Primates
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ORIGINAL ARTICLE

Using an ensemble modeling approach to predict the potential distribution for the Kashmir gray langur (*Semnopithecus ajax*)

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Abstract
Comprehensive species distribution data is crucial for assessing threat levels, conservation status and formulating effective conservation strategies. Globally, over half of the primate species remain unstudied, particularly those inhabiting challenging and remote environments. Endemic to the North-Western Himalayas, the Kashmir gray langur (*Semnopithecus ajax*) is a primarily arboreal forest-dwelling folivorous primate. Its shy behavior and the steepness of the inhabiting terrain in the high-altitude ecosystem makes it highly elusive and challenging to study. We employed an ensemble modeling approach to (i) predict the distribution of species in the Kashmir Himalayas and, (ii) gain insight into the importance of various environmental factors that influence the occurrence of the Kashmir gray langur. Our model, based on 35 environmental variables and 144 occurrence points, depicted forested mountainous areas with moderate slopes at mid elevations and with low human disturbance as suitable habitats for the Kashmir gray langur. The model showed strong discrimination (mean AUC = 0.926; mean TSS = 0.78), with predicted areas corresponding to the observed species locations, thereby supporting both its validity and ecological relevance. Variable response curves indicated a strong association of the species with areas characterized by pronounced precipitation seasonality, moderately sloping terrain, and optimal diurnal temperature ranges. These conditions typify temperate deciduous and coniferous forests, and these forests are increasingly threatened by ongoing climate change and require climate-adaptive management strategies for their conservation. We recommend integrating the findings of this preliminary yet important study into devising effective conservation and management strategies, as well as enhancing regular population monitoring to generate a comprehensive database on the species for long-term conservation implications.

Keywords Conservation · Distribution · Ensemble modeling · Kashmir gray langur · Primate

Introduction

Primates play crucial ecological roles in maintaining ecosystem structure and function (Marshall and Wich 2016). However, in recent decades primate populations have sharply declined with over 65% of species facing imminent extinction risks worldwide (Fernández et al. 2022). The conservation status of Asian primates is particularly alarming with 73% of the species facing extinction and 95% experiencing population decline (Estrada et al. 2017). Most

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primate species face declining populations and shrinking geographical ranges due to anthropogenic activities, including land-use changes, hunting, habitat loss, and fragmentation (Hameed et al. 2023; Rabanal et al. 2010; Wich et al. 2014). However, commercialized hunting and capturing of wild primates and their body parts for food, traditional medicine, pets, and use in biomedical research has emerged as a significant threat to affecting almost 70% of primate species globally (Garber et al. 2024). Climate change poses an additional threat potentially exacerbating the impact of other drivers especially in sensitive high-altitude ecosystems such as the Himalayas (Dahal et al. 2021), with *Semnopithecus ajax* expected to be one among the most severely affected species (Graham et al. 2016).

Globally, over half of primate species remain unstudied particularly those inhabiting challenging and remote environments (Rode et al. 2013). Comprehensive distribution data are crucial for assessing threat levels, defining conservation status, and formulating effective conservation strategies. Unfortunately, such data are often scarce and challenging to gather (Anderson et al. 2002). However, species distribution models (SDMs) have proven their applicability in understanding species ecology and biogeography (Araújo and Peterson 2012) to assist in biodiversity assessments, species management, and spatial conservation prioritization (Ahmed et al. 2020; Condro et al. 2021; Hurtado and Burton 2022; Vasquez et al. 2021). The key characteristics influencing the habitat suitability of most primate species include topographic features, forest characteristics, and anthropogenic factors (Choudhury et al. 2022; Mercado Malabet et al. 2020; Moraes et al. 2020; Smith and Lusseau 2022). Therefore, the identification of environmental variables associated with species habitat selection is critical for species conservation (Fitzgerald et al. 2018). Machine learning models based on the relationship between species occurrence data and user-defined environmental variables (Booth et al. 2014) are innovative and effective tools for estimating habitat suitability, species occurrence, or potential distribution of a species (Franklin 2009; Hirzel et al. 2006) as well as facilitating inferences about environmental variables associated with species presence (Fourcade et al. 2014; Liu et al. 2020). Moreover, the use of ensemble SDM approach has gained popularity because it is considered statistically robust and brings significant improvement in the accuracy of SDMs by combining their predictions and reducing the predictive uncertainty of single models (Grenouillet et al. 2011).

Endemic to the North-Western Himalayas, the Kashmir gray langur (*Semnopithecus ajax*, Pocock 1928) is an arboreal forest-dwelling folivorous alloprimate (Fig. 1), with a patchy distribution stretching from Himachal Pradesh in the East to Jammu and Kashmir in the West (Hameed et al. 2024a; Groves 2015; Jahangeer et al. 2019). In the Kashmir Himalaya, the species prefers steep cliffs and rugged terrain in the altitudinal range of 1,600-3,000 m above sea level (Khaleel 2020), which coincide with temperate evergreen needle forests, broad-leaved deciduous forests and subalpine forests. These langurs are known to form uni- and multimale bisexual groups as well as all male groups (Singh and Thakur 2020), averaging 51 individuals (Jahangeer et al. 2019; Hameed et al. 2024a). They also show seasonal altitudinal migration primarily using moist temperate broad leaf and coniferous forests in winter and subalpine forests during the summer (Singh and Thakur, 2020; Hameed et al. 2024a). Additionally, to avoid predation by large carnivores, these diurnal langurs use taller trees for roosting in forest ecosystems (Minhas et al. 2010), suggesting their high dependence on specific forest ecosystems (Singh and Thakur 2017). The shy behavior and steepness of the inhabited terrains make them highly elusive (Schwitzer et al. 2014) and challenging to study. Thus, only patchy information is available for this species across its distribution range.

The Kashmir gray langur despite its ecological role in maintaining the structuring and functioning of an ecosystem by acting as seed dispersers, herbivores, pollinators, and seed predators, it is listed as Endangered in the IUCN Red List of Threatened Species (Kumar et al. 2020) and is the most vulnerable primate species owing to its declining population, restricted habitat range, and susceptibility to the severity of predicted climate change (Graham et al. 2016). Additionally, during the last few decades, deforestation and degradation of natural forests (Wani et al. 2016), coupled with constant changes in land-use patterns in the Kashmir Himalayas (Ahmed et al. 2021; Rasool et al. 2021), have resulted in habitat loss and fragmentation (Haq et al. 2020), thus affecting its distribution. Therefore, in order to generate robust ecological information that could facilitate long-term conservation of Kashmir gray langur in the region, we employed an ensemble modeling approach to (i) predict its current distribution in the region, (ii) determine the importance of various environmental factors that influence its occurrence, and (iii) identify and prioritize suitable habitats for population surveys to ensure its long-term conservation in the Kashmir Himalayas.

Study area

The Kashmir Himalaya (Fig. 2) is situated in the North-Western flanks of the Himalaya and is included in the Western Himalayan biodiversity hotspot (Mittermeier 2004). Kashmir Himalaya is characterized by temperate climate with pronounced seasonality (Romshoo et al. 2020), with a precipitation of ~124 cm year^{-1} (Bhat et al. 2022), and an

Fig. 1 Kashmir gray langurs in a mixed deciduous forest, Kashmir. Photo credit: Shahid Hameed

annual temperature ranging from −10 to 35 °C (Zaz et al. 2019). The biogeographical distinctive location, topographical complexities, altitudinal range, and phyto-climatically varied conditions make the Kashmir Himalaya slightly different, and one of the biologically hyper-diverse regions than rest of the Himalaya (Prasher 2015; Roy et al. 2015). The vegetation at 1600–2700 m is mainly coniferous forests interspersed with broad-leaved mixed forests, subalpine forests between 2700 and 3500 m represent silver fir and birch vegetation, and elevations beyond 3500 m represent alpine scrub vegetation commonly comprised of Juniperus, Rhododendron, Salix, and Lonicera (Dar and Khuroo 2013). In the North-Western Himalaya, the timberline falls between 3200 and 3600 m (Singh and Pusalkar 2020).

Our study area, encompassing the Kashmir Himalayas, extends between 35.158662°–32.275329° N and 73.397705°–76.806038° E in an elevation range of 199–6502 m AMSL. The landscape is bordered by Siwalik mountains in the south, Pir Panjal in the southwest, the Greater Himalaya in the northeast, and the lofty mountainous ranges of Zanskar in the east and Karakoram in the north. Our study area covered protected areas, such as Dachigam National Park, Kazinag National Park, Machiara National Park, Kishtwar high-altitude National Park, Hirpora Wildlife Sanctuary, Rajparian Wildlife Sanctuary, Limber Wildlife Sanctuary, Lachipora Wildlife Sanctuary, Overa-Aru Wildlife Sanctuary Tral Conservation Reserve, and Wangath Conservation Reserve, and non-protected areas.

Methods

Species occurrence data

We used primary and secondary species occurrence data for the distribution modeling of the Kashmir gray langur. Primary data on species occurrence (84 records) came from a double-observer survey we conducted in parts of the study area to assess species distribution and population estimation during 2020–2022 (Hameed et al. 2024a). Secondary data (60 records) were obtained from published literature (Minhas et al. 2012; Sharma and Ahmed 2017).

Predictor variables- climatic and topographic

The identification of predictor variables based on prior knowledge of the ecological drivers of species distribution

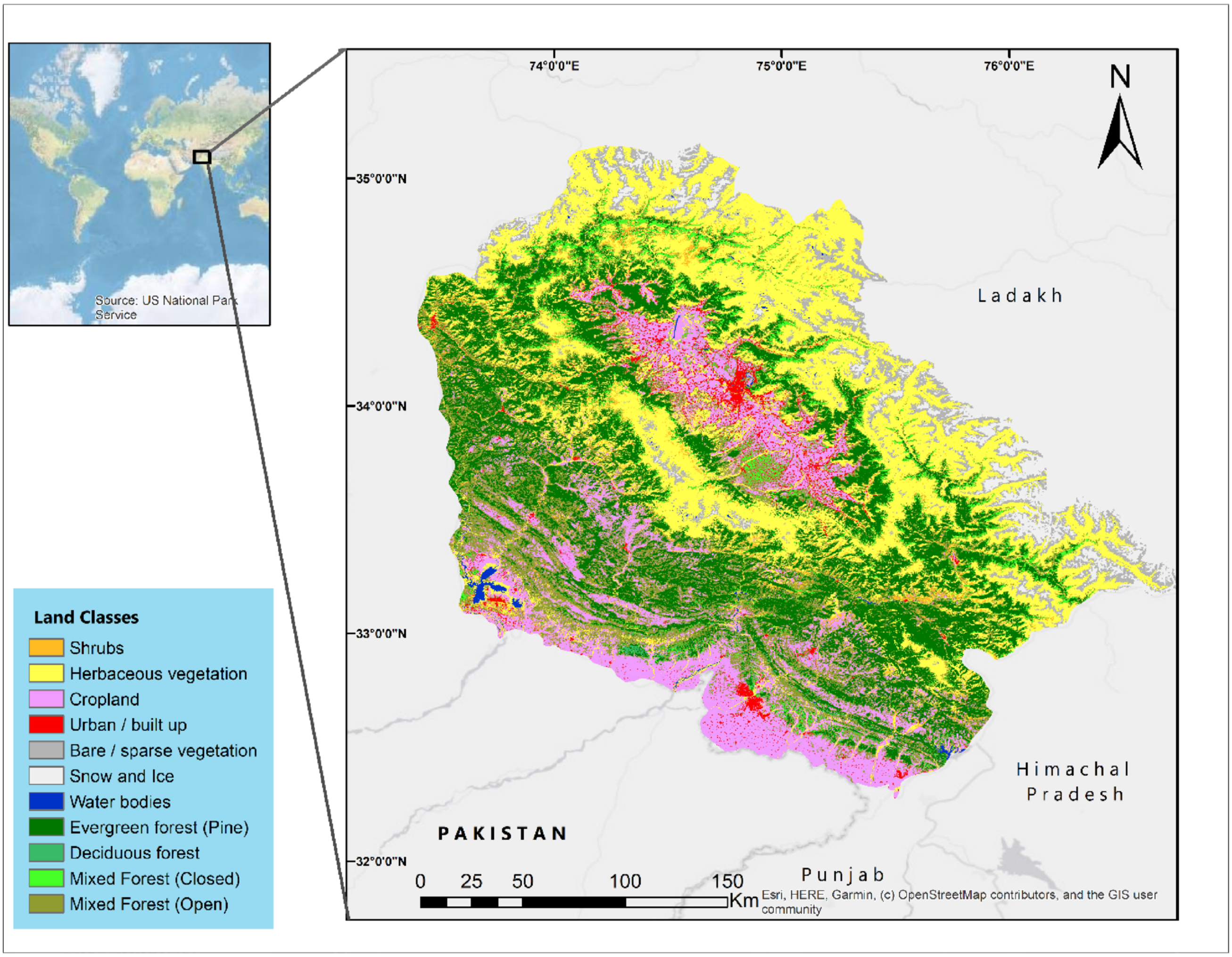

Fig. 2 Study area map showing various land use classes in Kashmir Himalaya, North-Western Himalayas. Data source https://land.copernicus.eu

enhances the accuracy and predictive ability of habitat suitability models (Guisan et al. 2017). Therefore, we selected predictor variables based on prior research on the behavior and ecology of the species (Thakur et al. 2022; Khaleel 2020; Asif et al. 2019; Mir et al. 2015; Minhas et al. 2010), and previous studies on the habitat suitability of high-altitude arboreal primates (Fitzgerald et al. 2018; Kufa et al. 2022; Liu et al. 2020; Parker et al. 2021). Predictor variables ($n=35$) (Table 1) were prepared using ArcMap Desktop (Version 10.8) and QGIS (Version 3.36.2). Bioclimatic variables ($n=19$) were downloaded from the WorldClim Database (Fick and Hijmans 2017; WorldClim-Global Climate Data 2022) at 30 arcseconds (~1 km × 1 km). The variables describing the landscape features ($n=13$) were calculated using the Geomorphometry and Gradient Metrics Toolbox in ArcMap (Evans et al. 2014) and QGIS, based on a digital elevation model (DEM) downloaded at 30 m spatial resolution from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER), Version V003 (ASTER 2019). Land use land cover (LULC) data and layers related to vegetation ($n=2$) were downloaded at a spatial resolution of 500 m from the FAO (FAO Global Land Cover 2022; Latham et al. 2014) and MODIS MOD13A1-LP DAAC (Didan 2015), respectively. A similar spatial resolution and extent among predictor variables is necessary for a consistent modeling environment (Guisan et al. 2017); therefore, we matched the spatial extent of all the environmental layers ($n=35$) by clipping them using the shape file of the study area and finally aligning them with the spatial resolution of bioclimatic variables (30 arc-seconds). To avoid autocorrelation between the variables, we transformed the predictors using Principal Component Analysis (PCA). The first five axes of the PCA were projected in space to be used as predictor variables using the NTBOX package in R (Osorio-Olvera et al. 2020).

Table 1 List of environmental variables included in developing an ensemble habitat suitability model for Kashmir Gray langur in the Kashmir Himalayas.

Environmental variables	Source	Description
Elevation	USGS	Height above sea level
Slope	USGS	Degree of rise/run
Aspect	USGS	Direction a slope faces
Integrated moisture index	USGS	Estimate of soil moisture based on topography
Topography roughness	USGS	Surface roughness
Hill shade	USGS	Shaded relief
Surface relief ratio	USGS	Describes rugosity
Surface area ratio	USGS	surface/area ratio
Slope position index	USGS	Slope position
Heat Load Index	USGS	A measure of how much heat an area receives based on slope steepness and aspect
Site exposure index	USGS	Exposure of an area based on surrounding topography
Landform/Concavity	USGS	concavity/convexity landform index
Topographic Wetness index	USGS	Steady-state wetness index
LULC	FAO Global Land Cover	Classification providing information on land cover types, and the types of human activity involved in land use.
NDVI	USGS	Index of photosynthetically active vegetation
EVI	USGS	Quantifies vegetation greenness similar to NDVI but corrects for some atmospheric conditions and canopy background noise and is more sensitive in areas with dense vegetation.
Bio1	WorldClim	The annual mean temperature
Bio2	WorldClim	The mean of the monthly temperature ranges (monthly maximum minus monthly minimum)
Bio3	WorldClim	Isothermality quantifies how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations
Bio4	WorldClim	The amount of temperature variation over a given period based on the ratio of the standard deviation of the monthly mean temperatures to the mean monthly temperature
Bio5	WorldClim	The maximum monthly temperature occurrence over a given year (time series) or averaged years (normal)
Bio6	WorldClim	The minimum monthly temperature occurrence over a given year (time series) or averaged years (normal)
Bio7	WorldClim	A measure of temperature variation over a given period
Bio8	WorldClim	This quarterly index approximates mean temperatures that prevail during the wettest season
Bio9	WorldClim	This quarterly index approximates mean temperatures that prevail during the driest quarter
Bio10	WorldClim	This quarterly index approximates mean temperatures that prevail during the warmest quarter
Bio11	WorldClim	This quarterly index approximates mean temperatures that prevail during the coldest quarter
Bio12	WorldClim	This is the sum of all total monthly precipitation values
Bio13	WorldClim	This index identifies the total precipitation that prevails during the wettest month
Bio14	WorldClim	This index identifies the total precipitation that prevails during the driest month
Bio15	WorldClim	This index is the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation (also known as the coefficient of variation) and is expressed as a percentage
Bio16	WorldClim	This quarterly index approximates the total precipitation that prevails during the wettest quarter
Bio17	WorldClim	This quarterly index approximates the total precipitation that prevails during the driest quarter
Bio18	WorldClim	This quarterly index approximates the total precipitation that prevails during the warmest quarter
Bio19	WorldClim	This quarterly index approximates the total precipitation that prevails during the coldest quarter

Occurrence probability modeling approach

Ensemble modeling, in which several algorithms are combined to quantify a range of predictions across multiple sets of uncertainty sources, has been shown to improve model predictions (Araújo and New 2007; Velazco et al. 2020) and circumvent the uncertainties associated with the utilization of a single algorithm (Thuiller et al. 2019; West et al. 2016). To map the occurrence probability and identify the topographic and climatic variables (Table 1) contributing to it, we built an ensemble species distribution model using the sdm package (Naimi et al. 2021; Naimi and Araújo 2016) in Program R (R 4.2.2, R Core Team, 2013). To overcome the errors of overestimation for broad-scale models, (1) the species' geographical ranges within the extent of occurrence should be limited based on the point locality and ecological preferences of the species (Rodrigues et al. 2004), and (2) habitat patches highly unsuitable for the species should be removed based on field knowledge of species-habitat relationships (Rondinini et al. 2006). To address these concerns and considering the habitat preference of the study species, we used a land-use map to obtain ten sets of 144 randomly selected pseudo-absences in non-forested areas (FAO's Global Land Cover map) between elevations higher than 1400 m and lower than 3600 m in the study area. The number of pseudo-absences was made equal to the number of presences to avoid imbalance issues (Japkowicz and Stephen 2002), while the use of 10 different sets fades random effect. For each set of pseudo-absences, we modeled the species using three machine learning algorithms with different approaches: Support Vector Machine (SVM; support vector algorithm), Mixture Discriminant Analysis (MDA; discriminant algorithm), and Radial Basis Function Network (RBF; neural network algorithm). We ran the algorithms ten times and used a 10-fold cross-validation by calculating the area under the receiver operating characteristic curve (AUC-ROC) and the true skill statistics (TSS) for each model, adding to a total of 3000 models. We optimized the TSS by considering the maximum sensitivity plus specificity and deleted models with AUC-ROC lower than 0.9 and/or TSS lower than 0.7. We ensemble the remaining 153 models using a committee average. This approach returns both an uncertainty map and an occurrence probability map, where the values range from zero to one. In this case, one is the value where all models agree with a presence, while 0.5 value indicates when half of the models agree with presence and the other half agree with absence. A raster value of zero indicates that all models agree with an absence.

To better visualize the potential spatial distribution of the Kashmir gray langur, we reclassified the final probabilistic SDM ensemble output into four habitat suitability categories based on the different threshold levels or degree of habitat suitability as: (1) high probability of occurrence (HI) with predicted probability ≥ 0.75, (2) moderate probability of occurrence (MID) with predicted probability ranging from ≥ 0.5 to < 0.75; (3) low probability of occurrence (LOW) with predicted probability ranging from ≥ 0.25 to < 0.5; and (4) Absent (ABS) with a predicted probability of < 0.25.

Variables influence

As we used PCA axes to build our models where the first five axes explained more than 74% of variance, environmental information was lost to the detriment of precision in the current distribution. Thus, it was not possible to access the contribution of variables using internal approaches from the sdm package. To understand the impact of each variable on species distribution, we extracted the occurrence probability of the species in each cell of our ensemble, together with environmental information from raw environmental data. We then calculated the Pearson's correlation between the ensemble and each of the variables. Finally, with this data, we drew line plots (response curves) for the six variables with higher influence on the ensemble (three positive and three negative influences).

Results

Distribution model performance

Our ensemble SDM AUC-ROC values ranged from 0.901 to 0.995, with a mean of 0.926 (SD = 0.020), whereas the TSS values ranged from 0.709 to 0.933, with a mean of 0.784 (SD = 0.057). The correlation plot (Fig. 3) depicts the relationship between the predictor variables and the probability of occurrence of the species in the ensemble model.

Species range

The ensemble species distribution model, we built, predicted the occurrence area for the species to be 25,369 km^2, accounting for 46.50% of the study area (54,549 km^2). The map from the final ensemble SDM output (Fig. 4) shows the probability of the occurrence of the Kashmir gray langur within our study area. This map illustrates the importance of the mid-elevation mountain corresponding to forest ecosystems as a habitat for this species. For the maximum training presence threshold (≥ 0.75), 76% of the landscape was classified as absent, and 24% as present for the species. The area in each of the probability of occurrence classes (Fig. 5a and d) was 13232.26 km^2 (HI), 12691.66 km^2 (MID), 7866.49 km^2 (LOW), and 20758.41 km^2 (ABS). The southeastern and northwestern mountainous areas were identified as having a high probability of occurrence and continuous habitat spaces for the Kashmir gray langur. The high probability areas are largely distributed along mountainous ecosystems with a 20–30-degree slope, have broad-leaved forests, mid-elevations, and are close to mountainous streams.

Factors influencing the species distribution

Response curves

The environmental variable response curves show that the predicted probability of occurrence of Kashmir gray langur was highly associated with areas having pronounced precipitation seasonality, moderate terrain slope, and optimal diurnal temperature ranges (Fig. 6a, b, c). The results show a gradual decline in the probability of occurrence with an increase in the disparity (>45%) between monthly

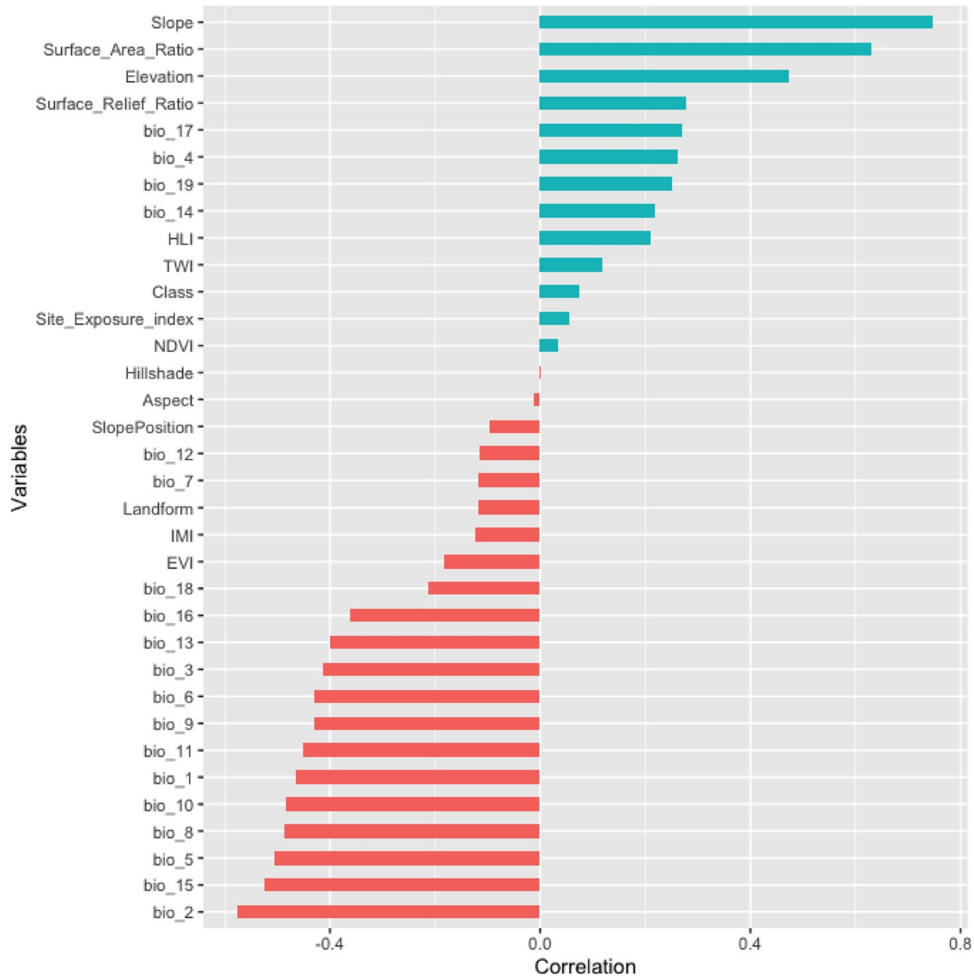

Fig. 3 Correlation (x-axis) between ensemble model projection and the predictor variables (Y-axis). The predictor variables with values close to zero indicate the least influence on the probability of occurrence; variables with positive values (cyan bars) suggest a positive influence, and variables with negative values (orange bars) indicate an inverted influence on the probability of occurrence of Kashmir gray langur in our study area

precipitation. A unimodal relationship between slope and probability of occurrence of langurs, with a peak at 23°, indicates that habitat areas with a moderate slope (mean slope = 10.53°) have a higher influence on species occurrence. Interestingly, the species is shown to thrive best in areas with the maximum temperature of the warmest month ranging between 15 and 28 °C, which represents typical temperate conditions (Fig. 6f). The probability of occurrence of langurs initially shows a negative relationship with the mean diurnal temperature range up to 9.6 °C followed by a steady increase till 10.7 °C, and a sharp decline beyond the mean diurnal temperature range of 11.2 °C. Moreover, we found that lowland areas (< 1400 m), highland areas (> 4000 m), and areas with low rugosity were associated with species absence or a very low probability of langur presence (Fig. 6d, e).

Discussion

The primary objective of this study was to develop a precise habitat suitability model, predict the patterns of distribution of the Kashmir gray langur in the Kashmir region, and assess factors that influence the same, with the ultimate aim to contribute towards its conservation and effective management. The high values of TSS (mean = 0.784) and AUC (mean = 0.926) indicate high model performance and suggest a strong predictive ability of the ensemble SDM, thereby providing an ecologically reliable projection of the areas suitable for the species. The results reveal that the probability of occurrence for the species is high in the peripheral mountainous areas of the Kashmir valley, with the southeastern and northwestern regions offering comparatively continuous and highly probable occurrence areas than the southwestern and northeastern regions. Furthermore, the results suggest that Kashmir gray langurs have high affinity for the land-use classes such as closed evergreen needle forests, closed evergreen broadleaf forests, closed deciduous broadleaved forests and also the highland herbaceous ecosystem surrounding the forests. The southeastern and northwestern

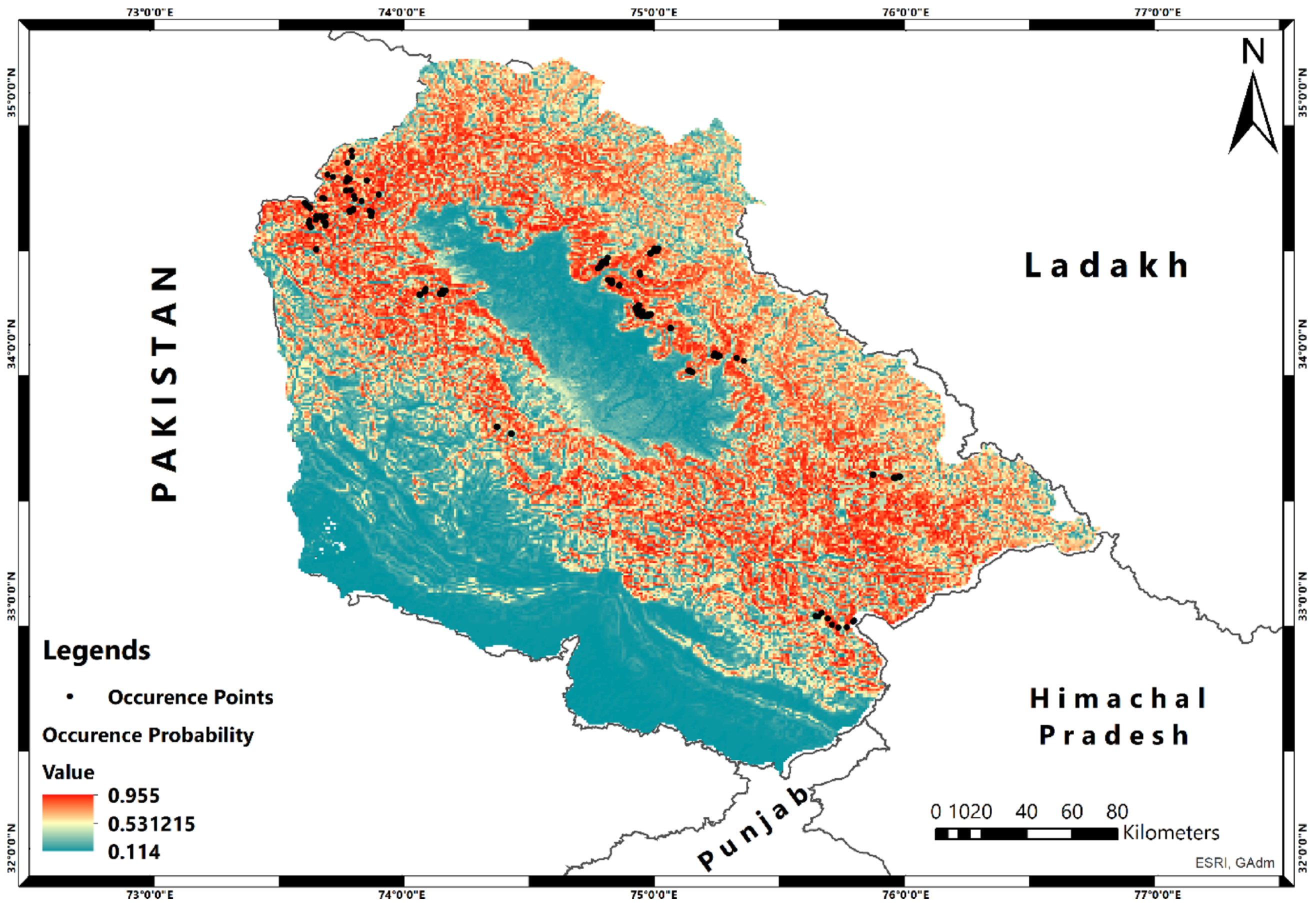

Fig. 4 Ensemble model showing the geographic distribution of KGL habitats across the Kashmir Himalayas. This gradient model output displays the probability of occurrence on a scale from 0 (low occurrence) to 1 (high occurrence)

parts of the study area are predominantly mountainous and overlap with forest ecosystems preferred by the species. Interestingly, the modeling output also showed the Kashmir valley areas and plains south to Pir Panjal mountain range with high levels of human disturbance (through urbanization, croplands, and roadways) and lack of natural forests to be highly unsuitable for the species, thus corroborating absence of Kashmir gray langur in these regions. Further, the results also showed that the probability of occurrence of Kashmir gray langur is either very low or decreases significantly in the areas coming under the influence of Zanskar mountainous range (3500–7500 m). Similar to the Pir Panjal range in Kashmir's southwestern flank, which acts as a major geographic and climatic barrier separating valley of Kashmir from the outer hot plains of Jammu, the Zanskar range in Kashmir's northeastern flank serves as a major geographic and climatic barrier separating valley of Kashmir from cold-desert plateau of Ladakh.

The model identified several environmental variables that were important in predicting the distribution of the species, including slope, elevation, mean diurnal temperature, precipitation seasonality, surface rugosity, and maximum temperature of the warmest month (Fig. 6a-f) as all these environmental variables affect the vegetation growth, seasonal food availability, and determine cover and shelter opportunities for the species that is primarily arboreal in nature. In Himalayan landscape, elevation serves as a proxy for vegetation, climate and human disturbance (Becker et al. 2007; Pokhriyal et al. 2012; Shah et al. 2019). The results of the occurrence probability modeling showed that the Kashmir gray langur is most suited to mid-elevational areas with the suitability peak at around 2600 m AMSL, coinciding with the transitional zone/ecotone between temperate (1600–2700 m) and subalpine (2700–3500 m) forests in Northwestern Himalaya (Hashim et al. 2023; Dar and Khuroo 2013). These are the elevations with moderate climatic conditions, offering the habitat spaces largely representing the temperate evergreen and deciduous forests with low human disturbance and moderate slope. The timberline in Kashmir Himalaya varies between 3200 and 3300 m and tree line varies between 3200 and 3700 m based on the aspect and configuration of the mountain (Singh et al. 2021). The probability of occurrence shows a significant decrease beyond 3600 m AMSL, mostly representing the

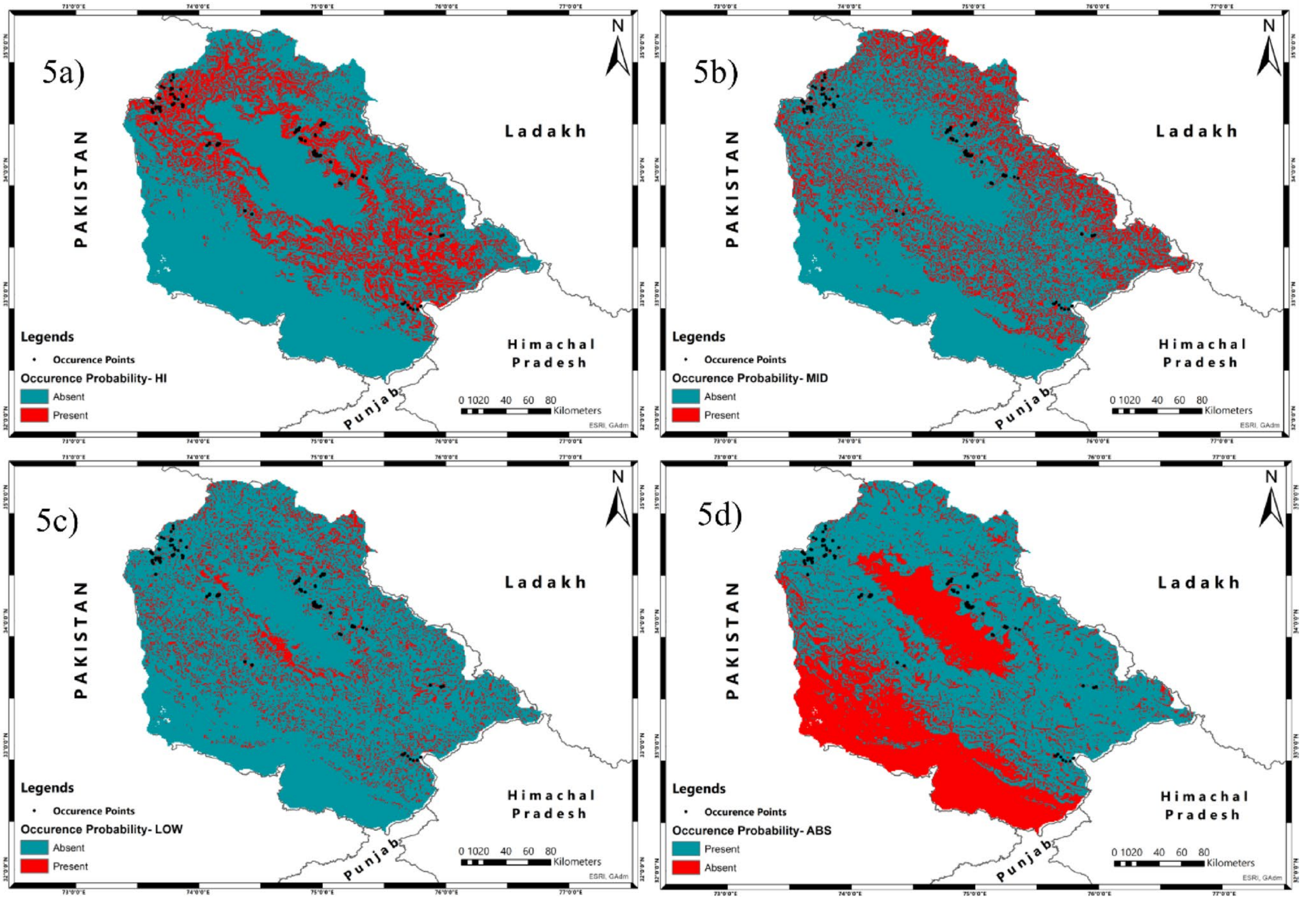

Fig. 5 Ensemble model output showing the distribution of suitable Kashmir gray langur habitat throughout the Kashmir Himalayas as a series of binary models of four different threshold values: (a) High probability of occurrence (HI) with predicted probability >= 0.75, (b) Moderate probability of occurrence (MID) with predicted probability ranged from >= 0.5 to < 0.75; (c) Low probability of occurrence (LOW) with predicted probability ranged from >= 0.25 to < 0.5; (d) Absent (ABS) with predicted probability ranged from < 0.25

treeless tundra vegetation particularly the alpine grasslands, as was expected with respect to our model parameters.

While NDVI depicts the degree of vegetation health (Meneses-Tovar 2011), land use classifies the various categories of land types (Huth et al. 2012), including the vegetation types. Though the model we built showed both the NDVI values and land-use classes to have positive influence on the distribution of Kashmir gray langur, the contribution of the later was much higher, suggesting higher association with particular vegetation classes such as temperate evergreen and deciduous closed forests. The species being folivorous and forest dependent (Khaleel 2020; Minhas et al. 2012), our model results showed success in capturing the important ecological signals related to Kashmir gray langur space use in Kashmir Himalaya.

Moreover, surface-to-relief ratio significantly influences Kashmir gray langur habitat suitability, showing the highest occurrence probability around a 0.5 ratio. This indicates that moderately rugged or hilly terrain, where the total surface area is about twice the elevation variation, is ideal for this species. These results are in consonance with the previously conducted studies on this species (Jahangeer et al. 2019; Khaleel 2020; Schwitzer et al. 2014), which showed preference of Kashmir gray langur to rugged and hilly terrain. In primates, predation has been shown to influence the habitat use, group size, and ranging behavior (Kamilar and Beaudrot 2018). Since there is a spatial variation of predation risk across various landscape features (Nowak et al. 2014; Parker et al. 2022) ascribed to the varying levels in predator and prey navigation, visibility and detection alike (Gaynor et al. 2019), the preference of these langurs to hilly terrains could be an evading strategy to avoid the predation. However, the effects of environmental stress on primate populations, scales dependent habitat selection has also been observed in few studies (Kamilar and Beaudrot 2018; Parker et al. 2021).

Abiotic stressors, such as temperature and precipitation, define the geographical boundaries for primate distributions (Kamilar and Beaudrot 2018; Williams et al. 2021). Primate behaviors can be influenced by these stressors, which can

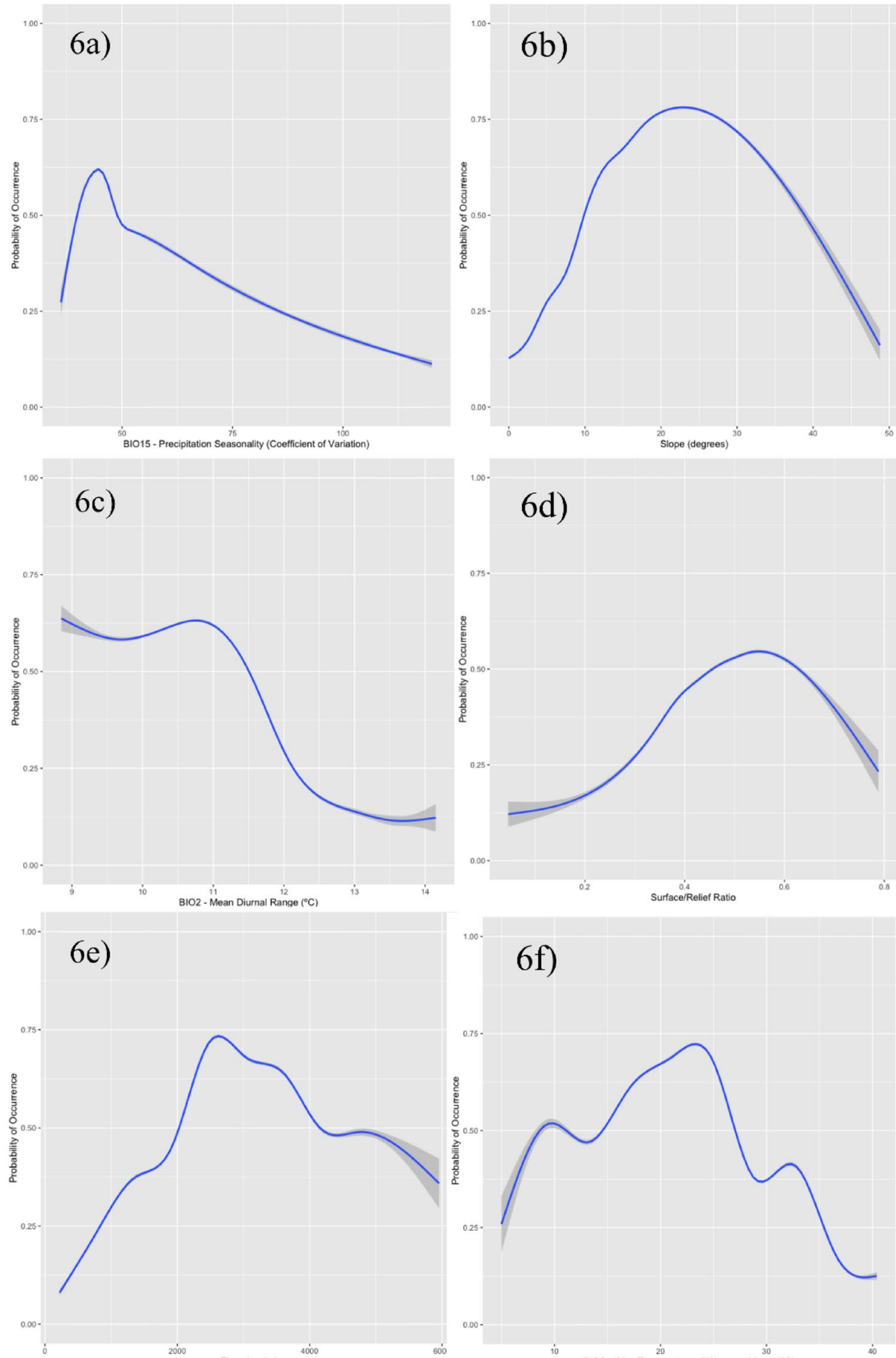

Fig. 6 Response curve plot generated with ensemble model showing the dependence of probability of occurrence of langur on the precipitation seasonality (6a), Slope (6b), mean diurnal temperate range (6c), surface relief ratio (6d), elevation (6e) and maximum temperature of the warmest month (6f). The curve shows the mean response of the ten-replicate ensemble SDM runs (blue) and the standard deviation (gray)

occur either through direct physiological demands such as thermoregulation or indirectly through changes in the vegetation of their habitat (Li et al. 2020; Wessling et al. 2018; Williams et al. 2021). Our results identified mean diurnal temperature range, a measure of temperature fluctuation, as the most influential variable affecting occurrence probability. The areas with daily temperature variation ranging from 10 °C to 11 °C have the highest probability of occurrence for these langurs. Nevertheless, we found that the probability of occurrence rapidly decreased beyond this threshold, i.e., the areas with significant fluctuations in diurnal temperatures. We found that the distribution of the Kashmir gray langur is limited by the temperature of the warmest month and precipitation seasonality. These langurs prefer habitats with specific temperature ranges and minimal variation in seasonal rainfall. Notably, range sizes of plant species are influenced by diurnal temperature ranges (Gallou et al. 2023) and seasonal precipitation (Harsch and HilleRisLambers 2016), while the temperature of the warmest month affects plant species richness (Gwitira et al. 2014). Therefore, the impact of these climate variables on Kashmir gray langur occurrence may be indirect, attributed to the vegetation distribution and structure determined by such factors.

Our findings demonstrated that, in addition to topographic variables, climatic variables such as precipitation and temperature are key limiting factors for Kashmir gray langur potential habitat distribution. However, the Kashmir Himalaya with higher-than-average global warming (Hamid et al. 2020) may experience temperature and precipitation regime change (Ahsan et al. 2022) at a faster rate thereby making it a highly vulnerable ecosystem to climate change (Dolezal et al. 2021), with potential multi-dimensional risks to the species (Graham et al. 2016). In the recent past, the mountainous areas in Kashmir Himalaya are known to have experienced an increasing trend in mean minimum temperature and decreasing trend in the precipitation (Shafiq et al. 2019), and this trend is expected to have negative environmental and ecological consequences. Moreover, the impact of climate change in the Kashmir Himalaya may have been intensified by habitat loss and fragmentation caused by changes in land use (Ahmed et al. 2021), ultimately posing a threat to the biodiversity within these ecosystems, particularly to Kashmir gray langur populations, which have low genetic diversity and a strong population genetic structure (Hameed et al. 2024b).

Of particular concern, our model shows that suitable habitats for the species largely overlap with sensitive high-altitude ecosystems highly exposed to climatic fluctuations. As a primarily forest-dwelling and folivorous primate with limited behavioral plasticity and low dispersal capacity, the Kashmir gray langur is unlikely to occupy habitats beyond its current elevational range or outside its preferred forest types. These forests provide key structural and microclimatic resources; tall trees for roosting and canopy cover dense forest canopies offer essential escape terrain from predators, protection from extreme weather, and safe sites for resting and social interactions. Consequently, even modest climatic shifts could jeopardize habitat availability and quality and further isolate already fragmented subpopulations.

From a conservation standpoint, these findings underline the need for proactive, climate-informed management. Additionally, effective planning should account for the sensitivity and exposure of the species to threats such as climate change, as well as its limited adaptive capacity arising from low behavioral plasticity, terrestriality, dispersal velocity, and habitat specialization. Hence, we recommend integrating the ensemble distribution maps into conservation planning for the Kashmir gray langur to enhance their resilience to climate and land-use change, as well as intrinsic threats such as low genetic diversity and strong population structure. Specifically, the outputs can guide prioritization of actions to restore and maintain forest connectivity across key mountain ranges, including Zabarwan, the Greater Himalayas, and Pir Panjal, to link isolated subpopulations across the River Sindh and Jhelum. We further recommend protecting refuge habitats, such as Dachigam National Park, which has been shown to serve both as a stronghold for the species and as a critical connectivity hub facilitating dispersal and gene flow between central and southern Kashmir populations.

Methodological and analytical considerations

Although, the findings of this study could prove helpful in designing a robust conservation strategy towards the long-term survival of Kashmir gray langur in Kashmir Himalaya, several limitations must be acknowledged and addressed in future research. One such limitation is the use of coarse resolution data, as topographic variables like aspect and slope, and vegetation proxies such as NDVI and forest type are likely to operate at a finer scale for langur distribution. Therefore, features like narrow ridges, forest gaps, and microclimatic refugia may not be well represented at this resolution. We also did not include specific anthropogenic disturbance variables such as distance to roads or natural barriers like rivers, instead relying on land use/land cover data that broadly captures human-nature interactions (Li et al. 2024). Future studies should incorporate fine-scale predictor data and expand survey areas to improve model accuracy and representation.

Due to limited data, we did not apply spatial autocorrelation corrections but minimized spatial bias by selecting widely spread occurrence points and using only one point per clumped occurrence. To reduce temporal bias, we used the most recent secondary data available. Further, considering the threshold criteria of at least 10 records for each predictor to be evaluated in the model analysis (Harrell et al. 1996), our limited dataset also restricted the ability to correct potential biases without losing data critical for model accuracy. However, we acknowledge that the use of random subsets in 10-fold cross-validation and the absence of spatial thinning may allow some residual spatial bias to influence model performance metrics and ecological inference. Sensitivity analyses at finer spatial resolutions were not feasible within current computational limits but are recommended for future work in this topographically complex region.

We did not rely on AIC for model selection as we used an ensemble modeling approach, with strong validation metrics (mean AUC = 0.926, mean TSS = 0.784) indicating a robust model unlikely to be overfit. Principal Component Analysis (PCA) was employed to reduce the dimensionality of environmental variables and avoid overfitting, which we considered more effective than Variance Inflation Factor analyses for our species distribution focus. Pseudo-absence data were generated conservatively to avoid overfitting, supported by high validation scores. However, for improved robustness, future studies with larger occurrence datasets should explicitly incorporate anthropogenic disturbance variables, apply spatial thinning, and use structured cross-validation methods to reduce spatial dependence and enhance prediction reliability for conservation planning. Additionally, integrating demographic, behavioral, and land-use data into future modeling frameworks will help refine predictions of habitat dynamics and enhance the ecological realism of conservation strategies for this endemic high-altitude primate.

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Author contributions Shahid Hameed: Conceptualization (equal), formal analysis (lead), methodology (equal), software (lead), data curation (lead), visualization (lead), writing—original draft preparation (lead), writing—review and editing (equal). Luíz Fernando Esser: Methodology (Supporting), formal analysis (lead), visualization (equal), writing—review and editing (equal). Chamba Wangmo data curation (lead), writing—review and editing (equal). Md. Niamat Ali: supervision (lead), writing—review and editing (equal). Tawqir Bashir: Conceptualization (equal), methodology (equal), supervision (lead), visualization (equal), writing—original draft preparation (equal), writing—review and editing (equal).

Declarations

Conflict of interest The authors declare no conflicts of interest.

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