

Projected climate change threatens Himalayan brown bear habitat more than human land use

S. A. Dar¹ , S. K. Singh¹ , H. Y. Wan² , V. Kumar¹, S. A. Cushman³ & S. Sathyakumar¹ 

¹ Wildlife Institute of India, Dehradun, India

² Department of Wildlife, Humboldt State University, Arcata, CA, USA

³ USDA Forest Service Rocky Mountain Research Station, Flagstaff, AZ, USA

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Correspondence

Sambandam Sathyakumar, Wildlife Institute of India, Chandrabani, Dehradun 248001, Uttarakhand, India.
Email: ssk@wii.gov.in

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Abstract

Climate change and land use change jointly are the largest drivers of population declines, range contraction and extinction for many species across the globe. Wide-ranging and large-bodied species are especially vulnerable to habitat loss and fragmentation due to their typically low population densities, reflecting their need for extensive and connected habitats. We used the multi-scale Random Forests machine learning algorithm to identify factors driving the habitat selection and future changes in habitat of Himalayan brown bear, an iconic wide-ranging and large-bodied species of high conservation interest, across a range of spatial scales. Habitat selection of brown bears was scale-dependent, with most variables selected at broad scales. Climatic variables such as maximum temperature of coldest month, minimum temperature of warmest month and the potential evapotranspiration of wettest quarter strongly influenced habitat selection of brown bears. Future projections indicate a strong difference between the high and low emission scenarios. Alarming, our model suggests that high emission scenarios, with or without land use change, may result in a decline of brown bear habitat of >90% by the end of the century. In contrast, low emission scenarios are projected to reduce brown bear habitat by <23%, with much of the species range shifting to higher elevations. This study provides an integrative understanding of scale-dependent variables in brown bear habitat selection, providing critical information for prioritizing areas for habitat management and conservation. Most importantly, our future projections imply that traditional conservation efforts, such as *in situ* conservation, will not be sufficient to protect the species without climate change mitigation. The incorporation of climate change mitigation and adaptation in conservation strategies will be one of the most pressing priorities in biodiversity conservation in this region.

Introduction

Human land use and climate change have altered landscapes and ecological processes across virtually all ecosystems on Earth. Given the high rate of anthropogenic change, many wildlife species are unable to adapt quickly enough to maintain their fitness in human-modified landscapes (Myers & Knoll, 2001). Increasing human activities, such as agriculture, urban development and the building of travel routes, have detrimental impacts on habitat availability and quality (Dixo *et al.*, 2009), reducing species survival (Cushman *et al.*, 2018; Kaszta *et al.*, 2019), dispersal (Cushman, Lewis & Landguth, 2014; Mateo-Sanchez, Cushman & Saura, 2014a), gene flow (Kaszta *et al.*, 2020) and other functional linkages between habitat patches (Scolozzi & Geneletti, 2012; Gao *et al.*, 2013). These negative impacts are often

exacerbated by climate change. As climate changes the suitable ecological conditions for species may shift such that the species must also shift its range (e.g. Shirk *et al.*, 2018). The interaction of anthropogenic habitat loss and climate driven range shifts creates a synergy that amplifies the negative effects of each stressor. For example, suitable climatic niche space may not be accessible due to limited ability of species to shift ranges as a result of habitat loss or fragmentation (Bellard *et al.* 2012).

Evaluating species-habitat relationships has become increasingly important as many species across the globe are facing the threat of extinction due to habitat loss, fragmentation and degradation (Marzluff & Sallabanks, 1998). Habitat loss and fragmentation disrupt dispersal and gene flow between populations and increase extinction risks (With & King, 1999; Flather & Bevers, 2002; Roques *et al.*, 2016).

Wide-ranging and large-bodied species are especially sensitive and vulnerable to habitat loss and fragmentation because they typically have low population densities, require large, continuous and diverse habitats, and have high individual space needs (Ripple *et al.*, 2014). Many of these species are geographically widespread and require conservation and management over large areas.

When analyzing species-habitat relationships, especially in complex landscapes, the scale at which the relationships are examined can influence the accuracy of model prediction (Mateo-Sanchez *et al.*, 2014a; Wan *et al.*, 2017). Because organisms perceive and respond to their environment at multiple spatial and temporal scales (Wiens, 1989), it is recommended not only to determine the underlying environmental factors that influence habitat selection, but also the scales at which these factors are most relevant to the species (Levin, 1992; Mateo-Sanchez *et al.*, 2014a; McGarigal *et al.*, 2016). Scale is the lens that focuses ecological relationships, and improper scaling in the analysis may distort species-habitat relationships and may lead to wrong conclusions (Rettie & Messier, 2000; Bradter *et al.*, 2013; McGarigal *et al.*, 2016).

One way to quantitatively identify the proper scales of predictor variables in species-habitat relationships is to employ a multi-scale optimization, that is, identifying the characteristic spatial scale at which the predictor variables best relate to habitat selection of a species (McGarigal *et al.*, 2016). An increasing number of habitat studies have indicated that using multi-scale approaches can improve model predictions and make more accurate inferences (e.g. Shirk *et al.*, 2012; Wasserman *et al.*, 2012a; Vergara *et al.*, 2015; Macdonald *et al.*, 2018, 2019). These studies demonstrate that species-habitat relationships are scale-dependent, with organisms selecting different resources across a hierarchy of spatial scales. For example, brown bears (*Ursus arctos*) at higher elevations reportedly select den sites at fine scales to escape harsh winters, minimize energy costs and ensure security of cubs (Libal *et al.*, 2012). Landscape features related to the dispersal and migration of brown bears are selected at broader scale (Naves *et al.*, 2003; Mateo-Sanchez *et al.*, 2014a, 2015). Thus, it is important to identify the appropriate scale at which habitat variables are most strongly related to different ecological processes.

The Himalayan region is characterized by extreme topography, diverse vegetation and widespread human influence, and supports exceptionally high biodiversity (Myers *et al.*, 2000). In recent years, the demand for natural resources in this region has increased many fold due to rapid human population growth, leading to extensive clearing of native forests and grasslands. This has resulted large and rapid reductions in the extent, and increased fragmentation, of wildlife habitat for many species in the region. The human population is still rapidly growing in this region (Apollo, 2017), and thus there are increasing pressures for more intensive human land use. Furthermore, the Himalaya is also one of the fastest warming regions in the world, with mean annual temperature expected to increase by 1°C–2°C by 2050 and 1.5°C–3°C by the end of 21st century (IPCC, 2013). Therefore, to develop effective biodiversity conservation strategies, a first step is to

characterize and map current species habitats, and to project how the extent, quality and fragmentation of habitat are likely to change under human land use and climate change.

The IUCN endangered Himalayan brown bear *U. a. isabellinus* is a potential indicator and umbrella species in the Himalayan ecosystem. The brown bear is broadly but sparsely distributed across the Palearctic and Nearctic faunal regions. It serves as a management indicator species for national conservation planning of other wide-ranging species (Simberloff, 1999; Carroll *et al.*, 2001; Dai *et al.*, 2019). The populations of Himalayan brown bear are declining (Sathyakumar *et al.*, 2012; McLellan *et al.*, 2017), low in density and largely isolated in the alpine and sub-alpine regions of the north-western and western Himalayan ranges (Sathyakumar, 2001; Sathyakumar, 2006a,b). Its decline is usually attributed to habitat loss and fragmentation due to land use change and increased human pressure (Sheikh & Molur, 2004; Nawaz, 2007). Furthermore, climate change emerges as a threat to the brown bear, causing displacement and range contraction (Shrestha, Gautam & Bawa, 2012; Su *et al.*, 2018). For example, a recent study indicated that climate change may lead to a substantial reduction in potential habitat for brown bears in Central Asia and Asian highlands (Su *et al.*, 2018).

The ecology of brown bears has been studied extensively across its range in North America and Europe (Haroldson *et al.*, 2020; Swenson *et al.*, 2020). However, in India and other parts of Asian highlands, the ecological information on brown bears is limited. The few existing studies are on phylogeography, feeding ecology, species distribution modelling, human-bear conflicts and daily activity patterns (Sathyakumar, 2002, 2006a,b; Mohanta & Chauhan, 2011; Lan *et al.*, 2017; Su *et al.*, 2018; Sharief *et al.*, 2020).

We used a combination of climatic, landscape composition, topographic and anthropogenic variables across a range of spatial scales to predict current and future brown bear habitat in the Western Himalaya. The aim was to test for scale-dependent factors driving brown bear habitat selection (e.g. Boyce, 2006; Ciarniello *et al.*, 2007; Mateo-Sanchez *et al.*, 2014a), and project future changes in brown bear habitat under the influence of human land use and climate change (e.g. Wasserman *et al.*, 2012b, 2013; Penteriani *et al.*, 2019). We hypothesize that (1) the spatial scales that most strongly influence brown bear habitat selection will vary by environmental variable, with (2) landscape composition affecting brown bear at fine scales and human disturbance variables at broad scales (following Mateo-Sanchez *et al.*, 2014a) and (3) projected human land use and climate change will substantially reduce habitat availability for the brown bear by 2070.

Methods

Study area

The Western Himalaya of India lies in the Oriental zoogeographic realm (Holt *et al.*, 2013). The study area covers 327 996 km² of the alpine and sub-alpine regions of Western Himalaya, encompassing the entire range of Himalayan brown bears in India (Fig. 1a). Topographic and physiographic

features are complex and typical of the region, which includes several major Indian mountain ranges, such as the Zaskar Range, Pir Panjal Range, Karakoram Range, Siwalik Range and the Great Himalayas. Elevation ranges from 181 to 8569 m (Fig. 1b). Mean annual temperature ranges from -24.1 to 32.5°C . The region contains distinct vegetation regimes that harbor 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 *Cervus hanglu*, blue sheep *Pseudois nayaur*, Tibetan antelope *Pantholops hodgsonii*, urial *Ovis orientalis* and musk deer *Moschus leucogaster* (Sathyakumar & Bashir, 2010). Temperature strongly contrasts between hot summer from June to August (mean temperature 32.5°C) and severe cold winter from December to February (mean temperature -24.1°C). Mean annual precipitation ranges from 34 to 2,934 mm, with $\sim 1,500$ mm from rainfall. Intensive rainfall and snowmelt from snow-covered peaks form a number of major river systems, including the Ganga, Yamuna, Jhelum, Chenab, Satluj and Beas rivers.

Vegetation in the study region changes along an elevational climatic gradient, and primarily includes, from lowest to highest elevation, alluvial grasslands, subtropical forests, conifer forests and alpine meadows. The forests of this region are characterized by Himalayan Temperate forest, Sub-alpine, Tropical Dry Deciduous Forest, Tropical Forest, Sub-tropical broad leaved, Temperate Broadleaved forest, Tropical Coniferous Forest, Dry Deciduous Forest, Moist Deciduous Forests and Sal Forest (Champion & Seth, 1968). The major tree species in this region are *Cedrus deodara*, *Abies pindrow*, *Picea smithiana*, *Pinus roxburghii*, *Pinus wallichiana*, *Quercus leucotrichophora*, *Q. floribunda*, *Q. Semecarpifolia*, *Q. lanuginosa*, *Aesculus indica*, *Betula utilis* and other species. Forests in this region are particularly important for maintaining biodiversity and providing ecosystem services to the north Indian plains. In recent years, rapid development of transportation infrastructure and increasing urban and suburbanization led to rapid deforestation.

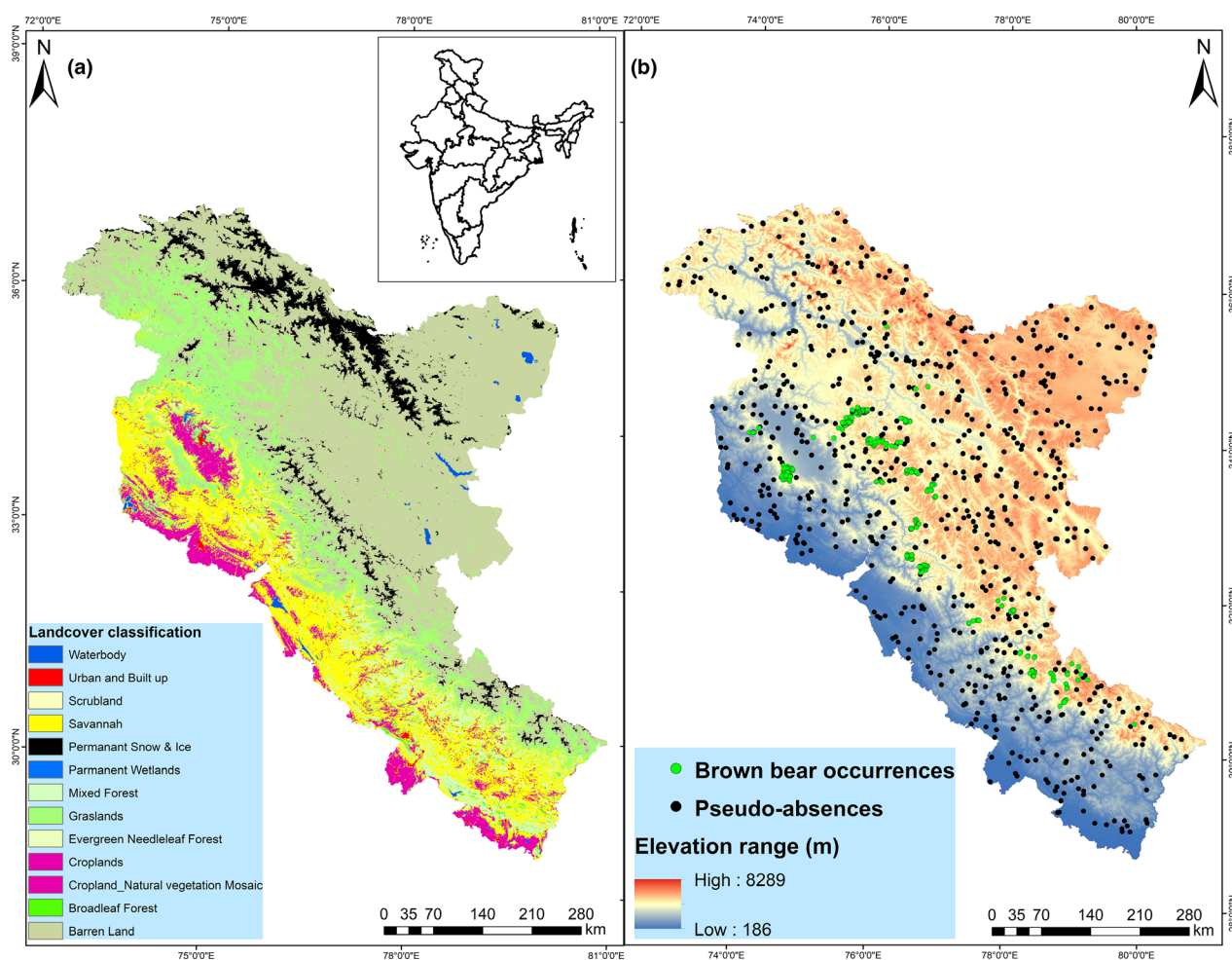


Figure 1 Study area the Western Himalaya (a) the landcover classes in the study area, (b) the elevation range of the study area. The green dots represent the brown bear occurrences and black dots represent the pseudo-absences.

Brown bear data

We conducted surveys and recorded presence locations of Himalayan brown bear from March to December in the years 2015–2017. A total of 165 trails of varying lengths (altogether 1337.9 km in length) were surveyed during the study period (Supporting Information Figure S1). While our surveys covered the entire study area, our efforts were more intense along natural trails, ridges, and *nullahs*. Both direct (i.e. sightings) and indirect evidences (i.e. scats) were recorded as presences (Fig. 1). To ascertain the species of indirect evidences, scat samples were collected from the field and genetically analyzed in the lab by amplifying the mitochondrial control region (Taberlet & Bouvet, 1994) and Cytb (Lan *et al.*, 2017). A total of 720 presence records were confirmed (25 direct and 695 indirect evidences). Our data represent an important source of Himalayan brown bear occurrence records in India, as no formal field survey has been previously attempted at this scope for this subspecies. The last assessment of the species across the whole distribution range in India was based on questionnaire survey (Sathyakumar, 2006a), and most of the studies were conducted in Kugti WLS and Lahul valley (Sharief *et al.*, 2020).

Generating pseudo-absences

Obtaining true absence data is especially challenging when studying cryptic, rare or highly mobile species. Yet, these species are usually of high conservation interest. When true absence data are unavailable, such as in this study, pseudo-absences are often used as a replacement (Ferrier *et al.*, 2002; Brotons *et al.*, 2004; Pearce & Boyce, 2006). Some studies demonstrated that an imbalance between the proportion of presence and absence classes can cause bias in the prediction and model-fit (Chawla *et al.*, 2003; Chen, Liaw & Breiman, 2004). Therefore, we generated 720 pseudo-absences, which is equal to the number of presence records. The pseudo-absences were generated in a spatially random pattern within the study extent, with the constraint that each pseudo-absence point was at least 2 km from presence and other pseudo-absence locations to reduce spatial dependence.

Habitat variables

We selected *a priori* 40 variables that are potentially related to habitat selection of brown bears in India based on published literature demonstrating the importance of these variables on brown bear occurrences (e.g. Clevenger *et al.*, 1997; Koren *et al.*, 2011; Nawaz, Martin & Swenson, 2014; Mateo-Sanchez *et al.*, 2014a; Su *et al.*, 2018; Sharief *et al.*, 2020). These variables represent climate, landscape composition, topography and anthropogenic influences in the region. All variables were projected to the 44N UTM projection and resampled to a 1 km spatial resolution in ArcGIS. Categorical variables were resampled using the nearest neighborhood method, whereas continuous variables were resampled using the bilinear interpolation method. The complete list of

variables, their description and source are given in Supporting Information Table S1.

Focal statistics at multiple scales

We calculated the focal mean of each variable around each presence and pseudo-absence locations across eight spatial scales: 1, 2, 4, 8, 16, 32, 64 and 128 km radii (e.g. Mateo-Sanchez *et al.*, 2014a) based on the average dispersal distance recorded in a species (108.3 km $\pm$ 27.4) (Støen *et al.*, 2006). To do this, we conducted a moving window analysis with the focal statistics tool in ArcGIS 10.3 (ESRI, Redlands, CA) using the scales described above as the search neighborhoods. This gave us an output raster of each variable at each scale across the study area, which allowed us to extract the focal mean at each location.

Multi-scale optimized multivariate modelling

We used the random forest algorithm to model habitat suitability for brown bears. Random forest is a machine learning algorithm that utilizes a decision tree-based bootstrap aggregation or bagging technique, and has shown to outperform other common assessment methods such as logistic regression (Evans *et al.*, 2011; Cushman *et al.*, 2017; Cushman & Wasserman, 2018). Random forest is non-parametric and does not assume independence. Therefore, unlike traditional regression-based approaches, it is not affected by spatial-autocorrelation. Still, we minimized the spatial autocorrelation among species presences by applying a spatial filter. Briefly, we buffered each sample locations by a 2-km radius, which was selected based on the mean daily movement of brown bears at ~4 km (Ćirović *et al.*, 2015; Almasieh, Rouhi & Kaboodvandpour, 2019). When any buffered locations overlapped, we randomly kept one of them and removed the rest.

We conducted the random forests using a two-step multi-scale optimization framework as suggested by McGarigal *et al.*, (2016), and implemented in random forests by Cushman *et al.*, (2017). First, we conducted a univariate scaling analysis to identify the spatial scale at which each variable was most strongly related to brown bear occurrences. Presences and pseudo-absences of brown bears were used as the response variable in random forests, and were tested against one habitat variable and one scale at a time. The best supported scale of each variable was determined based on the model with the lowest out-of-bag (OOB) error rate (Supporting Information Figure S2–S5).

Second, we used random forest to develop multivariate models to predict probability of brown bear occurrences using the suite of scale-optimized variables from step one. To identify the most parsimonious model, we filtered variables with two procedures: (1) we applied the multicollinearity function in the rUtilities R package to assess the potential correlation among all possible pairs of scaled variables and removed the variables that were highly correlated ($P < 0.05$), and (2) we used Model Improvement Ratio (MIR) to retain

only the most important variables (Murphy, Evans & Storfer, 2010). The MIR uses the permuted variable importance, represented by the mean decrease in OOB error, standardized from zero to one. The variables are subset using 0.10 threshold increments, with all variables above the threshold retained for each model. This subset is always performed on the original model's variable importance to avoid over-fitting (Svetnik *et al.*, 2004). We compared each subset model and selected the model that exhibited the lowest total OOB error and lowest maximum within-class error. We generated scaled variable importance and partial dependency plots for each variable selected in the final model. The partial dependency plots are useful in illustrating the relationship between the predicted probability of brown bear occurrence and each habitat variable in the model.

Prior to all random forest modeling, we determined the minimum number of trees required by testing 10 000 bootstrap samples and examined when the out-of-bag error ceased to improve. We determined that the OOB error stabilized between 500 and 1500 trees (Supporting Information Figure S6). To be conservative, we used 2000 trees in all models for the rest of the analysis. All random forest models were performed using the R package 'randomForest' (Liaw & Wiener, 2002).

Model validation

The performance of the model was assessed by random permutations, cross-validation using a resampling approach (Evans & Murphy, 2018), whereby, one-tenth of the data were withheld as a validation set for each permutation. The cross-validation at 99 permutations produces a suite of performance matrices including OOB error rate, Model error variance, and Kappa index of agreement. The OOB error rate measures the proportion of OOB samples that are incorrectly classified, and the Kappa index of agreement is a measure of agreement between predicted presences and absences with actual presences and absences corrected for agreement that might be due to chance alone. The statistical range of Kappa index of agreement ranges from 0 to 1: values <0 indicate no agreement, 0–0.20 as slight, 0.21–0.40 as fair, 0.41–0.60 as moderate, 0.61–0.80 as substantial, and 0.81–1 as almost perfect agreement (Landis & Koch, 1977).

Future land use and climate change scenarios

Using the multi-scale optimized multivariate model from above (i.e. the same set of variables), we projected future habitat suitability of brown bears in the 2050s (i.e. 2041–2060) and 2070s (i.e. 2061–2080) under several human land use and climate change scenarios. Climatic variables for future projection were obtained from the same source as our current climatic variables (i.e. WorldClim, Fick & Hijmans, 2017). These variables were based on Coupled Model Inter-Comparison Project (CMIP5) and contained climate projections under four representative concentration pathways (RCPs). We applied the MIROC5 (Model for

Interdisciplinary Research on Climate) (Watanabe *et al.*, 2010) general circulation model (GCM) and included a low emission (RCP 2.6) scenario and a high emission (RCP 8.5) scenario in our projections. Variations within and among different climatic models available at present pose problems in identifying the robust model to use and there is no clear guidance on how and which climatic models to select for a particular region (Perkins *et al.*, 2007; Beaumont, Hughes & Pitman, 2008). We picked MIROC5 model in our study, because Su *et al.*, 2018 used this model to assess the impact of climate change of potential habitat of brown bears in Asia highlands and showed promising results.

Future climatic variables such as Actual evapotranspiration (AET Post monsoon, AET Spring and AET Winter), Potential evapotranspiration (PET of wettest quarter), Maximum temperature of coldest month and Minimum temperature of warmest month were estimated using the 'envirem' R package (Title & Bemmels, 2018).

To project future landscapes with human land use changes, we used a layer of croplands and cropland/natural vegetation mosaics and urban/built up areas projected for years 2050 and 2100 from the GeoSOS global database (<http://geosimulation.cn/GlobalLUCCProduct.html>; Li *et al.*, 2017). Two future scenarios were included in this layer: A1B scenario – moderate increase in land use across all resources, and A2 scenario – high emphasis on development with adverse impact on the environment. We included both scenarios in our future projections. Other variables were held constant.

Together, we projected habitat suitability of brown bears under the following 12 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 2050s Low development scenario (A1B 2050)
- 6 2050s High development scenario (A2 2050)
- 7 2070s Climate change-only, low emission scenario (RCP 2.6 2070s)
- 8 2070s Climate change-only, high emission scenario (RCP 8.5 2070s)
- 9 2070s Low emission and low development scenario (RCP 2.6 2070s + A1B 2100)
- 10 2070s High emission and high development scenario (RCP 8.5 2070s + A2 2100)
- 11 2070s Low development scenario (A1B 2100)
- 12 2070s High development scenario (A2 2100)

Change detection

Using the multi-scale optimized multivariate models of current and future (2050s and 2070s) from above, we calculated changes in the potential habitat of brown bear in

Western Himalaya. To assess changes between current and future habitat predictions, we first used a threshold value of 0.5 to determine suitable habitats for the current and future scenarios. This threshold of 0.5 suggests that the probability of occurrence is greater than the probability of non-occurrence, and threshold is established in the literature and widely used in many studies (i.e. Manel *et al.*, 2001; Bailey, Haines-Young & Watkins, 2002; Stockwell & Peterson, 2002).

Then, we classified areas as either ‘gain’ (areas identified as habitat in the future scenario but not in the current scenario), ‘loss’ (areas identified as habitat in the current scenario but not in the future scenario), or ‘stable’ (areas identified as habitat in both the current and future scenarios).

Results

Scale optimization

The optimized multi-scale analysis showed strong relationships between brown bear habitat selection and scale of analysis for each variable (Table 1). The scale optimization revealed that most variables (77.27%) were selected at the broadest scales (equal to or greater than 64 km radius). Comparisons among the different scales revealed that all the landscape composition and human disturbance variables included in the final model were most strongly related to the brown bear habitat suitability at broad-scales (64–128 km). The minimum temperature of warmest month and river density were the only two variables most strongly related at the finest-scale (1–2 km).

Variable importance

The final multi-scale model included 22 variables after variable selection with the Model Improvement Ratio. 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 (Fig. 2).

Response of brown bear to environmental variables

Climatic variables

Brown bear occurrence had a non-linear relationship with climatic variables (Fig. 3a). Post-monsoon and winter AET showed a bimodal relationship with brown bear occurrence, peaking at 140 mm and 55 mm respectively. Brown bear appeared to prefer 55 mm of AET in spring. The probability of brown bear occurrence is highest in areas with relatively low minimum and maximum surface temperature in the warmest (7 to 12°C) and coldest (−6 to −1°C) months. PET during the wettest quarter was most related to brown bear occurrence between 45 and 85 mm. The brown bear preferred areas with low extent of permanent snow/ice and

Table 1 Optimal scales for the most important variables found in the Random Forests model for assessing the multi-scale habitat associations of brown bears

Class Variable	Variable	Optimal scale (km)
Climatic	AET of Post monsoon	128
	AET of spring	64
	AET of winter	128
	Maximum temperature of coldest month	16
	Minimum temperature of warmest month	2
	PET of wettest quarter	16
	Permanent snow/ice	64
	Natural barren land	64
Landscape composition	Mixed forest	128
	Grasslands with scattered trees	128
	Scrubland	128
	Evergreen needleleaf forest	128
	Grasslands	128
Topographic	Compound topographic index	64
	Permanent wetlands	128
	water bodies	128
	Elevation	32
	River density	2
Disturbance	Croplands & cropland/natural vegetation mosaics (Combined class)	128
	Human population	128
	Human footprint	64
	urban/built-up areas	128

Numbers in bold indicate broad scale.

occurrence probability dropped substantially when snow/ice is over 5%.

Landscape composition variables

Predicted probability of brown bear occurrences showed a non-linear relationship with vegetation variables (Fig. 3b). The probability of brown bear was predicted to be highest in areas with moderate amounts of barren land (30–40%). Brown bear preferred areas with low amounts of mixed forest (5%), scrubland (<1%) and grasslands with scattered trees (10%). Moderate (25%) to high (>40%) amount of evergreen needleleaf forest was related to higher probability of brown bear occurrence. Brown bear also was positively associated with grasslands (17–35%).

Topographic variables

Topographic variables also had non-linear relationships with brown bear occurrences (Fig. 3c). The compound topographic index showed a unimodal relationship with brown bear occurrence, with highest probability at 8.9 cti, indicating neither association with the bottom of large valleys, nor with the top of ridges, but indicating preference for intermediate topographies between valley and ridge locations. The brown

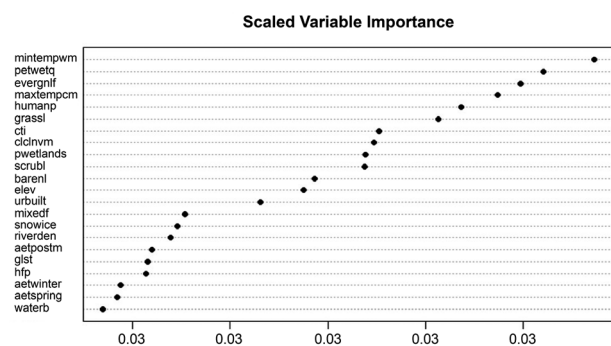


Figure 2 Variable importance plot for the predictor variables based on Model Improvement Ratio (MIR) from Random Forests classifications used for predicting occurrence of brown bears in the study area. Minimum temperature of warmest month was the most important variable and water bodies was the least important variable. The other variables are listed in order of their importance relative to minimum temperature of warmest month, with the x-axis indicating the relative additional model improvement when adding each successive variable. Variables: mintempwm = minimum temperature of warmest month, petwetq = potential evapotranspiration of wettest quarter, evergnlf = evergreen needleleaf forest, maxtempcm = maximum temperature of coldest month, humanp = human population, grassl = grasslands, cti = compound topographic index, clclnvm = croplands & cropland/natural vegetation mosaics, pwetlands = permanent wetlands, scrubl = scrubland, barrenl = barren land, elev = elevation, urbuilt = urban/built-up areas, mixedf = mixed forests, snowice = permanent snow, riverden = river density, aetpostm = actual evapotranspiration of post-monsoon, glst = grasslands with scattered trees, hfp = human footprint, aetwinter = actual evapotranspiration of winter, aetspring = actual evapotranspiration of spring, and waterb = water bodies.

bear was more likely to be found in areas with low density of permanent wetlands (<0.2%) and major water bodies (<0.6%), but with relatively higher river density (0.4–0.5 km/km²). The probability of brown bear occurrence was associated with higher elevations, with highest probability between 3,300 and 4,200 m.

Anthropogenic variables

Human disturbance factors also showed a non-linear relationship with the probability of brown bear occurrence (Fig. 3d). The probability of brown bear occurrence was highest in areas with a very low density of croplands and cropland/natural vegetation mosaics (10%) and urban/built-up areas (<1%). Additionally, brown bear occurrence was concentrated in areas with low human population density (75–150/km²) and relatively low levels of human footprint (25–27%).

Multi-scale optimized habitat suitability model

The habitat suitability map produced by the multi-scale optimized random forests model performed exceptionally well ($P < 0.001$, OOB error rate = 0.03; Table 2 and Fig. 4). The

model had high accuracy (PCC 97%, 0.94) with high sensitivity and specificity (Table 2). The area under the ROC curve (AUC) was 0.97 (Table 2), indicating excellent model performance in predicting occurrence of brown bears in Western Himalaya.

Gain and loss of habitat under future projections

Future projections under climate-only and combined climate and land use change scenarios indicated a substantial loss of potential habitat for brown bears under all scenarios (Supporting Information Figure S7–S8). In contrast, our future projections under land use change-only scenarios showed a low impact on potential habitat of brown bears under all scenarios (Supporting Information Figure S9). Our models projected a net loss of 3.6% and 34.7% of potential habitat for brown bears under RCP 2.6 and RCP 8.5 climate-only scenarios respectively in 2050s (Fig. 5b and c & Supporting Information Table S2). In 2070s, our models projected a net loss of 16.8% and 94.9% of potential habitat under RCP 2.6 and RCP 8.5, respectively (Fig. 5f and g & Supporting Information Table S2). Under the combined climate and land use change scenarios, potential habitat was further reduced (by 6.4% and 37.8% under RCP 2.6 and RCP 8.5 respectively in 2050s; Fig. 5d and e & Supporting Information Table S2). In 2070, the projected net loss was 23.0% and 96.0% under RCP 2.6 and RCP 8.5, respectively (Fig. 5h and i & Supporting Information Table S2). Under the land use change-only scenarios, our model projected a net loss of 1.4% and 1.2% of suitable habitat under RCP 2.6 and RCP 8.5 respectively in 2050s (Fig. 6b and c & Supporting Information Table S2). In 2070s, the suitable habitat was projected to decline by 5.0% and 1.6% under RCP 2.6 and RCP 8.5, respectively (Fig. 6d and e & Supporting Information Table S2).

Our future projections suggest that brown bear habitats will shift into new areas (indicated as ‘gain’ in our models; Fig. 5 and Supporting Information Table S2), particularly shifting from lower to higher elevations. Under RCP 8.5 scenarios, however, the ‘gain’ was projected to be <1.0% in 2070s, indicating the inability of brown bears to adapt to climate change through migration under high emission scenarios. Simultaneously, much of the current extent of suitable habitat is predicted to be lost.

Discussion

Scale dependence of habitat selection

Consistent with previous studies on this (Martin *et al.*, 2012; Mateo-Sanchez *et al.*, 2014a; Zarzo-Arias *et al.*,) and other species (Thompson & McGarigal, 2002; Grand *et al.*, 2004; Shirk, Raphael & Cushman, 2014; Vergara *et al.*, 2015; Chambers *et al.*, 2016; Wan *et al.*, 2017), habitat selection of the brown bear populations in Western Himalaya was scale-dependent. The majority of the habitat variables were selected at the broadest scale tested, indicating that brown

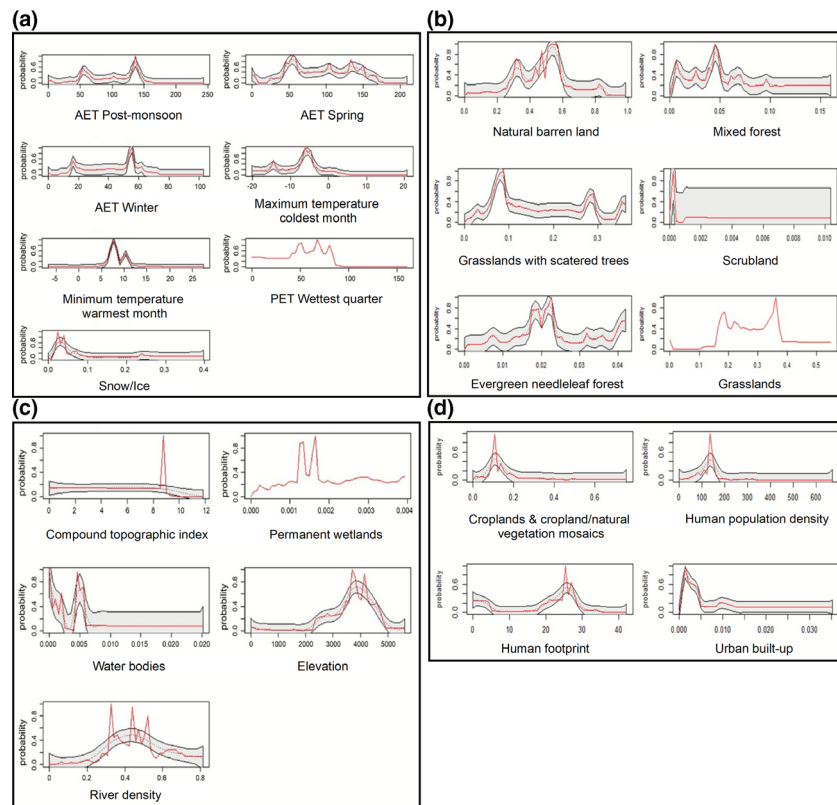


Figure 3 Partial dependency plots representing the marginal effect of habitat variables on predicted occurrence of Himalayan brown bear (a) climatic variables, (b) landscape composition variables, (c) topographic variables, and (d) disturbance variables. The gray area indicates the 95% confidence interval and the red line indicates the mean average.

Table 2 Cross-validated performance of the multi-scale random forest habitat suitability model for the Himalayan brown bear

Performance matrix	Value
Accuracy (PCC)	97.16%
Cohen's Kappa	0.94
Area under the ROC curve (AUC)	0.97
True Skill statistic	0.94
Sensitivity	0.97
Specificity	0.98
Cross-validation Kappa	0.94
Cross-validation OOB Error	0.03
Cross-validation error variance	2E-06

bears perceive landscape features mostly at larger scales. This is consistent with Mateo-Sanchez *et al.*, (2014a) who conducted one of the only full multi-scale optimized habitat modeling studies for brown bears. They found that most variables were selected at broad scales, and, consistent with our results, human land use and disturbance variables were

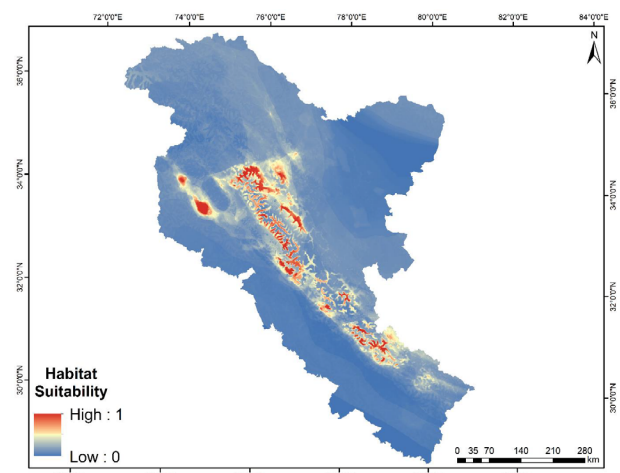


Figure 4 The habitat suitability map showing the predicted occurrence of brown bear based on multi-scale habitat modeling in Western Himalaya. The map displayed areas of low to high suitability represented in a gradient from the lowest probability of brown bear occurrence (blue) to the highest (red).

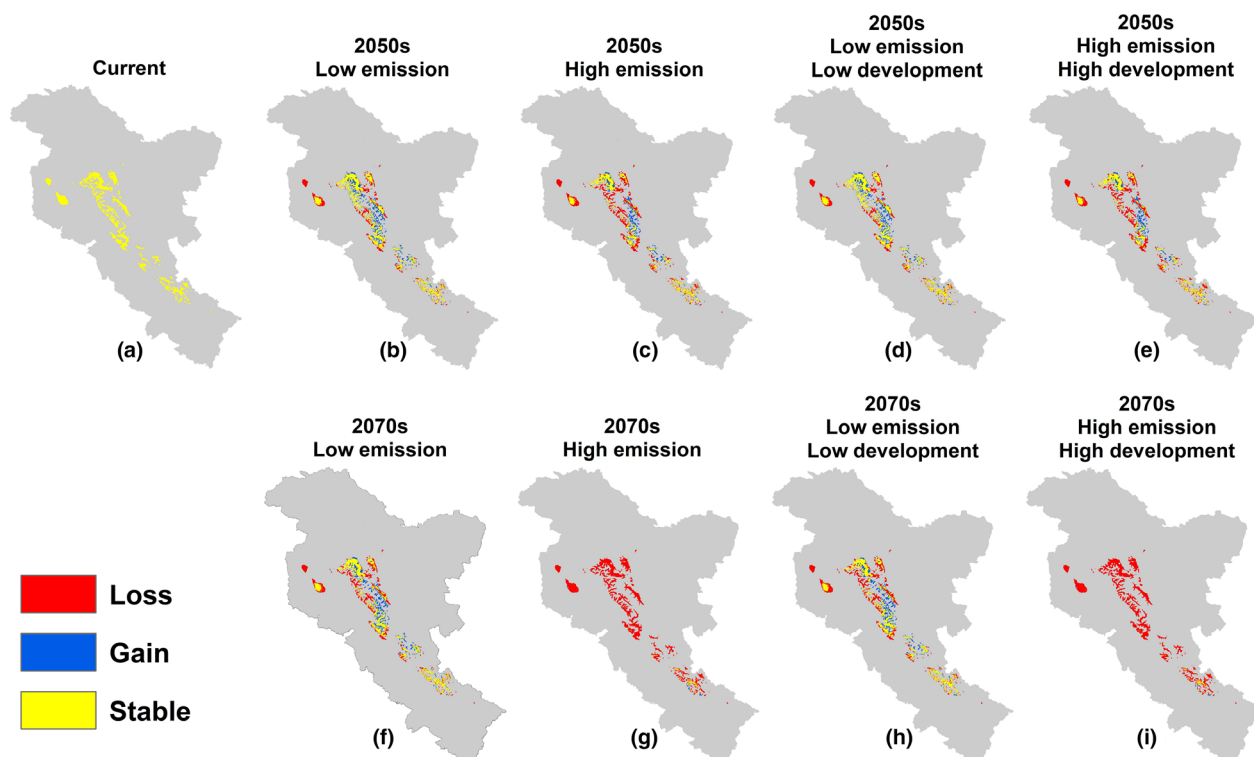


Figure 5 Future changes in potential habitat for brown bear in Western Himalaya based on multi-scale habitat modelling under the combined climate and land use change scenario in 2050s and 2070s.

all most influential at broadest scales. The broad-scale effect of human land use and habitat change effects is also seen in other carnivore species (e.g., Wasserman *et al.*, 2012a; Elliot *et al.*, 2014; Hearn *et al.*, 2018; Macdonald *et al.*, 2018, 2019). Our results are generally consistent with Fisher *et al.*, (2013), that larger species perceive and respond to landscape features at broader scales.

Our analysis provided insight into patterns of scale-dependent habitat selection in Himalayan brown bear. Specifically, the model shows that optimal brown bear habitat in Western Himalaya includes areas of relatively cold and wet climatic conditions, as measured by evapotranspiration and temperature. In the Western Himalaya, these climatic variables influence the bear habitat quality across a range of scales. Evapotranspiration of post-monsoon, winter and spring seasons were predicted to be important at the broadest scale. Evapotranspiration is regarded as a strong predictor of net primary productivity of terrestrial ecosystems (Rosenzweig, 1968), and is especially important to the brown bears in Western Himalaya because they predominantly forage on plants (Nawaz, 2008). These plants are patchy and sparsely distributed in this region, and thus brown bears often travel large distances when foraging. Minimum temperature of the warmest month and maximum temperature of the coldest month were important at finer scales. Temperatures affect daily activities and other crucial life history activities such as feeding and hibernation of brown bear (Schwartz *et al.*, 2010; Delgado *et al.*, 2018; González-Bernardo *et al.*, 2020), which is also considered to be

physiologically sensitive to warmer temperatures. These are all finer-scale processes in habitat selection.

Our models suggested that in the forested parts of the Western Himalaya, brown bears select portions of the landscape with large extent of grasslands and conifer forests, interspersed with low amounts of mixed forests and grasslands with scattered trees. However, in other parts of the region where forested areas are non-existent, brown bear select large extent of grasslands and natural barren lands. Our results indicate that brown bear occurrence is highest in intermediate to upper elevations, often in proximity to rivers, in areas with very low human population density and low human footprint, and that it avoids areas with extensive snow and ice cover. However, in other landscapes (e.g. in Western Europe) brown bears seem to avoid extremely high elevation areas, because the food resources are scarce compared to forested areas at lower elevations (Katajisto, 2006; G  thlin *et al.*, 2011; Martin *et al.*, 2012).

Landscape composition variables in this landscape influence the brown bear habitat quality at broader scales (Table 1). Martin (2009) found that landscape composition was important at a broad scale (15 000 m). Similarly, Mateo-Sanchez *et al.*, 2014a,b) found that extent of the most important cover types were related to brown-bear occurrence at broad scales (16 000–232 000 m). The broad scale association of landscape composition variables can be related to foraging decisions. Food resources for the brown bear are limited and sparsely distributed by vegetation types on the study landscape. Therefore,

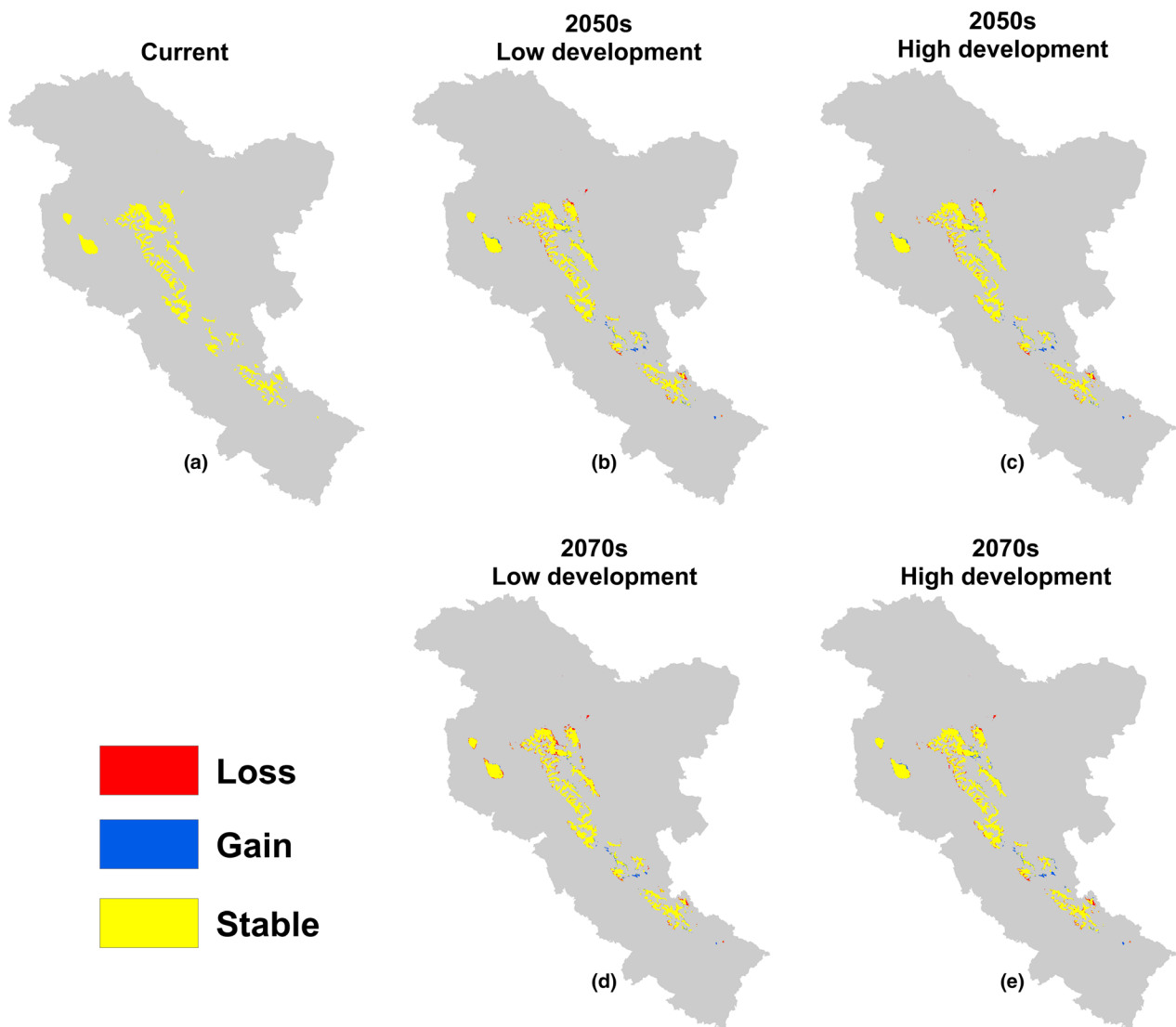


Figure 6 Future changes in potential habitat for brown bear in Western Himalaya based on multi-scale habitat modelling under land use change-only scenario in 2050s and 2070s.

the brown bear is likely to have to travel long distance to search for food. Additionally, broad-scale selection of landscape composition variables may suggest that they influence long-range dispersal and migration.

The optimal scales for topographic variables were highly variable (Table 1). Elevation was important at a mid-scale, which could be related to the foraging areas being limited to higher elevations in the study landscape. River density was important at finest scale, indicating the association of brown bears with riverine and riparian habitat, which is consistent with their ecology in other parts of their range, and likely reflects selection of areas with higher productivity of preferred food resources (Mateo-Sánchez *et al.*, 2016).

Human disturbance, such as croplands and cropland/natural vegetation mosaics, human population density, human footprint and urban/built-up areas were all important at the

broadest scale. This suggests that brown bears avoid human disturbances and prefer having large areas of habitat that has little or no human interference. This is consistent with a previous study which showed broad-scale cumulative effect of human disturbance on the distribution of brown bears in the Cantabrian Range, northwest Spain (Mateo-Sánchez *et al.*, 2014a,b; Zarzo-Arias *et al.*,).

Conservation strategies must integrate climate change

The most alarming finding in this study is that climate change alone may be disruptive enough to lead to near complete habitat loss for the brown bear by the end of the century in the Western Himalaya. Loss of potential brown bear habitat due to climate change has been observed in other

modelling studies (Su *et al.*, 2018; Penteriani *et al.*, 2019). Furthermore, the potential impact of climate change has also been observed in other species (e.g. Wong *et al.*, 2013; Li *et al.*, 2015). Warming climate can directly affect brown bears as it induces heat stress, which can lead to increased metabolic rate, reduced cub survival and reduced fitness (Pigeon, Stenhouse & Côté, 2016). Reproduction success can be negatively affected due to increased energy costs of torpor and reduced energy allocated to reproduction during warm winters (Post & Forchhammer, 2008; Albrecht *et al.*, 2017).

Our models suggest that temperature, actual evapotranspiration (AET) and potential evapotranspiration (PET) are strongly associated with the distribution of Himalayan brown bear in Western Himalaya. Our projections suggest that future changes in distribution of brown bear in the study landscape may be driven predominantly by changes in temperature and climatic water balance. Increasing temperature is predicted to increase the intensity of the summer monsoon in the Himalayan region (scenario RCP8.5, IPCC, 2013) causing increases in both evaporative demand and water availability. This can potentially increase AET and PET, and lead to changes in the vegetation cover of the landscape (Li *et al.*, 2013). This indicates that climate change also indirectly affects the brown bear by altering the vegetation (i.e. food resources and availability) on the landscape (Penteriani *et al.*, 2019). In the Western Himalaya, the brown bear forages mostly on plants (Nawaz, 2008). Plants are vulnerable to climate change due to being sessile and having limited ability to physically disperse to areas with suitable growing conditions (Parmesan, 2006). In particular, the temperate forests in Western Himalaya will be increasingly exposed to drought due to changes in rainfall patterns (Müller-Haubold *et al.*, 2013). Consequently, many plant species will decline and respond to changing climate through range shift, affecting both food and shelter for the brown bear (Shen, Cong & Cao, 2015).

Human land use is known to play a key role in range contraction of brown bears across its historical range (Zedrosser *et al.*, 2011; Wolf & Ripple, 2017). Several studies have highlighted the negative impacts of human land use on the distribution, foraging habit, cub matting and nursing, and survival rates of brown bears (Shannon *et al.*, 2016; Gaynor *et al.*, 2018). For example, Mateo-Sanchez *et al.*, (2014a) found that the density of human settlements in the landscape was universally the strongest predictor (negative relationship) of brown bear occurrence in Spain and had the largest influence at broad scales (16 km). Our results also suggest that human land use will lead to loss of brown bear habitat. We show that there is a strong association of brown bear distribution and human disturbances represented by the proportion of croplands and urban/built-up areas in Western Himalaya. Our projected models suggest that future changes in croplands and urban/built-up areas exert negative influence on the distribution range of brown bears in Western Himalaya (Supporting Information Table S2). The adverse effect of increases in croplands and urban/built-up areas on brown bear distribution is also reflected by other human disturbance

factors in our model. Our results suggest that brown bear occurrence is concentrated in areas with very low human population density and low human footprint, which is similar to results in other parts of the species range (e.g. Olson *et al.*, 1998; Martin *et al.*, 2010; Mateo-Sanchez *et al.*, 2014a; Wheat & Wilmsers, 2016).

Compared with climate change, however, human land use is expected to contribute only a small portion of habitat loss. This is perhaps in part because brown bear habitats are typically located at areas of rough terrain and relatively higher elevation, which are less desirable for human development. Thus, there is relatively lower projected change in human land use in the areas of highest suitability for brown bears. This, however, suggests that brown bears in the western Himalaya may have been excluded from other parts of their niche in more productive and lower elevation habitats by the high human footprint in these areas. Similar exclusion from lower elevation and higher productivity ecosystems has been seen for brown bears in the United States and Europe. Some studies also suggested that brown bear populations and their distributional range in the Himalayan region have changed drastically since 1990s due the habitat fragmentation and loss by anthropogenic activities (Nawaz, 2007; Nawaz *et al.*, 2014).

Our results show potentially large negative impacts of climate change leading to predicted loss of much currently suitable brown bear habitat. However, if brown bears are primarily associated with the high, cold conifer and grassland system due to exclusion by human disturbance and persecution from the lower elevation ecosystems then the projected change in range related to climate change may be larger than is likely to actually occur, assuming that human land use and impacts don't increase directly with climate change in the high elevation ecosystems of the Western Himalaya.

This discrepancy in interpretation arises from the difference between realized and fundamental niches (Hutchinson, 1957). Assuming the observed habitat relationship reflects the fundamental niche of the brown bear then projection of climate change suggests large contraction of range as suitable climate conditions move higher in elevation and decrease in extent (e.g. Wasserman *et al.*, 2012b, 2013). However, given the relatively wide ecological amplitude of the brown bear within its global range, we suspect that the observed relationship with climate is at least in part a restricted realized niche driven by exclusion by human persecution from lower elevation and warmer ecosystems. In that case, assuming the projection of climate reflects the likely change in bear range would be incorrect and over-estimate the likely effect of climate change on the species' distribution. It is notoriously difficult to delineate the differences between realized and fundamental niches, and this is one of the largest challenges in projecting and interpreting climate change effects on populations (e.g. Wasserman *et al.*, 2012b, 2013). This discrepancy suggests further research to quantify the relative limitations of brown bear distribution driven by climate and human factors independently. This will likely require meta-replicated studies (*sensu* Shirk *et al.*, 2014, and

e.g. Short Bull *et al.*, 2011) in which research is repeated in several ecosystems to determine in what circumstances particular habitat variables become limiting to brown bear distribution. For example, Short Bull *et al.*, (2011) conducted a meta-replicated study of American black bear genetic differentiation in 11 study areas across broad climatic and human disturbance gradients, and found that climate and human activities both were limiting to black bear gene flow, but in different ways depending on which factors were most limiting. Meta-replicated habitat selection studies for brown bear in the Himalaya region could be useful to separate the potential confounding of human impacts and climate dimensions of the species' realized niche. Furthermore, because our habitat models' predictions are dependent upon the climate data that we used, there are uncertainties involving the accuracy of the climate projection data.

Resolving the characteristics of the brown bear's fundamental habitat and climate niches is critical for more than ecological understanding. For example, traditional conservation strategies, such as setting aside protected areas and mitigating human disturbances, may be relatively robust if the brown bear's climate niche is wider than suggested in this analysis. However, if the species in fact has a narrow and limited tolerance for climate change, as suggested in our models, then the existing protected area network is unlikely to be robust in the future under climate change. In that case our results suggest there will be very little potentially suitable habitat for brown bear within or outside of protected areas by 2070.

Differences between high and low emission scenarios

Our results revealed a clear difference between the low and high emission scenarios. Our future model projections indicate that, although there will still be a substantial habitat loss under the low emission scenarios, some current habitats will remain along with some new potential habitats establishing in the higher elevation areas (Fig. 5). In contrast, almost no habitat will remain for brown bears under the high emission scenarios, with or without human land use change (Fig. 5). This could be most likely due to the lack of uphill available space that has the optimal climate condition for the species. A similar result was found for American marten by Wasserman *et al.*, (2012b, 2013) in the United States northern Rocky Mountains. Specifically, Wasserman *et al.*, (2012b, 2013) found that projected climate change would greatly reduce the extent and increase the fragmentation of suitable American marten habitat over much of the northern Rocky Mountains, leading to large decreases in genetic diversity. This suggests the importance of incorporating climate change mitigation strategies (i.e. emission reduction) in conservation strategies, and that traditional conservation efforts such as *in situ* conservation under the current Protection Acts will not be sufficient to protect this species if we do nothing to reduce the impact of climate change (Penteriani *et al.*, 2019).

Resolving the relative ability of *in situ* vs climate change mitigation scenarios will require resolving uncertainty about the extent of the realized vs the fundamental climate niche of brown bears in the Himalaya. For example, in the Himalaya region it would be useful to model brown bear climate and habitat relationships in Bhutan, where there is relatively low levels of human disturbance and persecution, which would provide a comparison of the predicted climate niche of the species in a region where there is relatively little displacement by human activities.

Conclusions

The multiscale modeling approach carried out in this study clarifies scale-dependent habitat selection of brown bear in the Western Himalaya region of India. We found strong associations with landscapes with cool and wet climates at middle to high elevations, with large extents of conifer forest and grassland, and low human footprint and low human population density. Current habitat of brown bears predicted by our models appears to be relatively fragmented, and projected future distributions show potentially large range contractions and further fragmentation. Future research should investigate population connectivity of brown bear in our system. Mateo-Sanchez *et al.* (2014b, 2015) used network connectivity algorithms to identify movement corridors for brown bears in northern Spain. We suggest using similar methods, including resistant kernel and factorial least cost path analysis (e.g. Cushman *et al.*, 2014) to identify current core areas and corridors for brown bear movement, and how they may change with future scenarios (e.g. Wasserman *et al.*, 2013; Cushman *et al.*, 2016). Furthermore, given that population size, genetic differentiation and genetic diversity are centrally important attributes for guiding conservation planning, we suggest using individual-based, spatially-explicit modeling to evaluate the influences of the alternative scenarios on population distribution, abundance, genetic diversity and genetic differentiation (e.g. Wasserman *et al.*, 2012b, 2013; Kaszta *et al.*, 2019, 2020). Finally, given that projection of shifting suitable habitat niche space does not equate to expected future occupied range, because of limitations of colonization and accessibility, we suggest using temporally dynamic dispersal and range-shift modeling (e.g. Cushman, 2015; Barros *et al.*, 2019) to project the ability of natural dispersal to enable colonization of future predicted habitat and identify areas where natural or anthropogenic obstacles may impede this colonization.

We projected substantial loss of brown bear habitat in the future that is predominantly driven by climate change, although human land use also plays a role. We note uncertainty in these projections due to difficulty in separating the realized and fundamental niche from a single observational study. We strongly suggest meta-replicated studies to confirm the breadth and structure of habitat and climate niches of Himalayan brown bear to improve projection of future range shift. In the interim, our results suggest potentially huge impacts of climate change on brown bear habitat, such that

under high emission scenarios little habitat is predicted to remain for brown bears by 2070. Our results suggest that setting aside protected areas and preventing development in wildlands will not be sufficient to save this charismatic species in this region. Therefore, we call for mitigation measures of climate change be incorporated into conservation plans to effectively conserve biodiversity in this region.

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Author contribution

Shahid Ahmad Dar contributed to methodology, formal analysis, investigation, data curation, writing - original draft, writing - review & editing, visualization, project administration. Sujeet Kumar Singh contributed to investigation and project administration. Ho Yi Wan contributed to conceptualization, methodology, formal analysis, writing - original draft and writing - review & editing. Vinay Kumar contributed to investigation. Samuel A. Cushman and S. Sathyakumar contributed to conceptualization, methodology, writing - review and editing.

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Supporting information

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

Supplementary Material