Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Future land use and climate change escalate connectivity loss for Himalayan brown bears

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Keywords
biodiversity; climate change mitigation; fragmentation; future projections; habitat loss; Himalayan brown bear; multi-scale; range shift; resistant kernels; UNICOR.

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Editor: Vincenzo Penteriani
Associate Editor: Vincenzo Penteriani

Received 28 April 2021; accepted 18 July 2022

doi:10.1111/acv.12813

Abstract

Climate and land use change are among the main drivers affecting virtually all species on earth. There were extensive studies projecting impacts of climate and land use changes on habitat loss and fragmentation but few on connectivity loss, and those that investigated connectivity did not disentangle the combined effects between climate change and land use change. This study uses the Himalayan brown bear (*Ursus arctos isabellinus)* as a case study to illustrate an approach for disentangling the effects of climate change and human land use on population connectivity in the future. First, we assessed the current spatial pattern of population connectivity by simulating cumulative resistant kernels and factorial least-cost paths with empirical field data. Then, we simulated the changes in connectivity due to future climate change under alternative emission scenarios (RCP 2.6 and RCP 8.5) in mid (2041–2060) and late (2061–2080) 21st century, which served as baseline scenarios of future connectivity. Finally, we estimated the changes in future connectivity due to human land use changes by adding a low and a high human land use activity scenario to the baseline climate change scenarios in our simulations. Alarmingly, all high emission scenarios, with or without human land use change, were projected to result in >99% reduction in current core areas of connectivity by the end of 21st century at 50th percentile threshold or above. This study demonstrates a spatially explicit scenario modeling approach to examine the interplay between future climate change and human land use on species connectivity. Our results suggest that regional land use regulations may be insufficient to conserve connectivity for HBB if nothing is done to reduce climate change at a global scale.

Introduction

Climate change and human land-use change together threaten the conservation and survival of many wildlife species worldwide (Gouveia *et al*., 2016), particularly those that are deemed endemic and face higher extinction risks (Lambers, 2015). Increasing human development and expected climate change are rapidly driving range shifts and are expected to continue to alter ecological systems and accelerate habitat loss and fragmentation at large scales over the next century (Parmesan, 2006; Shirk *et al*., 2018). For example, a meta-analysis of 1,700 species suggested range shifts of 6.1 km per decade on average towards poles or climatically equivalent elevation increases (Parmesan & Yohe, 2003).

Although habitat loss and fragmentation have frequently threatened species associated with lower elevations where human-induced drivers of biodiversity loss, such as agriculture, infrastructure development are generally higher, highland species in intact habitats are now facing the additional threat of warming temperatures (Miehe, Miehe, & Schlütz, 2009; Shrestha, Gautam, & Bawa, 2012; Elsen, Monahan, & Merenlender, 2020). Warmer climate pushes the suitable conditions for most species at high elevation areas upslope into smaller and increasingly isolated topographical habitat remnants interspersed with unsuitable lower elevation areas (Opdam & Wascher, 2004). Therefore, species already associated with higher elevation environments are likely to experience reduction in potential habitat and increasing fragmentation and isolation of habitat remnants (Schwartz *et al*., 2009; McKelvey *et al*., 2011; Cushman, Landguth, & Shirk, 2012; Wasserman *et al*., 2012; Wasserman, Cushman, & Littell, 2013). As a result, connectivity among the habitat remnants will decrease and wildlife populations will become more isolated (Cushman, 2006; Van Oort, Mclellan, & Serrouya, 2011), which can lead to reduced gene flow and genetic diversity, population declines and even local extinction (Coulon *et al*., 2004; Crooks *et al*., 2011, 2017; Wasserman *et al*., 2013).

Mountain environments are very sensitive to climate change, due to low productivity and extreme environmental conditions (Beniston, 2003, 2005). Thus, they often serve as indicators of climate change, and offer greater scope to assess the climate-related impacts on biodiversity (IPCC, 2014). Furthermore, despite their remoteness and inaccessibility, mountain ecosystems have not been spared from human-induced biodiversity loss. Human influence on mountain ecosystems has greatly increased in recent decades due to rapid population growth, urban sprawl and the expansion of utilities to meet increased energy demands, as well as border security and interdiction activities, especially in developing countries (Körner, 2004; Rodríguez-Rodríguez & Bomhard, 2012; Tiwari *et al*., 2018; Wang *et al*., 2019; Elsen *et al*., 2020). For example, in the Indian Himalayan mountains, 292 new hydroelectric projects are in various stages of planning and implementation to meet the increased energy demands projected from economic and population growth (Grumbine & Pandit, 2013). The increasing land use and climate change fragments mountain systems, leading to reduced resilience and sustainability. Many mountain wildlife species have to adapt to these human-modified landscapes in order to survive. However, information on impacts of climate and land use changes on mountain biodiversity is limited (Reyers *et al*., 2009). This lack of information is an obstacle for land managers and policy makers to making effective decisions for conservation of taxa currently associated with mountain ecosystems (Balsiger & Debarbieux, 2015).

Large carnivores are especially threatened by habitat fragmentation and isolation due to their large area requirements, slower life histories and low densities (Cardillo *et al*., 2004, 2005). Globally, a majority (77%) of large carnivores are declining, with populations of many species in a danger of local or global extinction due to climate and human pressure (Ripple *et al*., 2014; Hagen *et al*., 2015; Jackson *et al*., 2016; Recio *et al*., 2021). One of the most iconic large carnivores is the brown bear (*Ursus arctos*), having a circumglobal distribution in the northern hemisphere, with populations in North America, Europe and northern and central Asia (McLellan, Servheen, & Huber, 2008). Globally, the brown bear numbers and distributional range have decreased by more than 50% since the mid-1800s due to anthropogenic pressure and climate change (Servheen, 1990). These range contractions have fragmented the remaining populations of brown bears into many small isolates in need of strong conservation interventions (Zedrosser *et al*., 2001; Mattson & Merrill, 2002; McLellan *et al*., 2017). The Himalayan brown bear (*Ursus arctos isabellinus*; hereafter HBB) is an endangered subspecies under IUCN that occupies the high elevation habitats in the Himalayan region (Sathyakumar, 2001; Aryal *et al*., 2012; McLellan *et al*., 2017). HBB subpopulations are currently declining, with only around 300 individuals remaining in a patchy distribution at high elevations in northern Pakistan and the north and northwestern Himalayan regions of India (Sathyakumar, 2006; Sathyakumar *et al*., 2012; Abbas *et al*., 2015; Mclellan *et al*., 2017). The major threats HBB face in this region include habitat loss, habitat fragmentation due to human land use change and increasing human pressure, and retaliatory killings subsequent from human bear conflicts (Nawaz, Swenson, & Zakaria, 2008; Aryal, Sathyakumar, & Schwartz, 2010; Aryal *et al*., 2012; Dai *et al*., 2021). Furthermore, recent studies show that the distribution and connectivity of HBB subpopulations are heavily jeopardized by climate change (Aryal, Brunton, & Raubenheimer, 2014; Su *et al*., 2018; Dai *et al*., 2021; Dar *et al*., 2021; Mukherjee *et al*., 2021). However, these studies have not considered the uncertainty related to the dispersal movement ability, as connectivity is considered to be more sensitive to the species dispersal ability (Cushman, Landguth, & Flather, 2013; Cushman *et al*., 2016).

Studies examining effects of climate change and human land use change on species connectivity seldom disentangle the effects between the two (Su *et al*., 2018; Dai *et al*., 2021; Mukherjee *et al*., 2021). The disentanglement of these effects can provide insights in addressing climate change mitigation and conservation policies. Here, we demonstrate an approach that utilizes scenario modeling to assess and disentangle the potential effects of future climate change and land use change on population connectivity of species associated at higher elevations. To demonstrate our approach, we used HBB as a case study species and predict the current and future connectivity between the remnant subpopulations of HBB across the Western Himalayan mountains. The brown bear is an ideal species to elucidate the effects of climate change and increasing human pressure on population connectivity of highland species because of its association with high elevation habitats, large area requirements and high mobility. Further, brown bear serves as a management indicator or umbrella species and confers habitat and connectivity protection of other co-existing species (Peterson, 1988; Noss, 1993; Roberge & Angelstam, 2004).

We hypothesize that the expected future climate change and land use changes will substantially disrupt the connectivity between the potential habitats of HBB across the study landscape. In addition, we hypothesize that future land use change will considerably bolster the negative impact of climate change on HBB connectivity, and that impact of future climate and land use will intensify as the dispersal of HBB decreases.

Materials and methods

Study area

The study area encompasses 327,996 km^2 in the Western Himalayan mountains in India (Fig. 1). It is topographically diverse with extensive mountain ranges interspersed with intermountain valleys and high plains. Elevation ranges from 181 to 8,569 m. The study region is characterized by distinct vegetation regimes along elevational gradients, and harbors some of the world’s rarest wildlife species, such as snow leopard (*Panthera uncia*), Asiatic black bear (*Ursus thibetanus*), Himalayan wolf (*Canis lupus*), Kashmir red deer

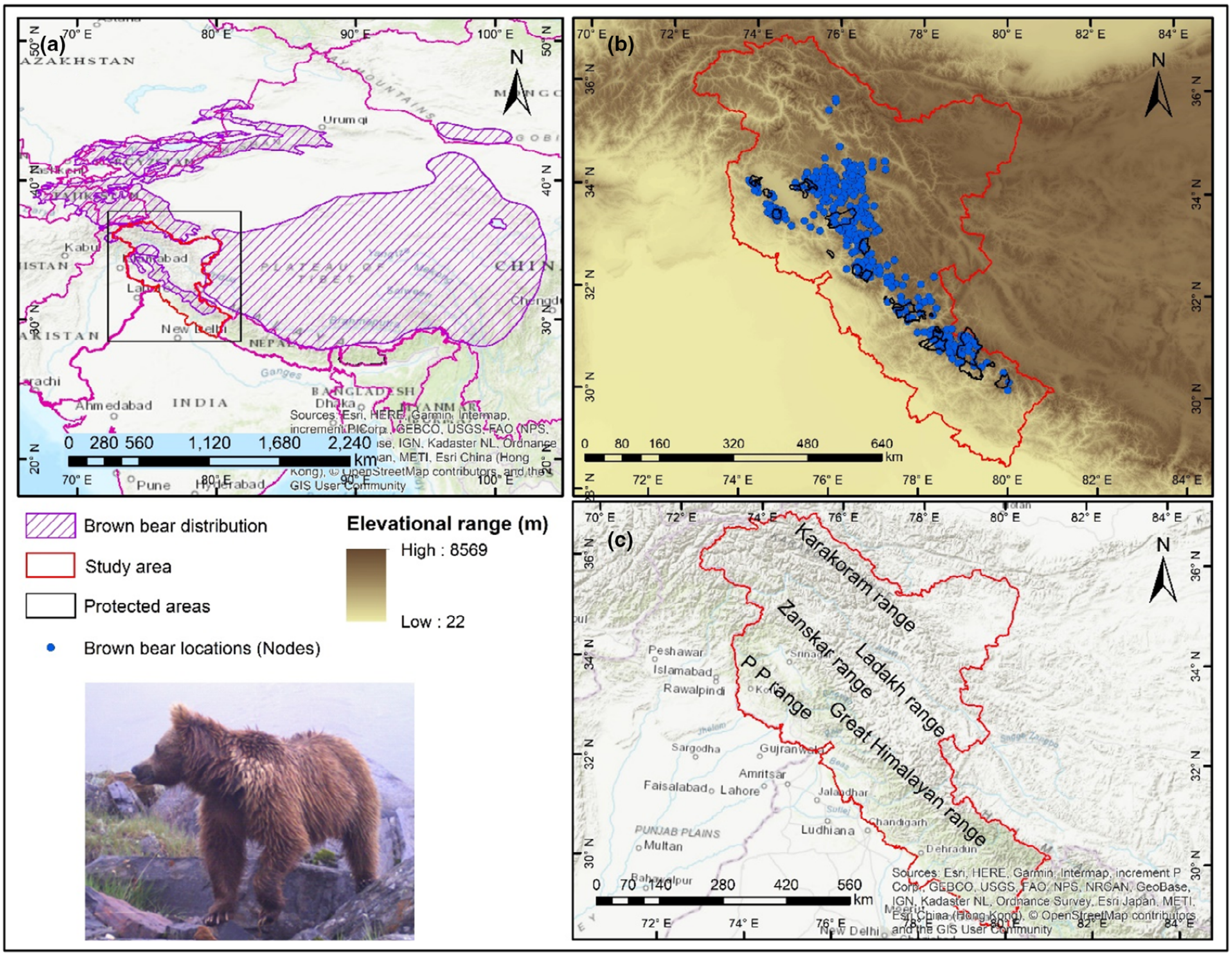

Figure 1 Location of the study area, the Western Himalaya. (a) the distribution of brown bear in Asia (IUCN), (b) The blue dots represent the nodes used in the connectivity analysis, (c) Main mountain ranges in the study area. Light yellow-brown background color represents elevational gradient.

(*Cervus hanglu*), blue sheep (*Pseudois nayaur*), Tibetan antelope (*Pantholops hodgsonii*), urial (*Ovis orientalis*) and musk deer (*Moschus leucogaster*) (Sathyakumar & Bashir, 2010).

Shrestha *et al*. (2012) documented increases in temperature over Himalayas by 1.5 °C from 1982 to 2006, an average rate of 0.06 °C/year. The temperature in the region is projected to increase in the range of 0.5°C to 1°C by 2020s and 1°C to 3°C by mid-century (Kulkarni *et al*., 2013; Wu, Xu, & Gao, 2017). The average annual mean temperature over the Himalaya mountains is projected to increase by about 3°C by the 2050s and about 5°C by the 2080s (Kumar *et al*., 2006; IPCC, 2007*a*,*b*).

Landscape resistance

We used a previously developed predicted habitat suitability maps for HBB (Dar *et al*., 2021) to generate landscape resistance surfaces for our connectivity analysis. Briefly, Dar *et al*. (2021) used a multi-scale optimization (sensu McGarigal *et al*., 2016) machine learning approach (e.g. Cushman *et al*., 2018) to predict the potential distribution of HBB across the study area, and then projected future habitat suitability of HBB in the 2050s (i.e. 2041–2060) and 2070s (i.e. 2061–2080) under several human land use and climate change scenarios. They collected 720 HBB occurrences from the study area and used them as the response variable in the model. For predictors, they used a set of a priori 40 variables that represent climate, landscape composition, topography and human disturbance in the region (see Supplementary Information Table S1 for a summary of the variables and their sources). The future climatic variables were obtained from the same source as the current climatic variables (i.e. WorldClim, Fick & Hijmans, 2017). To project future landscape patterns integrating human land use changes, a layer of croplands and cropland/natural vegetation mosaics and urban/built up areas projected for years 2050 and 2100 were used obtained from the GeoSOS global database (Li *et al*., 2017). Each variable was evaluated across eight spatial scales (1, 2, 4, 8, 16, 32, 64 and 128 km) in a univariate scaling analysis, with the scale with lowest out-of-bag (OOB) error rate chosen for inclusion in multivariate models. Dar *et al*. (2021) found that the habitat selection of HBB was scale dependent, and most of the variables was selected at the broadest scale. The final multiscale model included 22 variables, and the most important variables were minimum temperature of warmest month, PET of wettest quarter, evergreen needleleaf forest, maximum temperature of coldest month, human population, grasslands, compound topographic index and the least important was water bodies.

We obtained our resistance surfaces by converting the suitability maps using an exponential decay function following Wan, Cushman, & Ganey (2019). We used 1000 as the base of our exponential decay function, resulting in low-cost resistance in areas with >0.3 habitat suitability. We rescaled the resistance values to a range between 1 and 150 by linear interpolation, such that minimum resistance (R_{min}) was 1 when HS was 1, and maximum resistance (R_{max}) was 150 when HS was 0 (Fig. 2). While converting future habitat suitability maps into resistance surfaces, minimum resistance (R_{min}) was adjusted as per the maximum HS value of future habitat suitability maps. Several past studies on other species have shown that this approach using negative exponential transformations best describes the relationship between habitat suitability and resistance values for brown bears (e.g. Mateo-Sánchez *et al*., 2015*a*,*b*). All resistance surfaces used in connectivity models were at a spatial resolution of 1 km.

Future land use and climate change scenarios

We projected landscape connectivity for HBB under the following 8 future scenarios:

(1) 2050s Climate change-only, low emission scenario (RCP 2.6 2050s)
(2) 2050s Climate change-only, high emission scenario (RCP 8.5 2050s)
(3) 2050s Low emission and low development scenario (RCP 2.6 2050s + A1B 2050)
(4) 2050s High emission and high development scenario (RCP 8.5 2050s + A2 2050)
(5) 2070s Climate change-only, low emission scenario (RCP 2.6 2070s)
(6) 2070s Climate change-only, high emission scenario (RCP 8.5 2070s)
(7) 2070s Low emission and low development scenario (RCP 2.6 2070s + A1B 2100)
(8) 2070s High emission and high development scenario (RCP 8.5 2070s + A2 2100)

Current and future habitat connectivity and corridor simulation

We used UNICOR (Landguth *et al*., 2012) to predict current and future HBB connectivity patterns. To do this, we used

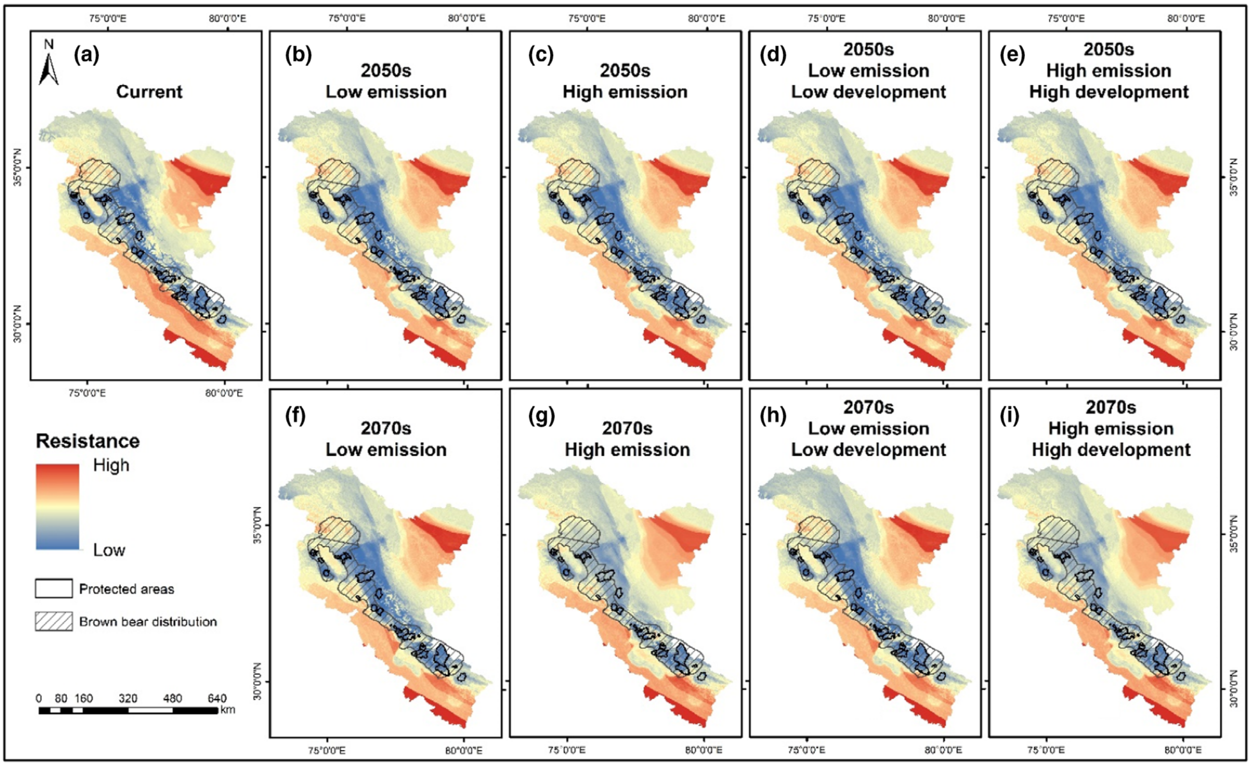

Figure 2 Landscape resistance surfaces across the study area for HBB, under current and future climate and land use scenarios based on exponential decay function. Higher resistance values indicate less probability of dispersing individual brown bears.

the predicted probability map of suitable habitat described above to randomly generate 1,000 habitat suitability weighted nodes on the landscape (i.e. higher predicted habitat suitability had more random nodes). Thereafter, we applied a spatial filter such that each node was at least 5 km from its nearest node. We randomly selected 300 nodes, approximately the number of HBB in the study region. We applied two methods—cumulative resistant kernel (Compton *et al.*, 2007) and factorial least-cost path (Cushman, McKelvey, & Schwartz, 2009)—in UNICOR to map the connectivity network. For the factorial least-cost paths, we also applied a Gaussian kernel estimate buffer of 2 km around all paths. The factorial least-cost path analysis produces the sum of predicted least-cost paths from each source point to each destination point. For the cumulative resistant kernel, it calculates the least-cost dispersal kernels around each source nodes and the summation of all kernels produce a density map of dispersing individuals on the landscape (Compton *et al.*, 2007). Unlike other methods of predicting and mapping dispersal corridors, the resistant kernel approach is spatially synoptic, estimating the predicted dispersal rates of each and every pixel within the study area, rather than just few selected 'linkage areas' (e.g. Compton *et al.*, 2007; Cushman, Lewis, & Landguth, 2014). Furthermore, in resistant kernel modeling approach, scale dependency of dispersal ability can be explicitly incorporated to analyze how landscape fragmentation affects species of varied vagilities (e.g. Cushman, Chase, & Griffin, 2010).

Because of scarcity of information regarding the dispersal movement of HBB, we ran the models across three levels of dispersal ability: 90 km (low dispersal ability), 250 km (medium dispersal ability) and 467 km (high dispersal ability), corresponding to maxima of the COSTDISTANCE (i.e. Edge Distance) function of 900,000, 2,500,000 and 4,670,000 cost units, respectively, on a uniform landscape of resistance equal 1. The expected value of dispersal distance across the landscape is the 'Edge Distance' dispersal ability divided by the average resistance of the landscape. Using a range of dispersal distances allows us to assess and quantify uncertainty related to dispersal movement ability (Cushman *et al.*, 2013, 2016). Further, the dispersal distances used in the analysis are comparable to known dispersal distances from empirical studies of brown bears in other regions (e.g. Støen *et al.*, 2006; Bartoń *et al.*, 2019).

Analysis of resistant kernel maps

To quantify the extent and connectivity of HBB dispersal habitat, and to assess the impact of climate and land use scenarios, we first calculated four connectivity percentiles on our base scenario, that is 0th (All above 0), 25th, 50th and 75th, and then used those percentile values as thresholds to extract the dispersal areas of high connectivity for all scenarios. Any cell with values above the threshold was classified as connected and the rest were classified as nonconnected. Then, we used FRAGSTATS (McGarigal *et al.*, 2002) to calculate several landscape metrics on the binary resistant kernel maps, including percentage of the landscape (PLAND), correlation length (GYRATE_AM), largest patch index (LPI), total edge (TE), edge density (ED), contiguity index (CONTIG), number of patches (NP), patch area, clumpy (CLUMPY) and aggregation index (AI) predicted by the resistant kernel model. These metrics are sensitive indicators to changes in landscape connectivity (Cushman *et al*, 2013) and have been frequently used to study fragmentation and climate change effects on connectivity (Wasserman *et al.*, 2012, 2013; Chambers *et al.*, 2016). We calculated these metrics for the current and future scenarios and across the four connectivity percentile thresholds.

Change detection

To evaluate connectivity change between current and future (2050s and 2070s) scenarios, we used the binary resistant kernel models from above and classified areas as either 'gain' (areas identified as connected in the future scenario but not in the current scenario), 'loss' (areas identified as connected in the current scenario but not in the future scenario) or 'stable' (areas identified as connected in both the current and future scenarios). In order to assess the impact of future climate and land use change on long dispersal corridors, we extracted the corridors with greater than zero value (All above 0).

Results

Resistance surface

Areas of low resistance to movement for HBB were mostly concentrated around intermediate topographies between valley and ridge locations, with low amounts of anthropogenic pressure and at middle to upper elevations (Fig. 2).

Current connectivity

Current HBB connectivity is shown in Fig. 3. Dispersal ability and the range of connectivity thresholds showed a substantial effect on the extent and patterns of core areas of high connectivity for HBB. Unsurprisingly, the extent of core area increases with increasing dispersal ability and decreases with higher levels of connectivity thresholds (Fig. 3). For example, at the most liberal threshold (cumulative kernel density value greater than 0) the dispersal core area under high dispersal ability was predicted to be a single large connected patch with an extent of 187,501 km^2 (Fig. 3c; Table 1). Similarly, with medium movement scenario (250 km), a single connected patch was predicted as a core habitat with an extent of 139,093 km^2 (Fig. 3b; Table 1). Under low dispersal ability (90 km), however, the core areas were predicted to be broken into three isolated patches with a total extent of 88,222 km^2 (Fig. 3a; Table 1). The percentage of dispersal core areas decreases with increasing connectivity threshold across all dispersal scenarios used in the analysis (Fig. 3; Table 1).

The resistant kernel connectivity models highlight four key areas of high priority for management efforts in Western

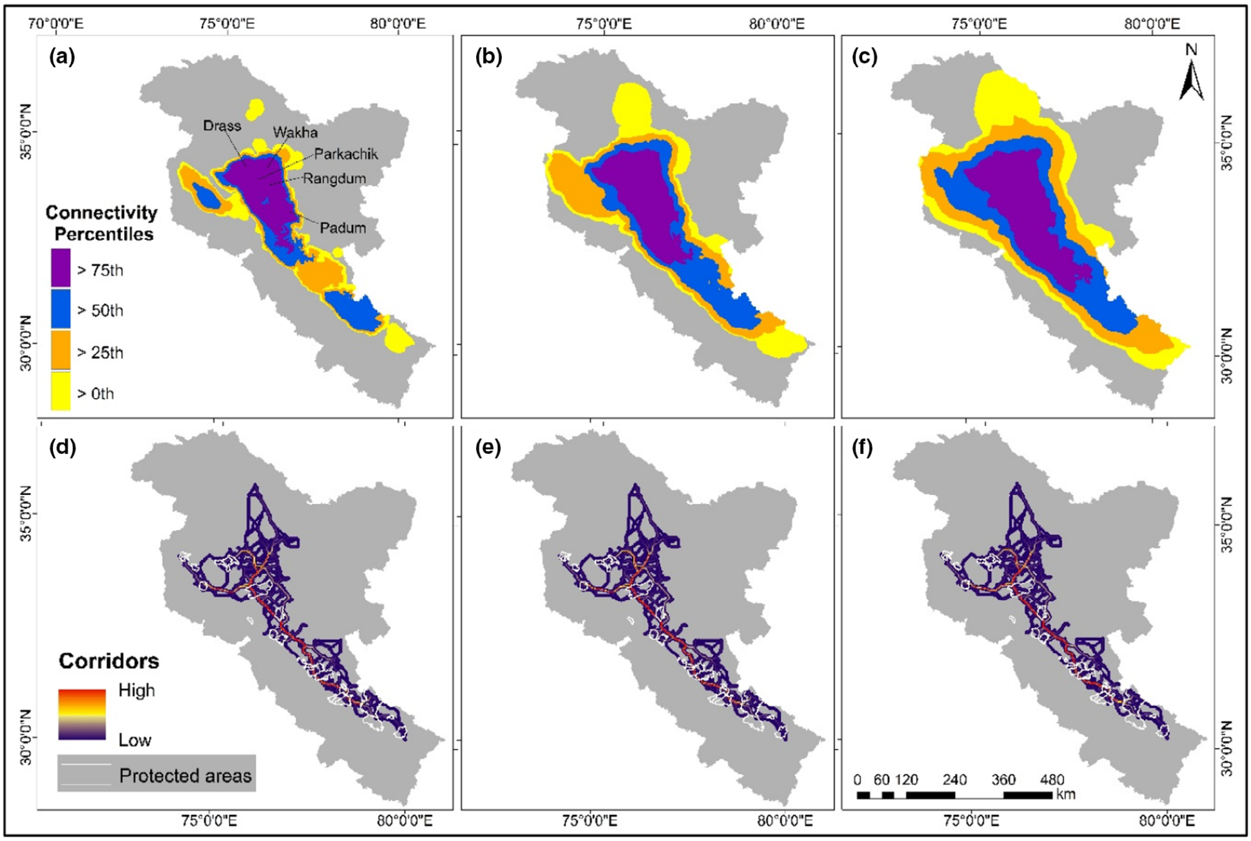

Figure 3 Resistant kernel and least-cost path connectivity maps of HBB for current scenario under three dispersal ability scenarios. (a, d) low dispersal ability (90 km), (b, e) medium dispersal ability (250 km) and (c, f) high dispersal ability (467 km).

Table 1 Dispersal core areas and landscape matrices of HBB under current scenario across three dispersal scenarios and across the range of four connectivity thresholds

Connectivity Threshold	Dispersal core area (km^2)	LPI (%)	Correlation length (km)	NP
Cost Distance Threshold 90 km				
>0th	88222	26.1	170.3	3
>25th	66175	17.8	136.8	2
>50th	44115	9.9	71.6	3
>75th	22053	6.7	65.7	1
Cost Distance Threshold 250 km				
>0th	139093	42.4	195.9	1
>25th	104312	31.8	170.7	1
>50th	69548	21.2	145.0	1
>75th	34775	10.6	86.1	1
Cost Distance Threshold 467 km				
>0th	187501	57.2	208.4	1
>25th	140624	42.9	185.0	1
>50th	93751	28.6	154.1	1
>75th	46873	14.3	106.5	1

Abbreviations: LPI, Largest Patch Index; NP, Number of Patches.

Himalaya. First, the Zanskar mountain range is predicted to have high levels of HBB movement across a wide area. This suggests that linkage between different HBB subpopulations residing in different geographic areas (such as Drass, Wakha, Parkachik, Rangdum and Padum) of this region ultimately depend on these group of mountains (Figa. 1 and 3). However, the models under low dispersal distance indicate restricted movement around northern areas of Lahul and Spiti (Fig. 3a). Furthermore, this region will be a potentially important movement route connecting HBB subpopulations of India and Pakistan (Deosai National Park). Second, the Great Himalayan mountain range has moderate to high levels of connectivity. The connectivity across this range may provide linkages between different existing HBB subpopulations in different protected areas (Figs. 1 and 3). In addition, this range is connected with Pir Panjal range via the Kishtwar mountains of Doda district, and also with the Zanskar range of Trans-Himalayan region via kargil (Ladakh) and Lahul and Spiti (Himachal Pradesh) (Figs. 1 and 3). Third, the Pir Panjal range shows low to moderate levels of connectivity connecting the north western (Kazinag NP), central (Gulmarg) and south eastern (Poonch and Hirpora) HBB subpopulations of this range (Figs. 1 and 3). Finally, the northwestern region of Ladakh range contains some corridors especially at low movement threshold.

Our factorial least cost paths results reflect the optimal movement network connecting the HBB subpopulations and reveal a low amount of high-intensity movement pathways for HBB across the landscape (Fig. 3). The high connectivity corridors in the Himalayan mountain range connect the different extant HBB subpopulations such as Kishtwar, Sechu-Tuan, Kugti, Tundah, Kullu, Sangla valley, Govind and Gangotri. Furthermore, the least cost pathways showed low to moderate connectivity corridors in Zanskar mountain range (Fig. 3). A potentially important route is also highlighted around the eastern edge of Great Himalayan range, through the Kishtwar mountains connecting HBB subpopulations between Great Himalayan range and Pir Panjal range. The network of predicted least cost pathways also shows extensive areas of lesser corridor intensity for HBB in this landscape (Fig. 3).

Effects of climate and land use change on population connectivity

Climate and land use change were predicted to substantially reduce the extent and connectivity of core areas for HBB across all future scenarios, but varied greatly in the magnitude of their effects (Figs. 4, 5 and 6; Supplementary Information Tables S2-S13, Figures S2-S13). In addition, our future connectivity change results are in relation to the percentile thresholds set based on the current scenario, and our findings imply that the negative impact of land use and climate change differed significantly across the percentile thresholds used in the analysis. Corroborating with our prediction, the negative impact of climate and land use changes increases as the dispersal distance decreases. Under high dispersal ability, our results revealed that at lower connectivity threshold (>0), the loss of core dispersal areas ranged from 1.2% to 7.0% in 2050 and 2.3% to 18.8% in 2070 climate-only scenarios (Fig. 6; Supplementary information Table S10, Figure S10). This effect slightly increases under combined climate and land use change scenarios. The percentage of loss, however, increases substantially with decreasing dispersal ability. For example, at medium dispersal ability the predicted loss of connectivity ranged from 3.4% to 10.0% in 2050 and 4.6% to 23.8% in 2070 climate-only scenarios (Fig. 5; Supplementary information Table S6, Figure S6), and at low dispersal ability the predicted loss of connectivity ranged from 6.9% to 16.3% in 2050 and 8.4% to 39.0% in 2070 climate-only scenarios (Fig. 4; Supplementary information Table S2, Figure S2). Similarly, the loss of core dispersal areas increases with increasing connectivity threshold. For example, at medium connectivity threshold (>50th Percentile) the loss of connectivity under high dispersal ability ranged from 51.5% to 87.6% in 2050 and 59.8% to 100% in 2070 climate-only scenarios (Fig. 7). At medium dispersal ability the predicted loss of core dispersal areas ranged from 52.2% to 92.6% in 2050 and 59.6% to 100% in 2070 climate-only scenarios (Fig. 7), and at low dispersal ability the loss ranged from 87.9% to 100% in 2050 and 91.4% to 100% in 2070 climate-only scenarios (Fig. 7).

Landscape metrics indicated that high dispersal core areas will decrease in size and isolated patches will increase in number in the future. For example, at low connectivity

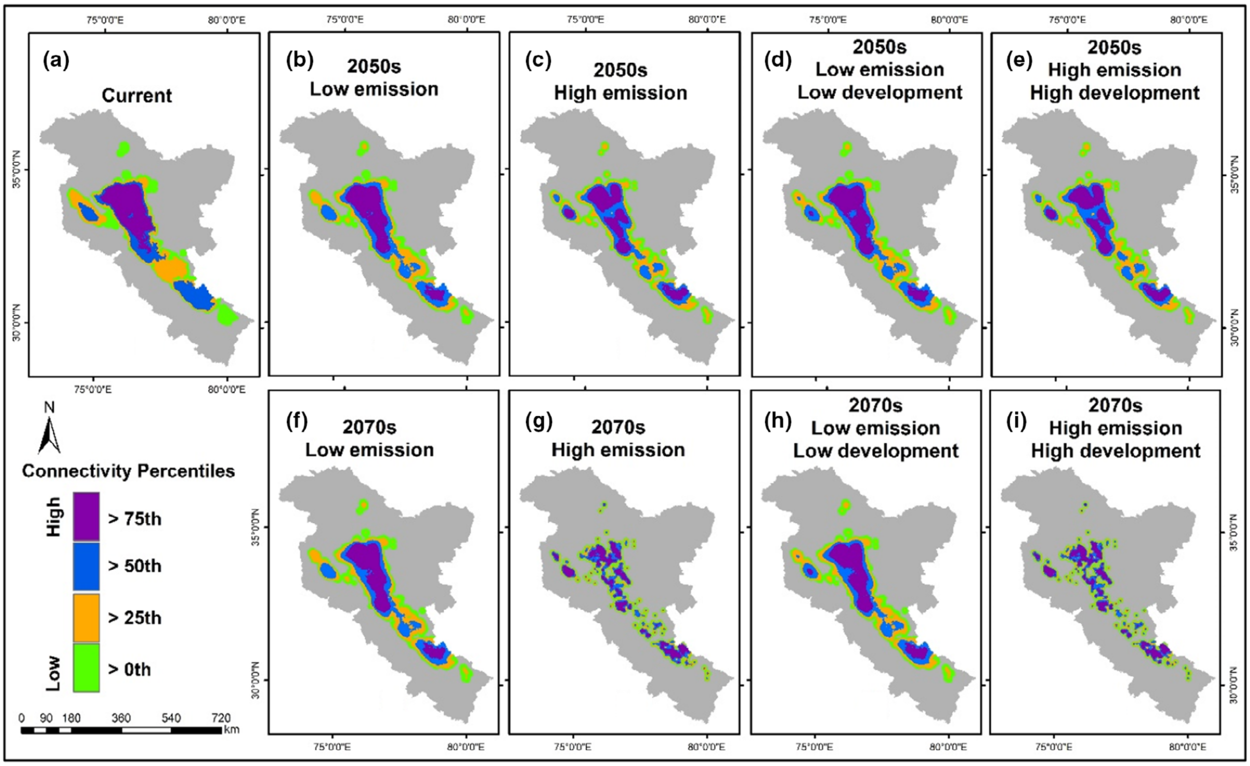

Figure 4 Resistant kernel connectivity maps of HBB under low dispersal ability (90 km) for current and eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

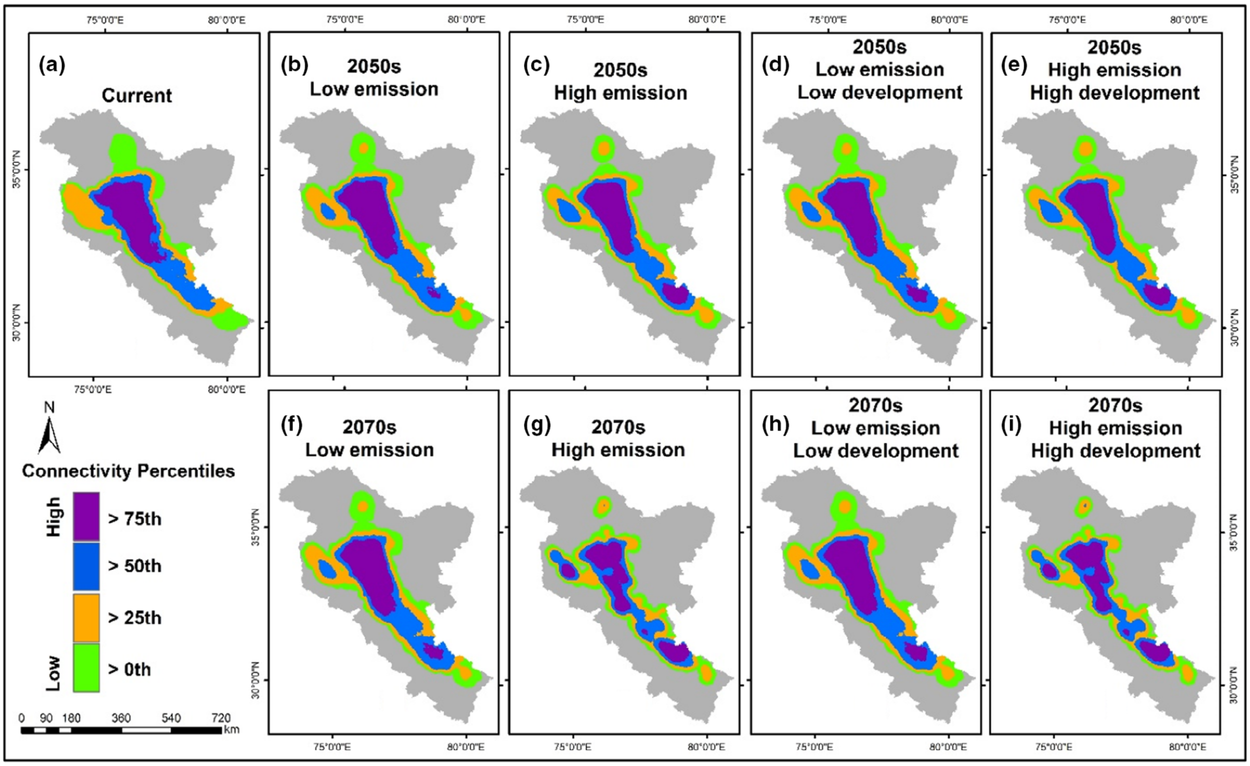

Figure 5 Resistant kernel connectivity maps of HBB under medium dispersal ability (250 km) for current and eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

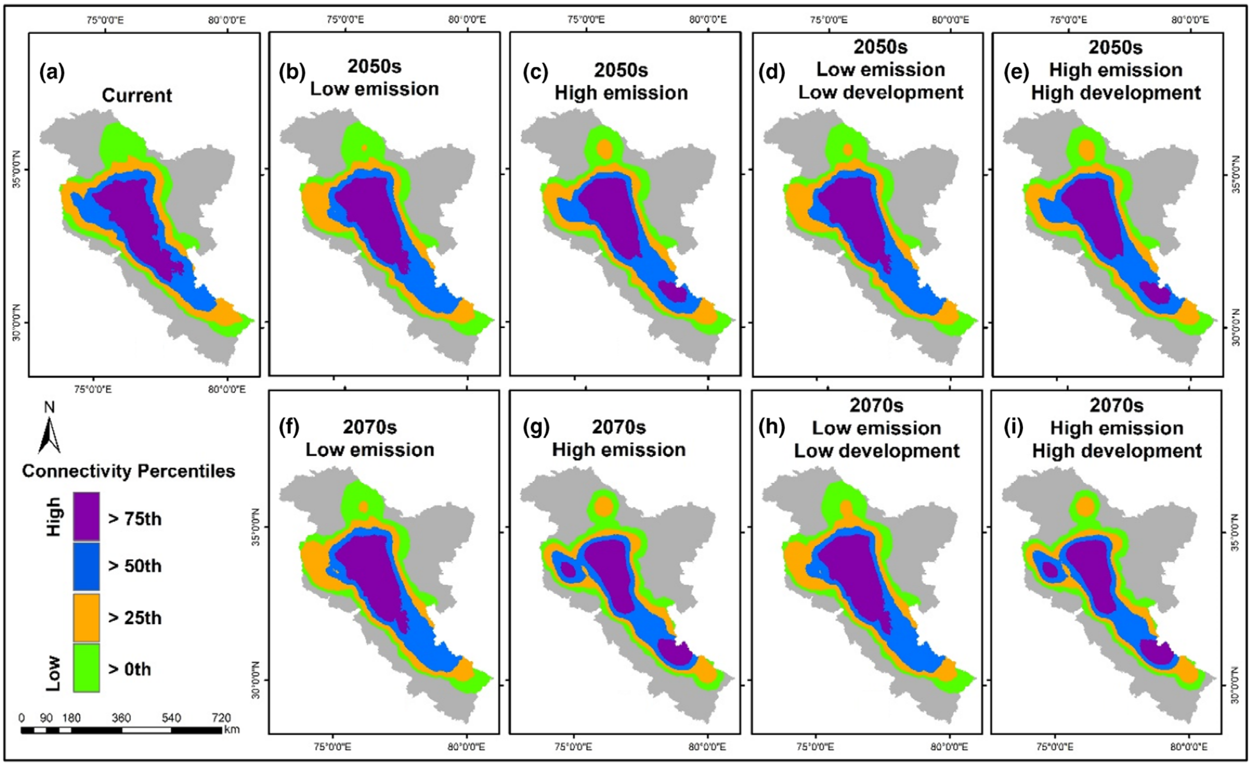

Figure 6 Resistant kernel connectivity maps of HBB under high dispersal ability (467 km) for current and eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

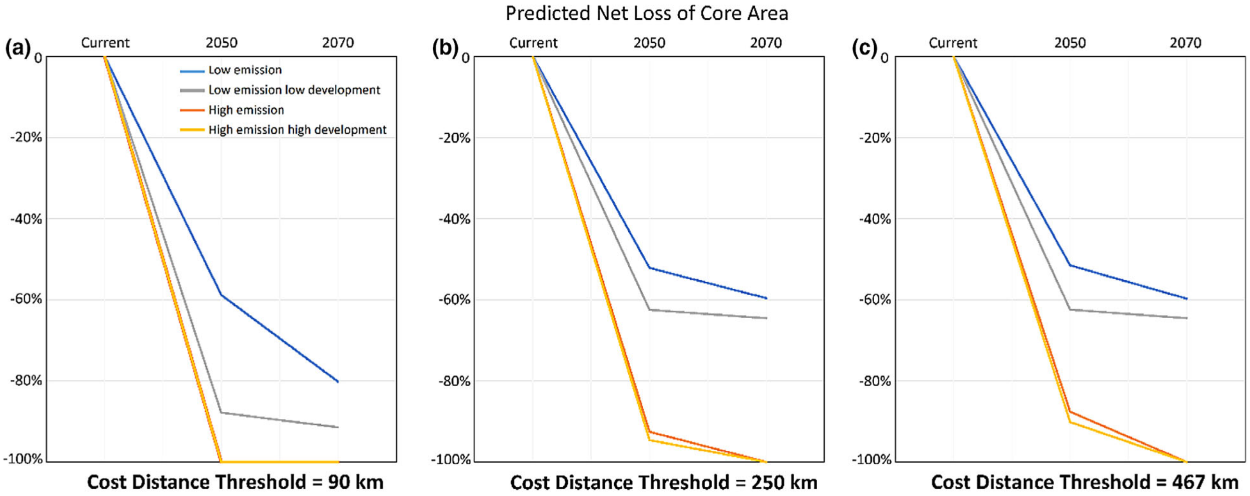

Figure 7 Future changes in dispersal core areas for brown bear in Western Himalaya at medium connectivity threshold (>50th, set based on current scenario) under three dispersal distances across eight future climate and land use change scenarios in 2050s and 2070s.

threshold, the core area was predicted to be fragmented into 15 isolated patches under low dispersal ability in 2070 future scenarios (Fig. 4; Supplementary information Table S2). However, at high dispersal ability the core area was predicted to remain a single patch (Fig. 6; Supplementary information Table S10).

Our future modeled connectivity suggests that, at lower connectivity thresholds, the dispersal habitat of HBB will shift into new areas under low emission and low development scenarios (indicated as 'gain' in our models; Supplementary Information Figures S1, S2, S6, S7, S10, S11 & Tables S2, S3, S6, S7, S10, S11); however, the gain was projected to be <3.0%, indicating the inability of low dispersing HBB to disperse between core areas. In addition, our models predicted massive connectivity loss under all climate change and all dispersal scenarios, with near total loss predicted at 25th percentile threshold or above (set based on the current scenario).

Discussion

The work presented here is the first extensive attempt to evaluate the ecological impacts of climate change and land use change on connectivity of species with high mobile capacities in the Indian Himalayan mountains. Although human land use change was projected to have a negative impact on the connectivity of HBB predicted by our models, it was to our surprise that such negative impact was relatively moderate when compared with the impact of climate change. In addition, the results of connectivity change vary greatly across the percentile thresholds used to classify connected vs. non-connected areas. With or without human land use change, all high emission scenarios in our models show a substantial loss of dispersal habitat for HBB at 50th percentile threshold or above, with 100% loss by the end of this century. This suggests that the extent and connectivity of HBB is extremely sensitive to climate, and is already on a climate tipping point, where projected warming drives rapid loss of habitat extent and connectivity. Climate change may be pushing HBB to higher elevations and further away from areas where humans prefer to settle, which can explain the relatively moderate effect of land use. Our dire predictions at 50th percentile threshold or above suggest that moderating these effects will need to go beyond local habitat conservation efforts. Our results suggest that there will still be a substantial loss of connectivity for HBB in the future if emissions are not reduced, but some low and very fragmented dispersal habitat may remain in the future especially at 25th percentile threshold or lower (Figs. 4, 5, and 6). As a result, local conservation efforts will be crucial to mitigate the impacts of climate change on HBB connectivity and facilitate its adaptation to climate change. Our results suggest that under several scenarios, especially low emission scenarios, the Zanskar mountain range and Great Himalayan mountain range are of particular importance for conservation and protection (Fig. 1). However, the overall very dire predictions of our results suggest that ultimately worldwide efforts to reduce greenhouse gas emissions may be required to conserve HBB population connectivity in the western Himalaya.

Consistent with previous studies on other species (Ashrafzadeh *et al.*, 2020; Cushman *et al.*, 2013, 2016), our landscape connectivity analysis indicated that the landscape connectivity of brown bears is extremely sensitive to the dispersal ability used for the analysis. Similarly, Cushman & Landguth (2012a), and Mohammadi *et al.*, (2021) found a greater effect of dispersal ability on landscape connectivity predictions than variations in resistance or habitat pattern, which highlights the importance of dispersal behavior in landscape connectivity. At low dispersal ability, which corresponds to female dispersal behavior, HBB are expected to have fragmented and isolated subpopulations. Conversely, the high dispersal scenarios suggest that HBB could potentially move between subpopulations, which would likely be driven by the natal dispersal of young males, the most active dispersal demographic group for bears (Stoen *et al.*, 2006). Male dispersers are generally less risk averse and disperse much further than females. Overall, HBB in this landscape may be able to maintain the genetic connectivity between existing subpopulations; however, as females are critical to recolonize and reproduction, their limited dispersal ability might result in reduced ability to recolonize or expand in new areas. Furthermore, brown bears are a highly mobile species and typically require large, continuous and diverse habitats, and have high individual space needs (Swenson *et al.*, 2000; Ripple *et al.*, 2014). Thus, it is likely that protection of large and well-connected habitat areas is crucial to support the viable population of this species in the study landscape (Ripple *et al.*, 2014), as has been shown in other regions (e.g. Mateo-Sánchez *et al.*, 2014, 2015*a*,*b*). Examination of predicted resistant kernel maps depicts that highest level of connectivity resides in three mountain ranges, Zanskar mountain range, Great Himalayan mountain range and Pir Panjal range. The linkage between different existing HBB subpopulations in this region may ultimately depend on these mountain ranges. Our findings are in accordance with previous studies conducted on this species, which also showed high connectivity in these ranges (Dai *et al.*, 2021; Mukherjee *et al.*, 2021).

Climate change and population connectivity of Himalayan brown bear

Future climate change and land use change were predicted to have substantial negative impact on the population connectivity of HBB across its range in Western Himalaya. Loss of connectivity for HBB has been observed in other modeling studies in this region as well (Dai *et al.*, 2021; Mukherjee *et al.*, 2021). Our results revealed that the impact of climate and land use change varied greatly across future scenarios, as well as across the three dispersal scenarios used for the analysis. Therefore, substantial effort should be focused in enhancing understanding of dispersal behavior and functional connectivity of the species to clearly understand the impact of future climate and land use change on their population connectivity in this landscape.

Moreover, our results also depict the shift of dispersal core areas to higher elevations in low emission and low development scenarios, which is similar to results of other studies on this species (Dai *et al.*, 2021; Mukherjee *et al.*, 2021) and other species (e.g. Wasserman *et al.*, 2012, 2013). However, our findings predicted a lower amount of new connected areas than shown by Dai *et al.*, (2021) and Mukherjee *et al.*, (2021). This difference might be because of modeling approach they have used (i.e. circuit theory approach), which did not incorporate the scale dependency of dispersal ability, which has shown to dominate the predictions of connectivity (Cushman, Compton, & McGarigal, 2010, 2013, 2016; Ash *et al.*, 2020).

Our factorial least-cost path analysis enabled us to map the optimal long dispersal routes between the existing HBB subpopulations in the study region, which, in turn, enables our analysis to prioritize areas for conservation action to facilitate the connectivity for current and future scenarios (e.g. Cushman *et al.*, 2013, 2018; Kaszta, Cushman, & Macdonald, 2020). Importantly, our results suggest that the current corridor linkages connecting different HBB subpopulations are predicted to be broken and shifted by future climate and land use change (Supplementary information Figure S1), similar to results for other mountain species climate connectivity assessments (e.g. Wasserman *et al.*, 2012, 2013). This spatially explicit information on long dispersal corridors can guide the conservation managers to develop landscape conservation strategies (e.g. assisted migration) and helps in identifying the most important current and climate resilient routes for HBB.

Our results suggest that at low to medium connectivity percentile thresholds, climate change and land use change will contribute to an increase in habitat fragmentation by the end of this century (high emission scenarios), but eventually, habitat fragmentation will decrease as most fragmented remnant habitat patches will turn into complete losses at higher connectivity thresholds across all scenarios. Such prediction resembles those of Wasserman *et al.* (2012, 2013) in which they also predicted increasing habitat fragmentation and eventual habitat losses for the American marten under projected climate change.

Genetic diversity declines when populations are fragmented into isolated patches (Shirk & Cushman, 2011), which has previously been shown to be particularly relevant for carnivores experiencing habitat and connectivity contractions due to climate change in mountain ecosystems (Wasserman *et al.*, 2012, 2013). As a result, our projections of large reductions in habitat extent and connectivity in the future landscape suggest that HBB may suffer severe demographic and genetic consequences. The HBB subpopulations in the western Himalayas are declining (Dar *et al.*, 2021), with just 130–220 individuals left between Pakistan and India (McLellan *et al.*, 2017, Sup. Info of IUCN assessment), necessitating climate change mitigation and adaptation conservation efforts for long-term survival of this species.

The spatial connections in meta-populations are crucial for long-term persistence of species, and can lead to regional conservation planning (Santini, Saura, & Rondinini, 2016). In the present study, the predicted loss of dispersal core areas may hamper the meta-population dynamics of HBB in this region and reduce their genetic diversity (e.g. Cushman *et al*, 2012, 2013). This may reduce the population's evolutionary capacity (Noel *et al.*, 2007), leading to inbreeding depression (Van Noordwijk, 1994), and ultimately resulting in population extinction (Lacy, 1997; Tanaka, 2000; Frankham, 2005).

Scope and limitations

While our models were developed using data collected with the most rigorous surveying efforts for HBB in the region, it is also worth noting that connectivity models based on presence points and habitat selection models have shown to underperform for some species in other studies (Mateo-

Sánchez *et al.*, 2015; Zeller *et al.*, 2018) because of potential differences in the requirements between movement habitat and residence habitat (LaRue & Nielsen, 2008; Ziółkowska *et al.*, 2012; Trainor *et al.*, 2013). Our prediction is based on observed patterns of occurrence in relation to environmental variables, which does not necessarily reflect the fundamental niche limitations of the species (in fact certainly does not give the wide amplitude of HBB occurrence across its range). This, in turn, suggests that our predictions might be improved by studying the functional connectivity based on empirically optimized resistance models using movement data (e.g. Cushman & Lewis, 2010; Elliot *et al.*, 2014*a*,*b*; Mateo-Sánchez *et al.*, 2015*a*,*b*; Ziółkowska *et al.*, 2016) and genetic data (e.g. Shirk *et al.*, 2010; Wasserman *et al.*, 2010), which likely are more closely related to the actual patterns and processes that limit HBB connectivity in this region than realized niche and observed occurrence patterns.

Another limitation of our model is that they relied on climate and human land use and did not incorporate different land cover models. However, the future climatic variations could change the vegetation covers and shift the plant species to new areas in higher elevations (Roberts, Nielsen, & Stenhouse, 2014; Manish *et al.*, 2016). In this case, our predicted new connected habitat in future scenarios could be underestimated. This discrepancy suggests that future research should focus to project the joint effects of climate change on vegetation and disturbances and then relate that to habitat suitability and connectivity for HBB.

Conclusion

We found a substantial loss of connectivity for HBB, indicating connectivity may be a limiting factor for future HBB subpopulations in Western Himalaya. Specifically, climate change under the high emission scenarios may completely eliminate the connectivity for HBB by year 2070 in our study area. However, ongoing climate and land use change can also impact other ecosystems and species in this landscape. Therefore, a comprehensive assessment of climate and land use change impact on a range of species representing the vulnerable ecosystems of this landscape is needed using comparable methodologies to produce a multi-species connectivity assessment that can be used to guide comprehensive conservation planning (e.g. Cushman & Landguth, 2012b; Cushman *et al.*, 2013).

We believe that the work presented here constitutes a substantial and informative evaluation of the potential effects of several, realistic, ongoing climate and land use scenarios on HBB. As such, we believe our results can be used immediately to prioritize the most climate-resilient areas for conservation and protection, particularly of the most important core areas and the corridors between them identified in our results. Furthermore, we hope that this study will be useful to guide future research. For example, future research should focus on acquiring HBB movement and genetic data, and should prioritize optimizing the resistance model by using multivariate optimization of geneflow models (Shirk *et al.*, 2010; Mateo-Sánchez *et al.*, 2015*a*,*b*), or by landscape relationships between movement behavior and landscape features (Cushman & Lewis, 2010; Zeller *et al.*, 2014; Elliot *et al.*, 2014a).

Finally, our study demonstrates a practical approach to predict and disentangle effects of climate change and human land use change on species connectivity, and highlights the importance of climate change mitigation in effective conservation. We hope that this study will motivate and provide a conceptual toolkit to officials, readily applicable to different regions and species. In the interim, we believe that our results will provide a basis for geographically focused conservation efforts to protect the biodiversity from severe genetic consequences under the influence of climate and land use changes.

Acknowledgments

We are thankful to the Department of Science and Technology, Government of India for providing financial support to this study (Grant ID: SERB/F5154/2014-2015). The first author thank The Council of Scientific and Industrial Research for providing the monthly fellowship (Award letter no. 09/668(0009)/2018-EMR-I). We thank wildlife departments of Jammu and Kashmir, Himachal Pradesh and Uttarakhand for necessary permission to conduct the study in Western Himalaya. We thank Dr. S. P. Goyal for his incredible support and suggestions. We are also thankful to the field assistants for their hep during fieldwork.

Author contributions

Shahid Ahmad Dar: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Sujeet Kumar Singh:** Investigation, Data curation, Project administration, Writing – review & editing. **Ho Yi Wan:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Supervision, Writing – review & editing. **Samuel A. Cushman:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Tawqir Bashir:** Investigation, Writing – review & editing. **Sambandam Sathyakumar:** Conceptualization, Methodology, Supervision, Writing – review & editing, Project administration.

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Supporting information

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

Figure S1. Least-cost path connectivity maps showing the long dispersal corridors for Himalayan brown bear under low dispersal ability (90 km) for current and eight future climate and land use change scenarios in 2050s and 2070s. The factorial least-cost paths show the similar pattern across the three dispersal distances used for all future scenarios.

Figure S2. Future changes in dispersal core areas for brown bear in Western Himalaya under low dispersal ability (90 km) assuming a connectivity threshold of 0th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S3. Future changes in dispersal core areas for brown bear in Western Himalaya under low dispersal ability (90 km) assuming a connectivity threshold of 25th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S4. Future changes in dispersal core areas for brown bear in Western Himalaya under low dispersal ability (90 km) assuming a connectivity threshold of 50th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S5. Future changes in dispersal core areas for brown bear in Western Himalaya under low dispersal ability (90 km) assuming a connectivity threshold of 75th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S6. Future changes in dispersal core areas for brown bear in Western Himalaya under medium dispersal ability (250 km) assuming a connectivity threshold of 0th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S7. Future changes in dispersal core areas for brown bear in Western Himalaya under medium dispersal ability (250 km) assuming a connectivity threshold of 25th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S8. Future changes in dispersal core areas for brown bear in Western Himalaya under medium dispersal ability (250 km) assuming a connectivity threshold of 50th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S9. Future changes in dispersal core areas for brown bear in Western Himalaya under medium dispersal ability (250 km) assuming a connectivity threshold of 75th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S10. Future changes in dispersal core areas for brown bear in Western Himalaya under high dispersal ability (467 km) assuming a connectivity threshold of 0th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S11. Future changes in dispersal core areas for brown bear in Western Himalaya under high dispersal ability (467 km) assuming a connectivity threshold of 25th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S12. Future changes in dispersal core areas for brown bear in Western Himalaya under high dispersal ability (467 km) assuming a connectivity threshold of 50th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S13. Future changes in dispersal core areas for brown bear in Western Himalaya under high dispersal ability (467 km) assuming a connectivity threshold of 75th percentile across eight future climate and land use change scenarios in 2050s and 2070s. The future connectivity is in relation to the percentile thresholds set based on the current scenario.

Figure S14. Future changes in dispersal core areas for brown bear in Western Himalaya at low connectivity threshold (>0th, set based on current scenario) under three dispersal distances across eight future climate and land use change scenarios in 2050s and 2070s.

Figure S15. Future changes in dispersal core areas for brown bear in Western Himalaya at medium connectivity threshold (>52th, set based on current scenario) under three dispersal distances across eight future climate and land use change scenarios in 2050s and 2070s.

Figure S16. Future changes in dispersal core areas for brown bear in Western Himalaya at high connectivity threshold (>75th, set based on current scenario) under three dispersal distances across eight future climate and land use change scenarios in 2050s and 2070s.

Table S1. Description of variables used by Dar *et al.* (2021) to predict the potential distribution of brown bears in Western Himalaya.

Table S2. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at low dispersal ability (90 km) assuming a connectivity threshold of 0th percentile under future projections.

Table S3. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at low dispersal ability (90 km) assuming a connectivity threshold of 25th percentile under future projections.

Table S4. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at low dispersal ability (90 km) assuming a connectivity threshold of 50th percentile under future projections.

Table S5. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at low dispersal ability (90 km) assuming a connectivity threshold of 75th percentile under future projections.

Table S6. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at medium dispersal ability (250 km) assuming a connectivity threshold of 0th percentile under future projections.

Table S7. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at medium dispersal ability (250 km) assuming a connectivity threshold of 25th percentile under future projections.

Table S8. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at medium dispersal ability (250 km) assuming a connectivity threshold of 50th percentile under future projections.

Table S9. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at medium dispersal ability (250 km) assuming a connectivity threshold of 75th percentile under future projections.

Table S10. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at high dispersal ability (467 km) assuming a connectivity threshold of 0th percentile under future projections.

Table S11. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at high dispersal ability (467 km) assuming a connectivity threshold of 25th percentile under future projections.

Table S12. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at high dispersal ability (467 km) assuming a connectivity threshold of 50th percentile under future projections.

Table S13. Change in dispersal habitat (Gain, Loss and Net Change) and landscape matrices of brown bears in Western Himalaya at high dispersal ability (467 km) assuming a connectivity threshold of 75th percentile under future projections.