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Landscape connectivity for mammalian megafauna along the Iran-Turkmenistan-Afghanistan borderland

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ABSTRACT

Habitat fragmentation threatens biodiversity, causes population isolation and reduces the availability of resources. When species ranges span geopolitical borders, management of transboundary populations and securing their connectivity can be compromised by different conservation priorities and juridical efforts. Using a combination of species distribution modelling and circuit theory, we modelled suitable habitats for four conservation-dependent mammalian megafauna in northeastern Iran, bordering Turkmenistan and Afghanistan which is part of the larger Kopet Dag Ecoregion in central Asia. Our multispecies approach aimed to identify key habitats and potential national and international corridors for Persian leopard (*Panthera pardus*), bezoar goat (*Capra aegagrus*), urial (*Ovis orientalis*) and goitered gazelle (*Gazella subgutturosa*) based on environmental variables. Between 18 to 34% of the study area was identified as suitable habitat for each species with a moderate variability in coverage by conservation network, ranging between 14 to 43%). Importantly, we identified three key landscapes which can enhance the connectivity between main populations of the species in northeastern Iran as well as neighboring countries. Most of the suitable landscapes along the Iran-Turkmenistan borderlands are protected on the Iranian side, providing a source for landscape connectivity across the border. In contrast, the main suitable landscapes for megafauna in northeastern Iran are located far from the Afghan border. Our multispecies approach provided an empirical framework for spatial conservation planning for the mammalian megafauna across the Kopet Dag Ecoregion and can direct future survey efforts to identify critical wildlife areas in Turkmenistan and Afghanistan, two countries with scarce data on biodiversity.

1. Introduction

Habitat conversion, degradation and fragmentation, mediated by growing pressures from human actions, threaten biodiversity (Tittensor et al., 2014). Future population growth and economic development are forecasted to impose unprecedented levels of extinction risk on many species worldwide, especially large mammals of Africa, Asia and South America (Crist, Mora, & Engelman, 2017; Tilman et al., 2017).

Although geopolitical borderlands are typically rich in biodiversity, protecting these landscapes is often challenging. Borderlands are characterized by dynamic social, political, economic and sometimes even ecological transitions which, at extremes, involve armed conflicts and political instability (McNeely, 2003; Trouwborst et al., 2017). Expansion of border security barriers, particularly across Eurasia is recognized as a threat to wildlife because they can cause mortality, obstruct access to seasonally important resources, and reduce effective population size and viability (Linnell et al., 2016).

Borderlands between Iran-Turkmenistan-Afghanistan, which are part of the larger Kopet Dag Ecoregion (Memariani, Zarrinpour, & Akhani, 2016; Olson & Dinerstein, 1998) is a shared steppe landscape hosting various conservation-dependent mammals, such as Persian leopard (*Panthera pardus saxicolor*), bezoar goat (*Capra aegagrus*), urial (*Ovis orientalis*) and goitered gazelle (*Gazella subgutturosa*) (Atamuradov, Fet, Fet, Valdez, & Feldman, 1999; Farhadinia, Moll et al., 2018; Kaczensky & Linnell, 2015; Moheb & Bradfield, 2014). Nonetheless, national conservation programs have created a heterogeneous landscape across the border. There is no established network of conservation areas on the Afghan side of the border (Kanderian, Lawson, & Zahler, 2011). In Turkmenistan, many established reserves suffer from limited conservation resources (Kaczensky & Linnell, 2015). On the Iranian side, the expanded network of reserves hosts populations of the mammalian megafauna (Farashi, Shariati, & Hosseini, 2017;

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Farhadinia, Moll et al., 2018; Ghoddousi et al., 2016) and can potentially play as a source role for the neighbouring countries. As a transboundary biodiversity-rich landscape, the Kopet Dag Ecoregion can benefit from inter-governmental conservation initiatives.

Although some mammalian species move across the border (Farhadinia, Johnson, Macdonald, & Hunter, 2018; Kaczensky & Linnell, 2015), there is no coordinated collaboration for biodiversity conservation. Two mammalian species, Asiatic wild ass (*Equus hemionus*) and Asiatic cheetah (*Acinonyx jubatus venaticus*), both assumed to depend on transboundary movement have already disappeared from one side of the border in Iran, and Turkmenistan, respectively (Farhadinia et al., 2017; Kaczensky & Linnell, 2015; Mallon, 2007). Developing a rigorous spatial conservation framework, along with encouraging political willingness, can facilitate a transboundary partnership between the countries.

A protective strategy in environments that are facing fragmentation is creating a network of habitats through connecting corridors (Di Minin et al., 2013; Foster, Love, Rader, Reid, & Drielsma, 2017; Moqanaki & Cushman, 2017). Corridors can improve the connectivity between isolated patches and, therefore, increases the landscape's capacity to sustain individuals, populations and meta-populations (Haddad et al., 2015; Khosravi, Hemami, & Cushman, 2018). Such a landscape-based conservation initiative requires measures that are supported by accurate information on distribution patterns and dispersal possibilities (Moqanaki & Cushman, 2017). Species Distribution Models (SDM) and circuit theory are increasingly combined to prioritize critical habitat patches and connectivity areas (Ahmadi et al., 2017; Carroll, McRAE, & Brookes, 2012; McRae & Beier, 2007).

Some mammalian megafauna, due to their extensive spatial and habitat requirements, can potentially be an umbrella for conservation planning of co-occurring species (Brodie et al., 2015; Closset-Kopp, Wasof, & Decocq, 2016; Khosravi, Hemami, Cushman et al., 2018). Assessing environmental conditions for multiple umbrella species with various habitat requirements can benefit the functionality of ecological corridors for a wider range of taxa (Brodie et al., 2015; Closset-Kopp et al., 2016; Khosravi, Hemami, Cushman et al., 2018). Accordingly, we tailored this approach to four conservation-dependent mammalian species with various habitat requirements, including Persian leopard, goitered gazelle, bezoar goat and urial which occur at all sides of the borderland between Iran, Turkmenistan and Afghanistan in central Asia.

Using a combination of species distribution modelling and circuit theory, we modelled suitable habitats for the species in northeastern Iran which is part of the larger Kopet Dag Ecoregion. Our study site was limited to Iran because species occurrence data as well as updated environmental layers were unavailable from the Turkmen and Afghan sides. We also assessed landscape connectivity among important habitat patches. Finally, we evaluated the efficacy of the existing conservation network in safeguarding the focal mammalian community in the region. Our modelling approach develops a spatial framework for launching inter-governmental transboundary partnerships across the Kopet Dag Ecoregion and can direct future survey efforts to identify critical wildlife areas in Turkmenistan and Afghanistan, two countries with scarce data on biodiversity.

2. Study area

We conducted our study in northeastern Iran, across two provinces of North Khorasan (28,434 km^2) and Razavi Khorasan (118,854 km^2) (38.28º to 33.46 °E and 55.90º to 61.26 °N) (Fig. 1). Our study area is part of the larger Kopet Dag Ecoregion which with an area of almost 165,000 km^2 mainly spans across northeastern Iran and southern Turkmenistan (Memariani et al., 2016). The study area has three different climate zones that includes cold in the north, mild-semi desert in the center and desert in the south (Bannayan, Lakzian, Gorbanzadeh, & Roshani, 2011). Elevation ranges between 300–3211 m.a.s.l, including two parallel mountain chains, i.e. the northern chain (Kopet Dag and Hezar Masjed mountains) and the southern chain (Binaloud, Aladagh and Golestan mountains) (Afshar-Harb, 1994). This zoogeographical region was named as the Iranian Cradle of speciation by Misonne (1959). It includes a total of 53 conservation areas, including 3 National Parks, 27 Protected Areas, 5 Wildlife Refuges and 18 No-Hunting Areas, and with an area of 23,103 (km^2) it covers 14% of the region.

3. Methods

3.1. Data collection

We collected occurrence data for the four focal species during field samplings by authors and rangers of the Department of Environment (DoE), spanning between 2008 and 2017. We only included occurrence records with hard evidence, such as carcasses, photos or live captures in the database. A total of 108, 44, 48, and 42 occurrence records were compiled for Persian leopard, goitered gazelle, bezoar goat and urial, respectively, covering most of the known localities of each species in the region.

3.2. Environmental variables

Optimal spatial resolution is critical for SDMs' performance to avoid misleading results (Connor et al., 2018; Guisan, Graham, Elith, Huettmann, & Group, 2007; Seo, Thorne, Hannah, & Thuiller, 2008). We therefore modeled each species distribution at five different spatial resolutions (1, 2, 4, 8, 16 km^2).

Land cover data was obtained from the Iranian Forests, Range and Watershed Management Organization as well as DoE, prepared in 2014. The ratio of different cover types (i.e. the natural background of the landscape) in a 1-km radius from the centre of each cell was calculated using neighbourhood analysis. Normalized Difference Vegetation Index (NDVI) data was derived from 30 m Landsat TM imagery at a 1-km spatial resolution for 2017. Two of 19 bioclimatic predictors were collected from the World Clim 1.4 database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at the 1 km spatial resolution (Table 1). Topographic variables included mean and standard deviation (SD) of elevation and mean of slope for all raster cells in a 1 km radius, calculated based on the digital elevation model generated by the National Cartographic Center of Iran. A correlation test was performed for all pairwise combinations of environmental variables, and correlated predictor pairs with $r > 0.7$ were excluded from analysis (Table 1).

3.3. Model construction

We used an algorithm based on the maximum entropy principle (MaxEnt), which outperform other modelling approaches across different sample sizes of species' occurrence records in a comparison of species distribution modelling framework (Philips, Anderson, & Schapire, 2006). In order to avoid autocorrelation and bias among occurrences, a simple systematic filtering was used because the simple systematic approach has proven to consistently outperform other methods (Kramer-Schadt et al., 2013; Fourcade, Engler, Rödder, & Secondi, 2014). MaxEnt already discards redundant records that occur in a single cell. A grid of 5 km spatial resolution was created and randomly sampled one occurrence per grid cell. This spatial resolution was chosen based on mean of reported home range size of studied species (e.g. Stevenson-Jones, 1977; Jacobson et al., 2016).

We used Jackknife as an efficient assessment of accuracy to evaluate the contributions of predictor variables for the best fitting model. The continuous map provided by MaxEnt was reclassified into a binary presence/absence prediction map for each species using the probability threshold corresponding to each model's maximum Kappa value. The binary maps were compared with current protected areas in IDRISI TerrSet to assess any possible overlap. Presence points were randomly

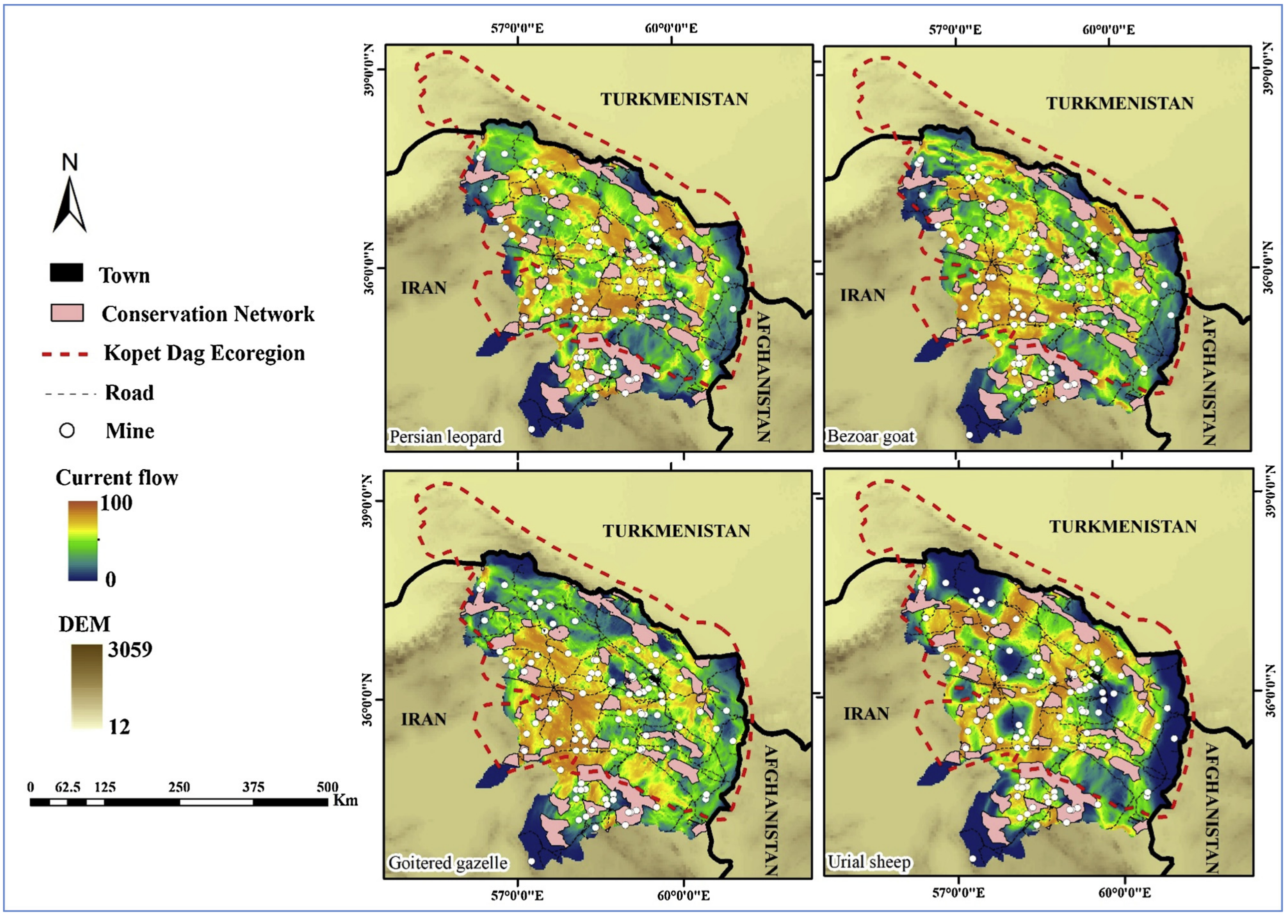

Fig. 1. Model of cumulative current flow used to evaluate habitat connectivity for the four mammalian megafauna in northeastern Iran.

divided into training and test datasets (80% and 20%, respectively). We ran 100 bootstrap replicates and used the area under the ROC-plot curve (AUC; Fielding & Bell, 1997) and the True Skill Statistics (TSS; Allouche, Tsoar, & Kadmon, 2006) to evaluate our models. AUC values between 0 and 1 mean the worst and best prediction respectively, with 0.5 corresponding to a random prediction. For TSS, -1 and 1 mean the worst and best prediction respectively, with 0 corresponding to a random prediction. The analysis was performed in MaxEnt version 3.3.3 (Philips et al., 2006) with default settings (regularization multiplier $\beta = 1$; auto features; convergence threshold = 0.0000, background points = 200). We evaluated the performance of five different spatial resolutions (1, 2, 4, 8, 16 km2) by AUC and TSS to select the best model.

3.4. Habitat connectivity analysis

A circuit model was used to estimate the actual connectivity inside the conservation network based on electrical circuit theory. The power of circuit theory can be used to measure the connectivity or isolation of habitat patches (Ahmadi et al., 2017; McRae & Beier, 2007). We chose the all-to-one mode and the option to connect a cell with eight of its neighbors. In the one-to-all mode, connectivity is calculated between all nodes (McRae & Shah, 2009). To parameterize Circuitscape models for each species, we designated the nodes as conservation areas (53 conservation areas, Fig. 3). The connectivity maps for each species were overlapped to delineate the final connectivity within the conservation network. An isolation-by-resistance analysis was conducted using Circuitscape 3.5 (McRae & Shah, 2009). The inverse of the habitat suitability map was generated for the studied species as a measure of habitat connectivity.

4. Results

Evaluation of modeling results using 14 independent environmental variables based on the TSS and AUC values showed that the MaxEnt model performed significantly better than random prediction at the five spatial resolutions (Table 1). For all four mammalian species, a spatial resolution of 2 km outperformed other resolutions (Table 1). Roughness was associated with increasing habitat suitability for all species, except the goitered gazelle. The distance to woodlands was associated with habitat suitability for all species, except bezoar goat which had less suitable habitats near woodlands (Fig. 2).

Between 18 to 34% of the entire study area was modelled as suitable habitat for each mammalian species (Table 2 and Figs. S1–S4). Importantly, suitable habitat coverage by conservation networks showed moderate variability between the species, varying between 14 and 43% (Table 2). In total, 58% of the study area was identified as suitable for at least one of the focal species. Analysis of landscape connectivity revealed that none of the conservation areas are completely isolated from other areas and there is a high potential to improve landscape connectivity, particularly across western parts (Figs. 1 and 3). Moreover, our results highlighted the existence of several pinch points (areas where is funneled within linkages) across the predicted linkages, which can constrain the species distribution (Fig. 1).

The Iran's leopard range is widely connected to the Turkmen side, while weak functional connectivity is seen for the species along the Iran-Afghanistan borderland (Fig. S1). Similarly, for both montane dwelling ungulates, i.e. bezoar goat and urial, the Iranian populations are mainly connected to the Turkmen's (Figs. S3–S4). In contrast, the suitable habitats of goitered gazelles are mainly connected to the Afghan side, along with parts of the Turkmenistan border (Fig. S2). The

Table 1
Environmental variables and their relative contributions to model habitat suitability for the four mammalian species at multiple spatial resolutions in northeastern Iran.

Environmental variables	Min-Max	Mean ± SD	Persian leopard					Goitered gazelle					Bezoar goat					Urial				
			Resolution (km^2)					Resolution (km^2)					Resolution (km^2)					Resolution (km^2)				
			1	2	4	8	16	1	2	4	8	16	1	2	4	8	16	1	2	4	8	16
Climatic variables																						
Annual mean temperature	22.0-197.0	139.3 ± 31.5	0.6	9.3	7.2	1.0	15.8	34.8	34.8	42.9	38.3	39.0	0.2	0.0	0.0	0.0	1.4	2.6	1.7	0.2	0.1	0.0
Annual precipitation	94.0-369.0	219.7 ± 55.2	3.0	9.3	3.5	6.7	1.2	4.3	3.7	1.0	1.4	8.2	4.5	4.7	6.5	9.0	10.1	0.3	0.4	0.1	0.1	0.7
Topographic variables																						
Roughness*	0.6-483.1	78.4 ± 68.8	42.1	47.6	44.6	40.1	40.7	4.9	2.9	3.3	1.5	1.1	53.8	46.2	49.8	25.0	38.8	24.1	15.8	11.2	18.4	17.3
LU/LC variables																						
Distance to urban area	0.0-106827.0	21415.8 ± 15160.9	3.3	2.2	2.1	1.8	2.7	5.1	3.4	0.9	0.5	5.0	1.0	0.8	1.1	1.6	7.1	0.0	0.3	0.3	0.9	4.2
Distance to rural area	0.0-56384.8	3477.4 ± 4305.3	2.0	1.6	1.6	1.6	0.6	10.6	7.1	2.8	2.4	1.4	0.7	1.0	0.7	1.9	4.3	0.1	3.0	5.5	0.3	3.9
Distance to High way	0.0-145784.0	29869.9 ± 19125.5	2.7	2.0	2.1	0.9	0.8	5.8	7.1	6.1	15.8	8.2	0.1	0.1	0.3	0.3	1.0	0.6	0.1	0.0	0.0	0.2
Distance to Road	0.0-71310.9	11994.9 ± 10714.0	2.6	2.8	1.9	3.2	2.3	0.6	0.2	2.9	3.2	1.0	2.3	1.0	2.7	1.2	1.2	3.6	3.2	4.7	1.9	9.5
Distance to Agriculture	0.0-67575.8	3703.4 ± 5966.4	1.2	0.8	1.1	2.1	0.2	0.9	5.4	3.5	0.3	1.3	4.6	8.5	6.9	34.6	13.1	1.2	3.8	5.1	11.9	0.2
Distance to Scrubland	0.0-93921.5	29829.3 ± 19943.2	1.5	0.8	1.3	2.2	0.0	4.2	5.2	3.6	6.6	0.2	1.4	0.5	1.2	0.8	0.9	3.1	1.1	0.9	2.0	0.5
Distance to Woodland	0.0-331166.5	96759.7 ± 87353.6	8.9	12.3	11.3	3.8	27.0	18.0	15.8	18.5	18.0	13.2	24.7	29.0	21.2	19.9	9.6	54.7	60.7	64.5	59.5	53.5
Distance to Range area	0.0-19659.5	983.6 ± 1945.5	1.0	0.9	3.4	2.9	0.2	0.5	0.7	0.1	0.5	4.9	2.4	2.6	2.5	1.4	0.7	0.5	2.1	2.5	1.3	1.0
Distance to Rocky area	0.0-96784.5	32224.0 ± 18829.1	5.5	2.5	2.5	6.2	1.0	5.0	5.8	4.4	4.7	4.8	3.1	1.7	1.6	1.5	2.4	0.0	3.5	1.4	1.8	5.4
Distance to Mine	0.0-95770.5	23371.8 ± 15095.3	4.0	4.5	4.5	5.0	5.1	3.6	5.2	8.5	4.3	2.7	1.1	3.0	4.7	0.5	2.9	1.7	6.2	3.0	1.0	0.1
NDVI	−0.3-0.8	0.1 ± 0.0	21.8	3.4	12.9	22.5	2.4	1.6	2.9	1.6	2.5	9.2	0.0	1.0	0.7	2.2	6.3	1.5	0.8	0.7	0.6	3.6
Accuracy index																						
AUC	———	———	0.95	0.96	0.93	0.89	0.92	0.90	0.98	0.93	0.91	0.92	0.90	0.96	0.94	0.92	0.97	0.95	0.99	0.97	0.97	0.96
TSS	———	———	0.93	0.97	0.92	0.87	0.90	0.89	0.96	0.92	0.90	0.94	0.91	0.95	0.90	0.90	0.94	0.92	0.97	0.92	0.93	0.93

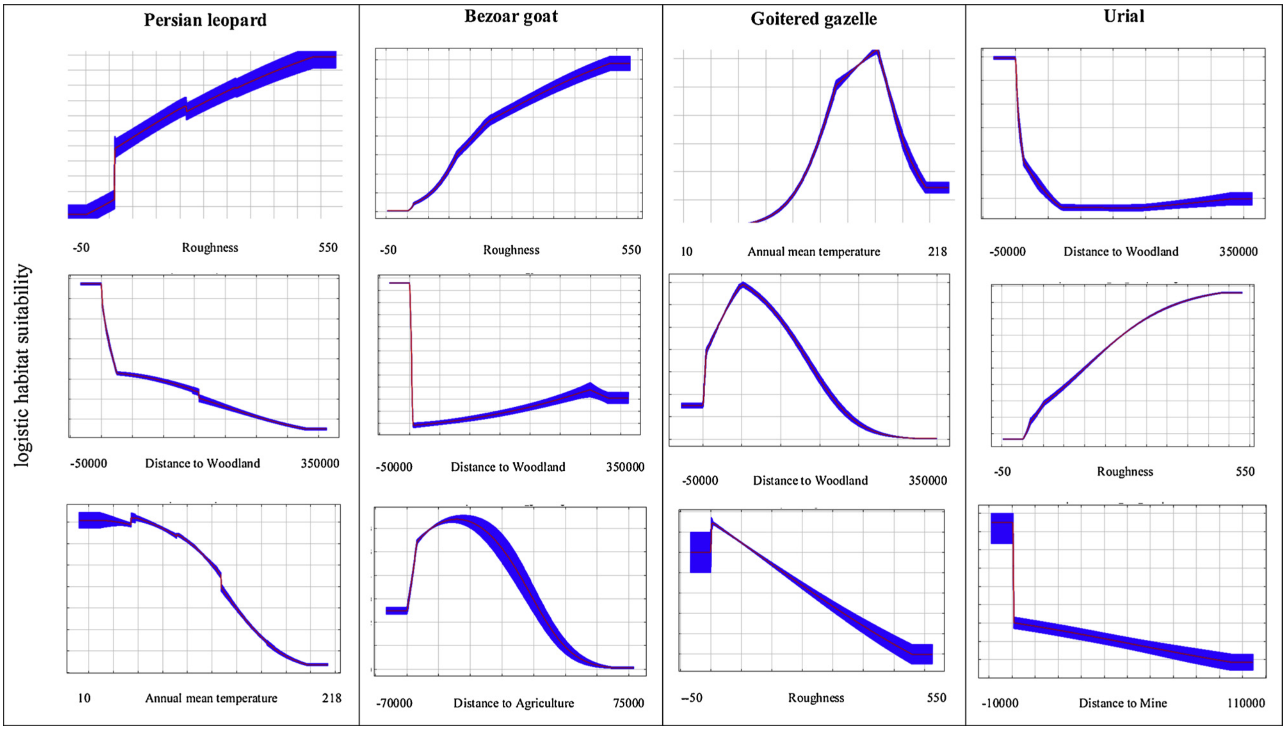

Fig. 2. Response curves of MaxEnt model for the four studied focal species in northeastern Iran at 2 km spatial resolution based on Jackknife test.

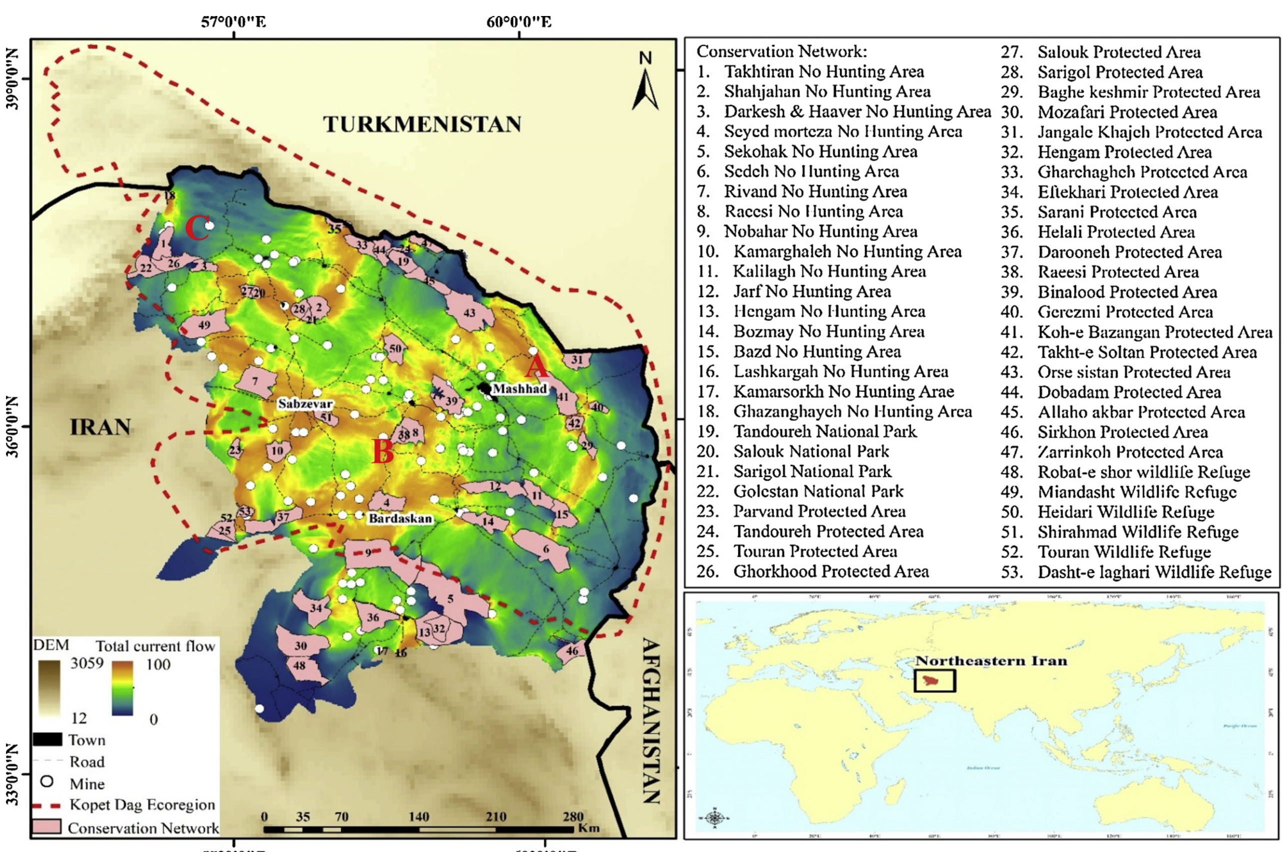

Fig. 3. Ensemble model of cumulative current flow used to evaluate habitat connectivity for Persian leopard, urial, bezoar goat and goitered gazelle megafauna in northeastern Iran. Red capital letters denote key landscapes in the northeast of Iran which are of high importance for survival of the focal species: A) northern Mashhad, B) southern Sabzevar-Neyshabour and C) northern Golestan National Park, towards Turkmenistan.

Table 2
Area and proportion of protection granted to the four mammalian megafauna in northeastern Iran.

Species	% Suitable habitat	% Suitable habitats protected by conservation network
Persian leopard	34%	24%
Bezoar goat	26%	29%
Urial	18%	43%
Goitered gazelle	27%	14%

ensemble model of cumulative current flow of the four mammalian species is shown in Fig. 3.

5. Discussion

Our multispecies approach provided an empirical framework for spatial planning to conserve the four mammalian megafauna in northeastern Iran. We also quantified the combined effects of topographic features and law enforcement to delineate functional niches for these mammals. Finally, our modelling effort revealed the potential connectivity across dozens of conservation areas in northeastern Iran as well as across international borders with Turkmenistan and Afghanistan.

The species' response to environmental predictors supports habitat associations known from the past literature for leopards (Ashrafzadeh, Naghipour, Haidarian, & Khorozyan, 2018; Ebrahimi, Farashi, & Rashki, 2017; Farhadinia et al., 2015; Khosravi, Hemami, Cushman et al., 2018), urial and bezoar goat (Bashari & Hemami, 2013; Makki, Fakheran, Moradi, Iravani, & Senn, 2013), and goitered gazelle (Farashi et al., 2017; Khosravi, Hemami, Malekian et al., 2018). Accordingly, mountains provide a refugia for all species, except goitered gazelles which unsurprisingly are confined to lowlands.

On average, almost one third of each species' suitable habitats are within the existing network of conservation areas which is equivalent to 14% of the entire study area (Figs. S1–S4). Moderate connectivity exists between the conservation areas. However, highways are a major impediment for functional permeability across the region (Ahmadi et al., 2017; Mohammadi et al., 2018; Moqanaki & Cushman, 2017). Importantly, we identified three key landscapes which can enhance the connectivity between main populations of study species in northeastern Iran (Fig. 3): A) north of Mashhad, B) south of Sabzevar-Neyshabour and C) northern areas of Golestan National Park, close to Turkmenistan. Areas south of Sabzevar-Neyshabour (landscape B) are exclusively suitable for goitered gazelle; the other two landscapes (A and C) can facilitate connectivity for all focal species.

Most of the suitable landscapes along the Iran-Turkmenistan borderlands are protected on the Iranian side, providing a source for species dispersion across the border (Fig. 3). Importantly, these border reserves can serve as sources of species transboundary connectivity between the two countries (Atamuradov et al., 1999; Farhadinia, Johnson et al., 2018; Kaczensky & Linnell, 2015). The two landscapes A and C can supplement the border conservation network through providing more support for transboundary connectivity of the focal species. In contrast, our modeling approach showed that the main suitable landscapes for mammals in northeastern Iran are located far from the Afghan border. Equally important, there is no conservation area on the Afghan side of the border, where many mammalian megafauna are heavily exploited (Kanderian et al., 2011). Nonetheless, Sirkhon Protected Area (Fig. 3: number 46) can play as a potential source to recover mammalian megafauna, particularly goitered gazelle in western Afghanistan. Biodiversity surveys are needed to evaluate the occurrence of any of the focal species in western Afghanistan.

Although large parts of northeastern Iran are modeled as suitable habitats with a moderate percentage lying within conservation networks, the focal species are generally unlikely to occur outside the conservation network. As an exception, Persian leopards are widely detected outside the conservation network, perhaps due to their large spatial requirements and shortage of food resources, which drive them to occasionally raid livestock in rural areas (Farhadinia, Johnson et al., 2018; Farhadinia, Moll et al., 2018; Ghoddousi et al., 2016; Khorozyan, Soofi, Hamidi, Ghoddousi, & Waltert, 2015). In contrast, as is the case in many Asian countries, ungulates are spatially confined to the conservation network since poaching and interactions with livestock threaten their persistence outside established reserves (Bashari & Hemami, 2013; Bleyhl et al., 2019; Khosravi, Hemami, Malekian et al., 2018; Mallon & Zhigang, 2009).

Northeastern Iran is an important region for migratory mammalian species in central Asia and has an extensive network of conservation areas with moderate connectivity. Two of our focal species, Persian leopard and goitered gazelle, are listed in the Appendix II of the 1979 Bonn Convention on the Conservation of Migratory Species of Wild Animals (CMS) which is an international instrument focusing on the conservation of transboundary wildlife (Karlstetter & Mallon, 2014; Trouwborst et al., 2017). Also, they are part of the Central Asian Mammals Initiative (CAMI) priority species. Our study provides a spatial framework to expand national and transboundary conservation across the Kopet Dag Ecoregion.

Author contributions

MAHSHID HOSSEINI: data analysis, AZITA FARASHI*: study design and writing, ALI KHANI: fieldwork, MOHAMMAD S. FARHADINIA: fieldwork and writing.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2019.125735.

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