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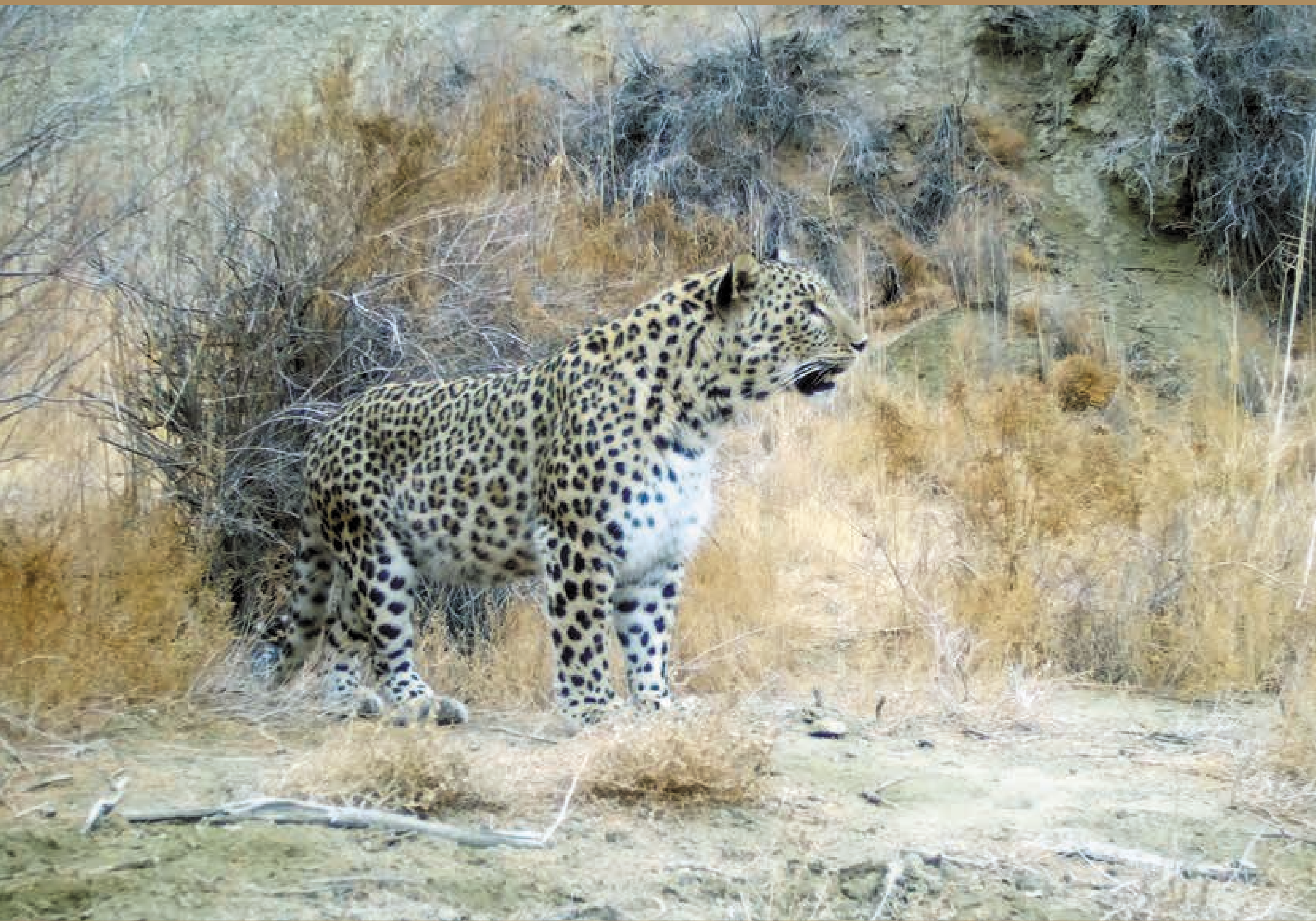
CAT news

The Persian Leopard



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CATnews is the newsletter of the Cat Specialist Group, a component of the Species Survival Commission SSC of the International Union for Conservation of Nature (IUCN). It is published twice a year, and is available to members and the Friends of the Cat Group.

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Cover Photo: Persian Leopard in Kazakhstan © USNR/CADI/ACBK, camera trap picture taken 1 January 2020, photo was provided by Tatjana Rosen

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Mapping the distribution and habitat of Persian leopard across its historical range

Persian leopards *Panthera pardus tulliana*, once widespread across Western and Central Asia, currently only occupy a fraction of their historical range. Identifying areas for restoring, connecting, and expanding extant populations is therefore important to safeguard this subspecies. Here, we used a large dataset of Persian leopard occurrences from 11 countries to map Persian leopard habitat across its historical range. We identified widespread potentially suitable habitat (about 1,290,000 km²), particularly in mountain regions. We highlight five clusters of habitat patches that could potentially host leopard metapopulations: the Caucasus (Armenia, Azerbaijan, Georgia, Iran, Russia, Turkey), the Alborz-Kopetdag Mountains (Iran, Turkmenistan), the Taurus Mountains (Turkey), the Zagros Mountains (Iran, Iraq, Turkey), and the Hindu Kush-Western Himalayas (Afghanistan, Pakistan). Further, we identified 174 core habitat patches with more than 250 km² of highly suitable habitat. Most of the core habitat patch area is found in Iran (204,005 km²; 38%), Turkey (100,651 km²; 19%), and Pakistan (51,868 km²; 10%), highlighting the importance of these countries for Persian leopard conservation. We then assessed the proportion of core patch area that is currently protected (9%) and updated the historical and current distribution maps, using all information gathered in this Special Issue. This revealed that 151 of all 174 potential habitat patches we found were historically occupied (i.e., overlapped with our historical distribution; 87%) and 53 patches are likely currently occupied (i.e., overlapped with our extant distribution; 30%). Finally, we mapped potential corridors among core habitat patches and identified three priority regions for population recovery, with clusters of unoccupied patches that have a high connectivity to currently occupied patches: the southern Caucasus, the southern Zagros Mountains, and the Hindu Kush-Spin Ghar. In sum, our analyses suggest a major potential for larger, viable Persian leopard metapopulations within their historical range, given conservation measures are implemented to halt and reverse ongoing population declines and local extinctions.

Many large carnivores today occupy only fractions of their historical ranges, persisting in small, fragmented populations (Ripple et al. 2014). The Persian leopard *Panthera pardus tulliana* is no exception. Once widespread across Anatolia, the Caucasus, and Western and Central Asia, only a few isolated populations remain today (Jacobson et al. 2016, Breitenmoser et al. 2017). Like other large carnivores, Persian leopards are mainly threatened by habitat destruction and fragmentation, illegal killings that often result from human-carnivore conflict, and prey depletion (Ghoddousi et al. 2017, 2020, Soofi et al. 2019, 2022). They require large areas of habitat and often roam beyond protected area boundaries and national borders (Ghoddousi et al. 2020, Farhadinia et al. 2021). Leopards often come into conflict with people, mainly over livestock depredation, and may get killed as a precaution or in retaliation (Ghoddousi et al. 2020, Soofi et al. 2022). Identifying suitable and safe areas to inform conservation where it might be possible to increase current population sizes, establish new populations, and work towards reducing human pressure is therefore urgently needed to safeguard leopards.

There are several regions that might still hold patches of suitable habitat within the historical Persian leopard range (e.g. in the Caucasus and Iran; Ahmadi et al. 2020, Bleyhl et al. 2021). Most of these habitat patches are however too small to host viable leopard populations (Zimmermann et al. 2007, Farhadinia et al. 2014). Therefore, regions should be identified that contain several large enough and safe habitat patches that are connected through functional corridors. In such regions, conservation efforts could seek to establish leopard metapopulations, consisting of several connected subpopulations that occur within the habitat patches (Bleyhl et al. 2021).

Achieving viable metapopulations is challenging. Often, there is a lack of information on which potential habitat patches are occupied and which would be the most promising sites to foster range expansions. Identifying candidate sites for leopard metapopulations has been done at country and regional levels (e.g., for the Caucasus; Farhadinia et al. 2015, Rozhnov et al. 2020a, Bleyhl et al. 2021), but needs to be scaled up to a range-wide level to develop a coordinated conservation strategy to safeguard Persian leopards in the future (Breitenmoser et al. 2007, Zimmermann et al. 2007, Gavashelishvili & Lukarevskiy 2008). Such information would help guiding (pro-)active conservation measures to mitigate human-leopard conflict and is further a requirement to distribute limited conservation funds most effectively. Knowledge on the current leopard distribution, patch sizes, and whether and how habitat patches are protected is thereby essential for robust conservation decisions. Additionally, it is often unclear whether functioning corridors exist between patches and where they are located. Without such corridors, population growth inside core patches can lead to a constant loss of individuals and high rates of conflict in sink areas (Khorozyan & Abramov 2007, Maharramova et al. 2018, Ghoddousi et al. 2020).

A range-wide assessment of habitat distribution is a key requirement to develop a coordinated strategy for the conservation of Persian leopards. Conservation planning is needed to safeguard existing populations, promote connectivity among them, and identify the most promising areas for natural range expansions and reintroductions. All this needs maps of the distribution of leopards and potentially suitable habitat, yet an up-to-date range-wide assessment of this kind is missing. Here, we used a large dataset of leopard occurrences from 11 range countries to map the historical, present, and potential Persian leopard distribution across the full range. Based on that, we identified core habitat patches and corridors among these patches and highlight candidate regions to establish leopard metapopulations and priority regions for population recovery. More specifically, we asked the following research questions:

1) What is the distribution of potential Persian leopard habitat?
2) How do Persian leopard habitat patches relate to the historical and current leopard distribution and how well are they connected?
3) Which regions are particularly promising for conservation interventions aimed at establishing viable Persian leopard meta-populations?
4) Which regions are particularly promising for leopard range expansion and population recovery?

Methods

Mapping potential Persian leopard habitat

As our study region, we used a broad area across Western and Central Asia comprising the Persian leopard range (Fig. 1; Jacobson et al. 2016). To make sure we map suitable habitat across the full range, we included contact zones and partly areas from neighbouring subspecies (i.e., Indian leopard *P. p. fusca* and Arabian leopard *P. p. nimr*, Jacobson et al. 2016). We considered all available leopard presence locations from the regional status reports (this Special Issue; in total 2,301 locations). From this, we only used records from 2010–2021 that had an exact location and were classified as C1 (hard fact, verified records such as photographs, camera-trap pictures, and results of genetic or biochemical analyses) or C2 (expert-confirmed records) according to the Status and Conservation of the Alpine Lynx Population (SCALP) criteria (Molinari-Jobin et al. 2012). Further, we excluded locations associated with leopard mortality and livestock kills (n = 66), because they might be in areas that are not safe, and filtered the remaining data to only retain one location per 1x1 km² cell. This resulted in a final dataset of 850 locations from 11 range countries: Afghanistan (n = 3), Armenia (n = 43), Azerbaijan (n = 24), Georgia (n = 1), Iran (n = 667), Iraq (n = 20), Kazakhstan (n = 10), Pakistan (n = 48), Russia (n = 3), Turkey (n = 2), and Turkmenistan (n = 29). To characterise habitat suitability, we used species distribution models. Species distribution models identify suitable habitat based on presence locations of species, absence, pseudo-absence, or background records, and a set of predictor variables (Franklin 2009). We used ten predictor variables related to landscape structure, landscape composition, climate conditions, and human disturbance (see SOM Table T1 in the Supporting Online Material for an overview). Regarding landscape structure, we used elevation data from the Shuttle Radar Topography Mission (SRTM; NASA JPL 2013) at 30-m resolution and calculated the terrain ruggedness index (TRI) at 1 km cell level as the square root of the sum of the squared differences between the centre pixel and its eight neighbours (Riley et al. 1999). Additionally, we calculated the mean proportion of tree and shrub cover as well as the proportion of grassland and water bodies from the Copernicus Global Land Service Land Cover Map for 2015 in each 1 km cell (Buchhorn et al. 2020). Regarding climate, we used the mean proportion of permanent snow as a predictor (Buchhorn et al. 2020) and assigned a habitat suitability of 0 to our final model predictions for all cells with a mean elevation >4,000 m, because in areas with permanent snow at high elevations, harsh winter conditions limit the range of Persian leopards and most of their prey (Lukarevsky et al. 2007a, Farhadinia et al. 2020). While data on snowfall intensity or snow depth would better characterise habitat constraints, such data is not consistently available across our study area. Regarding human disturbance, we calculated the mean distance to human settlements per 1-km cell, based on Euclidean distances to settlement centre points on a 100 m grid, as well as road density from Open Street Map data (categories for settlements: allotments, city, farm, hamlet, isolated dwelling, town, village; categories for roads: motorway, trunk, primary, secondary, tertiary; www.openstreetmap.org; downloaded on 10 September 2021). Additionally, we used the Copernicus Land Service Land Cover Map to

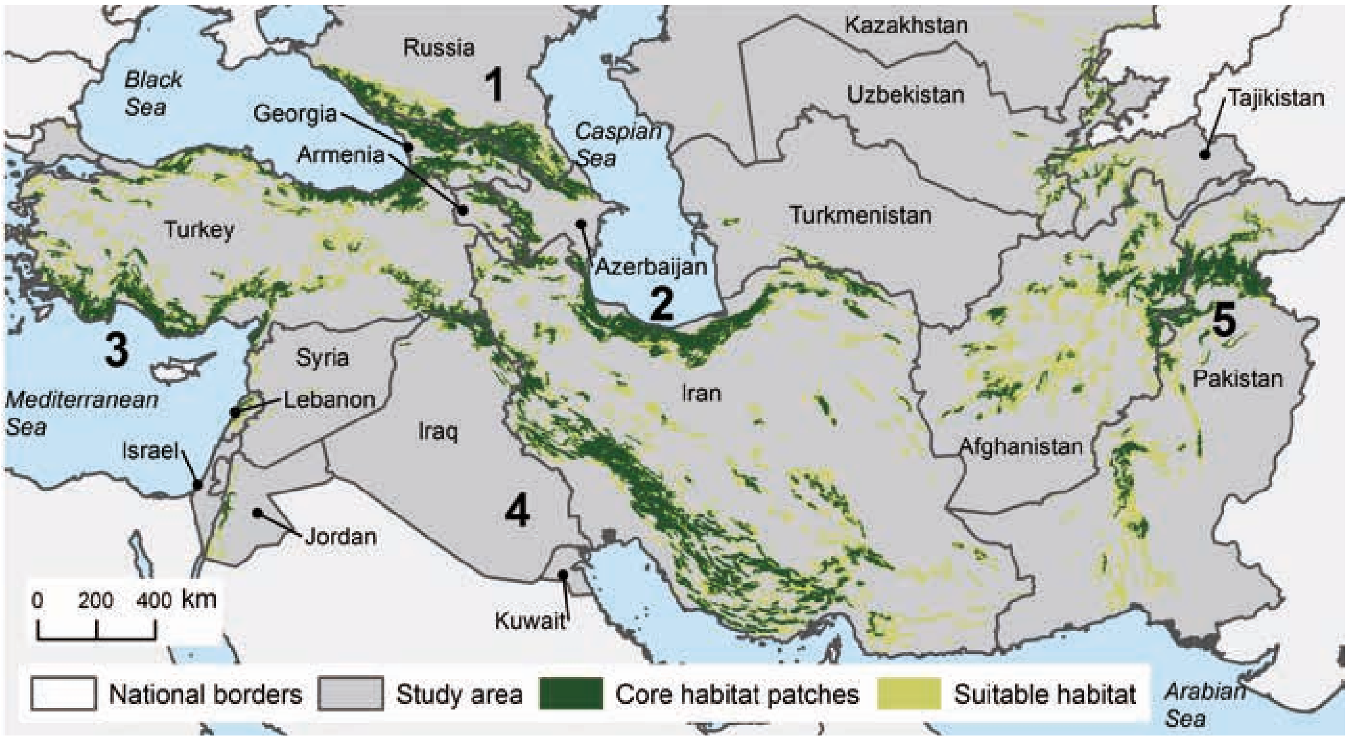

Fig. 1. Study area (dark grey), predicted suitable habitat (light green) and core habitat patches (dark green) for Persian leopards across their range. Numbers indicate the five candidate regions to host viable leopard metapopulations: (1) the Caucasus, (2) the Alborz-Kopet-dag Mountains, (3) the Taurus Mountains, (4) the Zagros Mountains, and (5) the Hindu Kush-Western Himalayas.

Table 1. Core patch area, number of core patches per range country, and the respective proportion of these patches that is under protection*, sorted by decreasing core patch area. We here list only countries with core habitat area. The proportion of each country to our study area refers to the area delineated in Fig. 1 in dark grey.

Country	Proportion of total study area (%)	Core habitat area (km^2)	Number of core patches**	Area under protection (%)	Area under strict protection (%) (IUCN cat. I and II)
Iran	24	204,005	78	9.09	0.95
Turkey	12	100,651	31	9.41	0.01
Pakistan	13	51,868	16	4.79	0.02
Afghanistan	10	43,120	26	2.39	1.99
Russia	5	35,403	3	35.97	11.11
Georgia	1	33,704	4	12.16	10.44
Azerbaijan	1	17,501	4	24.18	12.89
Iraq	7	12,958	4	8.39	0.00
Tajikistan	2	8,964	9	11.22	4.46
Uzbekistan	7	6,661	7	26.68	23.30
Armenia	1	6,332	3	25.17	15.05
Turkmenistan	7	2,869	4	20.69	18.9
Jordan***	1	1,532	1	18.09	11.02
Lebanon	1	1,350	1	4.86	0.71
Kazakhstan	7	890	2	58.84	57.76
Syria	3	81	0	0.00	0.00

* The proportion under protection is based mostly on the global WDPA dataset (IUCN & UNEP-WCMC 2021; except for the Caucasus Ecoregion and Turkey), and therefore, we might underestimate protected area coverage for some countries (You et al. 2018).
** Patches crossing international borders were counted for each country if at least 250 km^2 were located in the respective country (i.e., some patches are counted multiple times in this column, once for each country with at least 250 km^2 of that patch).
*** Part of the Arabian leopard range (*P. p. nimr*) but might comprise a contact zone to Persian leopards.

calculate the proportion of cropland at the 1 km scale (Buchhorn et al. 2020), which can be a strong determinant of human-leopard conflict (Ghoddousi et al. 2020). Finally, we used a human population density map (Center for International Earth Science Information Network - CIESIN - Columbia University 2018). We resampled all our predictors to a 1-km resolution and projected them to an Albers equal-area projection. Correlation among our predictor variables was low ($r < |0.65|$).

To map potential leopard habitat, we used three species distribution modelling algorithms: boosted regression trees (BRT), a generalised linear model (GLM), and Maximum Entropy modelling (Maxent). We used these three algorithms to have a gradient from a statistical regression-based approach (GLM) to more complex ensemble (BRT) and machine-learning (Maxent) approaches and avoid having to choose one best algorithm (Hao et al. 2020). We ran all models in the R programming language (R Core Team 2021) using the *dismo* package (Hijmans et al. 2017). As pseudo-absence and background data, we randomly sampled the same number of presence points for our BRT and GLM models (i.e., n = 850) and 10,000 points for Maxent. We split our presence and pseudo-absence/background data into training (80%) and test (20%) sets to validate our models. For each model, we calculated the continuous Boyce index (CBI; Hirzel et al. 2006) and the area under the Receiver Operating Characteristics curve (AUC; Fielding & Bell 1997). The continuous Boyce index measures correlation between the predicted habitat suitability and the predicted to expected ratio of the frequency of validation points with a moving window of differing widths (negative values indicate an inverse model, values around zero a random model, and one a perfect model; Boyce et al. 2002, Hirzel et al. 2006). The AUC value contrasts sensitivity and specificity across all possible thresholds, with values ranging from 0 to 1 (1 indicating a perfect model; Jiménez-Valverde 2012). Finally, we predicted potential habitat for each algorithm and calculated an average prediction across all three algorithms, weighted by the respective AUC values, as our final potential habitat map (i.e., using the weighted arithmetic mean, where predictions from the model with the highest AUC contribute most to the average prediction). This map had habitat suitability values ranging from 0 (unsuitable) to 1 (highly suitable).

Identifying and assessing Persian leopard core habitat patches

To identify suitable core habitat patches, we converted our continuous habitat maps into binary maps using the training sensitivity plus specificity threshold (Liu et al. 2013). We then identified core habitat patches as contiguous cells with a habitat suitability above the 25th percentile of values at our presence locations (Pitman et al. 2017, Bleyhl et al. 2021) and a cumulative area of at least 250 km^2 (i.e., the minimum area for breeding populations in Iran; Farhadinia et al. 2018). While smaller minimum areas have been reported in very suitable habitat (Farhadinia et al. 2019), we chose 250 km^2 across the whole range for a conservative estimate. Based on the distribution of these core patches, we highlighted areas with clusters of core habitat by visual interpretation of our maps as regions that can potentially host a viable leopard metapopulation.

In a next step, we assessed the core habitat patches based on a range of different criteria. First, we assessed which patches were historically occupied and which patches are potentially currently occupied. To do so, we updated the historical (i.e., before the start of the Industrial Revolution) and current leopard

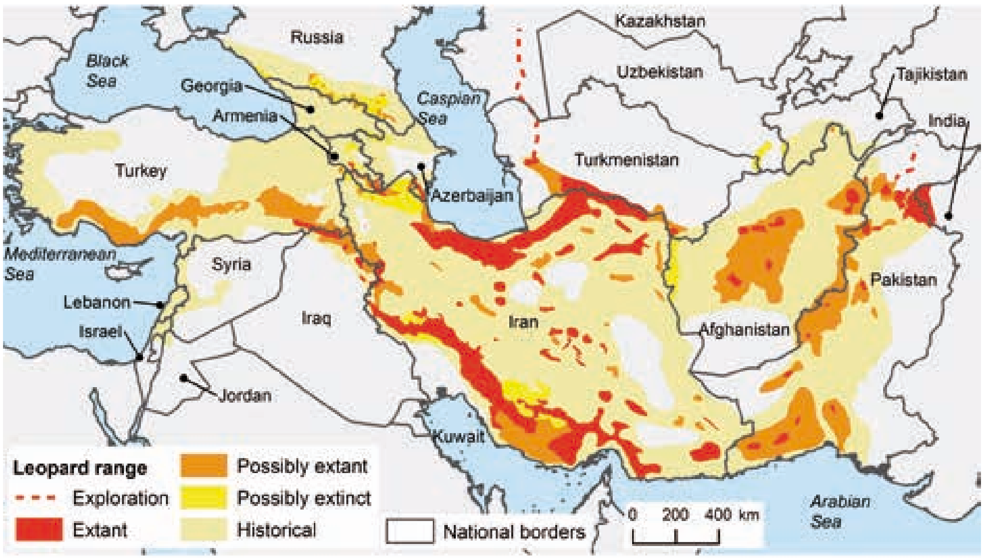

Fig. 2. Persian leopard range and historical distribution. Exploration lines are based on recent (post-2010) C1 records of leopards outside of the historical range in Turkmenistan, Kazakhstan, and Pakistan.

distributions from Jacobson et al. (2016) using the new leopard presence locations available through this Special Issue, and the results of our habitat model. The IUCN Red List Assessment for *Panthera pardus* (Stein et al. 2020) served as a basis for this procedure. For mapping the present distribution, we followed the IUCN mapping standards (IUCN Red List of Threatened Species 2021) to identify "Extant" and "Possibly Extant" areas. "Extant" areas are regions where leopards are confirmed by recent hard fact records (i.e., C1 records) or are very likely to occur within remaining suitable habitat. "Possibly extant" areas are regions where leopards may possibly occur, but recent (i.e., post 2010) hard fact records are not available. Possible occurrence is based on expert opinion or hard fact records prior to 2010 within areas of remaining suitable habitat. "Possibly extinct" areas are regions where the leopard used to occur, but no recent records are confirmed and, according to expert opinion, they are unlikely to be present due to habitat loss or other threats. "Extinct" areas are regions previously known or highly likely to support leopards, but it has been confirmed that the species no longer occurs, because exhaustive searches have failed to produce recent records and the intensity of threats could plausibly have extirpated the species. Additionally, we show advances of transient individuals (post-2010 C1 records) beyond the historic range into Kazakhstan, Turkmenistan, and Pakistan with "exploration" lines. To delineate the current distribution, we used C1 and C2 records from 2010 onwards and adjacent areas of potential leopard habitat (i.e., results of our habitat model prediction). Finally, we used existing local range maps and absence data from various local surveys to refine the distribution boundaries (i.e., from the regional status reports: Farhadinia et al. 2022a, Ghoddousi et al. 2022a, Khorozyan et al. 2022, Ostrowski et al. 2022).

Second, we calculated the area of each patch and the proportion of each patch that was officially protected using the World Database on Protected Areas (WDPA) and regional databases for the Caucasus Ecoregion and Turkey (IUCN, wwfcaucasus.net & UNEP-WCMC 2021). We acknowledge that WDPA data availability differs substantially across countries, and therefore, we might underestimate protected area coverage in some areas (You et al. 2018).

Third, we measured the connectivity of each unoccupied habitat patch (i.e., not overlapping with our extant distribution) to its closest neighbouring occupied patch (i.e., overlapping with our extant distribution). We measured connectivity as the length of least-cost corridors between patches based on our inverted habitat suitability map as a cost layer (with low length = high connectivity). For that, we used the Linkage Mapper Toolkit to calculate cumulative costs among core habitat patches and to identify least-cost paths (i.e., single-cell paths with the lowest cumulative cost from one patch to another; McRae & Kavanagh 2011). In case of disjunct constellations of patches (i.e., discrete clusters of patches that are only connected with corridors among themselves), we added corridors to their closest neighbouring patches until all constellations were connected (McRae & Kavanagh 2011). Based on this, we highlighted areas with clusters of unoccupied patches with high connectivity to current populations as promising regions for population recovery.

Fourth, to assess general connectivity among habitat patches, we also mapped least-cost corridors between all patches (McRae & Kavanagh 2011). We calculated least-cost paths between closest neighbouring patches in the Linkage Mapper Toolkit and defined corridors as those areas around the least-cost paths with a cumulative resistance below 200-km cost-weighted distance (McRae & Kavanagh 2011). Finally, to assess the permeability of the wider landscape towards leopard movement, we used Circuitscape in the programming language Julia and mapped current flow between 40 nodes randomly placed in a buffer around our study area (buffer width: 25% of the study area extent = 560 km in north-south and 1,250 km in east-west direction; Koen et al. 2010, Hall et al. 2021). Circuitscape models permeability between nodes as electric flows of current density (McRae et al. 2013). We also tested placing 50 nodes and found no substantial differences in the results. Placing the nodes randomly around our study area is a way to acknowledge that animals often have no predefined direction during dispersal and to attain a more general estimate of landscape permeability, compared to our corridor mapping (Koen et al. 2010, Pitman et al. 2017).

Results

Potential Persian leopard habitat

The three different species distribution modelling algorithms we used to map potential habitat across the Persian leopard range (i.e., BRT, GLM, and Maxent) performed similarly well, as evidenced by their high AUC and CBI values (all AUC > 0.88, all CBI > 0.92). Habitat suitability predictions did not differ substantially across algorithms (Pearson correlation coefficient r>0.7). Across all algorithms, ruggedness (TRI) was the most important predictor variable, followed by the proportion of tree cover and road density, as shown by high relative importance and percent contribution. In general, habitat suitability was highest at intermediate levels of ruggedness and increased with increasing tree and shrub cover and decreasing road density and cropland proportion (see SOM Table T1 for variable response types). Using an ensemble prediction across the three algorithms, we identified widespread areas of suitable habitat, most of which were located in the mountainous areas across our study region (in total 1,289,591 km²; Fig. 1).

Persian leopard core habitat patches and distribution

Based on our ensemble habitat map, we identified 174 core habitat patches with highly suitable habitat (i.e., areas with habitat suitability higher than at the 25th percentile of our presence locations) and a contiguous area of at least 250 km² (Fig. 1). Together, these patches covered about 528,000 km² (mean patch size = 3,035 km², median = 602 km², SD = 10.360 km²). The largest cumulative area of core patches was found in Iran (204,005 km²; 38%), followed by Turkey (100,651 km²; 19%) and Pakistan (51,868 km²; 10%; Table 1). In total, only 11% of the core patch area is currently under protection (3% under IUCN categories I and II), with substantial variation among range countries (Table 1). Among the five countries with the most habitat predicted, Russia had the highest proportion protected (36%) and Afghanistan the lowest (2%; Table 1). We then identified five regions with clusters of core habitat patches as candidate regions for hosting viable leopard metapopulations: (1) the Caucasus (Armenia, Azerbaijan, Georgia, Iran, Russia, Turkey), (2) the Alborz-Kopetdag Mountains (Iran, Turkmenistan), (3) the Taurus Mountains (Turkey), (4) the Zagros Mountains (Iran, Iraq, Turkey), and (5) the Hindu Kush-Western Himalayas (Afghanistan, Pakistan; Fig. 1).

We then compared our core habitat patches to an updated version of the historical and current leopard distribution developed in this study (Fig. 2). In total, our updated historical Persian leopard range covered an area of 3,314,667 km². In the west, it ranged from north-western Anatolia along the coast of the Aegean Sea to the southern coast of Anatolia and along the Mediterranean Sea and the Taurus Mountains to eastern Anatolia, Iran, Iraq, and to north-western Syria. From there, the distribution extended along the mountain ranges parallel to the Mediterranean coast of Syria and Lebanon to northern Israel, border-ing the Arabian leopard range (Jacobson et al. 2016). From there, the historical distribution extended north of the Tigris River across the northern and eastern parts of Iraq, but in contrast to Jacobson et al. (2016), we found no evidence of a former permanent leopard occurrence in the historical region of Mesopotamia within the Tigris-Euphrates River system. In the south, the range was limited by the coasts of the Persian Gulf, the Gulf of Oman, and the Arabian Sea. Leopards occurred throughout most of Iran (except for central and eastern desert regions, such as the Dasht-e-Kavir and Dasht-e-Lut; Fig. 2) and across large parts of Afghanistan. In the east, the range extended to the Indus River in Pakistan, bordering that of the Indian leopard (Jacobson et al. 2016). In the northern border region of Pakistan and India, east of the Indus, there is a contact zone where both subspecies, *P. p. tulliana* and *P. p. fusca*, have been genetically identified (Asad et al. 2019). The northern limit of the range included south-ern Turkmenistan and the southern parts of Uzbekistan and Tajikistan, and then the whole Greater and Lesser Caucasus. We found only 27% of the historical distribution to be still occupied (i.e., "extant" or "possibly extant" in our map). Most of our core patches were located within the historical range (151 patches/93% of the total patch area). Exceptions were the core patches in northern Turkey and in Kazakhstan, north-western Tajikistan, Uzbekistan, and Jordan (Fig. 3).

Overlaying our updated extant leopard distribution with the core habitat patches, we found that of all 174 core patches, 53 were currently likely occupied (i.e., overlapped with our extant distribution). Additionally, we ranked all potentially unoccupied core

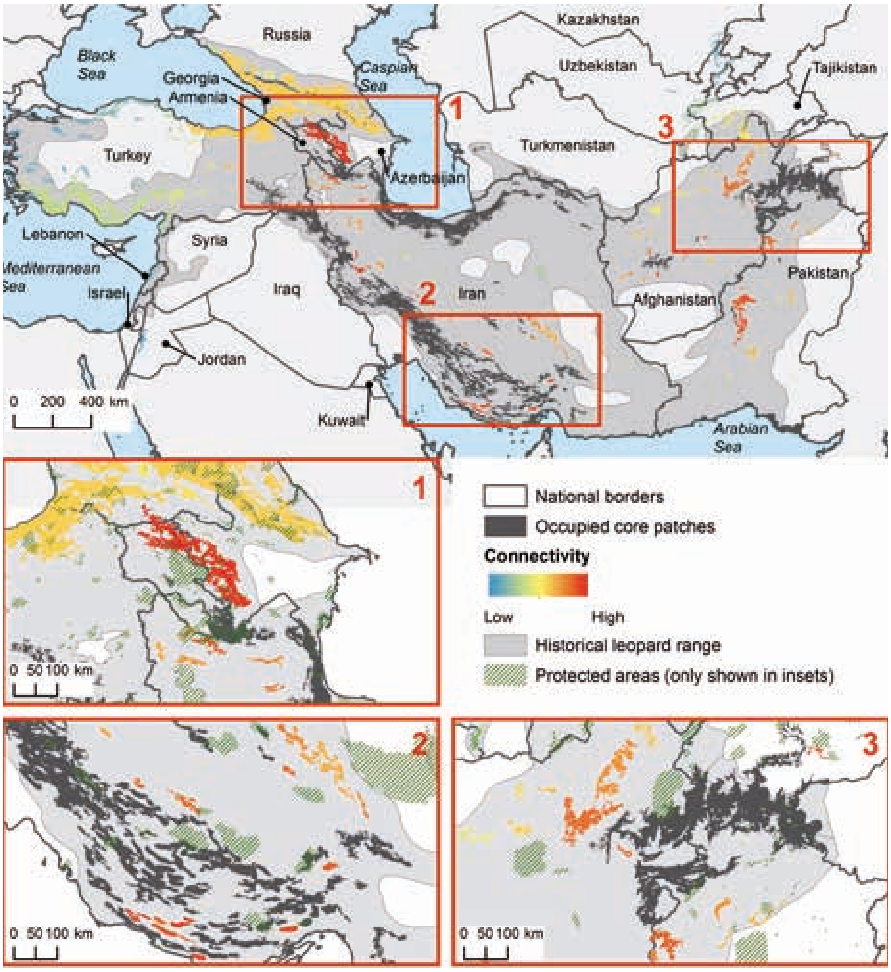

Fig. 3. Connectivity of each unoccupied patch (i.e., patches not overlapping with our extant distribution; coloured patches in the map) to its closest occupied patch (i.e., patches that overlap with our extant distribution; dark grey patches in the map). The three inset maps show the most promising regions for population recovery (clusters of unoccupied patches with high connectivity to current populations): (1) the southern Caucasus, (2) the southern Zagros Mountains, and (3) the Hindu Kush-Spin Ghar.

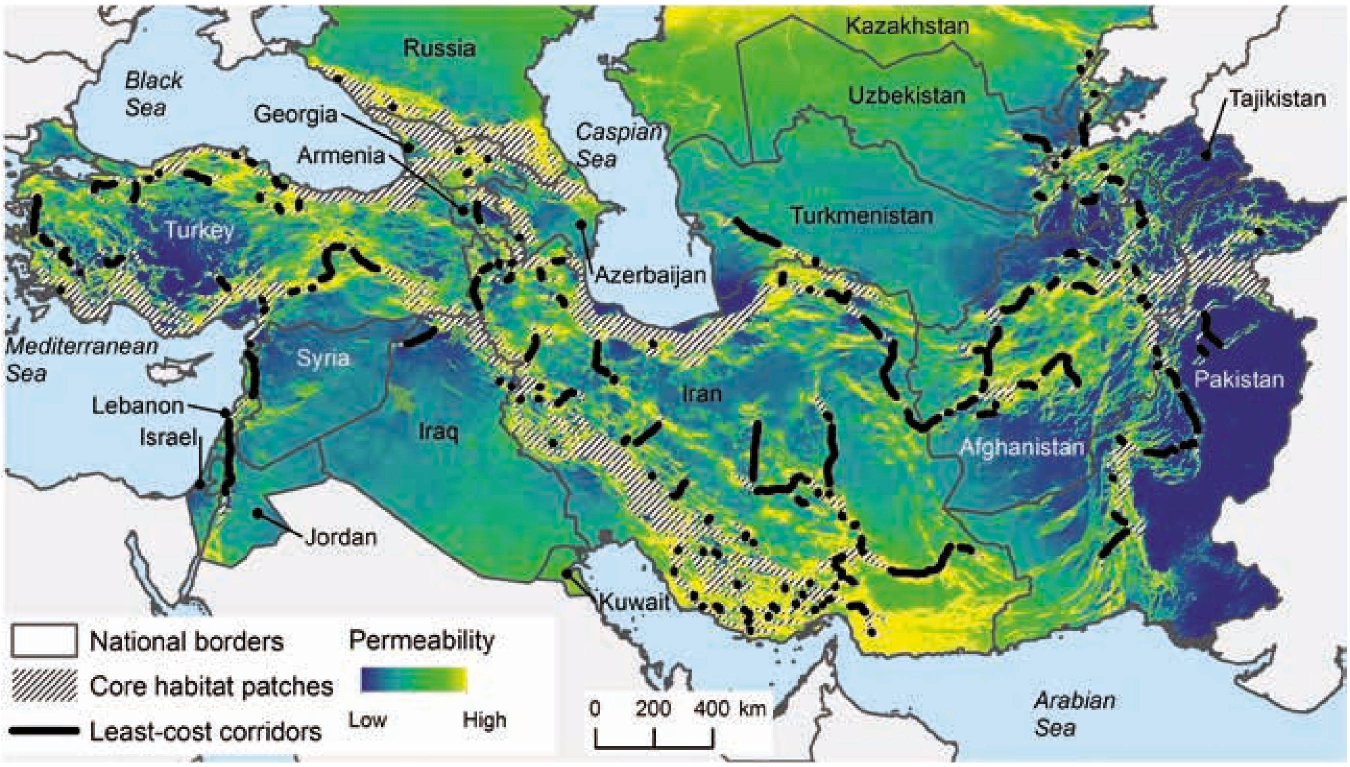

Fig. 4. Location of the least-cost corridors from each core habitat patch to its closest neighbouring patch and to the closest neighbouring disjunct group of patches and the general permeability of the landscape towards leopard movement.

habitat patches according to their connectivity to the closest occupied habitat patch. Thereby, we identified three regions as most promising areas for population recovery: (1) the southern Caucasus, (2) the southern Zagros Mountains, and (3) the Hindu Kush-Spin Ghar (Fig. 3).

Finally, we assessed the general landscape connectivity of our study area and the connectivity among core habitat patches. To do so, we first identified corridors among core habitat patches (Fig. 4). These corridors were on average 31 km long (range: 1–235 km, median: 12 km, SD: 43 km). From all 173 corridors, 7 corridors crossed international borders and 24 corridors passed through protected areas. In total, the corridors covered an area of 120,785 km², of which 6% is currently protected. The majority of the total corridor area (69%) was located in potential leopard habitat. The average cost of movement for leopards along the least-cost path between core habitat patches was 43 (range: 27–87, median: 43, SD: 9; lowest/highest possible cost: 1/100). The general permeability of the landscape towards leopard movement was moderate according to our analyses (mean current flow = 0.42; Fig. 4). Permeability was lowest in central Turkey and the eastern parts of the study area (i.e., southern Afghanistan, eastern Pakistan, and Tajikistan).

Discussion

Persian leopards today only occur in a fraction of their historical range (Jacobson et al. 2016). Restoring their populations and managing towards viable metapopulations requires the identification of clusters of suitable habitat patches and corridors among them. Here, we used a large dataset of presence records from 11 range countries to map potential Persian leopard habitat across its range. We identified widespread habitat, much of which is currently unlikely to be occupied (~70%). Our results suggest a large potential for restoring current populations and fostering recolonisations of formerly occupied habitat, and we highlight areas where conservation efforts could most effectively foster the establishment of viable metapopulations and population expansions.

Overall, our habitat model predictions were in line with regional studies that mapped suitable habitat across parts of our study area (Zimmermann et al. 2007, Gavashelishvili & Lukarevskiy 2008, Farhadinia et al. 2015, Ahmadi et al. 2020, Rozhnov et al. 2020b, Bleyhl et al. 2021). Mostly, suitable habitat was distributed across mountainous areas. This is likely due to the fact that leopards rely on either topographic heterogeneity or woody vegetation to ambush prey and find enough refuges, and because mountain areas are often less intensively used by humans (Lukarevsky et al. 2007b, Farhadinia et al. 2020).

Based on our habitat map, we identified 174 core habitat patches with at least 250 km² of highly suitable habitat. Most suitable core habitat was found in Iran, underlining the importance of the country for the survival of the Persian leopard as a whole (Jacobson et al. 2016). Particularly the Talysh-Alborz-Kopetdag Mountains and the Zagros Mountains stood out as regions with relatively large contiguous habitat, found also in other regional studies (e.g., Ahmadi et al. 2020). Nevertheless, our presence locations were biased towards records from Iran (78% of our presence locations used for the models were from Iran) and we cannot rule out that we underestimated habitat suitability in other areas (e.g., in Afghanistan and Turkmenistan). With more data becoming available, our habitat model should be updated to make sure to highlight all areas potentially suitable for Persian leopards across their range. Additionally, we did not take prey availability into account, because of a lack of consistent data across the whole study area. Prey availability is a key factor for large carnivore survival, and therefore should be integrated in any follow-up regional studies wherever possible, for example by using atlas data (Wolf & Ripple 2016, Khosravi et al. 2021). Finally, with continuous monitoring data becoming available, methods that account for imperfect detection and survey effort such as occupancy models can substantially improve predictions of which areas are likely to be occupied (Guillera-Arroita 2017, Ghoddousi et al. 2022b).

We identified five main clusters with large contiguous patches of suitable habitat: the Caucasus, the Alborz-Kopetdag Mountains, the Taurus Mountains, the Zagros Mountains, and the Hindu Kush-Western Himalayas. In the Caucasus, there is currently only a small number of leopard individuals present, mostly in the south towards Iran (Askerov et al. 2015, 2019). Yet, the Persian leopard population might naturally expand towards north, as shown by records from the Karabakh Upland, northern Armenia, and Georgia, likely a result of extensive conservation efforts in the last two decades (Askerov et al. 2015, Breitenmoser et al. 2017). Additionally, there are sporadic sightings of leopards in the Greater Caucasus (Yarovenko & Zazanashvili 2016), and the ongoing reintroduction programme in Russia could complement a possible range expansion (Rozhnov et al. 2020a, 2022). Nevertheless, the establishment of a viable metapopulation in the Caucasus likely depends on substantial conservation actions, particularly to mitigate human-leopard conflict, reduce leopard persecution, increase prey availability, and establish connectivity towards Iran and among core habitat patches, including to the Greater Caucasus (Moqanaki et al. 2013, Farhadinia et al. 2015, Babrgir et al. 2017, Maharramova et al. 2018, Rozhnov et al. 2020a, Bleyhl et al. 2021). The second cluster of core habitat patches we found is in the Alborz-Kopetdag Mountains in northern Iran and Turkmenistan. This area is a stronghold for leopards, given the high densities of leopards within the national parks (Hamidi et al. 2014, Farhadinia et al. 2019). However, recent surveys indicate that increased poaching in response to livestock depredation might have severely decimated local populations, particularly in the Alborz region (Kaczensky et al. 2019, Soofi et al. 2019, 2022, Farhadinia et al. 2022a). Nevertheless, the availability of prey, high landscape connectivity and the existence of a protected area network make this cluster likely the most important region for the survival of the Persian leopard, possibly hosting the largest population within the entire range (Kiabi et al. 2002, Hamidi et al. 2014, Ghoddousi et al. 2016, Farhadinia et al. 2019). Further west, the Taurus Mountains in south-western Turkey were highlighted as a cluster of suitable habitat patches. Information on the status of leopards in this area are very limited. At the time of writing, no breeding leopards were reported from the Taurus Mountains (Karataş et al. 2021). Additionally, the Taurus Mountains are relatively isolated from larger current source populations (Fig. 1), suggesting that active translocations could be needed to establish a viable metapopulation there. A fourth cluster of larger patches with suitable habitat was located along the Zagros Mountains, underlining the general suitability of that area for leopards (Kaboodvandpour et al. 2021). Several protected areas in Iran's Zagros Mountains (e.g., Bamu National Park, Dena National Park) are known to host small but stable leopard populations (Ghoddousi et al. 2010, 2022a). Additionally, recent records from the border region between Iran, Iraq, and Turkey indicate that this region might still host a small leopard population but conservation measures need to be ramped up to establish a larger viable metapopulation (Avgan et al. 2016, Karataş 2021). Finally, a large contiguous region with core habitat patches was found in the Hindu Kush and western Himalayas. This region had larger patches towards eastern Afghanistan and northern Pakistan and is relatively isolated from the remaining Persian leopard populations (Hosseini et al. 2019), yet connecting to the east with the Indian leopard in the northern Indus area of Pakistan (Asad et al. 2019). Additionally, in this area, leopards suffer from a loss of habitat and wild prey, leading to an increase in human-leopard conflict over livestock depredation, while armed conflicts often hinder the enforcement of conservation regulations (Shehzad et al. 2015, Kabir et al. 2017, Ostrowski et al. 2022).

Almost 70% of our core habitat was identified as currently not occupied in our analyses (or, given that parts of our study area are not frequently surveyed, not known to be occupied). Additionally, Persian leopards likely lost 73% of their historical range according to our updated distribution maps (in line with Jacobson et al. (2016), who estimated 72–84% range loss). This suggests that Persian leopards are under considerable pressure across their range, which likely prevents a natural recolonisation of these historically occupied patches and the establishment of metapopulations. One of the main reasons for suitable but unoccupied habitat is persecution, particularly in retaliation or fear of leopards killing livestock (Bleyhl et al. 2021, Soofi et al. 2022). Such killings can have devastating effects on small leopard populations and are often hindering population recoveries (Ghoddousi et al. 2020, Soofi et al. 2022). In addition to direct persecution, insufficient prey in otherwise suitable habitat can prevent the colonization of habitat patches, which in turn is often a result of poaching on prey (Ghoddousi et al. 2017). Indeed, only 11% of the core habitat patch area is currently protected, which might make conservation measures to reduce anthropogenic pressure on leopards and their prey challenging. Yet, given the large home range sizes and territories of Persian leopards (Farhadinia et al. 2018), a key aspect of their conservation is likely to foster coexistence with people and restore prey species particularly also outside protected areas (Ghoddousi et al. 2020). Additionally, we likely missed protected area coverage in some areas, relying mostly on the global standardised WDPA data (You et al. 2018). Finally, limited connectivity to current populations can prevent dispersal to unoccupied habitat patches. Because the underlying constraints for re-occupation of suitable habitat likely differ across areas, local studies are needed to identify the most effective conservation measures at place to facilitate range expansion.

Based on the connectivity of unoccupied to currently occupied core habitat patches, we identified three priority regions for population recovery in the near future: the southern Caucasus, the southern Zagros mountains, and the Hindu Kush-Spin Ghar (Fig. 3). While the southern Caucasus is currently likely experiencing a recovery of its leopard population (Askerov et al. 2019, Khorozyan et al. 2022), the situation is unclear for the southern Zagros Mountains and the Hindu Kush-Spin Ghar. In the southern Zagros, natural fragmentation, the low elevation of the mountains, and the low prey availability create more vulnerable conditions for the Persian leopard. Nevertheless, sporadic leopard sightings show the potential of the area for recovery, once conservation interventions are in place (Ghoddousi et al. 2022). In the Hindu Kush-Spin Ghar area, insecurity and resulting limited scientific investigations are current constraints for a better picture of the status of the Persian leopard populations and the potential for recovery. Despite severe habitat fragmentation due to fast increasing human populations, the potential for recovery in this area exists but would require, perhaps here more than elsewhere, genuine enforcement of existing regulations, engagement with communities, and a continued political commitment at all levels (Ostrowski et al. 2022).

Our connectivity analysis further revealed the best areas for corridors among core leopard patches (Fig. 4). The distribution of these corridors was in general in line with other regional connectivity studies (Farhadinia et al. 2015, Bleyhl et al. 2017, Hosseini et al. 2019). Most corridors were relatively short, meaning that most core patches were located in close distance (Euclidean as well as cost-distance) to other core patches. Persian leopards can disperse across large distances (> 80 km), often undetected, which indicates their potential to recolonise suitable habitat, given that persecution is prevented and prey species are available (Farhadinia et al. 2018, Maharramova et al. 2018, Askerov et al. 2019). Yet, several corridors crossed international borders (e.g., between Iran and Iraq, and Iran and Afghanistan), highlighting the importance of transboundary conservation for wide-ranging species, where border walls or fences might be impenetrable barriers (Linnell et al. 2016, Farhadinia et al. 2021, 2022b).

Using a large training dataset, we highlighted that potential habitat for Persian leopards is still widespread across the subspecies' former range. Much of this habitat is currently unoccupied, indicating high pressure on current leopard populations that prevents a substantial range expansion. Our modelling results indicate areas where populations could most easily recover, but conservation measures are needed, particularly to mitigate human-leopard conflict, restore prey populations, and foster connectivity (Farhadinia et al. 2015, Ghoddousi et al. 2020, Bleyhl et al. 2021). Protected areas can play an important role to implement such measures (currently, only 11% of all core habitat and 6% of all corridor areas are protected), but need to be accompanied by measures targeted at multiple-use landscapes, particularly in terms of conflict mitigation, prey recovery, and connectivity restoration (Babrgir et al. 2017, Ghoddousi et al. 2020). Effects of climate change can pose an additional threat on possible population recoveries, particularly because a large part of the range is vulnerable to drought, which could make vast areas climatically unsuitable and further intensify depredation on livestock due to prey decline (Khorozyan et al. 2015, Ashrafzadeh et al. 2019). Effects of climate change can additionally lead to substantial structural changes in habitat suitability and the corridors we mapped here, and therefore local assessments are needed to complement our range-wide assessment with fine-scale climate change predictions. More broadly, our study highlights the potential for viable Persian leopard metapopulations across their historical range, but only if conservation measures were implemented and coordinated among range countries. Transboundary efforts such as the Bern Convention, the Ecoregional Conservation Plan for the Caucasus (Zazanashvili et al. 2020), and the Central Asian Mammals Initiative CAMI under the Convention on the Conservation of Migratory Species of Wild Animals CMS are important steps towards coordinating range countries in their conservation efforts (Farhadinia et al., 2022b) and ultimately managing towards the recovery of Persian leopards across their historical range.

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Supporting Online Material Table T1 is available at www.catsg.org.

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