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Predicting range shifts of Asian elephants under global change

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Abstract

Aim: Climate change alters the water cycle, potentially affecting the distribution of species. Using an ensemble of species distribution models (SDMs), we predicted changes in distribution of the Asian elephant in South Asia due to increasing climatic variability under warming climate and human pressures.

Location: India and Nepal.

Methods: We compiled a comprehensive geodatabase of 115 predictor variables, which included climatic, topographic, human pressures and land use, at a resolution

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of 1 km^2, and an extensive database on current distribution of elephants. For variable selection, we first developed 14 candidate models based on different hypotheses on elephant habitat selection. For each candidate model, a series of 240 individual models were evaluated using several metrics. Using three climatic and one land use change datasets for two greenhouse gas scenarios, ensemble SDMs were used to predict future projections.

Results: Nine predictor variables were selected for ensemble SDMs. Elephant distribution is driven predominantly by changes in climatic water balance (>60%), followed by changes in temperature and human-induced disturbance. The results suggest that around 41.8% of the 256,518 km^2 of habitat available at present will be lost by the end of this century due to combined effects of climate change and human pressure. Projected habitat loss will be higher in human-dominated sites at lower elevations due to intensifying droughts, leading elephants to seek refuge at higher elevations along valleys with greater water availability in the Himalayan Mountains.

Main conclusions: Changes in climatic water balance could play a crucial role in driving species distributions in regions with monsoonal climates. In response, species would shift their range upwards along gradients of water availability and seasonal droughts. Conservation and management of elephant populations under global change should include design of movement corridors to enable dispersal of the elephant and other associated species to more conducive environments.

KEYWORDS

Asian elephant, climate change, habitat loss, range shift, seasonality, South Asia, species distribution modelling, water balance

1 | INTRODUCTION

Presently, the Asian elephant (*Elephas maximus*), an endangered species, occupies only a small fraction of its historical range (Choudhury et al., 2008; Sukumar, 2006). Between 26,390 and 30,770 elephants are reported in India, and between 100 and 125 are found in Nepal (Choudhury et al., 2008). The two countries harbour the bulk (more than 60%) of the total population of wild Asian elephants (Choudhury et al., 2008; DNPWC, 2008). The species survives in human-dominated habitats with human densities varying from approximately 149 to 292 people per km^2 (Worldometers, 2017), and is under threat from land use changes due to the continuous conversion of its habitat to agriculture, urbanization, transportation and industry. Elephant populations are usually small and mostly restricted to protected areas (Choudhury et al., 2008; Sukumar, 2006), which have not been planned to account for range shifts (Alagador, Cerdeira, & Araújo, 2016; Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004).

It is well known that climate change will cause redistributions of species (García-Valdés, Svenning, Zavala, Purves, & Araújo, 2015; Jetz, Wilcove, & Dobson, 2007) directly through (a) temperature and water availability, indirectly through (b) further habitat modification and additionally (c) through feedback loops between climate and vegetation, agricultural practices and land use (Tripathi & Mishra, 2017; Tsarouchi & Buytaert, 2018; Vanderwal et al., 2013). Higher temperature and its variability will lead to increased elephant mortality (Mumby, Courtiol, Mar, & Lummaa, 2013).

Even though climate change is projected to generally increase rainfall in South Asia in the near future (IPCC, 2013; Jayasankar, Surendran, & Rajendran, 2015), the intensity of changes will vary spatially and depend upon location (Rajendran, Sajani, Jayasankar, & Kitoh, 2013). Climate change is expected to increase the occurrence of monsoon break periods, delay monsoon onset and reduce summer precipitation by the end of 21st century (Ashfaq et al., 2009; Schewe & Levermann, 2012). The increase in the frequency, intensity and duration of weak spells or breaks can lead to enhanced drought (Rajeevan, Gadgil, & Bhate, 2010 and their Figure 1).

Warming will lead to shifts in the distributions of species poleward or to higher altitudes, mostly due to changes in temperature (Hickling, Roy, Hill, & Thomas, 2005; Moritz et al., 2008). Plants' distributions are influenced by actual evapotranspiration and water deficit (Stephenson, 1998; Stephenson & Das, 2011). Ultimately, climate-driven geographical redistribution of plant and animal species affects ecosystem functioning, human well-being and the dynamics of the climate system (Lenoir & Svenning, 2015; Pecl et al., 2017).

Land use change, one of the direct threats to the elephant (Choudhury et al., 2008), will also amplify the effects of climate

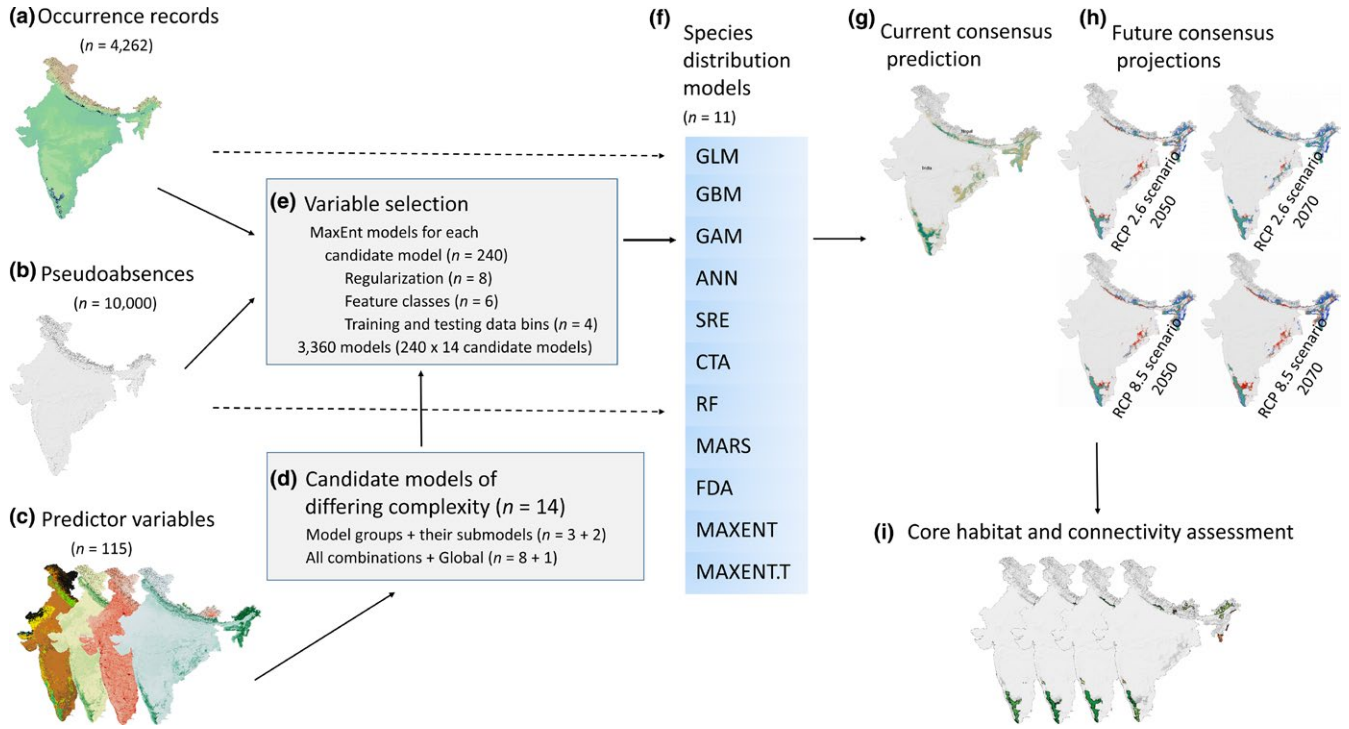

FIGURE 1 Methods for ensemble species distribution modelling for Asian elephant in India and Nepal (a–f); current consensus prediction (g); projection of models into future climate and land use change scenarios (h); assessment of core habitat and connectivity (i). See section species distribution modelling and evaluation for details of the SDMs used in the ensemble approach for the consensus projections

change indirectly due to alterations in surface energy budgets and thus temperatures at the local scale (Lenoir et al., 2010; Vanderwal et al., 2013). Changes in monsoon dynamics with increased variability in surface temperature and rainfall will affect climate water balance (Singh, Tsiang, Rajaratnam, & Di, 2014), thereby disrupting plant community structure and productivity (Condit, Engelbrecht, Pino, Perez, & Turner, 2013). Availability of forage and water influenced by seasonality is known to drive the habitat utilization of elephants (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014). Consequently, the interaction between climate change and land use will compound existing threats to the elephant.

Ensemble modelling approaches, which combine a series of species distribution models (SDMs), have become one of the widely used tools to forecast the anthropogenic climate change impact on species distributions (Araújo & New, 2007; Coetzee, Robertson, Erasmus, Van Rensburg, & Thuiller, 2009), as they produce consensus projections that usually outperform single SDMs (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). However, when a large set of predictor variables are considered for analysis, mainly due to the multidimensional abundance of environmental components, the model complexity increases and may lead to the development of heavily parameterized and overfitted models (Merow et al., 2014). Moreover, different SDMs and their underlying modelling decisions about inputs and settings further add to model complexity (Merow et al., 2014; Radosavljevic & Anderson, 2014). One way to reduce model complexity and avoid overfitting is to use an intermediate step of predictor variable selection before embarking into ensemble modelling. This step consists of developing candidate models of differing complexity by grouping the predictor variables based on their environmental types (Carroll, Dunk, & Moilanen, 2010) and on different hypotheses on the mechanisms governing species' habitat selection. These models can be fitted to the observed (presence-only) data, using widely used modelling technique such as MaxEnt (Phillips, Anderson, & Schapire, 2006). MaxEnt is known to facilitate species-specific tuning of modelling decisions for improved performance and the calibration and evaluation of models via spatially independent training and test datasets to reduce model overfitting (Muscarella et al., 2014). The performance of the fitted models can be assessed through the Akaike information criterion (Burnham & Anderson, 2004) and other adequate evaluation metrics (Muscarella et al., 2014). The variables identified by the most parsimonious model can then be used in the ensemble modelling approach.

In this study, we compiled a large database on environmental variables (115) covering India and Nepal with presence observations of Asian elephants (4,262), and subsequently used ensemble modelling and consensus projections to assess the current geographical distribution of the elephant and impacts due to future climate and land use change. We expect that seasonal variation in temperature and precipitation under the monsoonal regime and human disturbance plays a dominant role in driving the distribution of elephants. Our specific objectives were to (a) assess the relative contributions of climatic factors and their seasonal variation, human-induced disturbance, vegetation and topography on

elephant habitat suitability; (b) map the current and future elephant habitat suitability under different projections of global climate and land use change; and (c) assess the habitat quality of corridors linking fragments for current and future habitat suitability projections for elephant in India and Nepal.

2 | METHODS

2.1 | Study area

Our study area includes India and Nepal (8°–37°N, 68°–97°E), encompassing areas of 32,872,631 km^2 and 147,181 km^2, respectively (Balasubramanian, 2017; Karki, Hasson, Schickhoff, Scholten, & Böhner, 2017). The physiographical distribution is classified into three broad regions in Nepal, Lowlands (Terai and Siwalik), Mid-Mountains and Hills and High Mountains (Duncan & Biggs, 2012), and five broad regions in India, Himalayas and other ranges (including lowland Terai and Siwalik and hilly tracts of Western and Eastern Ghats in the south), Indo-Gangetic Plain, Thar Desert, Peninsular Plateau, and Coastal belts and Islands (Balasubramanian, 2017). The current distribution of Asian elephant in India and Nepal can be separated into four major regions (Choudhury et al., 2008): the Himalayan foothills and lowlands in northern India and southern Nepal (N), the eastern Himalayan foothills and Lowlands in north-eastern India (NE), the forests tracts in eastern India (E) and the Western and Eastern Ghats in southern India (S), which are representative of the broad ecological conditions governing elephant distribution in this region.

Our study area has a complex topography ranging from sea level in the south of India to elevation higher than 8,000 m in Himalayas in the north (Supporting information Figure S1). Two major weather systems dominate the general climate: the summer and winter monsoon circulations in India and the former in Nepal. The average annual rainfall in India and Nepal is about 1,190 mm and 1,530 mm, respectively, with heterogeneous spatial and temporal distribution (Li & Deng, 2017; Purohit & Kaur, 2017). The study area experiences four climatological seasons reflecting changes in precipitation patterns: winter (India: January and February; Nepal: December–February), pre-monsoon or hot weather season (March–May), summer monsoon season (June–September) and post-monsoon season (India: October–December; Nepal: October–November) (De, Dube, & Rao, 2005; Karki et al., 2017).

2.2 | Asian elephant data

Asian elephant occurrence records, which included direct observation and indirect evidences such as dung, track and debarking, were obtained from field surveys that ranged from one-time surveys to long-term monitoring of elephant populations in various time periods in India and Nepal (see Supporting information Appendix S1 for details). Most field surveys were carried out between the years 2002 and 2017, with few surveys done between 1990 and 2002. Overall, 4,262 Asian elephant occurrence records were collected.

Besides locations from field surveys, we obtained 135 elephant locations from the Global Biodiversity Information Facility (http://gbif.org) and the India Biodiversity Portal (http://indiabiodiversity.org) databases. Additionally, we obtained coordinates and digitized elephant occurrence locations from published literature and reports (see Supporting information Appendix S1).

Each georeferenced position was verified against a coarse spatial outline of the distributional range of Asian elephant provided by the IUCN Red List of Threatened Species (http://www.iucnredlist.org). In order to reduce spatial autocorrelation in our dataset (i.e., pseudoreplication) that may bias parameter estimates and increase type I error rates (Dormann et al., 2007), we selected only locations which were a minimum of 5.6 km apart from each other. This spatial thinning resulted in 631 locations. We selected this distance because it represents the radius of the minimum circular home range size of elephants, which is approximately 100 km^2 in the study area (Desai, 1991; Sukumar, 1989a).

2.3 | Environmental data

We focused on the environmental variables that were important in affecting the distribution of Asian elephants (see Supporting information Tables S1 and S2). As most of our field data were from the years 2000–2017, whenever possible, we compiled our environmental variables to cover this period. We assembled data on land use composition and human disturbances from various sources, as both habitat and human influence are likely to affect the distribution of Asian elephants. We obtained land cover variables and a time series of various vegetation indices from the MODIS database (https://lpdaac.usgs.gov). We then calculated for each variable several metrics across time (i.e., minimum, maximum, mean and *SD*) to be used as input into our models. We provided a detailed explanation of the collection and preparation of our environmental data in the digital Supporting information (see Appendix S2 and Table S2).

We also included various climatic factors and their seasonal variation (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Title & Bemmels, 2017; Supporting information Table S2). We obtained a total of 115 predictor variables: 60 climatic, 16 human disturbance, 29 forest and vegetation and 10 topographic variables. All analyses were done at a grid resolution of 1 km. We obtained our predictor variables at the resolution that was available at source. Variables with a finer resolution were combined by taking the average of grid cell at a particular neighbourhood. Variables with a coarser resolution were converted to fine resolution using bilinear interpolation.

2.4 | Candidate model construction and predictor variable selection

To make projections of elephant habitat suitability in space and time, we proceed in two steps: first (this section), we reduced the set of predictor variables by removing correlated variables and testing several models that are based on different hypotheses on elephant habitat selection, and second (next section), we used the variables of

TABLE 1 Evaluation metrics of the most parsimonious model (in bold) in comparison with the other candidate models of differing complexity (fitted in MAXENT) ordered based on increasing AICc score

Model	No. of (uncorrelated) variables	FC	RM	Mean AUC_{TEST}	Variance AUC_{TEST}	Mean AUC_{DIFF}	Variance AUC_{DIFF}	Mean OR_{10}	Variance OR_{10}	Mean OR_{min}	Variance OR_{min}	AICc
$C_m + D_m$	**9**	**H**	**1**	**0.914**	**0.006**	**0.052**	**0.005**	**0.310**	**0.099**	**0.041**	**0.002**	**15,945.096**
C_m + D	17	LQHP	2	0.890	0.016	0.073	0.020	0.340	0.169	0.078	0.013	15,972.336
Global	41	LQHP	3.5	0.902	0.028	0.065	0.030	0.304	0.178	0.094	0.031	16,030.156
C + D_m	11	LQHP	2.5	0.909	0.006	0.059	0.006	0.394	0.119	0.016	0.000	16,106.187
C_m + VT	25	H	0.5	0.812	0.152	0.039	0.007	0.289	0.130	0.019	0.001	16,135.832
C + D	19	LQHP	3	0.885	0.028	0.076	0.028	0.345	0.156	0.099	0.036	16,162.394
C + VT	27	LQHP	3.5	0.872	0.036	0.090	0.032	0.413	0.190	0.127	0.026	16,193.254
C	8	LQHP	2	0.884	0.015	0.081	0.012	0.410	0.190	0.025	0.000	16,419.696
VT + D_m	25	LQHP	3.5	0.899	0.005	0.041	0.007	0.229	0.030	0.025	0.003	16,621.494
VT + D	33	LQHP	3.5	0.858	0.020	0.080	0.026	0.292	0.055	0.062	0.015	16,656.668
C_m	5	LQH	1.5	0.892	0.010	0.065	0.006	0.301	0.054	0.027	0.002	16,692.181
VT	21	LQHP	2.5	0.879	0.005	0.049	0.006	0.189	0.006	0.024	0.002	16,931.975
D	12	H	0.5	0.800	0.017	0.117	0.015	0.336	0.038	0.043	0.006	17,229.808
D_m	4	LQH	0.5	0.820	0.002	0.071	0.002	0.236	0.005	0.010	0.000	17,514.816

Notes. Models were constructed by grouping the predictor variables based on their environmental types and the available knowledge on elephant habitat selection. For each model type, 240 individual models were fitted in order to improve performance and reduce overfitting, resulting in total of 3,360 individual models. Models used 10,000 random background locations. The model with the lowest evaluation metric scores (i.e., that showed less severe overfitting; bold) and its predictor variables were used to fit the 11 SDMs in the ensemble modelling approach for the consensus projection. C: climate; VT: vegetation and topography; D: human disturbance; subscript *m* indicates the minimal model in that model category. Variables with high correlation (Pearson's correlation coefficient r, with $|r|>0.6$) in each candidate model were removed before MaxEnt fit. See Supporting information Table S3 for all the variables in the candidate models.

RM: regularization parameter; AUC_{TEST}: value of the area under the curve of the receiver operating characteristic plot calculated based on testing data of k-fold cross-validation bins; AUC_{DIFF}: the difference between training and testing AUC, with high values for overfit models; OR_{min} and OR_{10}: two omission rates that quantify model overfitting with 0 and 10% omission rate of the training localities under which the proportion of test localities with MAXENT output values falls. High values for these two metrics indicate overfit models (Muscarella et al., 2014). The letters under the column FC indicate MAXENT variable transformations with L: linear; Q: quadratic; H: hinge; P: product; T: threshold.

the most parsimonious of these models in an ensemble of SDMs to project habitat suitability in space and time.

First, we grouped the environmental variables into three groups that correspond to basic hypotheses on elephant habitat selection: vegetation and topography (VT), human disturbance (D) and climate (C) (Supporting information Table S2). The candidate models were then assembled by the combinations of these three groups, thus ranging from specific models reflecting only one hypothesis (e.g., D) to general models containing variables of all three groups (i.e., VT + D + C). Whenever possible, we also defined "minimal" models, denoted by subscript m in italic (i.e., D_m and C_m) that contained only those variables expected a priori to be the most important ones. In total, we developed in this way 14 candidate models of differing complexity (see Supporting information Table S3 for details). We then performed a variable reduction procedure in each candidate model based on Pearson's correlation coefficient *r*, excluding variables with $|r| > 0.6$ (see Tables 1 and Supporting information Table S3).

To fit the candidate models to the data, we used MAXENT, one of the most commonly used presence-only methods (Phillips et al., 2006). MAXENT models the statistical relationships between explanatory variables at observed locations of species, and "background" locations in the study region. It incorporates flexible relationships by transformations of the original predictor variables into various feature classes. This higher flexibility, however, can lead to model overfitting (Muscarella et al., 2014; Radosavljevic & Anderson, 2014).

To improve the performance of MAXENT and avoid overfitting, we used methods described in Muscarella et al. (2014): we (a) first generated spatially independent splits of data for training and testing (e.g., Madon, Warton, & Araújo, 2013), (b) second fit a series of models to these data partitions across different combinations of feature classes and regularization values and (c) finally characterized the performance of the models using evaluation metrics (Muscarella et al., 2014). Here, we selected a set of 10,000 random background locations to use in all our model fits (Figure 1). To partition the occurrence and background locations into separate training and test datasets for k-fold cross-validation, we used a "block" method that partitions data according to the latitudinal and longitudinal lines, resulting in four bins (of equal numbers) (e.g., Madon et al., 2013; Muscarella et al., 2014).

We then built a series of individual MAXENT models (to each candidate model) to the partitioned training and test datasets with regularization values ranging from 0.5 to 4.0 (increments of 0.5) and with six different feature class combinations (L, LQ, H, LQH, LQHP and LQHPT; where L = linear, Q = quadratic, H = hinge, P = product and T = threshold) (Muscarella et al., 2014). Additionally, we also built a model using the entire, full dataset that was used to calculate the Akaike information criterion corrected for small samples sizes (AIC_c). Besides AIC_c, we calculated four other evaluation metrics as described in Muscarella et al. (2014): AUC_{TEST}, averaged value of the area under the curve of the receiver operating characteristic plot calculated based on testing data of *k*-fold cross-validation bins; AUC_{DIFF}, the difference between training and testing AUC, with high values for overfit models (Warren & Seifert, 2011); and two omission rates that quantify model overfitting with 0 and 10% omission rate of the training localities under which the proportion of test localities with MAXENT output values falls.

For each candidate model, we built 240 individual models (eight regularization values ×six feature classes × (four training and testing data bins + one full dataset)); this resulted in total of 3,360 individual models (240 × 14 candidate models). We selected the most parsimonious model, which was then used in the ensemble approach (see section "Species distribution modelling and evaluation" below), in two steps. First, for each candidate model, we selected the best performing model by AICc (i.e., $\Delta AIC_c = 0$). Then, among all the best performing candidate models, we selected the most parsimonious model that had lower AICc score, higher AUC value and overfit less severely than others by comparing the various evaluation metrics scores.

2.5 | Species distribution modelling and evaluation

An ensemble of species distribution models (SDMs) (Araújo & New, 2007) was generated using the variables identified in the best performing MAXENT model of the previous step (Figure 1). We considered 11 algorithms: generalized linear model (GLM), generalized additive model (GAM), generalized boosting model (GBM), artificial neural network (ANN), surface range envelope (SRE), classification tree analysis (CTA), random forest (RF), multiple adaptive regression splines (MARS), flexible discriminant analysis (FDA), maximum entropy (MAXENT) and low-memory multinomial logistic regression (MAXENT.Tsuruoka, noted below MAXENT.T).

The occurrence and background locations were split into 80% being a random sample to train the models, and the remaining 20% of the data were used to evaluate the fitted models using true skill statistic (TSS) as measure of accuracy with TSS = sensitivity + specificity – 1 (Allouche, Tsoar, & Kadmon, 2006) and the area under the curve of the receiver operating characteristic (AUC, Fielding & Bell, 1997). Models were run five times, each time the training samples were taken randomly to be evaluated against a random test partition. Models with the TSS scores >0.8 were kept in the consensus analysis. The final consensus prediction was based on the mean weighted probability of occurrence of elephants in each 1-km grid cell and a proportional decay, with more weight given to the models that had better TSS scores. The continuous ensemble prediction values were converted into binary ones (suitable/unsuitable) based on the optimal threshold identified by the TSS.

2.6 | Future projections under climate and land use scenarios

The ensemble model was then projected to climatic conditions around 2050 (i.e., 2041–2060) and 2070 (i.e., 2061–2080) based on several global change scenarios to project the likely changes in suitable habitats for elephants. We obtained the climatic variables

for future projections from the same sources as our current climatic variables (i.e., WorldClim). We obtained future climatic variables from three Coupled Model Inter-Comparison Project (CMIP5) Global Circulation Models (Taylor, Stouffer, & Meehl, 2012), GCMs: Centre National de Recherches Météorologiques Coupled Global Climate Model, version 5 (CNRM-CM5); Hadley Centre Global Environmental Model, version 2-Earth System (HadGEM2-ES); and Max Planck Institute Earth System Model, low resolution (MPI-ESM-LR), and for two representative concentration pathways (RCPs): RCP 2.6 and 8.5. The models were then projected for 2050 and 2070 under the two RCPs by averaging the climate variables across the three GCMs.

To obtain scenarios for land use changes, we focused on the MODIS land use variable (i.e., the combined class of croplands and cropland/natural vegetation mosaics, Supporting information Table S2) and used the future projections at 1-km resolution available for years 2050 and 2,100 from GeoSOS global database (http://geosimulation.cn/GlobalLUCCProduct.html; Supporting information Appendix S3). The remaining disturbance variables in the final model were held constant while forecasting the future predictions, due to unavailability of their future spatial data distribution.

2.7 | Assessing core habitat and connectivity

To identify core habitat areas throughout the study area, we used the Core Mapper tool within the Gnarly Landscape Utilities package (Shirk & McRae, 2013). Using a moving window with a 9.4 km radius (i.e., average home range 278 km^2; Fernando et al., 2008), this tool identified highly suitable (>0.64) habitat patches in the study area (Supporting information Appendix S4). To assess the potential connectivity among cores, we defined a resistance surface (i.e., resistance = 1/habitat suitability). The resistance value is then multiplied with the minimum distance of this cell from the core area to obtain an effective distance. The cells within an effective distance of 60 km (Sukumar, 1989b) are included into the extended core habitat area. This establishes connectivity between nearby cores that are within a reachable distance, resulting in fewer but larger cores.

All analyses were conducted in R (R Core Team, 2016) using the package ENMeval (Muscarella et al., 2014) for MAXENT fits for evaluating candidate models and BIOMOD2 (Thuiller et al., 2016) for ensemble approach. For the latter, we used the default options, except for MAXENT (Phillips) for which the RM and FC combinations were selected in consistence with the best performing MAXENT model (see section Candidate models construction and predictor variables selection).

3 | RESULTS

3.1 | Candidate model evaluation and predictor variable selection

Overall, candidate models generally exhibited good performance (mean AUC_{TEST} > 0.8), especially models that included climatic variables, and the final model was selected from including combination of the climate and the disturbance groups comprising nine predictor variables (Table 1). The final model (C_m + D_m) was selected based on its low AICc scores and evaluation metric scores for overfitting (Table 1).

3.2 | Species distribution models

The selected nine predictor variables were chosen to model suitable habitat for elephants. TSS scores were low for the SRE and MAXENT.T approaches (TSS < 0.8), and consequently, these two

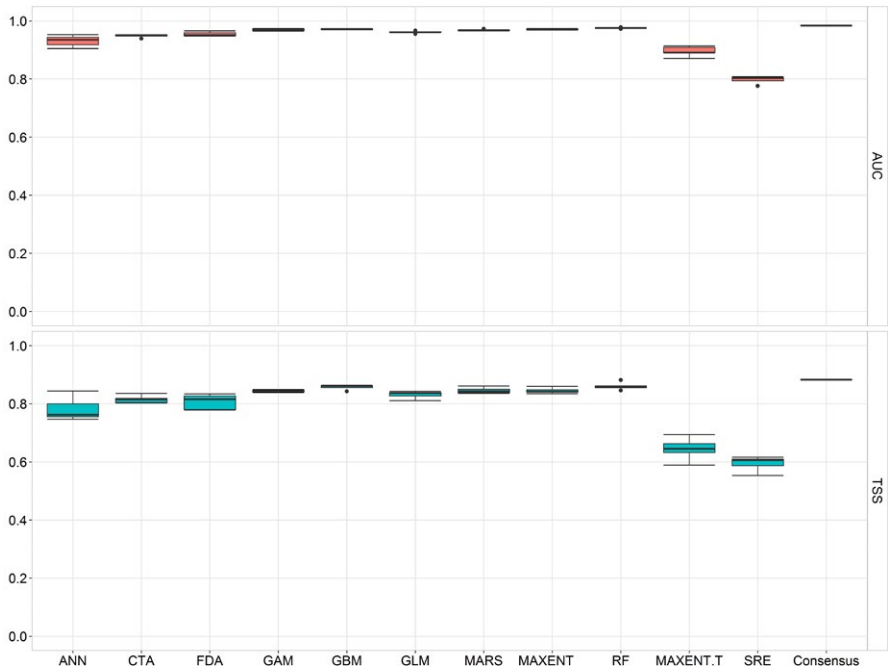

FIGURE 2 Boxplots for AUC and TSS model evaluation scores for five cross-validation runs on test data for the 11 species distribution modelling techniques used for predicting Asian elephant distribution in India and Nepal. For comparison, the evaluation scores for the consensus model are also shown. The boxes represent the first and third quartiles, with the median represented by the black line. The whiskers represent the data within 1.5× the interquartile range, and the individual points represent the outliers. The consensus model does not include MAXENT.T and SRE (TSS < 0.8). See text for model abbreviations

modelling techniques were removed from the ensemble approach (Figure 2). The evaluation scores for the consensus model were higher than for the individual modelling techniques. Within climate group, the minimum of actual evapotranspiration (AET) across the twelve monthly means accounted for 58.4% of the total statistical contribution (Table 2). This was followed by presence of land cover class "Croplands and Cropland/natural vegetation mosaic" (15.7%), isothermality (13.3%), potential evapotranspiration (PET) in the driest quarter (7%) and the variation of monthly AET over the year (5.6%). The contributions of remaining four variables were <5%.

The response curves for the predictor variables that contributed substantially (% contribution > 5; see Table 2) to the consensus model showed that elephants prefer habitat that experience higher AET (Figure 3, Supporting information Figure S2), that is, active vegetation. This indicates that elephants potentially avoid areas that experience enhanced seasonal droughts and desert areas. On the other hand, elephants avoid areas of high human influence in the form of increasing presence of croplands. The resulting spatial pattern of habitat suitability based on the ensemble approach is shown in Figure 4. Around 256,518 square kilometres was estimated as suitable for elephants, based on the optimal prediction value threshold of 0.513 identified by the TSS.

3.3 | Future projections

The future projections under the combined climate and land use changes predict a heavy loss of potential elephant habitats under all scenarios in relatively low altitude, human-dominated regions (Figure 5a,b), with no gain of suitable habitat in the eastern (E) and southern (S) regions. Overall, a loss of around 41.8% of potential suitable habitat is expected in the study area under the combined climate and land use change scenario of RCP8.5 in 2070 (Figure 5b and Supporting information Figure S4a). Under the climate-only change scenarios, the loss of potential habitat is more moderate (Supporting information Figure S3), but still substantial with a 17.1% loss under RCP8.5 in 2070 (Supporting information Figure S4b). Gain in potential habitat areas is indicated in the northern (N) and north-eastern (NE) habitats particularly along the valleys towards north avoiding high mountains (Figure 5a,b), with a maximum gain of 42.2% under climate-only change scenario of RCP8.5 in 2070 (Supporting information Figure S4b). Further, a possible northward shift along the valleys in the northern populations' distribution (N) is expected, while losing the relatively flat habitat areas in the foothills (Figure 5a,b).

3.4 | Cores and habitat connectivity

The Core Mapper tool identified several core habitat areas ("cores") in the study area (Figure 6a–d and Supporting information Figure S5). In particular, two large cores with high habitat quality (mean habitat suitability value around 0.91) were identified in the southern (S) part of the study area (S; Figure 6a and Supporting information Figure S5). Although the total area of cores of current elephant habitat was lower for the northern (N) and north-eastern (NE) regions compared to southern (S) region of the study area, the number of cores is comparable and increased under cost-weighted dispersal, especially in north-east under RCP2.6 in 2070, due to area gains of some patches smaller than 600 km^2 (Figure 6d), revealing the fragmented nature of these habitat areas in terms of high suitability values (Figure 6c,d and Supporting information Figure S5).

4 | DISCUSSION

The historical range of the Asian elephant has shrunk due to anthropogenic land use change (Choudhury et al., 2008). Currently, we show that seasonal rainfall patterns and human disturbance are strongly associated with the distribution of extant Asian elephant populations over the majority of its range in the Indian subcontinent. Our model projections suggest that future changes in the

TABLE 2 Statistical contribution of variables in the final consensus model. See Supporting information Table S2 for definition of variables

Variables	% contribution
Climate	
Actual evapotranspiration (AET mean monthly minimum)	58.4
Isothermality (mean monthly temperature diurnal range/annual range between maximum temperature of warmest month and minimum temperature of the coldest month)	13.3
Potential evapotranspiration (PET) of driest quarter	7
Actual evapotranspiration (*SD*)	5.6
Aridity index—Thornthwaite	1.5
Disturbance	
Combined land cover—croplands and cropland/natural vegetation mosaic (%)	15.7
Fire probability in June–August 1982–1999	3.4
Human population density (mean)	2.7
Fire probability in September–November 1982–1999	1.1

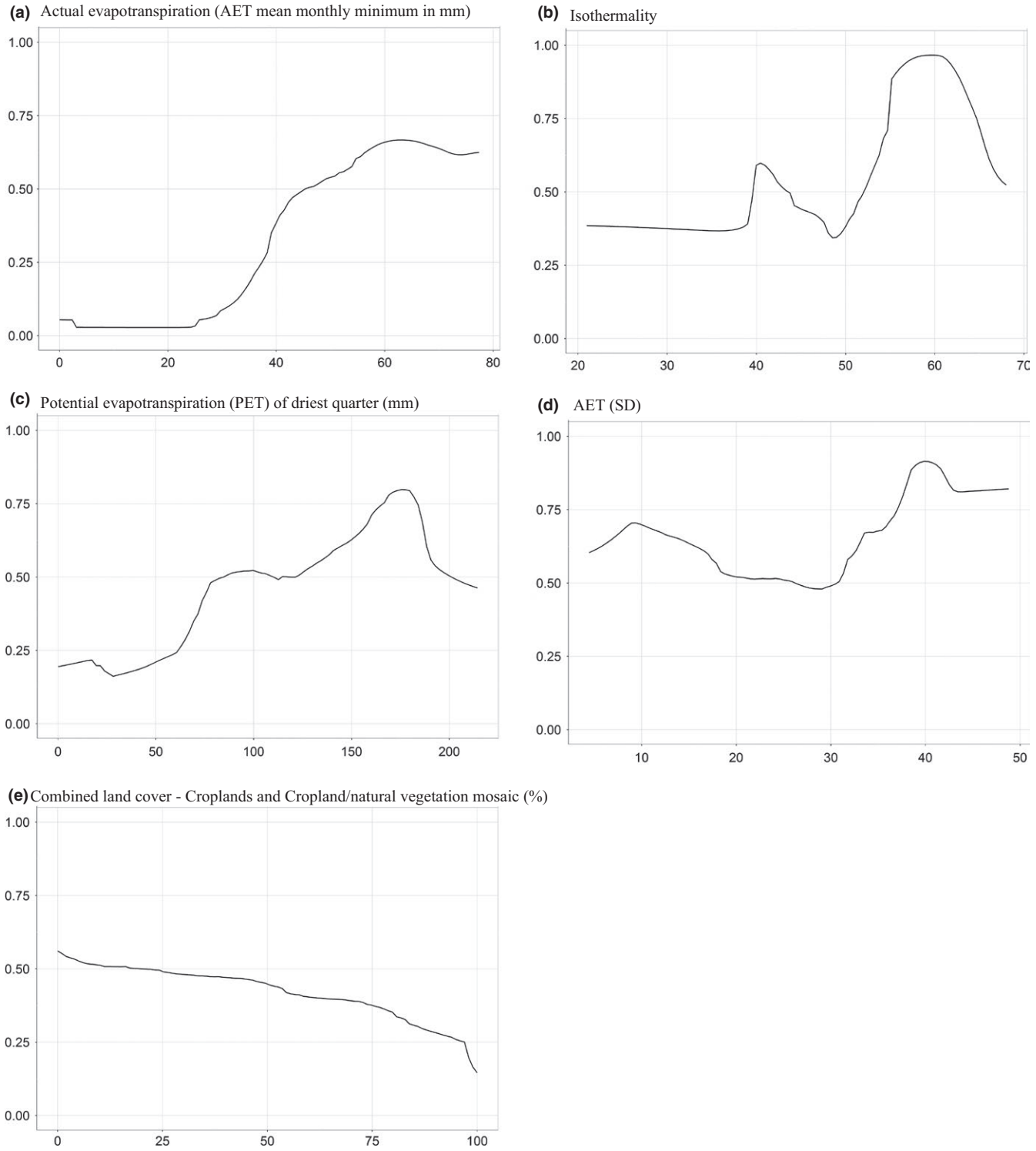

FIGURE 3 Response curves for the environmental variables that contributed substantially (% contribution > 5; see Table 2) to the consensus model for Asian elephant in India and Nepal

distribution of the elephants in India and Nepal would be driven predominantly by changes in climatic water balance, followed by changes in temperature and other ongoing human-induced disturbance. We anticipate that elephant range would likely shift towards higher elevations in the Himalayas and along a gradient of water availability, that is, low elevation valleys in the mountains, instead of a simple unidirectional range shift towards higher elevations and latitudes typically expected when temperature is the principal factor (Hickling et al., 2005; Lawler et al., 2009; Moritz et al., 2008). Our study also outlines complex local-scale interactions among precipitation and temperature, complicated by seasonal monsoon, and land use changes in the distribution of elephants in South Asia.

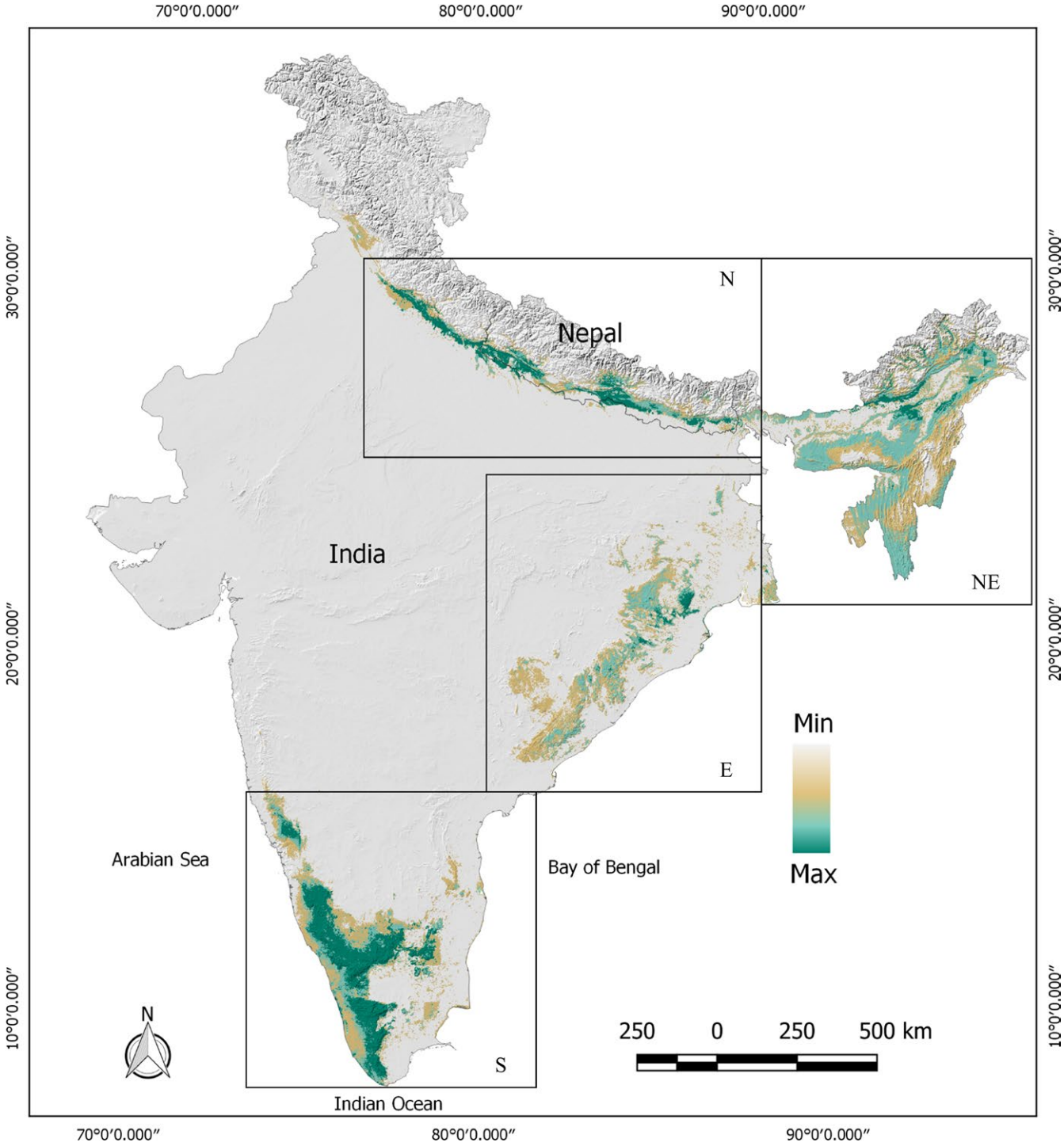

FIGURE 4 Map of predicted habitat suitability (on top of hillshade map) for Asian elephant in India and Nepal using the consensus model derived from the ensemble approach. Map projection: Universal Transverse Mercator zone 44 N

4.1 | Effect due to climatic factors

Forage and water availability is critical for elephants (Sukumar, 2006). Actual evapotranspiration (AET) is a strong predictor of aboveground net primary productivity for terrestrial ecosystems as it simultaneously measures water availability (rain plus other water sources) and energy (heat and solar radiation), the key factors that enhance photosynthetic rates (Rosenzweig, 1968; Stephenson & Das, 2011). For the past several decades, both India and Nepal have been experiencing significant changes in spatial–temporal patterns of monsoon rainfall, with breaks in wet spell and the prolongation of the dry spell leading to seasonal droughts (Karki et al., 2017; Vinnarasi & Dhanya, 2016). Prolonged dry seasons have been observed to cause drought-related mortality in African elephant

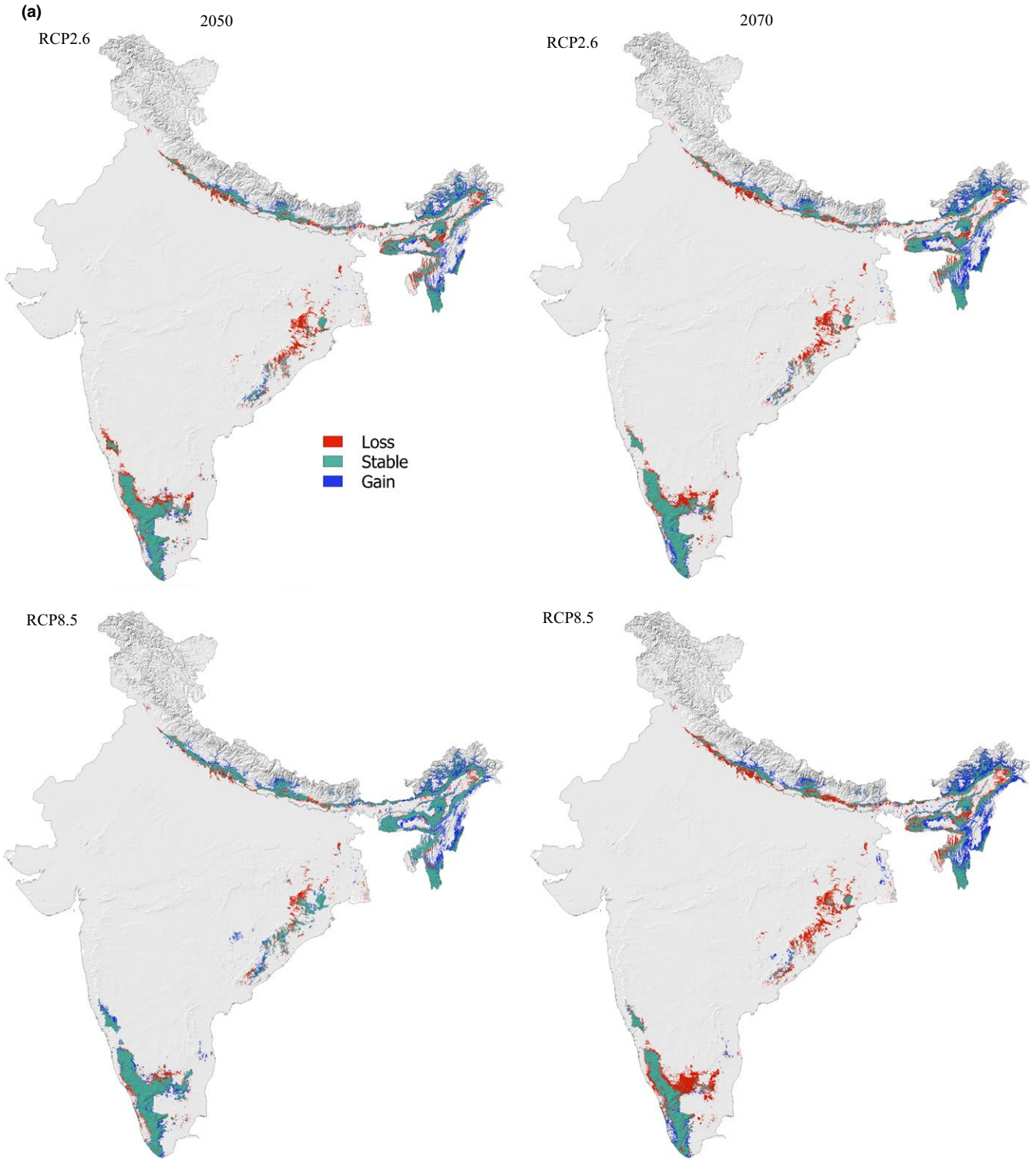

FIGURE 5 Future changes in consensus projections for Asian elephant in India and Nepal under climate change and land use change scenarios (a); different elephant population zones are magnified for RCP8.5 in 2070 (b). Variables Human population density and Fire probabilities were held constant (see Table 2). Green: stable, red: lost, blue: gain, grey: unsuitable. Note the projected habitat loss in relatively low altitude, human-dominated regions and gain of habitat in the valleys of Himalayan Mountains. Map projection: Universal Transverse Mercator zone 44 N

populations in arid and semi-arid savannas (Foley, Pettorelli, & Foley, 2008; Wato et al., 2016). Seasonally driven rainfall affects vegetation dynamics and water availability, and elephants are known to respond to those changes to their habitat, especially in dry seasons, by moving to more suitable sites (Birkett, Vanak, Muggeo, Ferreira, & Slotow, 2012; Bohrer et al.., 2014).

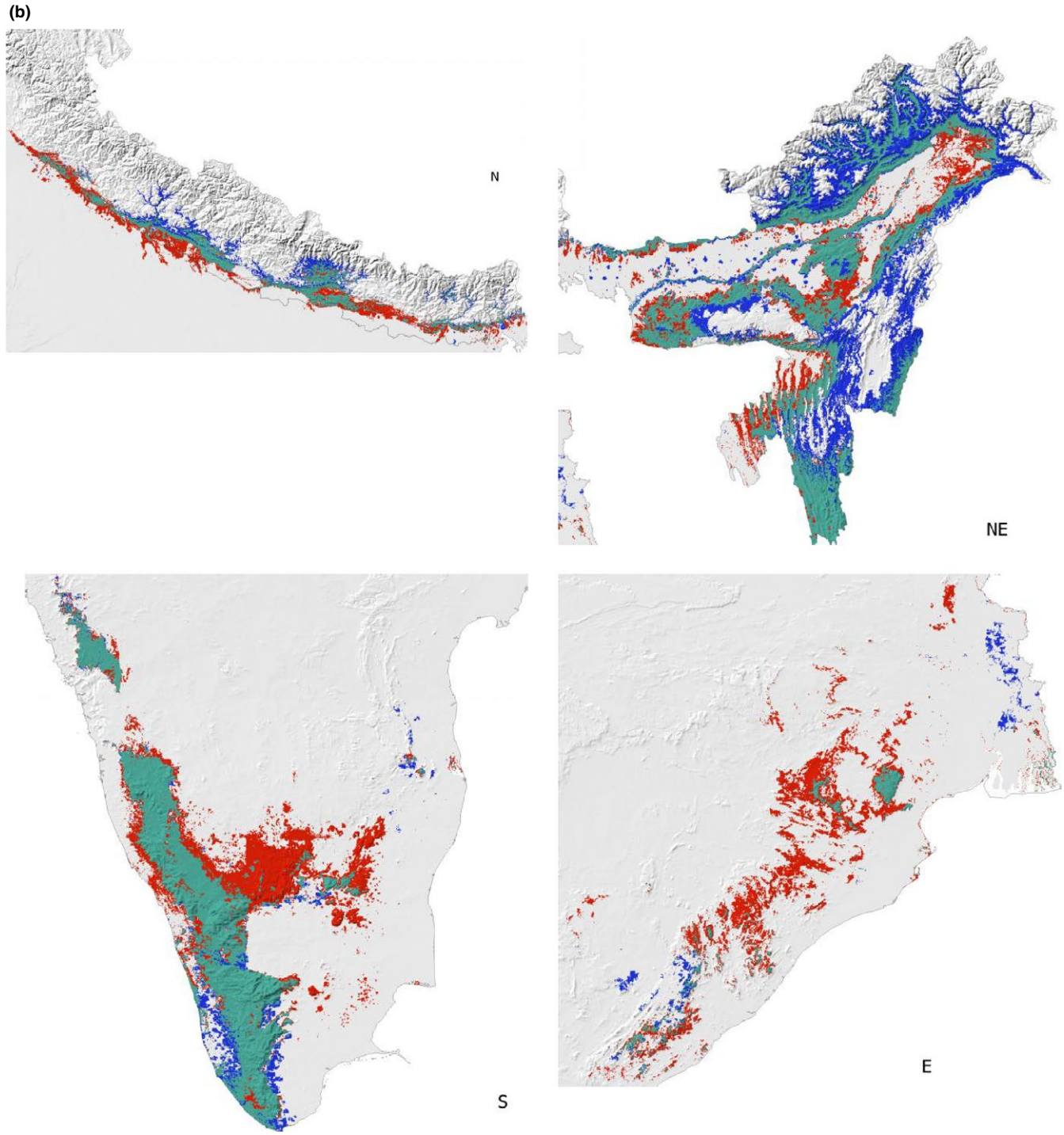

FIGURE 5

Continual rise in greenhouse gases and, thereby, temperatures is predicted to increase the intensity of the summer monsoon in India (scenario RCP8.5; IPCC, 2013; Jayasankar et al., 2015) causing increase in evaporative demand and water availability. This can potentially increase AET and lead to shifts in species' ranges towards higher elevations and latitudes (Hickling et al., 2005; Lawler et al., 2009). Although increase in water availability alone can lead to range expansion within an elevation belt (Stephenson & Das, 2011), additional increase in evaporative demand may modify this pattern in unexpected ways depending on its magnitude relative to water availability. Our results show that this can cause range shifts towards higher elevations but along the water availability gradient (Figure 5a,b). The elephant range is projected to contract in the human-dominated, flood-prone low altitude tropical climate regions (i.e., the Terai areas of India and Nepal in the Himalayan region and central and southern parts of India; Figure 5a,b and Supporting information Figure S3). These regions experienced an increasing warming trend (1961–2000; Sheikh et al., 2014). Recent studies suggest that

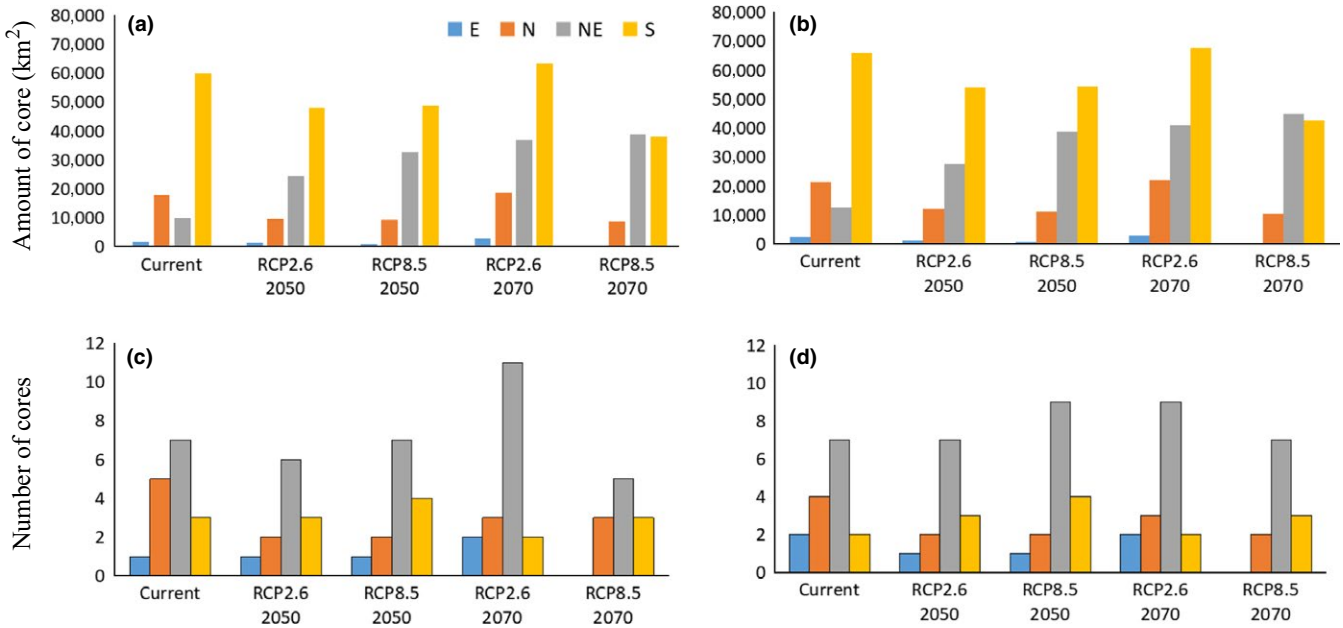

FIGURE 6 Amount of core habitat in the identified cores and the number of core habitat areas in the suitable habitat as predicted for Asian elephant in India and Nepal by the final consensus model for the current and future scenarios. (a) Identified core habitat areas and (b) under cost-weighted dispersal. (c) Number of identified cores and (d) under cost-weighted dispersal

the onset of the summer monsoon could be delayed and lead to a rapid decrease in rainfall by the turn of the 22nd century (Ashfaq et al., 2009; Schewe & Levermann, 2012). This will additionally increase the magnitude of evaporative demand in relation to available water and would shift suitable elephant habitat further northwards in the Himalayan region and accelerate habitat loss at lower altitudes.

The adverse effect of increases in global temperature and anomalies in seasonal monsoon rainfall on elephant distribution is also reflected by other climatic factors in our model. Our results suggest that elephants were fewer in areas that experience high minimum surface temperature in the warmest month, smaller day-to-night temperature oscillation relative to the annual oscillations (isothermality) and low PET during the driest quarter of the year in the model (Table 2). These results are in agreement with a study of Mumby et al. (2013) that found that an average monthly temperature increase of ~1°C over 35 years (between 1965 and 2000) increased mortality in calves and young elephants.

4.2 | Effect of human disturbance

Human disturbance and land use change have historically been the main drivers of elephant population decline (Choudhury et al., 2008). Several studies have highlighted the sensitivity of Asian and African elephants to human disturbances (Buij et al., 2007; Jathanna, Karanth, Kumar, Karanth, & Goswami, 2015; Srinivasaiah, Anand, Vaidyanathan, & Sinha, 2012). Our results indicate here that human disturbances represented by the proportion of croplands in a 1.5 × 1.5 km area exerted negative influence on elephant occurrence patterns (Figure 3). The loss of habitat is projected to occur mostly in the human-dominated regions, that is, the Central-Eastern (Eastern Ghats) and the Southern Western Ghats of India and in the relatively flat areas of the Himalayan region (Figure 5a,b). Loss of native forests (Puyravaud, Davidar, & Laurance, 2010) and land degradation, which affects about 18% of its territory (Bai, Dent, Olsson, & Schaepman, 2008), are major threats to India's biodiversity that will decrease the availability of forage for wild herbivores (Jathanna et al., 2015; Madhusudan, 2004). Climate change will further amplify these threats leading to species declines and eventual extinction (Thomas et al., 2004).

4.3 | Importance of habitat connectivity

Our habitat model predicts only the suitability for a given 1-km^2 grid cell without accounting for the movement capacity of elephants and their home range sizes. We therefore added an analysis of core areas, being contiguous high suitability areas larger than the size of two average home ranges, and an analysis of connectivity of core areas that considers the maximal displacement capacity of elephants. The core area analysis identified the major habitat patches, such as two large core areas in the southern part of India that had the highest mean habitat suitability compared to the patches of the other three regions (Supporting information Figure S5). Indeed, field estimates document that the southern region holds by far the largest population of the elephants in the world (Madhusudan et al., 2015). The connectivity analysis suggests that the fragmented core areas that are located along the foothills forests and floodplains of the Himalaya in the northern part of India and Nepal could be connected by a mixture of poor- and high-quality habitat that should form specific targets for management. These analyses provide a first assessment of areas that could provide connectivity among core

areas, and future studies using more detailed least-cost path analysis (Cushman, Lewis, & Landguth, 2014) or individual-based movement models (Kanagaraj, Wiegand, Kramer-Schadt, & Goyal, 2013) can test specific management actions in their effectivity to provide connectivity.

4.4 | Modelling constraints

Although our modelling approach makes a number of simplifications, for example, that the vegetation shifts are in equilibrium with climate shifting immediately after climate changes or that some variables are held constant (e.g., population density, fire probability), it is the best we can do at the moment to assess the sensitivity of elephant habitats to potential changes in climate and land use. Though such limitations inevitably affect the accuracy and generality of projections, there are independent tests demonstrating that correlative models, especially when placed in the context of ensemble forecasting, provide inferences that are useful (Araújo, Whittaker, Ladle, & Erhard, 2005) and as powerful as more complex mechanistic models (Fordham et al., 2017). We acknowledge the inaccuracy associated with combining two IPCC assessments, but our approach of combining low emissions with balanced resources scenario and high emissions with adverse impact on the environment scenario provides a balanced approach to make the best use of available data.

4.5 | Conservation implications

Loss of local species is considered to be a major driver altering ecosystem structure and function in any region (Hooper et al., 2012). Our study area covers several biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) and has a high proportion of threatened species; for example, India supports approximately 4.9% of the world's total threatened plant and faunal species (MEFI, 2009; Squires, 2014), and its extinction risk has increased in the recent past, primarily due to habitat loss and illegal hunting (Secretariat of the Convention on Biological Diversity, 2010). Given the limitations in human and financial resources and political will in conserving all desired species and their habitats in South Asia (Persha, Fischer, Chhatre, Agrawal, & Benson, 2010), prioritizing biodiversity conservation, strengthened by management shortcuts such as umbrella-species concept, should remain high priority in this region. The umbrella-species concept has shown promise in forest restoration and conserving biodiversity (e.g., Bell, 2015; Yamaura, Higa, Senzaki, & Koizumi, 2018), and can be used as an effective strategy for conservation in the South Asian region. Further, the centrepiece of biodiversity conservation always remains to be conservation of remaining habitat from any further loss. By studying a charismatic megafauna and a flagship of conservation, we have not only quantified and mapped the current suitable habitat and projections for this species under a warming climate and land use change scenarios, but also provided conservation opportunities for a large number of other species that co-occur under elephants' umbrella. For example, our suitability maps and future projections can be effectively used to identify critical habitat areas that require immediate conservation attention in order to minimize biodiversity loss through habitat degradation and loss. Further our fine-scale maps at 1-km^2 resolution can be used by park managers and conservationists to identify and prioritize the conservation requirements of those critical habitat areas, for example, preservation of critical remnant patches and connective habitats (e.g., corridors) that are projected to be lost in the future.

Adding to our difficulties in conservation of biodiversity in this region is the changing climate, which is predicted to affect the seasonal monsoon system, leading to variation in local climates. Our comprehensive treatment of relevant climatic factors at the spatial resolution of 1 km^2 enabled us to capture the variation in local climates over a major land part of the South Asian monsoon domain and assess its influence on the current and future distribution of elephants in this region. The wide array of scenarios tested here revealed clear tendencies in the expected habitat changes and provides an understanding of how climate and human-induced threats can influence the elephant distribution, critical prerequisite for the management of endangered species that will help mitigate potential threats. Habitat loss/degradation and range shift of the elephants in human-dominated landscape will also cause increase in human–elephant conflict (Lamichhane et al., 2018). Our study also provides a first assessment on the effect of climate change on the distribution of the Asian elephant in its major habitats in India and Nepal, which could help other assessments over its entire range across South and South-East Asia, and be useful for developing management plans for wildlife conservation under the aegis of climate change.

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DATA ACCESSIBILITY

All environmental layers and part of species locations are freely available online, see in-text references. Remaining species locations are available on request.

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REFERENCES

Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2016). Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. *Methods in Ecology and Evolution*, *7*(7), 853–866. https://doi.org/10.1111/2041-210X.12524

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L., & Williams, P. H. (2004). Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, *10*(9), 1618–1626. https://doi.org/10.1111/j.1365-2486.2004.00828.x

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, *22*(1), 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Araújo, M. B., Whittaker, R. J., Ladle, R. J., & Erhard, M. (2005). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, *14*(6), 529–538. https://doi.org/10.1111/j.1466-822X.2005.00182.x

Ashfaq, M., Shi, Y., Tung, W., Trapp, R. J., Gao, X., Pal, J. S., & Diffenbaugh, N. S. (2009). Suppression of south Asian summer monsoon precipitation in the 21st century. *Geophysical Research Letters*, *36*(1), L01704. https://doi.org/10.1029/2008GL036500

Bai, Z. G., Dent, D. L., Olsson, L., & Schaepman, M. E. (2008). Proxy global assessment of land degradation. *Soil Use and Management*, *24*(3), 223–234. https://doi.org/10.1111/j.1475-2743.2008.00169.x

Balasubramanian, A. (2017). *Physiographic divisions of India*. Mysore: University of Mysore.

Bell, D. (2015). *Forest restoration guided by an umbrella species. Will measures to protect the white-backed woodpecker benefit saproxylic beetles?* Umeå, Sweden: Swedish University of Agricultural Sciences.

Birkett, P. J., Vanak, A. T., Muggeo, V. M. R., Ferreira, S. M., & Slotow, R. (2012). Animal perception of seasonal thresholds: changes in elephant movement in relation to rainfall patterns. *PLoS One*, *7*(6), e38363. https://doi.org/10.1371/journal.pone.0038363

Bohrer, G., Beck, P. S. A., Ngene, S. M., Skidmore, A. K., & Douglas-Hamilton, I. (2014). Elephant movement closely tracks precipitation- driven vegetation dynamics in a Kenyan forest- savanna landscape. *Movement Ecology*, *2*(2), 1–12. https://doi.org/10.1186/2051-3933-2-2

Buij, R., McShea, W. J., Campbell, P., Lee, M. E., Dallmeier, F., Guimondou, S., … Alonso, A. (2007). Patch-occupancy models indicate human activity as major determinant of forest elephant *Loxodonta cyclotis* seasonal distribution in an industrial corridor in Gabon. *Biological Conservation*, *135*(2), 189–201. https://doi.org/10.1016/J.BIOCON.2006.10.028

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Carroll, C., Dunk, J. R., & Moilanen, A. (2010). Optimizing resiliency of reserve networks to climate change: Multispecies conservation planning in the Pacific Northwest, USA. *Global Change Biology*, *16*(3), 891–904. https://doi.org/10.1111/j.1365-2486.2009.01965.x

Choudhury, A., Lahiri Choudhury, D. K., Desai, A., Duckworth, J., Easa, P. S., Johnsingh, A. J., Wikramanayake, E. (2008). Elephas maximus. The IUCN Red List of Threatened Species 2008. The IUCN Red List of Threatened Species 2008, 8235. https://doi.org/10.2305/IUCN.UK.2008.RLTS.T7140A12828813.en

Coetzee, B. W. T., Robertson, M. P., Erasmus, B. F. N., Van Rensburg, B. J., & Thuiller, W. (2009). Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*, *18*(6), 701–710. https://doi.org/10.1111/j.1466-8238.2009.00485.x

Condit, R., Engelbrecht, B. M. J., Pino, D., Perez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences*, *110*(13), 5064–5068. https://doi.org/10.1073/pnas.1218042110

Cushman, A. S., Lewis, S. J., & Landguth, L. E. (2014). Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. *Diversity*, *6*(4), 844–854. https://doi.org/10.3390/d6040844

De, U. S., Dube, R. K., & Rao, G. S. P. (2005). Extreme Weather events over India in the last 100 years. *Journal of Indian Geophysical Union*, *9*(3), 173–187.

Desai, A. A. (1991). The home range of elephants and its implications for management of the Mudumalai Wildlife Sanctuary, Tamilnadu. *Journal of Bombay Natural History Society*, *88*, 145–156.

DNPWC (2008). *The elephant conservation action plan for Nepal*. Kathmandu: DNPWC.

Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*(5), 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Duncan, J. M. A., & Biggs, E. M. (2012). Assessing the accuracy and applied use of satellite-derived precipitation estimates over Nepal. *Applied Geography*, 626–638. https://doi.org/10.1016/j.apgeog.2012.04.001

Fernando, P., Wikramanayake, E. D., Janaka, H. K., Jayasinghe, L. K. A., Gunawardena, M., Kotagama, S. W., … Pastorini, J. (2008). Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology*, *73*(1), 2–13. https://doi.org/10.1016/j.mambio.2007.07.007

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence / absence models. *Environmental Conservation*, *24*(1), 38–49. https://doi.org/10.1017/S0376892997000088

Foley, C., Pettorelli, N., & Foley, L. (2008). Severe drought and calf survival in elephants. *Biology Letters*, *4*(5), 541–544. https://doi.org/10.1098/rsbl.2008.0370

Fordham, D. A., Bertelsmeier, C., Brook, B. W., Early, R., Neto, D., Brown, S. C., … Araújo, M. B. (2017). How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, *24*(3), 1357–1370. https://doi.org/10.1111/gcb.13935

García-Valdés, R., Svenning, J.-C., Zavala, M. A., Purves, D. W., & Araújo, M. B. (2015). Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology*, *52*(4), 902–912. https://doi.org/10.1111/1365-2664.12453

Hickling, R., Roy, D. B., Hill, J. K., & Thomas, C. D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology*, *11*(3), 502–506. https://doi.org/10.1111/j.1365-2486.2005.00904.x

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., … Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*(7401), 105–108. https://doi.org/10.1038/nature11118

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Vol. AR5)*. Cambridge and New York, NY: IPCC. https://doi.org/10.1017/CBO9781107415324

Jathanna, D., Karanth, K. U., Kumar, N. S., Karanth, K. K., & Goswami, V. R. (2015). Patterns and determinants of habitat occupancy by the Asian elephant in the western Ghats of Karnataka, India. *PLos One*, *10*(7), 1–19. https://doi.org/10.1371/journal.pone.0133233

Jayasankar, C. B., Surendran, S., & Rajendran, K. (2015). Robust signals of future projections of Indian summer monsoon rainfall by IPCC AR5 climate models: Role of seasonal cycle and interannual variability. *Geophysical Research Letters*, *42*(9), 3513–3520. https://doi.org/10.1002/2015GL063659

Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*(6), e157. https://doi.org/10.1371/journal.pbio.0050157

Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., & Goyal, S. P. (2013). Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. *Biological Conservation*, *167*, 298–309. https://doi.org/10.1016/J.BIOCON.2013.08.030

Karki, R., Hasson, S., Schickhoff, U., Scholten, T., & Böhner, J. (2017). Rising precipitation extremes across Nepal. *Climate*, *5*(1), 4. https://doi.org/10.3390/cli5010004

Lamichhane, B. R., Subedi, N., Pokheral, C. P., Dhakal, M., Acharya, K. P., Pradhan, N. M. B., … Yackulic, C. B. (2018). Using interviews and biological sign surveys to infer seasonal use of forested and agricultural portions of a human-dominated landscape by Asian elephants in Nepal. *Ethology Ecology & Evolution*, *30*(4), 331–347. https://doi.org/10.1080/03949370.2017.1405847

Lawler, J. J., Shafer, S. L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R., & Bartlein, P. J. (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, *90*(3), 588–597. https://doi.org/10.1890/08-0823.1

Lenoir, J., & Svenning, J.-C.-C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., … Svenning, J.-C. (2010). Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, *33*, 295–303. https://doi.org/10.1111/j.1600-0587.2010.06279.x

Li, A., & Deng, W. (2017). Land use/cover change and its eco-environmental responses in nepal: an overview. In A. Li, W. Deng, & W. Zhao (Eds.), *Land cover change and its eco-environmental responses in Nepal* (p. 478). Singapore: Springer. https://doi.org/10.1007/978-981-10-2890-8

Madhusudan, M. D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology*, *41*(5), 858–869, https://doi.org/10.1111/j.0021-8901.2004.00950.x

Madhusudan, M. D., Sharma, N., Raghunath, R., Baskaran, N., Bipin, C. M., Gubbi, S., … Sukumar, R. (2015). Distribution, relative abundance, and conservation status of Asian elephants in Karnataka, southern India. *Biological Conservation*, *187*, 34–40. https://doi.org/10.1016/j.biocon.2015.04.003

Madon, B., Warton, D. I., & Araújo, M. B. (2013). Community-level vs species-specific approaches to model selection. *Ecography*, *36*(12), 1291–1298. https://doi.org/10.1111/j.1600-0587.2013.00127.x

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, *15*(1), 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

MEFI (2009). *India's Fourth National Report to the Convention on Biological Diversity*. New Delhi: MEFI.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., Mcmahon, S. M., Normand, S., … Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, *37*(12), 1267–1281. https://doi.org/10.1111/ecog.00845

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, *322*(5899), 261–264. https://doi.org/10.1126/science.1163428.

Mumby, H. S., Courtiol, A., Mar, K. U., & Lummaa, V. (2013). Climatic variation and age-specific survival in Asian elephants from Myanmar. *Ecology*, *94*(5), 1131–1141. https://doi.org/10.1890/12-0834.1

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210X.12261

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214–https://doi.org/10.1126/science.aai9214.

Persha, L., Fischer, H., Chhatre, A., Agrawal, A., & Benson, C. (2010). Biodiversity conservation and livelihoods in human-dominated landscapes: Forest commons in South Asia. *Biological Conservation*, *143*(12), 2918–2925. https://doi.org/10.1016/j.biocon.2010.03.003

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Purohit, M. K., & Kaur, S. (2017). *Rainfall statistics of India - 2016*. New Delhi: India Meteorological Department.

Puyravaud, J. P., Davidar, P., & Laurance, W. F. (2010). Cryptic destruction of India's native forests. *Conservation Letters*, *3*(6), 390–394. https://doi.org/10.1111/j.1755-263X.2010.00141.x

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643. https://doi.org/10.1111/jbi.12227

Rajeevan, M., Gadgil, S., & Bhate, J. (2010). Active and break spells of the indian summer monsoon. *Journal of Earth System Science*, *119*(3), 229–247. https://doi.org/10.1007/s12040-010-0019-4

Rajendran, K., Sajani, S., Jayasankar, C. B., & Kitoh, A. (2013). How dependent is climate change projection of Indian summer monsoon rainfall and extreme events on model resolution? *Current Science*, *104*(10), 1409–1418.

Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: prediction from climatological data. *The American Naturalist*, *102*(923), 67–74. https://doi.org/10.1086/282523

Schewe, J., & Levermann, A. (2012). A statistically predictive model for future monsoon failure in India. *Environmental Research Letters*, *7*(4), 044023. https://doi.org/10.1088/1748-9326/7/4/044023.

Secretariat of the Convention on Biological Diversity (2010). Global Biodiversity Outlook 3. *Journal of the American Podiatric Medical Association*, *104*, 94. https://doi.org/10.7547/0003-0538-104.3.A1

Sheikh, M., Manzoor, N., Ashraf, J., Adnan, M., Collins, D., Hameed, S., … Shrestha, L., M., (2014). Trends in extreme daily rainfall and temperature indices over South Asia. *International Journal of Climatology*, *35*(7), 1625–1637. https://doi.org/10.1002/joc.4081

Shirk, A. J., & McRae, B. H. (2013). *Gnarly landscape utilities: Core Mapper user guide*. Fort Collins, CO: The Nature Conservancy.

Singh, D., Tsiang, M., Rajaratnam, B., & Di, N. S. (2014). Observed changes in extreme wet and dry spells during the South Asian summer monsoon season. *Nature Climate Change*, *4*, 1–6. https://doi.org/10.1038/nclimate2208

Squires, D. (2014). Biodiversity conservation in Asia. *Asia and the Pacific Policy Studies*, *1*(1), 144–159. https://doi.org/10.1002/app5.13

Srinivasaiah, N. M., Anand, V. D., Vaidyanathan, S., & Sinha, A. (2012). Usual populations, unusual individuals: Insights into the behavior and management of Asian elephants in fragmented landscapes. *PLoS ONE*, *7*(8), e42571. https://doi.org/10.1371/journal.pone.0042571

Stephenson, N. L. (1998). Actual evapotranspiration and deficit: Biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, *25*(5), 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x

Stephenson, N. L., & Das, A. J. (2011). Comment on "Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations". *Science*, *334*(6053), 177–177. https://doi.org/10.1126/science.1205740

Sukumar, R. (1989a). Ecology of the asian elephant in southern india. i. movement and habitat utilization patterns. *Journal of Tropical Ecology*, *5*(01), 1–18. https://doi.org/10.1017/S0266467400003175

Sukumar, R. (1989b). *The Asian elephant: Ecology and management*. Cambridge: Cambridge University Press.

Sukumar, R. (2006). A brief review of the status, distribution and biology of wild Asian elephants. *International Zoo Yearbook*, *40*, 1–8. https://doi.org/10.1111/j.1748-1090.2006.00001.x

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experimental design. *Bulletin of the American Meteorological Society*, *93*(4), 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., … Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148. https://doi.org/10.1038/nature02121

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2016). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7. Retrieved from https://cran.r-project.org/package=biomod2

Title, P. O., & Bemmels, J. B. (2017). ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, *41*(2), 291–307. https://doi.org/10.1111/ecog.02880

Tripathi, A., & Mishra, A. K. (2017). Knowledge and passive adaptation to climate change: An example from Indian farmers. *Climate Risk Management*, *16*, 195–207. https://doi.org/10.1016/j.crm.2016.11.002

Tsarouchi, G., & Buytaert, W. (2018). Land-use change may exacerbate climate change impacts on water resources in the Ganges basin. *Hydrology and Earth System Sciences*, *22*(2), 1411–1435. https://doi.org/10.5194/hess-22-1411-2018

Vanderwal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., & Reside, A. E. (2013). Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, *3*(3), 239–243. https://doi.org/10.1038/nclimate1688

Vinnarasi, R., & Dhanya, C. T. (2016). Changing characteristics of extreme wet and dry spells of Indian monsoon rainfall. *Journal of Geophysical Research: Atmospheres*, *121*(5), 2146–2160. https://doi.org/10.1002/2015JD024310

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecological Applications*, *21*(2), 335–342. https://doi.org/10.1890/10-1171.1

Wato, Y. A., Heitkönig, I. M. A., van Wieren, S. E., Wahungu, G., Prins, H. H. T., & van Langevelde, F. (2016). Prolonged drought results in starvation of African elephant (*Loxodonta africana*). *Biological Conservation*, *203*, 89–96. https://doi.org/10.1016/J.BIOCON.2016.09.007

Worldometers (2017). World Population Clock: 7 Billion People - Worldometers. Retrieved from http://www.worldometers.info/world-population/

Yamaura, Y., Higa, M., Senzaki, M., & Koizumi, I. (2018). Can charismatic megafauna be surrogate species for biodiversity conservation? Mechanisms and a test using citizen data and a hierarchical community model. In F. Nakamura (Ed.), *Biodiversity conservation using umbrella species: Blakiston's fish owl and the red-crowned crane* (pp. 151–179). Singapore: Springer. https://doi.org/10.1007/978-981-10-7203-1_11

BIOSKETCH

Our multidisciplinary team includes experts in biodiversity conservation, climate change, macroecology and spatial modelling.

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SUPPORTING INFORMATION

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