Animal Conservation



Identifying human-brown bear conflict hotspots for prioritizing critical habitat and corridor conservation in southwestern Iran

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Abstract

Multiple studies have used species distribution models to identify human-wildlife conflict drivers. An important application of these models is spatial conflict resolution by accounting for habitat suitability and corridors. We used distribution and connectivity models to identify habitats and corridors for brown bear Ursus arctos in southwestern Iran with high risk of bear damages, and evaluated the effects of landscape composition and configuration on the predicted conflict hotspots. We used 154 locations of bear damage incidents along with a suit of predictors to develop risk models. To prepare predictive variables, we used brown bear occurrence data and a number of covariates to develop a suitability model. We then converted the suitability map into a resistance surface and used a connectivity model to predict corridors. Finally, the bear damages risk map, habitats and corridors were overlaid to prioritize conflict hotspots, corridors and habitats, and conflict-prone corridors. Proportion of suitable habitats, distance to village, density of forest patches, conservation areas and corridor bottlenecks were the main predictors contributing to bear damages risk. A total of 38.73% of habitats, and 6.24% of corridors across the 124 000-km² study area were identified as areas with high risk of bear damages. The risk of bear damage was also spatially associated with forests fragmentation and patchiness of habitat. Our results highlight the importance of landscape configuration and corridors when investigating the spatial patterns of bear damages. Our findings showed how the combination of distribution models and connectivity analysis can guide carnivore conservation planning aiming at reducing the risk of carnivore-inflicted damages.

Introduction

Habitat fragmentation due to rapid growth of human population and anthropogenic disturbances affects species by limiting their movement (Cushman, 2006). It also brings them closer to human settlements and increases the likelihood of human-wildlife conflict. The most common types of damages inflicted by wildlife include attacks on human, livestock depredations and damage to beehives and crops (Dickman, 2010). Animals involved in these damages are often deemed undesirable and eradicated by local communities.

Large carnivores are especially vulnerable to increasing human presence, especially at the edge of conservation areas (Pettigrew *et al.*, 2012; Rostro-García *et al.*, 2016; Broekhuis, Cushman, & Elliot, 2017). Due to large spatial requirements, these carnivores typically do not persist within isolated protected areas alone but rely heavily on suitable habitats outside of these regions and linkages between them (Ripple *et al.*, 2014; Cushman *et al.*, 2018). Where the network of conservation areas intermixes with human dominated landscapes, conflicts are more likely to intensify as the risk of carnivore damages increases due to increasing presence of humans and their properties, land use conversion and natural prey depletion (Pettigrew *et al.*, 2012; Morales-González *et al.*, 2020).

Although conservation efforts in some regions have been successful in increasing the distribution and population size of threatened carnivores (e.g. Chapron *et al.*, 2014), the expansion of these species into multi-use landscapes or reoccupation of habitats can increase the likelihood of carnivores damages and create a conflict between carnivores recovery efforts and human–wildlife conflicts (Hobbs *et al.*, 2012). This may inhibit conservation efforts, leading to reductions of carnivore populations and shrinkage of their

ranges, which often results in fragmentation into smaller isolated populations (Ripple *et al.*, 2015). Therefore, understanding factors that trigger human–carnivore conflicts and the trade-offs between species conservation and conflict management is a prerequisite step to delineate management strategies for human–carnivores coexistence in multi-use landscapes (Treves *et al.*, 2006).

The brown bear Ursus arctos can be considered as an umbrella species for conservation because of its large area requirement, charismatic appearance, umbrella capacity and low population density (Simberloff, 1999; Roberge & Angelstam, 2004). Human settlements, availability of anthropogenic resources, roads and recreational and industrial activities are the main threats to brown bears in humanmodified landscapes at the global scale, which may lead to human-bear conflicts, changes in behavioral and physiological patterns and reduced genetic variation (Morales-González et al., 2020). In the Middle East, the range of the species has contracted considerably, and now occupies only a small fraction of its historical range (Calvignac, Hughes, & Hänni, 2009; Ashrafzadeh et al., 2018; Burton et al., 2018; Moganaki et al., 2018). The species is at risk of local extinction in Iran, particularly in the Zagros Mountains, due to intensive habitat destruction and fragmentation, direct persecution and conflict with pastoralists and farmers (Ansari & Ghoddousi, 2018; Ashrafzadeh et al., 2018; Mohammadi et al., 2021). The southwestern parts of Iran are the southernmost distribution range of the brown bear globally (McLellan et al., 2017). Although a microsatellite-based genetic study did not detect genetic differentiation among brown bears in this area, mtDNA findings confirmed that brown bears in southwestern Iran form a genetically distinct sub-clade that is unique from brown bears in other parts of the country (Ashrafzadeh, Kaboli, & Naghavi, 2016; Ashrafzadeh et al., 2018).

Among wildlife species, brown bear damages to croplands and orchards in southwestern Iran is one of the causes of wildlife conflict with human activities (Unpublished data). This may promote illegal behavior of retaliatory killing of the species. Hence, human-bear conflict mitigation in this area is a high management priority to create a balance between bears' requirements and human livelihood.

Despite the fact that human-wildlife conflict is one of the most serious threats to carnivores (Ripple et al., 2014), the underlying factors attributed to these conflicts are often unknown. Although multiple studies have used distribution models to map predation risk by wildlife species (e.g. Miller, 2015; Rostro-García et al., 2016; Broekhuis et al., 2017), one important but fairly neglected application of these models is to evaluate conflict risks associated with migration corridors. While corridors facilitate individual movements and thus can help maintain connectivity between habitats, these linkages may increase the potential for conflict with human and human-induced mortality risk (Cushman, Compton, & McGarigal, 2010; Cushman et al., 2018). In addition, existing networks of conservation areas are fairly ineffective in protecting corridors of large carnivores due to their isolation, small size and also presence of anthropogenic and natural barriers (Macdonald *et al.*, 2019; Ashrafzadeh *et al.*, 2020). Therefore, conservation planning should consider the conflict risks both in conflict hotspots and corridors to support species persistence in human-dominated landscapes. Identifying the spatial relationship between migration corridors and human–wildlife conflict provides critical information for improving functional connectivity and for prioritizing areas and resources for conflict mitigation efforts (Cushman *et al.*, 2018).

Effects of landscape features, composition and configuration on conflict risks between human and carnivores are generally understudied (see Rostro-García *et al.*, 2016; Broekhuis *et al.*, 2017). Brown bears are more likely to cause damage to beehives, crops and livestock on landscapes characterized by a complex mosaic of forest habitat patches (Miller *et al.*, 2015). Conflict mitigation efforts, therefore, should consider the effects of forest composition and configuration on the intersection between carnivore activity patterns and human activities and resources (Sharma *et al.*, 2020).

In this study, we used correlative distribution models and habitat connectivity analysis to: (1) investigate spatial patterns of brown bear damage risk in southwestern Iran; (2) identify environmental and anthropogenic factors that may intensify the risk of bear damages, (3) identify spatial hotspots of brown bear damages where mitigation and prevention strategies should be adopted; and (4) assess the effects of landscape composition and configuration on bear damage risk.

Materials and methods

Study area

Our study area covers Fars Province in southwestern Iran, one of the brown bear's globally southernmost ranges (IUCN, 2006; Ansari & Ghoddousi, 2018), with an extent of 124 000 km² (27°-31° N to 50°-55° E; Fig. 1). The study area is characterized by semi-arid climate conditions and is dominated by rangelands, forests and croplands, which collectively account for 90% of the study area. The Zagros Mountains, stretching from the north-west to the south-west across the study area provide extensive deciduous forest habitats favored by the species. The wide range of elevation (80-3900 m) provides diverse habitats to support many native fauna and flora (Fars Provincial Office of Department of Environment [FDoE], 2020). A number of conservation areas with a total extent of 24 650 km² and in four main types including national parks (NPs; IUCN category II), wildlife refuges (WRs; IUCN category IV), protected areas (PAs; IUCN category V) and no-hunting areas (NHAs; no IUCN category) have been established to conserve and protect natural habitats and biodiversity. In addition to the brown bear, many species that are of conservation importance occur in the Zagros Mountains, including Persian leopard Panthera pardus, caracal Caracal caracal, gray wolf Canis lupus, mouflon Ovis gmelini, goitered gazelle Gazella subgutturosa and wild goat Capra aegagrus. The isolation and small size of conservation areas, as well as presence of

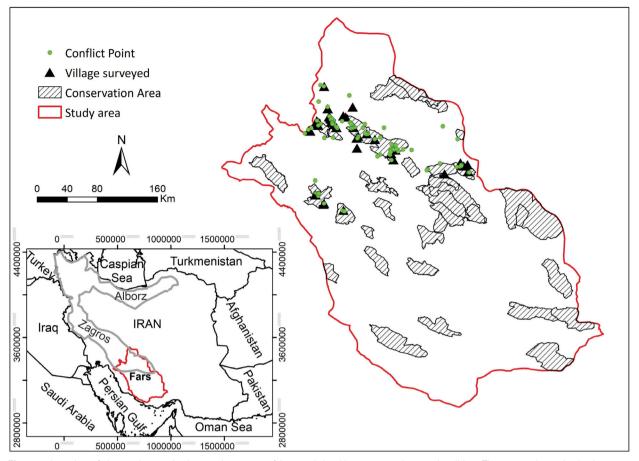


Figure 1 Location of the study area in the southwestern of Iran and the Ursus arctos damage localities. The gray polygon in the inset map indicates Alborz and Zagros Mountains.

anthropogenic (human land use) and natural (landscape heterogeneity) barriers between them, result in a system where carnivore populations extend beyond boundaries of conservation areas. Therefore, this protected network is insufficient to protect key habitats or corridors (Mohammadi *et al.*, 2021). Consequently, the intersection of key habitats and corridors with human activities may increase the likelihood of bear damages.

Ethical statement

Ethical approval and permission to conduct the questionnaire survey were provided by the FDoE (permit No: 15398-212495). We also received verbal consent from all individuals and assured them about the confidentiality and anonymity of their data.

Analytical framework

We carried out an analytical framework to predict the spatial patterns of bear damages risk (Fig. 2). The steps undertaken in the study are explained in detail below.

Brown bear conflict data

We compiled data on human-bear conflict (crop and beehive damage, domestic sheep and goat depredation and attacks on human) across the entire of the study area (Fig. 1) from two main sources:

First, from 2019 to 2020, we conducted surveys by making field visits and interviewing farmers, gardeners and beekeepers during the peak season of bear damages (i.e. June to October). We used semi-structured questionnaires to collect information from reported conflict incidents. The protocol was as follows: after each damage claim was filed by FDoE, our research team was notified by FDoE and visited the reported location and verified the claim by examining for signs of physical damages. Since most of the reported claims were related to crops raiding, we were able to assess the accuracy of the claims with confidence. Next, we conducted interviews only with individuals whose damage claim had been verified by our team. To initiate the interview, we first asked if the respondent was knowledgeable about the existence of bears. In these interviews, information was asked about the type of damage, time of occurrence of damage and

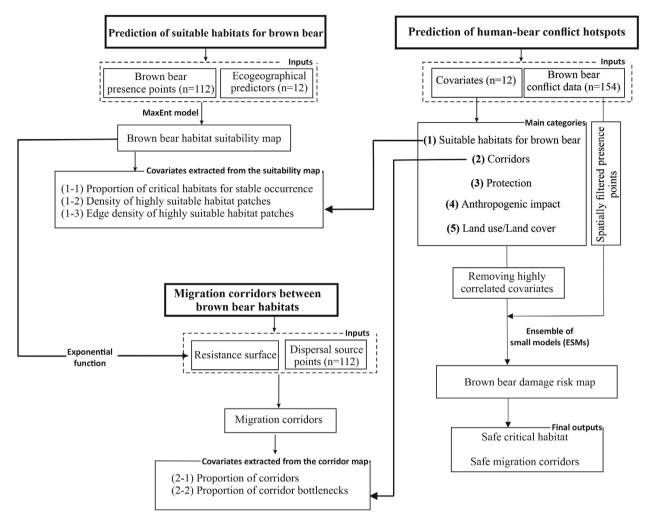


Figure 2 The analytical framework to predict Ursus arctos damage risk.

number of losses (in case of damage to livestock). In total, we conducted 90 interviews in 37 villages (the range of nearest neighborhood distances = 0.73-30.08 km, mean nearest neighborhood distance = 6.88 km; Fig. 1). Spatial coordinates where conflict occurred were recorded with handheld GPS Garmin 62 s.

Second, a database (N = 64) on the damage locations was provided by FDoE from 2011 to 2020, which is the responsible agency for conflict reports in the Fars Province. The reliability of these damage claims was verified by FDoE guards. Further, we mapped them in Google Earth version 7.1 to check for the accuracy of the coordinates. This database contains the coordinates of locations, dates and types of damages. We only used those reports that have information on spatial coordinates and the type of damage.

In summary, all damage data used in our study were verified data. We collected a total of 154 verified locations of bear damages (128 localities for crop damages, 5 for livestock depredation, 1 for attack on human and 20 for beehives damages; Fig. 1). Since factors influencing different types of bear damages (i.e. crop and beehive damage, livestock depredation and attacks on human) may be similar at broad spatial scales, we combined all data into a single response variable in the risk model.

We calculated global Moran's I for each covariate separately in R package raster (Hijmans, 2021) to assess the spatial pattern of the bear damage points and address the effects of spatial autocorrelation in localities due to uneven sampling efforts (Supporting Information Table S1). To avoid bias in prediction models due to unequal sampling effort, damage localities were spatially filtered to a minimum of 5-km distance from each other (Boria *et al.*, 2014) according to the bear movement (Falcucci *et al.*, 2009) using the SDM toolbox (Brown, 2014) in ArcGIS 10.6 (ESRI, Inc., Redlands, CA, USA).

Predictor variables

Considering previous studies on the conflict risk modeling of large carnivores (e.g. Dai *et al.*, 2019; Sharma *et al.*, 2020;

van Bommel et al., 2020; Zarzo-Arias et al., 2021), geographic and environmental characteristics, and bear ecology, we selected 15 predictors in six main categories, including brown bear suitable habitats, connectivity between highly suitable habitats, protection, anthropogenic impact, topography and land use/land cover (Supporting Information Table S2). All variables were resampled to a 50×50 m spatial resolution. We conducted bear damages risk modeling with a 78.5 km² circular moving-window (radius of 5 km) around each cell, hereafter focal cell. We chose this focal cell size based on the recommendation of Beier (2019), who recommended using a corridor width of >2 km when connecting habitat patches >80 km apart. Moreover, this focal size corresponds to the minimum habitat patch size required for the stable presence of at least one adult female bear (Maiorano et al., 2019), or equivalent to the minimum home range requirement of a brown bear.

Habitat suitability for brown bears

To predict habitat suitability for brown bears, we ran Max-Ent model (Phillips, Anderson, & Schapire, 2006) in the 'dismo' R package (Hijmans *et al.*, 2017) with 113 opportunistically collected occurrence points (bear signs and direct observations) collected during 2015–2019 by FDoE. We used a spatially filtration framework to reduce spatial autocorrelation in presence points (Falcucci *et al.*, 2009). Finally, the remaining presence points (N = 112) were used to calibrate and evaluate the MaxEnt model. To calibrate the MaxEnt model, we selected 12 covariates based on literature review (Ansari & Ghoddousi, 2018; Farashi, 2018; Almasieh, Rouhi, & Kaboodvandpour, 2019; Maiorano *et al.*, 2019). All covariates were calculated in a 50 × 50-m cell size (Supporting Information Table S3).

Covariates used for habitat suitability modeling (Supporting Information Table S3) and risk mapping (Supporting Information Table S2) were different to avoid model overfitting. To provide a better approximation of the bear's perception of the environment, we prepared the raster layers by applying a 450-m radius moving window. This moving window size was suggested by Falcucci et al. (2009), who determined this to be the representative scale at which bears view their immediate surrounding area as calculated by movement data of eight GPS radio-collared bears (Falcucci et al., 2009; Maiorano et al., 2019). For categorical variables, we calculated the proportion of each class within the mentioned moving window using FRAGSTATS (McGarigal, Cushman, & Ene, 2012). For continuous variables, we calculated the mean value of each variable assigned inside a given radius for the central pixel in ArcGIS 10.4.1. (ESRI, Inc.).

We ran MaxEnt using a 10-fold cross-validation. We kept other default parameters of the MaxEnt. The overall model's performance was evaluated by calculating the area under the receiver operating characteristic curve (AUC). This model produced a predicted map that shows two categories of brown bear habitats, as defined below, including highly suitable habitats, and critical habitat for stable occurrence. Specifically, we applied the 10th percentile training presence threshold to define highly suitable habitats (Hemami *et al.*, 2020; Khosravi *et al.*, 2021). Critical habitat for stable occurrence was defined as contiguous highly suitable habitats with an extent of more than 70 km² (Maiorano *et al.*, 2019). The 70 km² threshold corresponds to the minimum spatial requirement for the stable occurrence of an adult female bear (Maiorano *et al.*, 2019).

To examine how the extent and configuration of brown bear habitats may be related to bear damages risk spatially, we calculated the percentage of study area covered by critical habitat for stable occurrence within each focal cell in FRAGSTATS (i.e. PLAND index; McGarigal *et al.*, 2012). We also hypothesized that landscape fragmentation and configuration would affect the risk of bear damages. To test this hypothesis, we calculated two class-level configuration metrics, including the number (NP) and edge density (ED) of highly suitable habitat patches within each focal cell. Edge density represents the amount of perimeter of highly suitable habitat patches and standardizes edge to a per unit area basis that facilitates comparisons among landscapes of varying size (McGarigal *et al.*, 2012).

Connectivity between habitats

We assessed connectivity between predicted highly suitable habitat patches to depict the effects of brown bear corridors on the risk of bear damages. To do so, we used factorial least-cost path modeling (Cushman, McKelvey, & Schwartz, 2009) in the universal corridor network simulator (UNICOR version 2.0; Landguth et al., 2012). The factorial least-cost path method predicts the strongest linkages among source locations by summing the least-cost paths between all possible pairs of source points and create a cumulative density of optimal paths across the full landscape in a synoptic framework (Cushman, Landguth, & Flather, 2013). To predict connectivity, UNICOR requires a resistance surface that estimates the movement cost at any given location across the study area and source locations as inputs. We created the resistance surface by transforming the predicted habitat suitability map, using an exponential decay function (Wan, Cushman, & Ganey, 2019):

$$x = 1000^{-1*y} \tag{1}$$

where, x is the cost resistance value assigned to each pixel and y shows the predicted habitat suitability value. We rescaled cost resistances to a range between 1 and 10 by linear interpolation. Also, we followed the method developed by Kaszta, Cushman, & Macdonald (2020) to define source locations in connectivity analysis. First, the predicted suitable habitat for brown bears was rescaled between 0 and 1. Then, a random raster layer was created in an extent same as suitable map and distributed values of pixels from 0 to 1 uniformly. The created random raster layer subtracted from the rescaled suitable map to determine pixels with positive values. Finally, 112 points from these pixels were randomly selected. The selected source locations were spatially rarefied (one centroid every 5×5 km) to simulate the presence of the species across the study area. These source locations were used as nodes for connectivity analysis in UNICOR. Based on the predicted connectivity map, we calculated the mean value of predicted cumulative paths within each focal cell. We then used the predicted map of cumulative density of optimal paths to identify corridor bottlenecks across the study area. A high density of optimal paths indicates a lack of alternative paths and therefore, potential bottlenecks within a corridor. We defined corridor bottlenecks as regions with an optimal path density higher than the mean plus two standard deviations (Bleyhl *et al.*, 2017). Finally, we calculated the proportion of corridor bottlenecks within each focal cell as another predictor variable for bear risk mapping.

Protection

We considered conservation areas as a proxy for the level of human disturbance (including risk of anthropogenic mortality) and habitat quality (Moqanaki & Cushman, 2017; Ahmadi *et al.*, 2020). As suggested by Rostro-García *et al.* (2016) and Broekhuis *et al.* (2017), the extent of conservation areas within each focal cell may be more important in conflict risk mapping than the distance of each pixel to the boundary of the closest conservation area due to edge effects (Woodroffe & Ginsberg, 1998). We used both variables (i.e. shortest distance from each pixel to the border of the nearest conservation area, and the proportion of conserved pixels within each focal cell) in our damage risk modeling.

Anthropogenic impact

To address impacts of human activities on bear damages risk, the network of roads was classified into two main groups including main roads (e.g. highways and urban streets) and smaller roads (e.g. trails and countryside roads). For the former class, we calculated the Euclidean distance from the nearest road. For the latter, road densities within each focal cell were generated using the Line Density tool in ArcGIS. In addition, distance to villages was calculated using the layer of geographic localities of villages across the study area (Supporting Information Table S2).

Land use/land cover

We extracted two land use/land cover classes including forests and croplands using the land use/land cover map from the Iranian Forests, Rangeland and Watershed Management Organization (IFRWMO). These classes can represent habitat productivity, human disturbance, and cover for brown bears, and consequently bear damage risk. We hypothesized that landscape fragmentation and configuration affect the risk of conflict (e.g. Rostro-García *et al.*, 2016; Broekhuis *et al.*, 2017). To test this hypothesis, we used FRAGSTATS to calculate the spatial pattern of these land use/land cover classes using class-level metrics including forest patch density, forest patch ED, cropland patch density, and cropland patch ED per focal cell. Bears are often associated with riparian ecosystems due to higher productivity of vegetative forage and higher density of mammal prey in these areas (Hopcraft, Sinclair, & Packer, 2005). Thus, we calculated river density within each focal cell using Kernel Density function in ArcGIS.

To reduce the collinearity among variables, we first adopted hierarchical ascendant classification based on Pearson correlation with R package *virtualspecies* (Leroy *et al.*, 2016) to identify groups of intercorrelated variables. Then, we calibrated the model using each group of intercorrelated variables and selected the variable with the highest percent contribution. Finally, we calibrated the final model using the uncorrelated variables with highest percent contribution (Louppe *et al.*, 2020). Following the reduction process, 12 predictors were retained in the final risk modeling process (Supporting Information Table S2; Figures S1 and S2).

Brown bear damage risk modeling

We used the Ensembles of Small Models (ESMs) approach for modeling the relationship between bear damage risk and the predictor variables (Lomba et al., 2010; Breiner et al., 2018). We accomplished this with R packages ecospat (Broennimann, Di Cola, & Guisan, 2015) and biomod (Thuiller et al., 2009). The ESMs approach is an effective technique to overcome limitations of modeling the habitat suitability for species with limited occurrence data and performs significantly better than standard species distribution models (Breiner et al., 2018). To predict the risk of bear damage risk, 66 small and simple MaxEnt models were calibrated and evaluated (models that contain only two predictors at a time; bivariate models; Supporting Information Table S4). All bivariate models were calibrated with 10 000 background points and 70% of bear damage localities as training (n = 108) and 30% as evaluation (n = 46) data. All background and brown bear damages occurrence localities were weighted equally in the bivariate models. We calculated AUC (DeLeo, 1993) and Boyce index (Hirzel et al., 2006) to evaluate the performance of each bivariate model. Models with a Somers' D (Somers, 1962) lower than 0 were not included in the ESMs. Then, the final map was calculated using the weighted average of all resulting Somers' D (i.e. rescaled AUC) values of the bivariate models.

Identification of brown bear damage risk hotspots, safe habitat patches and corridors

We classified the brown bear damages risk map produced from the model into three categories (i.e. low, medium and high potential for conflict) using Jenks natural breaks (Jenks, 1967). Jenks natural breaks is a data clustering method that uses natural groupings inherent in the data to classify values into different classes. This method seeks to reduce the variance within groups and maximize the variance between them. We classified cells into three categories (i.e. low; 0-0.105, medium; 0.105-0.368 and high; 0.368-0.962) by finding points where between-group variability was highest while within-group variability was minimized using ArcGIS 10.5. Bear conflict hotspots were considered as areas with high potential for damage risk. The zone with high risk was then analysed with respect to spatial patterns of conservation areas, critical habitats and corridors. Then, we classified 'safe corridors' and 'safe habitats' by identifying corridors and critical habitats that have low to medium potential for bear damages risk. Finally, we identified high-risk critical habitats and corridors which require urgent conservation mitigation efforts due to the absence of alternative dispersal paths (Ghoddousi *et al.*, 2020).

Results

Brown bear damage risk modeling

The predicted bear risk model (Fig. 3a) had high prediction accuracy with mean AUC and Boyce index being 0.943 and 0.942, respectively. This indicates that the selected covariates were relevant predictors and that ESMs can reliably predict the risk of bear damages in our study area. According to the estimates of relative contributions of the variables, predictors that contributed most to predicting bear damages risk were proportion of critical habitats for stable occurrence, distance to village, density of forest patches, distance to conservation areas, proportion of corridor bottlenecks and density of highly suitable habitat patches.

The potential for the risk of bear damages showed a nonlinear relationship with the proportion of critical habitats for stable occurrence (Supporting Information Figure S3). With increasing values this variable, the risk of brown bear damage increased to its maximum and then leveled off. Distance to villages and conservation areas were negatively related to brown bear damage risk (Supporting Information Figure S3). The model predicted that the potential for bear damages increases with increasing density of forest patches, proportion of corridor bottlenecks and density of highly suitable habitat patches (Supporting Information Figure S3). Both landscape configuration and composition showed strong relationships with brown bear damage risk. Patch density of forests and density of highly suitable habitat patches showed significant positive relationship with bear damages risk (Supporting Information Figure S3).

According to Jenks natural breaks classification, 3.75% (4655 km²) and 6.91% (8574 km²) of the study area were predicted to be highly and medium suitable for bear damage risk, respectively (Fig. 3b). Overall, most areas with high risk of bear damages were located in the northern, central and western parts of the Fars Province (Fig. 3). A total of 10.80% (2662 km²) of the existing network of conservation areas overlap with areas of high predicted risk of bear damages. Geographically, Kooh-Khersi, Tang-e-Bostanak, Margoon, Arzhan and Parishan and Male Galeh conservation areas have the highest predicted risk (Fig. 3b).

High-risk habitats and corridors

Brown bear habitats and corridors spatially overlapped with areas of high bear damages risk at levels of 38.73%

 (2622 km^2) and 6.24% (430 km^2) of total area, respectively (Fig. 4a). Our analysis classified 93.76% of corridor as safe corridors (i.e. low to medium risk), with the remaining classified as corridors of high bear damages risk (Fig. 4b). Critical habitats of high bear damages risk mostly located in northern and central parts of the study area (Fig. 4a).

Discussion

Human-wildlife conflicts are complex with many environmental and anthropogenic factors in play. We demonstrated a way to explore some of the spatial aspects of these complexities by analysing the spatial pattern of conflict hotspots while accounting for their proximity to critical habitats and corridors. Our analysis provides spatially explicit information on human-bear conflict and pinpoints habitat and corridors that are at greater relative risk of conflict. Such information can aid management in prioritizing areas and resources for conflict mitigation measures.

Understanding factors that influence brown bear damages risk

The positive effects of villages may be attributed to its positive association of available croplands and livestocks, which increases the risk of bear damages (e.g. Miller, 2015; Rostro-García et al., 2016). Another important predictor of brown bear damages risk was distance to conservation areas, suggesting that bears were more likely to have conflict with local people near conservation areas. This relationship may be explained by the higher density of brown bears in these areas due to higher levels of protection and greater edge effects due to irregular boundaries of these areas, both of which increase the encounter rates between bears and human (Rostro-García et al., 2016; Broekhuis et al., 2017). Although conservation areas offer some degree of refuge to bears, more frequent and prolonged drought in recent years across the study area have led to food and water shortages for bears, especially in summer, which encourage bears to forage near human settlements (e.g. Doan-Crider, Tri, & Hewitt, 2017). Bear damages to local properties was more likely to occur near forest patches (e.g. Rostro-García et al., 2016). One possible explanation is that forest edges represent areas with easier access to anthropogenic food resources and may alter behavior and habitat selection of species (van Bommel et al., 2020; Tee et al., 2021).

The potential for bear damages was positively associated with increasing road density and negatively associated with distance to roads (e.g. Sharma *et al.*, 2020). Some possible explanations for the higher risk of conflict in areas with higher road density include attraction of roads as travel routes, easier access to food and water sources and the need to cross them to find suitable habitat (van Bommel *et al.*, 2020). This relationship should be interpreted with caution due to the possibility of sampling bias as human settlements are also more likely to locate near roads.

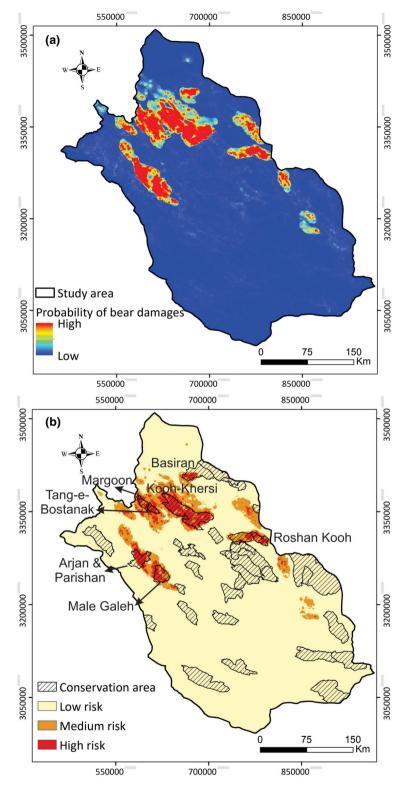


Figure 3 Predicted continuous (a) and classified (b) hotspots map of *Ursus arctos* damages risk using Jenks natural breaks threshold (low risk; 0–0.105, medium risk; 0.105–0.368, high risk; 0.368–0.962).

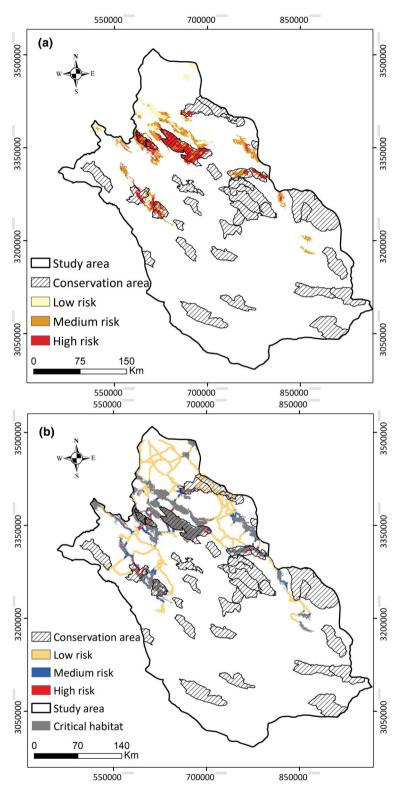


Figure 4 Intersection map of *Ursus arctos* damages risk with critical habitats (a) and corridor bottlenecks (b) to identify habitats and corridors with low to high risk of *U. arctos* damage. Factorial least-cost path modeling in the universal corridor network simulator was used to predict migration corridors. Corridor bottlenecks were defined as regions with an optimal path density higher than the mean plus two standard deviations.

Impacts of landscape composition and configuration on brown bear damages risk

In some studies, it has been suggested that, because of high mobility of large carnivores, landscape composition is more important than configuration (e.g. Mateo Sanchez, Cushman, & Saura, 2013). However, Sauder & Rachlow (2014) suggested that configuration has greater impacts on species with large body size, high trophic level and high habitat specialization. While habitat composition (i.e. extent of highly suitable habitats) and configuration (i.e. density of forest patches and highly suitable habitat patches) measures were both important in predicting bear damages risk in our model, patch density of forests and suitable habitats showed a larger effect. It has also been shown that bears are more likely to cause damage to beehives, crops and livestocks in more fragmented landscapes (Akhtar, Bargali, & Chauhan, 2004; Carter, 2007; Tee et al., 2021). Similar relationships have also been reported for other carnivores including Bengal tiger Panthera tigris and leopard P. pardus in Bhutan (Rostro-García et al., 2016), leopard, Bengal tiger and Asiatic elephant (Elephas maximus) in Nepal (Acharya et al., 2017), African lions (P. leo) in southwestern Kenya (Broekhuis et al., 2017) and leopard in north of Iran (Ghoddousi et al., 2020).

Many fragmented forest landscapes have become humanwildlife conflict hotspots (Michalski et al., 2006; Acharya et al., 2017). These fragmented forests typically contain smaller key habitat areas with reduced natural food and water availability and access, lower overall connectivity and greater human presences, which may alter carnivore behaviors such as increasing their aggressiveness (Acharya et al., 2017). In addition, forest fragmentation in our study area is often associated with the conversion of forests to agricultural lands, which leads to higher presence of livestocks and crops and thus greater risk of bear damages. Density of suitable habitat patches was important likely because of brown bears preference for anthropogenic food sites. When natural prey are scarce or depleted in natural habitats, bears are more likely to move into surrounding croplands for food (Bargali, 2012; Cozzi et al., 2016). The intersection of natural and human habitat provides cover for bears to move along and between the human habitat with lower risk of encountering with humans and to access anthropogenic food. Moreover, small and patchy suitable habitats provide low structural and functional connectivity, which likely increase human-wildlife conflict for species that require large area for movement, such as the brown bear.

Safe and high-risk corridors

Migration corridors are critical for species dispersal and gene flow, especially in a fragmented landscape, but human-wildlife conflict pose threats to these linkages and undermine their functionality (e.g. Cushman *et al.*, 2018). Large-bodied carnivores are especially susceptible to these conflicts along migration corridors in human-dominated landscapes (e.g. Michalski et al., 2006; Inskip & Zimmermann, 2009; Elliot et al., 2014).

Ignoring the risk of human-wildlife conflict in landscape connectivity assessments may lead to an overestimation of corridor extent and functional connectivity (e.g. Ash et al., 2020; Ghoddousi et al., 2020). We identified some corridor bottlenecks with high conflict risks between predicted critical habitats and conservation areas (such as between Kooh-Khersi and Tang-e-Bostanak; Fig. 4b). Considering high-risk corridors in future conservation plans is important for two main reasons: (1) high-risk corridors may act as ecological traps and increase bear mortality due to conflict (Ghoddousi et al., 2020), which can then lead to reduced gene flow and genetic diversity in the long run; and (2) high-risk corridors may act as risk diffusion paths (Dai et al., 2019) and increase conflict risks in areas connected to these paths. Based on our findings, risk diffusion paths may exist in the central and northern parts within the study area (i.e. corridors with high risk of conflict; Fig. 4b), which may increase the risk of bear damages in the future. Particularly, high-risk corridors between Kooh-Khersi no-hunting area and Tang-e-Bostanak protected area may act as a diffusion path. Currently, brown bear damages frequently occur inside and at the peripheral regions around Kooh-Khersi. This area contains some of the largest key habitats for brown bears. We think that bears may diffuse from Kooh-Khersi to Tang-e-Bostanak along these high-risk corridors in search of human food resources. Although the local people living around the high-risk corridors are more likely to suffer damages from bears, these corridors serve as important linkages for brown bears and must be protected. Hence, it is essential that authorities and decision-makers focus on short-term, locally affordable, mitigation approaches and involve law enforcement. In addition, for long-term solutions, educating and working with the locals to develop conservation strategies that can protect the species while assuring the livelihood of local communities should be considered.

Scope and limitations

Although our predation risk model performed well in mapping bear damages risk, we recognize some potential limitations of our model: (1) we combined all human-brown bear conflict types due to small sample sizes of bear damage incidents. This may affect our model since each type of damage caused by bears may be related to a different set of environmental factors (Zarzo-Arias et al., 2021). In addition, drivers of predation risk can be prey species-specific (Milanesi et al., 2019). Therefore, developing a separate predation risk model for each livestock species may improve our understanding on damages risk and help formulate mitigation solutions targeting each livestock. (2) We did not include other environmental, economic and social factors, such as natural food availability, availability of livestocks or beehives, husbandry methods that might affect the risk of damages. However, since >83% of damage reports were related to cropland raiding, we think that our model still paints an overall picture of the most important factors contributing to conflict risk. (3) We used habitat-based models to create resistance surfaces for connectivity analysis, which represented the best available method to produce such an analysis given the data we had. We acknowledge that the use of empirical movement data for parameterizing resistance surfaces may improve the connectivity analysis (Zeller *et al.*, 2018). The efficiency of habitat suitability-based landscape resistance have been acknowledged by Mateo-Sánchez *et al.* (2015) and Zeller *et al.* (2018) in cases where resource limits prohibit the collection of GPS collar or genetic data.

Conservation implications

With continual human expansion into wildlife species' primary habitat, human-wildlife conflicts will only increase if anthropogenic attractants are not effectively managed (Baruch-Mordo *et al.*, 2014). Actively managing these attractants across a broad landscape can be unfeasible. In this context, our study serves to provide critical information for prioritizing management and conservation efforts. Particularly, the predicted brown bear damage risk hotspots and high-risk habitats and corridors can help guide deployment of conflict mitigation actions.

Considering that farming significantly contributes to rural economy in this part of Iran, minimizing damages risk through efficient and spatially precise conflict mitigations can strengthen both economic livelihood and biodiversity conservation. Based on our findings, we recommend the following nonlethal mitigation efforts: (1) managing harvest of forest products by local people during conflict seasons (May-July; Parchizadeh & Belant, 2021). For example, wild pistachio (Pistacia atlantica) forests in the predicted conflict hotspots in the north of the study area (Kooh-Khersi and Tang-e-Bostanak) provide critical food for the species and should be protected against overharvesting, (2) restricting conversion of natural habitats to orchards especially in brown bear core habitats. The results of land use changes show that approximately 450 km² have been added to the extent of croplands and orchards over a period of 30 years in areas with medium to high risk of brown bear damage (3.4% of medium to high-risk areas; Unpublished data by Khosravi et al., 2021), (3) avoiding overgrazing pastures by livestock and limiting the activities of herders to the specific pastures according to their official grazing permits in regions with high risk of livestock depredation by bears (e.g. Margoon and Barm-e-Firooz protected areas), (4) removing livestock carcasses and other anthropogenic-derived food and food waste from human-dominated landscapes, (5) installing electric fences around orchards, and (6) adopting payment for ecosystem services scheme (PES) and conservation performance payments (CPP) in human-bear conflict hotspots. Direct compensation schemes are often not sustainable and viable long-term solutions (Zabel et al., 2011). Therefore, CPP which establishes a direct link between monetary payments and the production of desired conservation objectives, have been increasing used in recent years to promote carnivorehuman coexistence (Nelson, 2009; Dickman, Macdonald, & Macdonald, 2011; Persson, Rauset, & Chapron, 2015).

Conservation areas with relatively fewer restrictions on human activities (e.g. no-hunting areas) that are located near predicted risk hotspots should be prioritized for management for two main reasons. First, these conservation areas are typically in close proximity to villages and agricultural land, which attract bears when there are forage shortages in natural habitats (Sharma *et al.*, 2020). Second, retaliatory killings may be more likely when conflict occur due to fewer regulations that are in place. Currently unprotected habitats in the central and northern parts of the study area may represent suitable candidates for the expansion of conservation areas. Establishing new conservation areas could provide the necessary law enforcement to curb potential land use change and conflict.

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References

- Acharya, K.P., Paudel, P.K., Jnawali, S.R., Neupane, P.R. & Koehl, M. (2017). Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecol. Indic.* 80, 74–83.
- Ahmadi, M., Farhadinia, M.S., Cushman, S.A., Hemami, M.-R., Nezami Balouchi, B., Jowkar, H. & Macdonald, D.W. (2020). Species and space: A combined gap analysis to guide management planning of conservation areas. *Landsc. Ecol.* 35, 1505–1517.
- Akhtar, N., Bargali, H.S. & Chauhan, N. (2004). Sloth bear habitat use in disturbed and unprotected areas of Madhya Pradesh, India. Ursus 15, 203–211.
- Almasieh, K., Rouhi, H. & Kaboodvandpour, S. (2019). Habitat suitability and connectivity for the brown bear (*Ursus arctos*) along the Iran-Iraq border. *Eur. J. Wildl. Res.* 65, 57.
- Ansari, M. & Ghoddousi, A. (2018). Water availability limits brown bear distribution at the southern edge of its global range. Ursus 29, 13–24.
- Ash, E., Cushman, S.A., Macdonald, D.W., Redford, T. & Kaszta, Ż. (2020). How important are resistance, dispersal ability, population density and mortality in temporally dynamic simulations of population connectivity? A case study of tigers in southeast Asia. *Landarzt* 9, 415–441.
- Ashrafzadeh, M.R., Kaboli, M. & Naghavi, M.R. (2016). Mitochondrial DNA analysis of Iranian brown bears (*Ursus arctos*) reveals new phylogeographic lineage. *Mamm. Biol.* 81, 1–9.
- Ashrafzadeh, M.R., Khosravi, R., Adibi, M.A., Taktehrani, A., Wan, H.Y. & Cushman, S.A. (2020). A multi-scale,

multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. *Biol. Conserv.* **245**, 108523.

Ashrafzadeh, M.-R., Khosravi, R., Ahmadi, M. & Kaboli, M. (2018). Landscape heterogeneity and ecological niche isolation shape the distribution of spatial genetic variation in Iranian brown bears, *Ursus arctos* (carnivora: Ursidae). *Mamm. Biol.* **93**, 64–75.

Bargali, H. (2012). Distribution of different species of bears and status of human-bear conflict in the state of Uttarakhand, India. *Adv. Biol. Res.* 6, 121–127.

Baruch-Mordo, S., Wilson, K.R., Lewis, D.L., Broderick, J., Mao, J.S. & Breck, S.W. (2014). Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. *PLoS ONE* 9, e85122.

Beier, P. (2019). A rule of thumb for widths of conservation corridors. *Conserv. Biol.* **33**, 976–978.

Bleyhl, B., Baumann, M., Griffiths, P., Heidelberg, A., Manvelyan, K., Radeloff, V.C., Zazanashvili, N. & Kuemmerle, T. (2017). Assessing landscape connectivity for large mammals in the Caucasus using landsat 8 seasonal image composites. *Remote Sens. Environ.* **193**, 193–203.

Boria, R.A., Olson, L.E., Goodman, S.M. & Anderson, R.P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Model.* 275, 73–77.

Breiner, F.T., Nobis, M.P., Bergamini, A. & Guisan, A. (2018). Optimizing ensembles of small models for predicting the distribution of species with few occurrences. *Methods Ecol. Evol.* 9, 802–808.

Broekhuis, F., Cushman, S.A. & Elliot, N.B. (2017). Identification of human–carnivore conflict hotspots to prioritize mitigation efforts. *Ecol. Evol.* 7, 10630–10639.

Broennimann, O., Di Cola, V., Guisan, A. (2015). *Ecospat:* spatial ecology miscellaneous methods. R package version 1.

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

Burton, A.C., Fisher, J.T., Adriaens, P., Treweek, J., Paetkau, D., Wikstrom, M., Callender, A., Vardanyan, R. & Stepanyan, A. (2018). Density and distribution of a brown bear (*Ursus arctos*) population within the Caucasus biodiversity hotspot. *J. Mammal.* 99, 1249–1260.

Calvignac, S., Hughes, S. & Hänni, C. (2009). Genetic diversity of endangered brown bear (*Ursus arctos*) populations at the crossroads of Europe, Asia and Africa. *Divers. Distrib.* 15, 742–750.

Carter, N. (2007). Predicting the ecological and social suitability of black bear habitat in Michigan's lower peninsula. MSc thesis, University of Michigan.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F. & Anders, O. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519.

Cozzi, G., Chynoweth, M., Kusak, J., Coban, E., Çoban, A., Ozgul, A. & Şekercioğlu, Ç.H. (2016). Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. *J. Zool.* **300**, 142–150.

Cushman, S.A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* **128**, 231–240.

Cushman, S.A., Compton, B.W. & McGarigal, K. (2010).
Habitat fragmentation effects depend on complex interactions between population size and dispersal ability: modeling influences of roads, agriculture and residential development across a range of life-history characteristics. In *Spatial complexity, informatics, and wildlife conservation*: 369–385. Cushman, S.A. & Huettmann, F. (Eds). Tokyo: Springer.

Cushman, S.A., Elliot, N.B., Bauer, D., Kesch, K., Bahaa-eldin, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D.W. & Loveridge, A.J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern africa. *PLoS ONE* **13**, e0196213.

Cushman, S.A., Landguth, E.L. & Flather, C.H. (2013). Evaluating population connectivity for species of conservation concern in the American Great Plains. *Biodivers. Conserv.* 22, 2583–2605.

Cushman, S.A., McKelvey, K.S. & Schwartz, M.K. (2009). Use of empirically derived source-destination models to map regional conservation corridors. *Conserv. Biol.* 23, 368–376.

Dai, Y., Hacker, C.E., Zhang, Y., Li, W., Li, J., Zhang, Y., Bona, G., Liu, H., Li, Y. & Xue, Y. (2019). Identifying the risk regions of house break-ins caused by Tibetan brown bears (*Ursus arctos pruinosus*) in the Sanjiangyuan region, China. *Ecol. Evol.* 9, 13979–13990.

DeLeo, J. M. (1993). Receiver operating characteristic laboratory (roclab): software for developing decision strategies that account for uncertainty. In *1993 (2nd) international symposium on uncertainty modeling and analysis*: 318–325. College Park, MD: IEEE.

Dickman, A.J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Anim. Conserv.* **13**, 458–466.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proc. Natl. Acad. Sci.* **108**, 13937–13944.

Doan-Crider, D.L., Tri, A.N. & Hewitt, D.G. (2017). Woody cover and proximity to water increase American black bear depredation on cattle in Coahuila, Mexico. Ursus 28, 208– 217.

Elliot, N.B., Cushman, S.A., Macdonald, D.W. & Loveridge, A.J. (2014). The devil is in the dispersers: predictions of landscape connectivity change with demography. *J. Appl. Ecol.* 51, 1169–1178.

- Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L. & Boitani, L. (2009). Assessing habitat quality for conservation using an integrated occurrence-mortality model. *J. Appl. Ecol.* 46, 600–609.
- Farashi, A. (2018). Identifying key habitats to conserve the threatened brown bear in northern Iran. *Russian J Ecol* 49, 449–455.
- Fars Provincial Office of Department of Environment (FDoE). (2020). https://fars.doe.ir
- Ghoddousi, A., Bleyhl, B., Sichau, C., Ashayeri, D., Moghadas, P., Sepahvand, P., Hamidi, A.K., Soofi, M. & Kuemmerle, T. (2020). Mapping connectivity and conflict risk to identify safe corridors for the Persian leopard. *Landsc. Ecol.* 35, 1809–1825.
- Hemami, M.R., Khosravi, R., Groves, C. & Ahmadi, M. (2020). Morphological diversity and ecological niche divergence in goitered and sand gazelles. *Ecol. Evol.* 10, 11535–11548.
- Hijmans, R. J. (2021). Geographic data analysis and modeling. R package raster version 3.4-10.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. & Hijmans, M.R.J. (2017). Package 'dismo'. *Circles* 9, 1–68.
- Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152.
- Hobbs, N.T., Andrén, H., Persson, J., Aronsson, M. & Chapron, G. (2012). Native predators reduce harvest of reindeer by Sámi pastoralists. *Ecol. Appl.* 22, 1640–1654.
- Hopcraft, J.G.C., Sinclair, A. & Packer, C. (2005). Planning for success: serengeti lions seek prey accessibility rather than abundance. J. Anim. Ecol. 74, 559–566.
- Inskip, C. & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43, 18–34.
- IUCN. (2006). 2006 IUCN red list of threatened species. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.
- Jenks, G. (1967). The data model concept in statistical mapping. In *International yearbook of cartography*, Vol. 7: 186–190. Frenzel, K. (Ed). Gutersloh: Bertelsmann Verlag.
- Kaszta, Ż., Cushman, S. & Macdonald, D. (2020). Prioritizing habitat core areas and corridors for a large carnivore across its range. *Anim. Conserv.* 23, 607–616.
- Khosravi, R., Hemami, M.-R., Malakoutikhah, S., Ashrafzadeh, M.R. & Cushman, S.A. (2021). Prey availability modulates predicted range contraction of two large felids in response to changing climate. *Biol. Conserv.* 255, 109018.
- Landguth, E., Hand, B., Glassy, J., Cushman, S. & Sawaya, M. (2012). Unicor: a species connectivity and corridor network simulator. *Ecography* 35, 9–14.
- Leroy, B., Meynard, C.N., Bellard, C. & Courchamp, F. (2016). Virtualspecies, an r package to generate virtual species distributions. *Ecography* **39**, 599–607.
- Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J. & Guisan, A. (2010). Overcoming the rare

species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. *Biol. Conserv.* **143**, 2647–2657.

- Louppe, V., Leroy, B., Herrel, A. & Veron, G. (2020). The globally invasive small indian mongoose *Urva auropunctata* is likely to spread with climate change. *Sci. Rep.* 10, 1–11.
- Macdonald, D.W., Bothwell, H.M., Kaszta, Ż., Ash, E., Bolongon, G., Burnham, D., Can, Ö.E., Campos-Arceiz, A., Channa, P. & Clements, G.R. (2019). Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*). *Divers. Distrib.* 25, 1639–1654.
- Maiorano, L., Chiaverini, L., Falco, M. & Ciucci, P. (2019). Combining multi-state species distribution models, mortality estimates, and landscape connectivity to model potential species distribution for endangered species in human dominated landscapes. *Biol. Conserv.* 237, 19–27.
- Mateo Sanchez, M.C., Cushman, S.A. & Saura, S. (2013). Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian range (NW Spain). *Int. J. Geogr. Inf. Sci.* 28, 1531–1546.
- Mateo-Sánchez, M.C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A. & Saura, S. (2015). A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? *Landsc. Ecol.* **30**, 1405–1420.
- McGarigal, K., Cushman, S. A. & Ene, E. (2012). *Fragstats v4: spatial pattern analysis program for categorical and continuous maps*. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at: http://www.umass.edu/landeco/research/ fragstats/fragstats.html
- McLellan, B., Proctor, M., Huber, D., Michel, S. (2017). Ursus arctos (amended version of 2017 assessment). The IUCN red list of threatened species. 2017: E.T41688a121229971
- Michalski, F., Boulhosa, R., Faria, A. & Peres, C. (2006). Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Anim. Conserv.* 9, 179–188.
- Milanesi, P., Puopolo, F., Fabbri, E., Gambini, I., Dotti, F., Sergiacomi, U., Zanni, M.L. & Caniglia, R. (2019).
 Improving predation risk modelling: prey-specific models matter. *Hystrix Ital. J. Mammal.* 30, 149–156.
- Miller, J.R. (2015). Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodivers. Conserv.* 24, 2887–2911.
- Miller, J.R., Jhala, Y.V., Jena, J. & Schmitz, O.J. (2015). Landscape-scale accessibility of livestock to tigers: implications of spatial grain for modeling predation risk to mitigate human–carnivore conflict. *Ecol. Evol.* 5, 1354– 1367.
- Mohammadi, A., Almasieh, K., Nayeri, D., Ataei, F., Khani, A., López-Bao, J., Penteriani, V. & Cushman, S. (2021).

Moqanaki, E. & Cushman, S. (2017). All roads lead to Iran: predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. *Anim. Conserv.* **20**, 29–41.

Moqanaki, E.M., Jiménez, J., Bensch, S. & López-Bao, J.V. (2018). Counting bears in the Iranian caucasus: remarkable mismatch between scientifically-sound population estimates and perceptions. *Biol. Conserv.* 220, 182–191.

Morales-González, A., Ruiz-Villar, H., Ordiz, A. & Penteriani, V. (2020). Large carnivores living alongside humans: brown bears in human-modified landscapes. *Glob. Ecol. Conserv.* 22, e00937.

Nelson, F. (2009). Developing payments for ecosystem services approaches to carnivore conservation. *Hum. Dimens. Wildl.* 14, 381–392.

Parchizadeh, J. & Belant, J.L. (2021). Brown bear and persian leopard attacks on humans in Iran. *PLoS ONE* **16**, e0255042.

Persson, J., Rauset, G.R. & Chapron, G. (2015). Paying for an endangered predator leads to population recovery. *Conserv. Lett.* 8, 345–350.

Pettigrew, M., Xie, Y., Kang, A., Rao, M., Goodrich, J., Liu, T. & Berger, J. (2012). Human–carnivore conflict in China: a review of current approaches with recommendations for improved management. *Integr. Zool.* 7, 210–226.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M. & Nelson, M.P. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I., Levi, T. & Lindsey, P.A. (2015). Collapse of the world's largest herbivores. *Sci. Adv.* 1, e1400103.

Roberge, J.M. & Angelstam, P. (2004). Usefulness of the umbrella species concept as a conservation tool. *Conserv. Biol.* 18, 76–85.

Rostro-García, S., Tharchen, L., Abade, L., Astaras, C., Cushman, S.A. & Macdonald, D.W. (2016). Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. *Landsc. Ecol.* **31**, 1277–1298.

Sauder, J.D. & Rachlow, J.L. (2014). Both forest composition and configuration influence landscape-scale habitat selection by fishers (*Pekania pennanti*) in mixed coniferous forests of the northern rocky mountains. *For. Ecol. Manage.* **314**, 75– 84.

Sharma, P., Chettri, N., Uddin, K., Wangchuk, K., Joshi, R., Tandin, T., Pandey, A., Gaira, K.S., Basnet, K. & Wangdi, S. (2020). Mapping human–wildlife conflict hotspots in a transboundary landscape, eastern Himalaya. *Glob. Ecol. Conserv.* **24**, e01284.

- Simberloff, D. (1999). Biodiversity and bears: a conservation paradigm shift. Ursus 11, 21–28.
- Somers, R.H. (1962). A new asymmetric measure of association for ordinal variables. Am. Sociol. Rev. 799, 123– 163.

Tee, T.L., van Manen, F.T., Kretzschmar, P., Sharp, S.P., Te Wong, S., Gadas, S. & Ratnayeke, S. (2021). Anthropogenic edge effects in habitat selection by sun bears in a protected area. *Wildl. Biol.* **2021**, wlb00776.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009). Biomod–a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006). Co-managing human-wildlife conflicts: a review. *Hum. Dimens. Wildl.* 11, 383–396.

- van Bommel, J.K., Badry, M., Ford, A.T., Golumbia, T. & Burton, A.C. (2020). Predicting human-carnivore conflict at the urban-wildland interface. *Glob. Ecol. Conserv.* **24**, e01322.
- Wan, H.Y., Cushman, S.A. & Ganey, J.L. (2019). Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. *Landsc. Ecol.* 34, 503–519.
- Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Zabel, A., Pittel, K., Bostedt, G. & Engel, S. (2011). Comparing conventional and new policy approaches for carnivore conservation: theoretical results and application to tiger conservation. *Environ. Resource Econ.* 48, 287–301.
- Zarzo-Arias, A., Delgado, M.d.M., Palazón, S., Afonso Jordana, I., Bombieri, G., González-Bernardo, E., Ordiz, A., Bettega, C., García-González, R. & Penteriani, V. (2021).
 Seasonality, local resources and environmental factors influence patterns of brown bear damages: implications for management. J. Zool. 313, 1–17.
- Zeller, K.A., Jennings, M.K., Vickers, T.W., Ernest, H.B., Cushman, S.A. & Boyce, W.M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Divers. Distrib.* 24, 868–879.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Spatial autocorrelation of the final predicted covariates used for brown bear damages risk mapping at occurrence localities.

Table S2. The initial list of covariates used in the human-brown bear damages risk modeling, with the

hypothesized effect of each variable on the probability of conflict risk.

 Table S3. List of variables used for predicting brown bear's habitat suitability map.

Table S4. The list of bivariate models, their performance (based on AUC), and the weighted average of all resulting Somers' D (i.e. rescaled AUC) values of the bivariate models.

Figure S1. Classification of the predictor variables for brown-bear damage risk modeling using hierarchical ascendant classification and Pearson correlation.

Figure S2. The map of the predicted variables used for modeling brown bear damages risk.

Figure S3. Response curves of the most influential predictors for brown bear damages risk.