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Environmental factors shaping habitat suitability of *Gyps* vultures: climate change impact modelling for conservation in India

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Abstract

Out of eight *Gyps* species in the world, three residents (*G. bengalensis*, *G. indicus*, *G. tenuirostris*) and two migratory (*G. fulvus*, *G. himalayensis*) inhabit Indian forests and other landscapes. While Himalayan and Eurasian *Gyps* are near threatened and least concerned species, respectively, the resident *Gyps* are critically endangered. They are facing modification in habitats caused by anthropogenic factors and are enduring climate change. The impact of climate change has been insufficiently studied. The aim of this study is to predict current and future habitat suitability for these vultures shaped by bioenvironmental factors using maximum-entropy species distribution modelling. Seventy-one robust predictions and models, species and scenario wise (AUC 0.780 to 0.981, TSS 0.478 to 0.852 and CBI 0.978 to 0.997) were generated. Whole Indian landscape (3,287,263 km²) was categorised into unsuitable, moderately suitable and highly suitable habitats and analysed floristic region-wise. There was a reasonable change in habitat suitability which showed a trend of decrease in the suitable area in the future (3287 to 65,745 km²). The key environmental variables shaping current and future habitat included land use/land cover, annual mean temperature (bio1), precipitation of coldest quarter (bio19), precipitation seasonality (bio15) and precipitation of warmest quarter (bio18). Our results on the potential habitat in different floristic regions and projected change in future habitat will aid national and regional managers to design proactive approaches towards conservation of endangered *Gyps* vultures. Management interventions like in situ conservation, habitat maintenance, advance planning of habitat improvement, expansion of favourable area and protection of suitable area have been proposed.

Keywords Habitat drivers · Habitat change · MaxEnt modelling · Resident Gyps · Wintering Gyps

Introduction

Vultures are among the most threatened birds throughout the world with a majority of the species at risk (Botha et al. 2017). India is endowed with six resident (bearded vulture, Egyptian vulture, Indian vulture, red-headed vulture, slender-billed vulture and white-rumped vulture) and three wintering (cinereous vulture, Eurasian griffon and Himalayan griffon) old-world vultures (MoEFCC 2020). Five of these

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Gyps vultures (Indian vulture *Gyps indicus* = INV, slenderbilled vulture *Gyps tenuirostris* = SBV, white-rumped vulture *Gyps bengalensis* = WRV, Eurasian griffon *Gyps ful*vus = EGV, Himalayan griffon *Gyps himalayensis* = HGV) are phylogenetically closer in comparison to four distant, non-*Gyps* vultures having different competitive behaviour. The former is comparatively more social and has the advantage of getting information early about carcass presence and stronger group defence but are disadvantaged when it comes to poisoned carcasses, where they are at higher risk. Therefore, the management requirements of these two groups differ significantly (Campbell 2016).

The populations of vultures, in general, have diminished or they have been eliminated in some of their distribution ranges due to habitat loss and other reasons like lack of food resources, exposure to livestock contaminated with drugs and direct persecution like poison or shooting (Green et al. 2004; Ogada et al. 2011; Ilanloo et al. 2020). Decimation of the population of vultures in India was also reported due



Fig. 1 Location, physiographic and climatic details of the study area, India. Top row: Geographic position of India in the world. Middle row: Land use/Land cover and elevation gradients, Bottom row: Mean annual precipitation and Temperature ranges

to shelter destruction along with food shortage and poor breeding success (Chhangani and Mohnot 2004). Hurtt et al. (2011) reviewed that habitat loss is the primary cause of species extinctions. However, Ilanloo et al. (2020) identified climate change as a major factor for species extinction along with changes in habitat distribution within the short span of a few decades. As reviewed by Thapa et al. (2021), climate change may cause redistributions of species directly through changes in temperature and water availability, and indirectly through further habitat modification.

An important step in the recovery of the diminished vulture population (Prakash et al. 2012, 2019; Galligan et al. 2020, 2021; UPFD and BNHS 2021) will be a gain in the knowledge of current and possible future habitats of vultures and their management. For this, ecological modelling having the potential to fill the knowledge gaps regarding species distribution, may provide insight into the impact of climate change and aid in conservation planning (Rodríguez et al. 2007; Mateo et al. 2013). Therefore, species distribution modelling (SDM) could be applied as a tool in determining environmental covariates of habitats, mapping of suitable habitats and predicting the impact of climate change on it (Angelieri et al. 2016). Many SDM algorithms exist, but machine learning approaches have gained popularity due to their ability to fit responses with high predictive performance (Elith and Graham 2009). MaxEnt is one such machine learning algorithm used the most by the ecological modelling community (Merow et al. 2013; Sesink-Clee et al. 2015; Morales et al. 2017; Mohammadi et al. 2019; Urbina-Cardona et al. 2019; Vu et al. 2019) due to its high reliability and statistical robustness among well-established SDMs (Phillips et al. 2004; Elith et al. 2006; Summers et al. 2012; Banag et al. 2015).

Under the above premise, the present study is aimed at the following using MaxEnt SDM: (a) identifying dominant environmental factors shaping the habitat of *Gyps* vultures; (b) predicting and mapping the current habitat suitability; (c) assessing predicted change in future habitat expanse due to climate change; and (d) proposing broad management interventions based on habitat quality.

This study covers whole India, a country once known for

widespread and abundant populations of *Gyps* species

Methods

Study area

(Gadhvi and Dodia 2006; Baral et al. 2013), now threatened (IUCN 2022). Topographical heterogeneity, climatic variation, land use/land cover (LULC) pattern, historical occurrence of *Gyps* vultures and delineation of the floristic regions (FRs) of the study area are presented in Fig. 1 and Fig. 2 along with some detailed features in Supplementary Table 1. Range of elevation, mean annual temperature and mean annual precipitation of the study area is -1 to 8583 m, -33.8 to 30.0 °C and 33 to 9312 mm, respectively. The forests in different regions provide nesting and foraging habitats to the vultures due to presence of large trees, mountain cliffs and wildlife population. Outside forests also there is a sizable population of livestock which is another source of carcasses (NDDB 2019).

Data collection and processing

Presence-only species distribution model like MaxEnt requires species occurrence locations and their environmental covariates. Therefore, nesting, roosting and foraging presence sites of the studied species were collected from published literature (Supplementary Table 2), citizen science repositories ebird (http://www.ebird.org, Sullivan et al. 2009) and iNaturalist (http://www.inaturalist.org, iNaturalist users and Ueda 2020), and author's field works. Since spatial filtering, also known as spatial rarefying (Brown et al. 2017), improves the performance of ecological niche models by reducing sampling bias (Boria et al. 2014), the occurrence data were cleaned, duplicates were removed and then rarefied. Out of several rarefying distances tried, 4 km gave optimum results in the present case. Original occurrence points of different Gyps species, 2767 (EGV), 10,653 (HGV), 5533 (INV), 617 (SBV) and 4939 (WRV), were reduced after duplicate removal and spatial rarefication to 529 (EGV), 1131 (HGV), 876 (INV), 114 (SBV) and 1163 (WRV), respectively.

The environmental variables like temperature, precipitation, LULC and elevation determine vultures' habitat in general and shelter in particular (Jha and Jha 2021b). Therefore, predictor environmental covariates like bioclimatic variables required by SDM were downloaded at 30 arc second resolution from https://www.worldclim. org/ (1970–2000; Fick and Hijmans 2017), LULC from Copernicus Global Land Service at 100 m resolution (Buchhorn et al. 2020) and elevation from SRTM 1 Arc second global data from https://earthexpoler.usgs.gov/ (USGS EROS 2018). These layers were resampled at 30 arc second spatial resolution before plugging in Max-Ent. The categorical variable, LULC, available in 23 fine classes was reduced to six (forest, water, scrubland, agriculture, built-up, wasteland) for the present study as suggested by Jha and Jha (2021b). All these environmental variables may possibly have collinearity among them and



Fig. 2 Vegetation based divisions of India and occurrences of *Gyps* vultures. Top row: different floristic regions and occurrence locations of *Gyps bengalensis* (white-rumped vulture), Bottom row: occurrence

ignoring the multicollinearity may lead to false ecological conclusions in modelling the spatial distribution of a species (Heikkinen and Luoto 2006; de Frutos et al. 2007). Therefore, Pearson correlation analysis was carried out at ± 0.8 threshold to identify and remove colinear covariates using "Remove highly correlated variables" tool of SDM tool box (Brown et al. 2017). The variables were

locations of *Gyps indicus* (indian vulture) and *Gyps tenuirostris* (slender-billed vulture), and *Gyps himalayensis* (Himalayan griffon) and *Gyps fulvus* (Eurasian griffon)

input alphabetically. Highly correlated variables namely, bio4, bio5, bio6, bio8, bio9, bio10, bio11, bio13, bio16, bio17 and Elevation were eliminated. For further improvement of the models, bias file was prepared using Correcting latitudinal background selection biases tool of SDM tool box (Brown et al. 2017). This was done for minimising overfitting and avoid sampling habitat outside of a species' known occurrence and account for collection sampling biases with coordinate data (Brown et al. 2017).

Climate model selection

There are several GCMs available with Representative Concentration Pathways (RCP2.6, RCP4.5, RCP6.0, RCP8.5) for different climate scenarios (Stocker 2014) but there is no consensus on which makes the most accurate one. However, Sutton et al. (2015) recommended ensemble of multiple GCMs to reinforce the accuracy of the projections. This is a very common approach for habitat projection (Stiels and Schidelko 2018). Therefore, we chose commonly used GCMs and downloaded precalculated 30 arc second data from WorldClim (Fick and Hijmans 2017): CCSM4 (de Luis et al. 2019), HadGEM2AO (Ahmad et al. 2019) and MIROC5 (Sony et al. 2018). Two RCPs namely, RCP4.5 (moderate) and RCP8.5 (extreme) (de Luis et al. 2019; Vu et al. 2019), for short-term (2041–2060 represented by year 2050) and long-term (2061–2080 represented by year 2070) prediction were chosen based on the hypothesis that a sharp cut in CO_2 emission will not happen (Lane 2018) and lower emission scenarios will be unlikely (Manning et al. 2010). Prediction averaging of the three GCMs was done in order to increase model accuracy of habitat suitability area (Dormann et al. 2018).

Distribution modelling

After processing presence locations and environmental variables in ArcGIS, they were used as the input of the MaxEnt model and predictions were made for the different scenarios. The model was run at default MaxEnt settings with a change in the run type, which was set as bootstrap with 10 replicates per prediction and a random test percentage of 25. Feature type used for model training was auto features and the number of background points was 10,000. Six model entities were studied (5 Gyps species and 1 aggregated all species of Gyps or "superspecies"). For each of the 5 species, 2 models (with 10 replicates) were trained: with-LULC and without-LULC models, while for the superspecies entity, only one model was trained (without LULC for comparison). Predictions for the present period were made by all of the models while predictions for the future periods were made by only the without-LULC model due to unknown longterm dynamics of landcover. Climatic predictors used for the future predictions were updated for the corresponding time period.

Tabulation and mapping

Area under receiver operator curve (AUC) values and variable contribution were tabulated, maps were reclassified and

jackknife bar charts and response curves were analysed to present the results. Other two model evaluators true skill statistics (TSS) and continuous Boyce index (CBI) were also computed in R using SSDM (Schmitt et al. 2017) and mod-EvA (Barbosa et al. 2013) packages, respectively. Most of the studies considered reclassification of continuous Max-Ent output range (0-1) into four classes (Vu et al. 2019; Zhang et al. 2019) in a smaller study area. Proposed classification for raptors including vulture by Zhang et al. (2019) was fine tuned in the present study into three categories of suitability (0-0.3 as unsuitable; 0.3-0.6 as moderate and 0.6–1.0 as high). This was done keeping into view coarse scaling in large study area (25 times larger than Zhang et al. 2019) based on previous field experiences (Jha and Jha 2020, 2021a, b). All MaxEnt outputs were also separately reclassified into two categories, unsuitable (0-0.30) and suitable (0.3-1.0), for calculation of future loss or gain in habitat area. The present prediction was then compared with each of the future scenarios to estimate the suitable area lost or gained as a result of climate change. ArcGIS 10.5 and Microsoft Excel were used to process the results. The huge study area (3.28 million km²) was divided into floristic regions of India (Sharma 2005). A map of different floristic regions was digitised using the data from Sharma (2005) and the output maps were analysed accordingly.

Results

Model predictors

The selected non-colinear covariates (Pearson coefficient ± 0.8) namely, bio1, bio2, bio3, bio7, bio12, bio14, bio15, bio18, bio19 and LULC contributed in varying proportions to prediction in different species, as detailed in the covariate contribution table of MaxEnt output. However, in the case of present models with LULC, the average cumulative contribution for all the species (top three covariates) was found to be 71.2% (range 65 to 86%). For the top five covariates, this was found to be 88.5% (range 86 to 97%). Without LULC, it differed marginally, 74.2% (range 62.9 to 91.6%) for the top three covariates and 89.2% (range 84.6 to 96.5%) for the top five covariates. Considering all the species together, the top five rankers or dominant variables (based on modified Likert ranking method; Bhattacherjee 2012), in decreasing order of importance, for without LULC models were bio1, bio19, bio15, bio18 and bio14. Species wise top three covariates were bio19, bio7 and bio18 (EGV); bio1, bio19 and bio14 (HGV); bio15, bio14 and bio1 (INV); bio18, bio1 and bio14 (SBV); and bio15, bio1 and bio12 (WRV). In the case of with LULC models, this order changed which is described in Supplementary Box 1. However, the jackknife chart of training gain (Figs. 3

Fig. 3 Jackknife chart of variable importance in resident *Gyps* species. Note dark blue, light blue and red bars in jackknife chart (top indian vulture, middle slender-billed vulture and bottom white-rumped vulture) showing importance with only variable, without variable and with all variables, respectively



and 4) showed some variation in the ranking of variables when compared to the variable contribution table. Response charts of LULC components are presented in Supplementary Fig. 1.

The response curves between dominant environmental variables and distribution probability of resident *Gyps* vultures (*G. bengalensis*, *G. indicus*, *G. tenuirostris*) and migratory (*G. fulvus*, *G. himalayensis*) drawn by Max-Ent reflected varied responses (Figs. 5 and 6). However, the most dominant climatic covariate bio1 (Annual mean temperature) showed a narrow range (around 24 °C) as the most suitable temperature for INV, SBV, WRV and EGV but HGV favoured a wider range towards lower temperature (1-24 °C). Bio18 (precipitation of warmest quarter), the next dominant variable, presented positive relationship in precipitation increase (500 mm onwards) with occurrence probability in all the *Gyps* species except *G. indicus* with inverse relation. Bio19 (precipitation of coldest quarter), yet another dominant covariate, recorded that in the case of resident *Gyps* this (precipitation, 200 mm onwards) had decreasing but migratory vultures had increasing correlation. Response of precipitation seasonality (bio15) towards species occurrence reflected positive relation in all the *Gyps* except minor variation of first decrease and then increase in the case of *G. himalayensis*.

Model performance

The distribution density of 10,036 occurrence points in different landcover classes was found to be 0.0112 km^{-2} (builtup area), 0.0064 km^{-2} (forest), 0.0054 km^{-2} (waterbody), 0.0050 km^{-2} (scrubland), 0.0013 km^{-2} (wasteland) and 0.0010 km^{-2} (agriculture). Using unique points for each species, 70 species-based predictions (EGV; HGV; INV; SBV and WRV) and one all vultures (superspecies) prediction for habitat assessment were developed. Species wise details of **Fig. 4** Jackknife chart of variable importance in migratory *Gyps* species. Note dark blue, light blue and red bars in jack-knife chart (top: Himalayan griffon and bottom: Eurasian griffon) showing importance with only variable, without variable and with all variables, respectively



model evaluators (AUC, TSS, CBI) are presented in Supplementary Table 3. The AUC, TSS and CBI values for models without LULC ranged between 0.781 and 0.976, 0.478 and 0.852, and 0.978 and 0.997, respectively. The CBI charts of different species are presented in Supplementary Fig. 2.

Habitat and floristic regions' suitability

Habitat suitability (pan-India) and floristic region's (vegetation based regional units) suitability in terms of area for different Gyps species are presented in Fig. 7 and Supplementary Table 4 and 5, respectively. All Gyps area suitability map is presented as Supplementary Fig. 3. Habitat suitability area of different species and floristic regions, modelled with LULC, are presented in Supplementary Tables 6 and 7, respectively. The projected pan-India suitable area for different species, in the present without LULC, in decreasing order was 50.2% (WRV), 28.4% (INV), 23.2% (EGV), 10.5% (HGV) and 3.9% (SBV) in the total available area of 3.287 million km². However, some areas were found to be overlapping among different species. When LULC was included as a modelling parameter, the area availability decreased from climatic projection by 12.1% (WRV), 6.5% (EGV), 4.5% (INV), 0.6% (SBV) and 0.1% (HGV), respectively, indicating a greater role of LULC in the former three species.

As regards the vegetation based regional suitability, suitable habitat for *Gyps* was found in all the FRs though in varying sizes. The habitat of resident vultures was spread

broadly all over the country from the northern-most region, Western Himalaya (33.636°N), to southern-most region, Malabar (09.179°N) while the habitat of wintering vultures was confined from Western Himalaya (35.837°N) to West Indian Plain and Central India (22.631°N). Among residents, *Gyps tenuirostris* (30.497°N–25.198°N) and, among wintering, *Gyps himalayensis* (35.348°N–25.565°N) had the narrowest habitat belts.

Since none of the species of vultures were reported from the Andaman and Nicobar and other Islands during the considered study period, we ignored this FR for the purpose of this study. Though all other FRs of India had suitable habitats for Gyps vultures, resident and wintering vultures showed some preferences when seen at the species level. Himalayan griffon remained confined to the northern FRs (Assam, Eastern Himalaya and Western Himalaya) but EGV expanded its presence further up to the central FRs (Assam, Central India, Eastern Himalaya, Gangetic Plain, West Indian Plain and Western Himalaya). The southern peninsular region of India lacked the presence of wintering griffons. Resident Gyps species showed better adaptation as indicated by the presence of suitable habitats in the southern region. Like HGV, SBV was also confined to the northern regions but in a much narrower belt of the Himalayan tarai plain. Unlike SBV, other two resident Gyps had a wider distribution. For example, INV had suitable habitats in all the floristic regions except Assam and Deccan; and WRV was present through all the floristic regions.

Fig. 5 Response curves of environmental parameters (rows 1 to 4; bio1 (annual mean temperature), bio18 (precipitation of warmest quarter), bio19 (precipitation of coldest quarter), bio15 (precipitation seasonality), respectively) in resident *Gyps* vultures (indian vulture, slender-billed vulture, white-rumped vulture)



On account of species richness, the most suited region is Western Himalaya (all the five species) and least suited is Deccan (two species only, INV and WRV). The floristic regions Assam, Eastern Himalaya and West Indian Plain supported four species while Central India, Gangetic Plain and Malabar harboured three species. However, these species had a suitable area expanse at 47% of 3.287 million km². Though overlapping among the species, their suitable area was distributed in different floristic regions in decreasing order: Central India (24%), Western Himalaya (15.9%), West Indian Plain (14.4%), Gangetic Plain (10.5%), Deccan (10.1%), Eastern Himalaya (9.6%), Malabar (8.2%) and Assam (7.3%). This indicated that Central India is the most important floristic region for *Gyps* species.

Impact of climate change on habitat

Predicted future emission scenarios RCP4.5 and RCP8.5 belonging to (i) the short term, i.e. year 2050, and (ii) the long term, i.e. 2070 (Figs. 8, 9 and 10, 11 and Supplementary Table 4), when compared with the present climatic model, showed changes in both unsuitable and suitable areas. Out of four, a minimum of three scenarios showed a decreasing trend in area suitability in EGV, HGV, INV and WRV. In the case of SBV, all four scenarios showed a decrease from the present prediction.

The "stable" area (suitable as well as unsuitable) along with "loss" of suitable area and "gain" from unsuitable area in future scenarios is presented in Supplementary Table 8. Both suitable and unsuitable area of the present prediction **Fig. 6** Response curves of environmental parameters (rows 1 to 4; bio1 (annual mean temperature), bio18 (precipitation of warmest quarter), bio19 (precipitation of coldest quarter), bio15 (precipitation seasonality), respectively) in migratory *Gyps* vultures (Eurasian griffon, Himalayan griffon)



Fig. 7 Habitat suitability classes distribution (yellow = unsuitable, blue = moderate, pink = high) of *Gyps* vultures in different floristic regions of India. Top row: *Gyps indicus* and *Gyps bengalensis*. Middle row: *Gyps tenuirostris*. Bottom row *Gyps tenuirostris*. Bottom row *Gyps tenuirostris* and *Gyps fulvus*. Distribution of *Gyps tenuirostris* and *Gyps himalayensis* may be seen confined to northern floristic regions with limited expanse



recorded a change in their status since their parts converted to unsuitable and suitable category, respectively, in both short and long terms. Eurasian griffon, SBV and INV showed a reduction in suitable area for both the RCPs and terms, while WRV showed a decreasing trend (except 2050 RCP4.5), and HGV showed an increasing trend (except 2050 RCP4.5). The amount of change was meagre between 0.1 and 2% but still sizable in expanse (3287 to 65,745 km²).

The conversion dynamics are depicted species-wise and residency class-wise in Supplementary Figs. 4 and 5 migratory/ wintering, and Supplementary Figs. 6 to 8 resident *Gyps* vultures.

The change in future habitat, especially the loss of suitable habitat, was observed to be the lowest in the Himalayan region (Western Himalaya and Eastern Himalaya) and the Nilgiri mountains (Malabar and Deccan) for any vulture. Most of the changes or habitat conversion were seen in the plains and at the fringes of suitable or unsuitable areas for all the species found therein. The West Indian Plain, Central India and Gangetic Plain FRs were found more prone to loss.

Discussion

This study has produced habitat suitability maps derived from statistical models for five Gyps species. Naoroji (2006), referring to the limitation of existing range maps, has recorded that exact distribution of a species depends on availability of suitable habitat. Bustamante and Seoane (2004) have further suggested that SDM generated maps are improvement of traditional range maps based on broad survey of species presence. This study also provides the first account of a national baseline of species-wise suitable projected habitat of Gyps vultures and possible changes in the future in different floristic regions using field surveys in > 17% of total area considered, citizen science and published occurrence records, bioclimatic variables and SDM. The resulting analysis has shown a concern for suitable area showing a decreasing trend in the future for critically endangered resident species. Though citizen science data is considered unstructured, integration of expert survey data with the filtered citizen science data has been in vogue and is known to result in improved inference, predictive ability and ultimately with increased extent of inference of the structured surveys or expert data (Robinson et al. 2020).

Our study is based on MaxEnt algorithm which uses presence-only data. Using presence-only data to calibrate distribution models has some known drawbacks which may limit model performance (Brotons et al. 2004; Alatawi et al. 2020). Importantly, presence-only methods probably overestimate species occurrence, because locations predicted to be suitable may not in fact be occupied, as a result of limited species dispersal. As a result, using presence-absence data is strongly recommended whenever available (Brotons et al. 2004). However, presence-only records often the only available information about species occurrences, and these are still informative about the true underlying distribution (Zaniewski et al. 2002). Despite using presence-only data, Maxent has been shown to perform well, generating predictive models even with biased data and small sample sizes (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008). Kaky et al. (2020) have also reviewed that though MaxEnt models were criticised by some researchers earlier, it continued to be frequently used to fit models across many different taxa, geographical areas, time periods and environmental scenarios (Achour and Kalboussi 2020; Anoop et al. 2020; Anand et al. 2021; Cable et al. 2021; Dobrev and Popgeorgiev 2021; Gao et al. 2021; Gao and Shi 2021; Grimshaw et al. 2021; Jha and Jha 2021a,b,c; Mushtaq et al.

2021; Oliveira et al. 2021; Panthi et al. 2021, among others). MaxEnt has numerous advantages like (1) it can work with a small sample size especially rare and threatened species (Hernandez et al. 2006; Wisz et al. 2008; Kumar and Stohlgren 2009; Abolmaali et al. 2018), (2) it is easy to use and very useful when presence-absence data collection is impractical (Phillips et al. 2006; Kumar and Stohlgren 2009; Angelieri et al. 2016), (3) both categorical and continuous environmental layers can be applied in this software and (4) it measures importance of each environmental variable using the jackknife test, in terms of gain (Elith et al. 2011; Groff et al. 2014).

Despite the universal use of MaxEnt software, Cobos et al. (2019) and de Andrade et al. (2020) have recently suggested use of R packages which allows robust processes of modelling and straightforward construction of complex ecological niche models. Therefore, it is advisable that R packages, such as "kuenm," "ENMTML," "maxnet," and "dismo," may be used for prediction improvement in future modelling. It is further proposed that future models must contain modelled future LULC for enhanced accuracy in prediction, since climatic prediction may be an overestimation without LULC (Jha and Jha 2021b). Preston et al. (2008) also stated that distribution models predicting species responses to climate change included mostly climate variables and rarely the biotic interactions.

Habitat determinants

Bioclimatic habitat determinants used in this study sourced from WorldClim follow the dynamic approach. Bede-Fazekas and Somodi (2020) recently discovered potential traps in the use of the widely applied dynamic approach but simultaneously stated that this approach cannot be ignored also. The models presented here were with good to excellent prediction power due to uncertainty removal (De Marco and Nobrega 2018). MaxEnt variable contribution table showed that major determinants of suitable habitat for Gyps species in the study area are land use/land cover (LULC), annual mean temperature (bio1) and temporal variants of precipitation, e.g. bio19 (precipitation of coldest quarter), bio15 (precipitation seasonality) and bio18 (precipitation of warmest quarter). This finding is in general agreement with Herrero et al. (2006) which states that the influence of vegetation cover on the distribution of animal species, in providing food and shelter, also acts as a limiting factor to the spread of species. Freeman et al. (2019) also had a similar observation suggesting that forest cover is a more vital driver as compared to climate for the current distribution of the target species.

However, climate variables, particularly rainfall and temperature, generally influence habitat quantity and quality affecting the structure, composition and dynamics of



◄Fig. 8 Short term projected habitat suitability (yellow=unsuitable, blue=moderate, pink=high) of resident *Gyps* vultures under moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Top row: *Gyps indicus*. Middle row: *Gyps tenuirostris*. Bottom row: *Gyps bengalensis*

wildlife species (Kupika et al. 2018). Jha and Jha (2020) also reported LULC as the most prominent determinant of the distribution of different vulture species, followed by iso-thermality, and precipitation seasonality in Central India. The findings of this study broadly concur with this but differ in order of preference of these determinants in different species when considered on a much larger scale at country level. More so, several studies suggested the influence of bioclimatic variables in habitat determination in raptors (Gschweng et al. 2012; Liminana et al. 2012) and vultures (Zhang et al. 2019; Anoop et al. 2020) although the set of covariates were not similar in these different and distant localities.

Moreover, the lowest spatiotemporal occupancy in agricultural landscape (0.0010 km^{-2}) and highest in builtup area (0.0112 km^{-2}) followed by forest (0.0064 km^{-2}) , water (0.0054 km^{-2}) , scrubland (0.0050 km^{-2}) and wasteland (0.0013 km^{-2}) could be speculated to play a role in the prediction of habitat suitability corresponding to their importance. As suggested by response bars, built-up area, land covered by buildings and other manmade structures (Buchhorn et al. 2020) including road, railway, paved land and urban park (Venter et al. 2016) favours the *Gyps* species in providing foraging materials, for example, accidental carcasses, direct disposal of dead animals, feed through slaughterhouses and bone mills etc. Forest is the next favourable area for nesting as well as foraging while agricultural landscape is the least suitable for lack of nesting sites.

Response curves indicated varied impact of the covariates on vulture presence. Habitat suitability is a product of interaction among numerous covariates in different quantities (grades), not a function of any single variable (Richard et al. 2018; Jha and Jha 2021b). Quite a few among these could be following Liebig's Law of the Minimum (a covariate behaving as limiting factor). Hence, considering a single variable in isolation may be misleading as the species choose their habitat based on the interaction of several factors (Golterman 1975; Jha and Jha 2021b). However, a thumb rule can be drawn from response curves that increase in mean annual temperature beyond 24 °C produces stress conditions. Another stressing factor is precipitation in coldest quarter (bio19) beyond 200 mm for resident Gyps, though migratory ones have no such impact. However, precipitation in warmest quarter (bio18) beyond 500 mm enhances the probability of occurrence for all the *Gyps* species except *G. indicus*. Further generalisation reveals that precipitation seasonality (bio15) will be useful for residency but mean annual temperature beyond 30 °C may become intolerable.

Model robustness

Despite the weakness of AUC as an inadequate model evaluator (Lobo et al. 2008; Fourcade et al. 2014; Jiménez-Valverde 2014), model performance is commonly evaluated by AUC values of the Receiver Operating Characteristic (DeLong et al. 1988), especially MaxEnt (Gao and Shi 2021). For example, it was preferred in recent studies on animals (Achour and Kalboussi 2020; Mori et al. 2020), birds (Tehrani et al. 2021), raptors (Regos et al. 2021) and vultures (Khwarahm et al. 2021), since AUC is one of those statistics which provides a good information to judge the model performance where only presence data are used (Proosdij et al. 2016; Anand et al. 2021). Although AUC is widely applied (Abolmali et al. 2018; Abdelaal et al. 2019; de Luis et al. 2019; Achour and Kalboussi 2020; Mori et al. 2020; Anand et al. 2021; Jha and Jha 2021b), many agree that it tends to be overoptimistic (Lobo et al. 2008; Shabani et al. 2016), and hence, it is often complemented by another measure of model goodness. Therefore, CBI and TSS may be used as additional and better assessment as suggested by Allouche et al. (2006), Breiner et al. (2015), Manzoor et al. (2018) and Shabani et al. (2018). The reason for this could be as suggested by Lobo et al. (2008, 2010) that AUC is influenced by species prevalence but TSS has been widely advocated as a suitable discrimination metric less dependent on prevalence (Allouche et al. 2006; Somodi et al. 2017). Additionally, Sun et al. (2021) suggested that AUC is suitable for evaluating models built based on presence-absence data, and the CBI (Hirzel et al. 2006) evaluates presence-only models such as MaxEnt used in this study.

Model performance could be assessed by their categories as suggested in different studies. For example, AUC closest to a value of 1 would be a perfect model and AUC = 0.5 would indicate that the model performed no better than random (Barragan -Barrera et al. 2019). However, models are excellent with AUC > 0.9, good with AUC between 0.8 and 0.9, fair with AUC 0.7–0.8 and uninformative with AUC < 0.7 (Swets 1988; Araújo et al. 2005). TSS values are categorised as excellent with>0.8, good between 0.6 and 0.8, fair with 0.4 and 0.6, poor or no predictive ability with < 0.4 (Rew et al. 2020). The Boyce index varies between -1 and +1. Positive values indicate a model in which predictions are consistent with the distribution of presences in the evaluation data set, values close to 0 mean that the model is not different from a random model, and negative values indicate counter predictions (Hirzel et al. 2006; Di Cola et al. 2017). All our predictions (AUC between 0.781 and 0.976, TSS between 0.478 and 0.852 and CBI between 0.978 and 0.997) are very useful and considered suitable for conservation planning (Pearce and Ferrier 2000).

The models for the present, both with and without LULC, predicted results which varied in the expanse of habitat. The

Fig. 9 Short-term projected habitat suitability (yellow = unsuitable, blue = moderate, pink = high) of wintering *Gyps* vultures under moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Top row: *Gyps fulvus*. Bottom row: *Gyps himalayensis*



former had a lesser spread of suitable area than the latter which could be attributed to the fact that the environmental umbrella is mostly smaller than the climatic umbrella due to the specific requirements of a niche, e.g. trees/cliffs, water and ungulate/cattle concentration (Jha and Jha 2021a,b). This implied that the actual suitable habitat area was an overestimation in the case of bioclimatic models. This was similar across all the future models which are bioclimatic in nature also supported by Preston et al. (2008).

Habitat availability

Species distribution modelling was used to predict the habitat suitability, shaped by environmental factors, which was then reclassified in two classes. The first was the class comprising moderately and highly suitable areas and the second comprising unsuitable area for different species of *Gyps* in India, for each floristic region. It is apparent that HGV and SBV have restricted suitable habitats in the north which also overlaps other species (WRV, EGV). The habitat of INV is distributed mainly in the central and south-western part, mostly overlapping with WRV everywhere and EGV in

northern part. This indicates lower availability of projected suitable area kilometrage per species due to inter species competition in particular regions for shelter, territory and available food. Possible reason for the overlap was assigned to availability of ample source of carrion and relatively low availability of nest sites (Ferguson-Lees and Christie 2001). For example, large vultures like Lammergeier and Himalayan griffon are reported to coexist in closer proximity along with Saker Falcon (Katzner et al. 2004). However, overlapping areas due to sympatric nature of the species should be highly valued and protected (Zhang et al. 2019) to maximise multispecies conservation. Ground verification of selected sites was done in Western Himalaya tarai, Gangetic Plain, Central India and West Indian Plain (Madhya Pradesh, Uttar Pradesh and Rajasthan). It was observed that WRV and SBV preferred trees while INV chose cliff nesting surrounded by forests. This agreed with many studies (Majgaonkar et al. 2018; Jha et al. 2021) in different provinces but with a couple of exceptions (Khatri 2015; Navaneethan et al. 2015). Vultures showed an affinity to localities closer to water sources, mostly rivers or large waterbodies. Anoop et al. (2020) also recorded the use of riparian forested area Fig. 10 Long-term projected habitat suitability (yellow = unsuitable, blue = moderate, pink = high) of resident *Gyps* vultures under moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Top row: *Gyps indicus*. Middle row: *Gyps tenuirostris*. Bottom row: *Gyps bengalensis*



in the Western Ghats (Malabar region) being used by WRV for nesting. Kumar et al. (2014) and Misher et al. (2017) had similar observations of cliff nesting in INV along a river in Central India. Nests were mostly found in areas free from disturbance but cases of nesting near human settlements was recorded in the case of WRV. Such plasticity was also reported elsewhere (Bahadur et al. 2019).

Impact of climate change

Climate is considered a primary factor in constraining the distribution of plant species (Banag et al. 2015). This could be a possible reason for the change in habitat area in the future in this study, since other anthropogenic factors have not been considered in modelling. The impact is evident from the change in habitat expanse in the short- and long-term future. As a result of loss of suitable area and Fig. 11 Long-term projected habitat suitability (yellow = unsuitable, blue = moderate, pink = high) of wintering *Gyps* vultures under moderate (RCP 4.5) and extreme (RCP 8.5) scenarios. Top row: *Gyps fulvus*. Bottom row: *Gyps himalayensis*



gain from unsuitable area, a trend of net loss is observed in different scenarios of emission and term tenures. Different observations of a decrease in suitable habitat of wildlife species in general (McDonald et al. 2019) and vultures specifically (Ilanloo et al. 2020) support our finding. However, such an expansion and contraction of habitat area may have a bearing on the *Gyps* species population as habitat is an important place for the survival, reproduction and population development of any organism. Any changes in the quantity, quality and distribution of habitat have a wide range of effects on spatial dynamics and can directly affect the distribution, quantity and survival rate of organisms (Zhang et al. 2019). Nevertheless, such areas require advance planning to mitigate the loss and exploit the gains. Another point of interest of conservation should be the highland areas where there was the lowest change in habitat due to climate change as also observed by Banda and Tassie (2018) in endemic bird species.

However, the highest number of floristic region (FR) as well as the largest area coverage in decreasing order, i.e. WRV (1,253,037 km², 8 FR) > INV (786,121 km², 6 FR) > EGV (548,181 km², 4 FR) > HGV (343,094 km², 3 FR) > SBV (108,091 km², 3 FR), indicated better adaptability and lower vulnerability to varied bioenvironmental conditions of the former ones than the latter ones. Therefore, priority must be given to conservation of species with lower adaptability or higher vulnerability against climate change.

Management implications

Predictive models are a useful tool for wildlife managers to make better decisions about biodiversity management and conservation (Rodriguez et al. 2007). This study provided potential habitat areas for different *Gyps* species based on predictive modelling under different scenarios. All the models are robust enough to be replicated but a point of concern could be the future predictions which do not consider land use while it is evident that there is a constant change in forest, agricultural, built-up and other landcover. Nevertheless, due to a timely intervention in the management of forests, a positive shift, i.e. increase in (very dense forest and) open forest but decrease in moderately dense forest (ISFR 2021), was seen. Therefore, it is assumed that there may not be a negative change in vulture habitat or at least it may remain unchanged on this account.

However, the prediction of suitable habitat for Gyps vultures combined and species-wise independently differed in the floristic regions. Highly suitable area in the all-species combined prediction was reduced when compared with species individually; for example, SBV in Assam, INV in Central India, WRV in Central India and West Indian Plain, and EGV in West Indian Plain had much larger expanses of suitable area. This is due to the fact that the algorithm of the SDM works on specific requirement of a species. In the case of all Gyps vultures, common minimum suitability criteria were considered and a projection was made. Such a prediction indicated that species-wise management planning should be a better option than combined conservation efforts wherever feasible. Nevertheless, in Indian context, all species information is equally important since the Forest Departments look after overall vulture conservation.

Keeping the above in view, the predictions from this study could be used for conservation planning in the study area. As regards the planning structure, Indian governance is federal in nature where the responsibility of making a standard policy for conservation, if needed, rests with the Centre while states are responsible for implementing this strategy at a local level. In such a scenario, a large research study area becomes useful for the formulation of a common management strategy by the central government for the states. The following measures could be considered based on the above findings.

This study provided the expanse of suitable area in different floristic regions for different species. However, it is important to focus on land use in the area for any conservation programme. For example, in the case of reintroduction of a species, availability of nesting, roosting, and foraging area all become important. The agricultural land falling in suitable areas may provide only foraging opportunity, while forests, tall trees, or cliffs, depending on species, would be a must for nesting and roosting requirement.

Vulture centric development of existing suitable areas must be carried out. The concept of Vulture Protection Area (overlapping areas of high suitability for multiple species) and Vulture Conservation Area (species wise high suitability area) must be introduced in order to secure fruitful conservation. This must include roosting, nesting and foraging area for vultures/species in the core zone and foraging area in the periphery for buffer function. Going by the area prediction, and availability of sufficient nesting structures, feasibility of Vulture Conservation Areas may be explored in different floristic zones, for example, SBV Protection Area in the eastern part of Eastern Himalayas, INV-WRV Conservation Area in the eastern and western part of Central India. The area expanse of such reserves could be as large as possible after taking into consideration threats and opportunities, since vultures are highly mobile organisms and are capable of long-distance foraging trips, up to 100 km (Moleón et al. 2020). Within these reserves and outside, if feasible, suggested activities could be (i) in situ conservation of vultures in highly suitable areas; (ii) habitat maintenance for expansion of territory in moderately suitable areas; (iii) planning in advance for habitat improvement in unstable areas since changing climate can cause changes in the geographic distribution of the amount and quality of habitat (Holyoak and Heath 2016); (iv) expansion of favourable area for vultures which have shown habit plasticity (Genero et al. 2020), an agroforestry model could also be adopted by including trees of moderate height for shelter and rearing of medium sized vertebrates for food (Hiraldo et al. 1991; Chhangani 2007) in the areas where only foraging is possible; and (v) above all there is a need to protect the landscape (moderate and highly suitable area) against human-induced large-scale habitat change like, deforestation for development, in order to slow down species extinction (Kentie et al. 2018).

Conclusion

Though the models generated in this study based on bioclimatic variables could be further improved by incorporating bioenvironmental variable like dynamic LULC layers for future prediction, they are strong enough and should be used as a starting point for immediate management planning of *Gyps* vulture conservation in various floristic regions.

Our study of *Gyps* vultures' habitat suitability impacted by impending climate change identified habitat variables and provided delimitation of stable and unstable habitats of suitable and unsuitable nature in Indian context for the first time. This has direct implication on management of imperilled vultures since stable and suitable area could be used for in situ conservation and reintroduction of the species. Unstable area could be used for habitat improvement by ensuring nesting and foraging resources for further use by vultures in expanding their territory for increasing population. In general, development of reserves, protection of large trees, adoption of agroforestry etc. could be useful in model predicted areas to attempt a reversal of the endangered status, to some extent, of indigenous vultures in different floristic regions. The study also indicated better adaptability and lower vulnerability to varied bioenvironmental conditions of the different *Gyps* species. Therefore, priority must be given to conservation of species with lower adaptability or higher vulnerability against climate change.

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Declarations

Competing interests The authors declare no competing interests.

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