variables, with concentration of suitable habitat, core areas and corridors along the major mountain ranges, particularly in northern and western Iran. We computed the intersection of these with protected areas and found that most habitat core and corridors are not currently protected. We advocate that additional protected areas should be designated to optimally protect the multispecies network of core and corridors we identified. We suggest that the Iranian Department of Environment should consider the findings of this and similar studies that use empirical data to predict habitat suitability and connectivity of multiple focal species, especially when planning and designing new Protected Areas and reviewing development plans (e.g., Kaszta et al. 2019, 2020b). Such spatially explicit prioritization is critical to balance the tradeoffs between development and conservation and ensure the viability of sensitive wildlife species.

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### Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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