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Predicting climate-driven habitat dynamics of adjutants for implementing strategic conservation measures in South and Southeast Asian landscape

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The storks (Ciconiiformes: Ciconiidae) are a fascinating group of birds known for their tall, wading stance, long legs, extended necks, and strong bills. The South and Southeast Asian region boasts the most diverse population of storks, necessitating immediate conservation efforts to protect their habitats and save them from the escalating threats of climate change. Within the genus *Leptoptilos*, three distinct species exist, two of which—the Greater Adjutant (*Leptoptilos dubius*) and the Lesser Adjutant (*Leptoptilos javanicus*)—have garnered attention as 'Near-Threatened' according to the IUCN Red List. However, the assessment overlooks the crucial aspects like ramifications of climatic shifts and anthropogenic-induced habitat fragmentation. Hence, this study endeavors to assess climatic impacts via an ensemble approach to species distribution modeling. The findings unveil alarming trends for both adjutants across South and Southeast Asia. The *L. dubius* is projected to undergo a severe decline of over 95% across all future scenarios (SSP245 and SSP585 in both time periods) from its current suitable extent of 38,686 km^2, which represents only 5.91% of its total extent. On the contrary, the *L. javanicus* experiences a spatial relocation towards Southeast Asia under the SSP245 and SSP585 scenarios, resulting in a decline of over 20% from its present suitable range of 239,490 km^2, which accounts 22.59% of its IUCN range. Furthermore, the resulting habitat fragmentation, propelled by climatic alterations, is severe, with the *L. dubius* losing numerous viable patches entirely and the *L. javanicus* experiencing discontinuity in its habitat. Furthermore, given the overlapping ranges of both adjutant species, the current scenario yields a niche overlap value of 0.370. Therefore, the present study advocates for the reassessment of both *L. dubius* and*L. dubius*, urging their IUCN assessment under threatened category. Furthermore, strategic conservation measures are proposed in this study, involving local communities, non-governmental organizations, and governmental entities, to safeguard these remarkable avian species.

The storks (Ciconiiformes: Ciconiidae) are a fascinating group of birds known for their distinctive characteristics: heavy-wading nature, long legs, elongated necks, and robust bills[1,2]. They can be found residing in a wide array of habitats including wetlands and marshes to grasslands, forests, and even urban areas worldwide[2]. Historically, this order included a diverse array of long-legged wading birds including the herons and ibises[2]. However, recent advancements in molecular based phylogenetic research have refined the classification of avian systematics.

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Large-scale genetic studies have revealed that the traditional order Ciconiiformes actually comprises three distinct evolutionary lineages[2–6]. These lineages are now recognized as separate orders viz., Ciconiiformes, Suliformes, and Pelecaniformes. Finally, all storks have been grouped into the order Ciconiiformes, which is separated from the other two orders of Aves[2–6]. Globally, storks comprise 20 species, predominantly inhabiting subtropical or tropical regions[1,7]. However, with the passage of over three decades, there has been no comprehensive evaluation of the scientific status of storks. Nonetheless, considerable progress has been achieved in elucidating the conservation needs of several stork species[7]. The majority of stork species worldwide are not classified as threatened in the IUCN Red List, which employs a blend of scientific evidence and expert counsel to ascertain species status especially in the tropical regions[7]. The South and Southeast Asian region boasts the highest diversity of storks, necessitating immediate conservation efforts to safeguard their habitats[7,8]. The genus *Leptoptilos* encompasses three distinct species, Greater Adjutant (*Leptoptilos dubius*), Lesser Adjutant (*Leptoptilos javanicus*), and Marabou (*Leptoptilos crumenifer*). The Marabou inhabits the African continent and is categorized as 'Least Concern' by the IUCN. However, both the *L. dubius* and *L. javanicus* are native to the Asian continent, specifically the South and Southeast Asia region, and were previously classified as threatened (*L. dubius*: Endangered from 1988 to 2016; *L. javanicus*: Vulnerable from 1988 to 2017) by the IUCN Red List[8–13].

The *L. dubius* is the second rarest stork species globally and was classified as 'Endangered' in the IUCN Red List[12,14]. This species ranks among the top 100 out of 9,895 bird species for evolutionarily distinct and globally endangered (EDGE) scores[15]. Historically, *L. dubius* had a wide distribution, spanning from Pakistan across northern India, Nepal, and Bangladesh to Myanmar, Thailand, Laos, Vietnam, and Cambodia[12]. Their preferred habitats are wetlands, where they nest in tall trees with dense canopies and exhibit a strong affinity for forested areas. The breeding is believed to coincide with the dry season to exploit abundant prey as water levels recede[16]. Furthermore, they have occasionally been spotted at altitudes of up to 1,500 m from the sea-level[17]. The historical observations indicate that the population of *L. dubius* numbered in the hundreds of thousands during the late 1800s[18]. However, extensive habitat destruction, logging, wetland drainage and pollution, poaching, and environmental pollutants led to a drastic decline of this species in the first half of the 20th century[14,19]. By the early 1990s, it was estimated that only around 400 individuals remained globally. Currently, *L. dubius* is restricted to Assam and Bihar in India and Cambodia with a population of 1,200 to 1,800 birds in total with a declining trend which represents less than 1% of its historic population from a century ago[14,20,21]. The *L. javanicus* represents another threatened species within the genus *Leptoptilos*[13]. The species has an extensive range spanning across Indian subcontinent extending eastward through the southern Himalayan foothills, encompassing Nepal, Bhutan, Bangladesh, Myanmar, and Sri Lanka. In Southeast Asia, *L. javanicus* has been sporadically reported in several countries, including Thailand, Laos, Vietnam, Cambodia, and Malaysia. It also occurs in the Sundaland Biodiversity hotspot encompassing the island ecosystems in Borneo, Sumatra, and Java[13]. During the 20th century, *L. javanicus* populations witnessed a dramatic decline, resulting in the abandonment of large sections of their former territories. The primary drivers of this decline were habitat loss and alteration, as well as hunting for bushmeat. The previous estimates suggested a total population of 5,000 individuals existed globally[13,22–24]. In Southeast Asia, the majority of the population of this species is concentrated in Cambodia (~ 1,500 pairs), Thailand (< 50 pairs), and an estimated 300 individuals in Malaysia. The *L. javanicus* commonly inhabits expansive rivers and lakes within densely wooded areas, freshwater wetlands amidst agricultural landscapes, and coastal wetlands such as mudflats and mangrove forests. They nest colonially in large trees, often in or near wetlands, sometimes utilizing small wetlands within the forested areas. However, during the dry season, shrinking pools and their limited availability can force them into proximity with human habitations[13].

Furthermore, both the species (*L. dubius* and *L. javanicus*) have been listed as 'Schedule I' species under the Indian Wildlife Protection Act of 1972. However, the recent assessment by the IUCN has reclassified both *L. dubius* and *L. javanicus* as 'Near Threatened', thus removing them from the threatened category due to observed population increases resulting from local conservation efforts[12,13]. Nonetheless, the assessment notes that both species remain dependent on conservation efforts in the future. However, since the IUCN assessment criteria do not currently incorporate the impacts of climate change on any species, it is imperative to include changes in species distribution resulting from population dynamics and anthropogenic pressures to make informed decisions[25–27]. Therefore, this study utilizes an ensemble approach to the Species Distribution Model (SDM) to further aid in spatial planning for both species. This ensemble approach employs multiple modeling algorithms to predict species distributions across geographic areas, harnessing the unique strengths of each model to account for diverse factors influencing distribution[26]. Hence, balancing the strengths and limitations of individual models, this integrated strategy enhances the accuracy and reliability of distribution predictions. This method has diverse applications in wildlife science and management by predicting avian distributions across landscapes, providing a robust tool for wildlife managers to implement effective conservation strategies[28–31].

Therefore, this study aims to utilize an ensemble approach with specific variables based on IUCN criteria for both adjutants (*L. dubius* and *L. javanicus*) in the entire South and Southeast Asia to: (i) ascertain the current distribution and the impacts of climate change on their habitats; (ii) country-wise habitat assessment for both species; (iii) evaluate habitat fragmentation under future climatic scenarios; and (iv) assess the niche overlap in present and future scenarios. The findings of the current study will assist in identifying specific priority sites as well as informing conservation decisions for both *L. dubius* and *L. javanicus* in South and Southeast Asian landscape.

Materials and methods

Study extent and species distribution records

Based on the distinctive IUCN ranges (extant, extant non-breeding, and possibly extinct) of *L. dubius* and *L. javanicus*, the entire Indian Subcontinent, China, and regions extending to Southeast Asia were selected as training areas for model development in the current study (Figs. 1 and 2). This approach facilitates the prediction of suitable habitats capable of accommodating both species. Over the past nine years (2015–2023), opportunistic field surveys have been conducted in both protected and unprotected areas of Northeast India, especially in Assam. During the survey tenure the locations points were collected from 10 geographical locations accumulating for *L. dubius* ($n = 133$) and *L. javanicus* ($n = 320$) using the the Garmin GPS eTrex 10 and photographic records were taken using Canon 7D MK 2 with Canon 100–400 mm Lens (Supplementary Table S1, Supplementary Figures S1, S2). Additionally, the study utilized location points secondary citizen science platforms GBIF (*L. dubius*, $n = 770$; https://doi.org/10.15468/dl.v76qg9 and *L. javanicus*, $n = 801$; https://doi.org/10.15468/dl.mez97a)32,33, iNaturalist (*L. dubius*, $n = 148$ and *L. javanicus*, $n = 200$), and previous literature (*L. dubius*, $n = 4$)[20]. Furthermore, the spatial correlation among the present locations was addressed at a resolution of 4.5 km^2 to align with the raster pixel size, effectively removing duplicates and minimizing redundancies. The spatial rarefaction was performed using spatially rarefy function in SDM Toolbox v2.4[34]. The final model was trained using 220 presence points for *L. dubius* and 507 presence points for *L. javanicus*.

Assessment of covariate selection for habitat suitability modeling

A comprehensive array of covariates, comprising bioclimatic, topographic, habitat, and anthropogenic variables, was selected to assess their influence on both species. The bioclimatic variables ($n = 19$) were obtained from the WorldClim website[28,35]. Meanwhile, topographic variables (elevation, slope, and aspect) were sourced from the NASA's Shuttle Radar Topographic Mission (SRTM) (http://srtm.csi.cgiar.org/srtmdata/) at a spatial resolution of 90 m. To evaluate the impact of different habitat types on both species, variables were chosen based on criteria outlined by the IUCN Red List[12,13]. Thus, habitat variables such as the Normalized Difference Vegetation Index

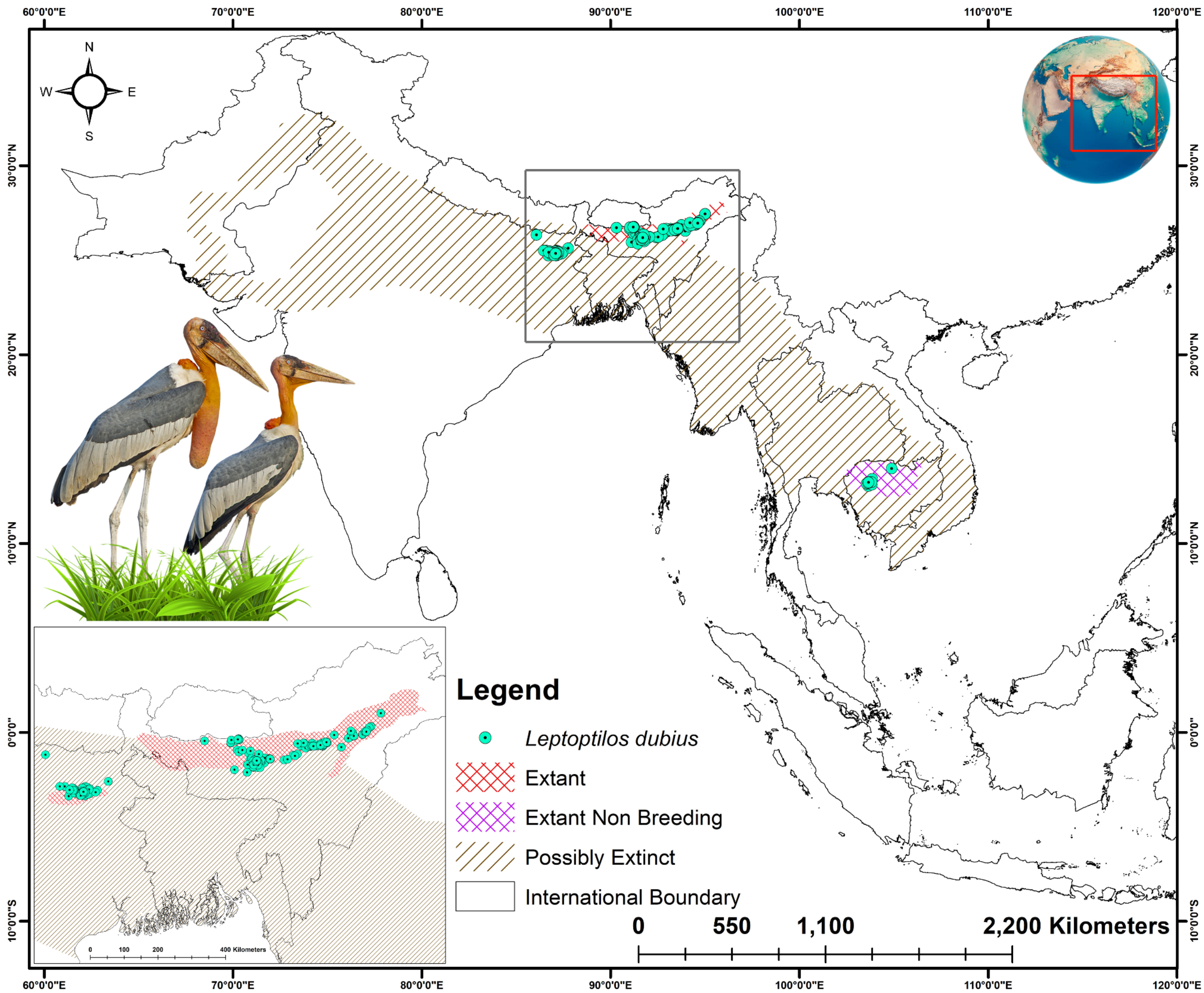

Fig. 1. The map shows the IUCN extent (non-breeding, extant and possibly extinct) of Greater Adjutant (*Leptoptilos dubius*), in South and Southeast Asia along with its presence location points collected through direct surveys and secondary citizen science platforms. The map was generated by using ArcGIS version 10.6. Inset earth map was captured from Google Earth. The species photograph was taken by Dhritiman Mukherjee and edited manually in Adobe Photoshop CS 8.0.

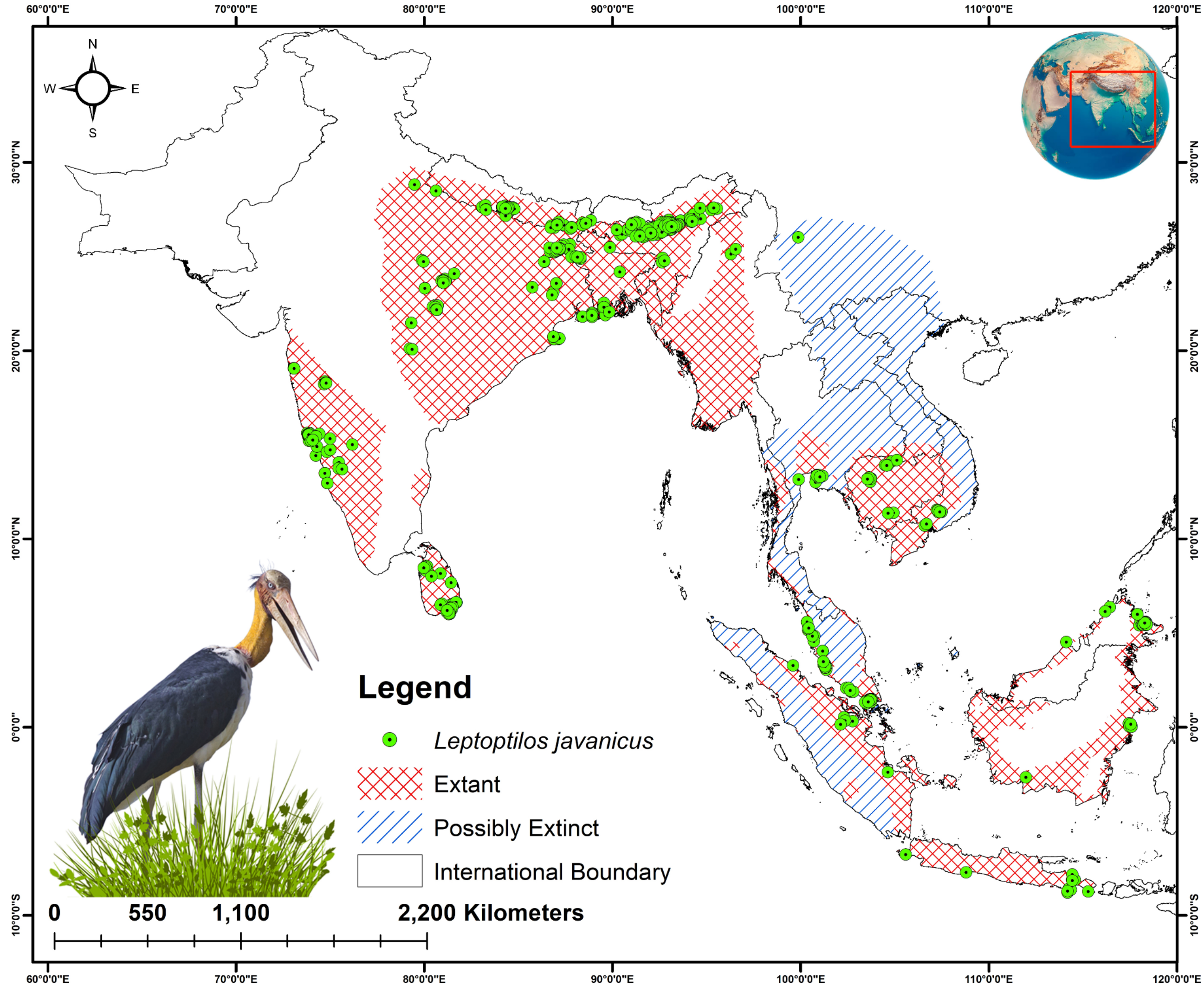

Fig. 2. The map shows the IUCN extent (extant and possibly extinct) of Lesser Adjutant (*Leptoptilos javanicus*), in South and Southeast Asia along with its presence location points collected through direct surveys and secondary citizen science platforms. The map was generated by using ArcGIS version 10.6. Inset earth map was captured from Google Earth. The species photograph was taken by Dhritiman Mukherjee and edited manually in Adobe Photoshop CS 8.0.

(NDVI), Evergreen Forest (euc_122), Deciduous Forest (euc_124), and Wetlands/Waterbodies (euc_water) were selected. Additionally, anthropogenic variables including built-up/urban (euc_built) and cropland (euc_40) were included to assess their influence on species distribution. The habitat and anthropogenic variables were determined using the Euclidean Distance function within ArcGIS, utilizing land use and land cover (LULC) class data from the Copernicus Global Land Service[36,38]. Following this, all variables were resampled to 2.5-minutes (~ 4.5 km^2) using the Spatial-Analyst Extension in ArcGIS 10.6. Spatial multicollinearity testing among the variables was carried out using the SAHM (Software for Assisted Habitat Modelling) package within the VisTrails software[39]. The covariates displaying a Pearson correlation coefficient (r) exceeding 0.8 were excluded from the analysis[40] (Supplementary Figures S3, S4). A qualitative assessment of suitable habitats across various countries within their present and future distribution range was conducted using the zonal statistics function in ArcGIS v.10.6[37,41].

Developing species distribution models

The distribution models were assessed by employing multiple modelling algorithms in an ensemble approach to develop the final distribution model for both species. Accordingly, five distinct algorithms—Maximum Entropy (MaxEnt), Random Forest (RF), Boosted Regression Tree (BRT), Generalized Linear Model (GLM), and Multivariate Adaptive Regression Splines (MARS)—were utilized[42–44]. These algorithms were implemented in the VisTrails software using the SAHM package[39,45]. The execution yielded probability surfaces ranging from '0' (indicating the lowest suitability) to '1' (indicating the highest suitability), and binary maps were generated using the minimum training presence as the threshold. Model evaluation relied on an Area Under the Curve (AUC) threshold of 0.75, with elimination criteria established accordingly[46–48].

The ensemble count map was created on a scale from '0' to '5', where each pixel represented the number of model agreements, with a value of '5' indicating unanimous agreement across all five models, facilitating habitat configuration analysis. Additionally, various evaluation metrics, including Area Under the Curve (AUC), True Skill Statistic (TSS), Cohen's Kappa, Proportion Correctly Classified (PCC), specificity, and sensitivity, were calculated to assess and compare model performance for both the training data and cross-validation sets ($n = 10$)[49–56].

Furthermore, future projections were made using potential climate change scenarios across two distinct shared socio-economic pathways (SSP): SSP245 and SSP585, spanning the periods 2041–2060 and 2061–2080. The study utilized the Hadley Centre Global Environment Model in Global Coupled Configuration 3.1 (HadGEM3-GC31 LL), the sixth Coupled Model Intercomparison Project (CMIP6) selected based on its recognized performance in South and Southeast Asia and its ability to capture temporal fluctuations and excel in representing temperature distribution, as evidenced by previous research[57–59]. Non-climatic raster data, including various habitat types (such as evergreen forest, deciduous forest, and wetlands), NDVI, and built-up/urban areas, remained constant in the future projections aiming to isolate the impact of climate change on the study objective. This approach constrained distribution probabilities within potential habitat zones in the study area and excluded projected regions like high ice-capped mountains and barren plateau areas from consideration[37,60]. Moreover, the centroid shift of both species from the present to future SSP scenarios, across both time frames, was analyzed using centroid change function in SDM Toolbox v2.4[34]. Hence, two ensemble models were developed for both species: the climate-change-only model and the climate-change-habitat model. The climate-change-only model included only bioclimatic and topographic variables, whereas the climate-change-habitat model incorporated bioclimatic, topographic, habitat, and anthropogenic variables for the final analysis.

Integrative assessment of habitat shape geometry and niche overlap dynamics

To evaluate the qualitative and geometric attributes of suitable patches in both current and projected future scenarios, a variety of class-level metrics were employed. The class descriptor tables were prepared based on the suitability argument, ranging from 0 to 5 suitability count models of past and future projections. The eight-cell neighborhood rule was applied with class metrics settings for the sampling strategy, user-provided tiles, and uniform tiles. The five-class layer was incorporated in .tif format for the assessment of shape geometry. These assessment metrics included the number of patches (NP), aggregate index (AI), patch density (PD), largest patch index (LPI), edge density (ED), total edge (TE), and landscape shape index (LSI), all calculated using FRAGSTATS version 4.2.1[61]. Additionally, these metrics carry ecological significance, providing insights into habitat processes and the effects of changes in suitable areas on landscape dynamics[62,63]. This approach allows for a comprehensive analysis of landscape characteristics across the species' distribution range, enabling an understanding of habitat features and fragmentation levels under various scenarios, including present conditions and future climate change projections.

Similarly, the niche overlap between both Asian adjutant species was computed using the ENM tool Ver.1.3[40,64]. The Schoener's D was calculated to assess the degree of niche overlap between the species using this tool. This ecological niche modeling tool is specifically designed to conduct the niche overlap test and explore potential niche radiation between species. The niche similarity test, based on Schoener's D, evaluates the estimated habitat suitability results derived from a multi-model ensemble. Schoener's D assesses the suitable range for the studied species based on probability distributions in a georeferenced cell. A value of '0' indicates no overlap between species in terms of environmental factors, while a value of '1' signifies equal suitability of geographic space cells for both species[40,64,65].

Results

Assessment of ensemble distribution model performance

After considering the correlation between variables, a total of 14 variables were chosen for inclusion in the final model for both species (Supplementary Figures S3, S4). Since both ensemble models for each species yielded similar results with only minor differences, the climate-change-habitat model was selected for further analysis and interpretation as it offers a holistic ecological and environmental envelope (Supplementary Table S2, Supplementary Figures S5, S6). This resultant model i.e., climate-change-habitat model performance demonstrated excellence across all participating models, showcasing strong performance on both training and cross-validation datasets. Given that the model threshold of AUC (> 0.75) was upheld for the final selection of algorithms, all models were incorporated into the final ensemble map. The models exhibited a range of AUC values from 0.954 to 0.993 in training and between 0.931 and 0.953 in cross-validation for *L. dubius*, whereas the AUC range for *L. javanicus* ranged from 0.931 to 0.987 in training and between 0.893 and 0.943 in cross-validation. Specifically, the ΔAUC value for *L. dubius* displayed the smallest discrepancy for RF, with a value of 0.001, whereas BRT demonstrated the highest ΔAUC values, reaching 0.049 across the replicate runs. Similarly, the ΔAUC value for *L. javanicus* was the smallest for RF, registering a value of 0.012, while the highest ΔAUC values were observed for BRT, reaching 0.094 across the replicate runs (Fig. 3; Table 1, Supplementary Figures S7–S10). These findings collectively underscore the sensitivity of the dataset utilized for model fitting across all algorithms. Moreover, the evaluation metrics, encompassing TSS, PCC, Kappa, sensitivity, and specificity, further affirm the models' high-quality performance in both the training and cross-validation phases (Fig. 3; Table 1, Supplementary Figures S7–S10). Among the five chosen models, MaxEnt utilized all variables provided in each replicate run, while BRT employed the fewest variables for both species. Specifically, BRT selected only seven variables for *L. dubius* and six variables for *L. javanicus* out of the total 14 variables available.

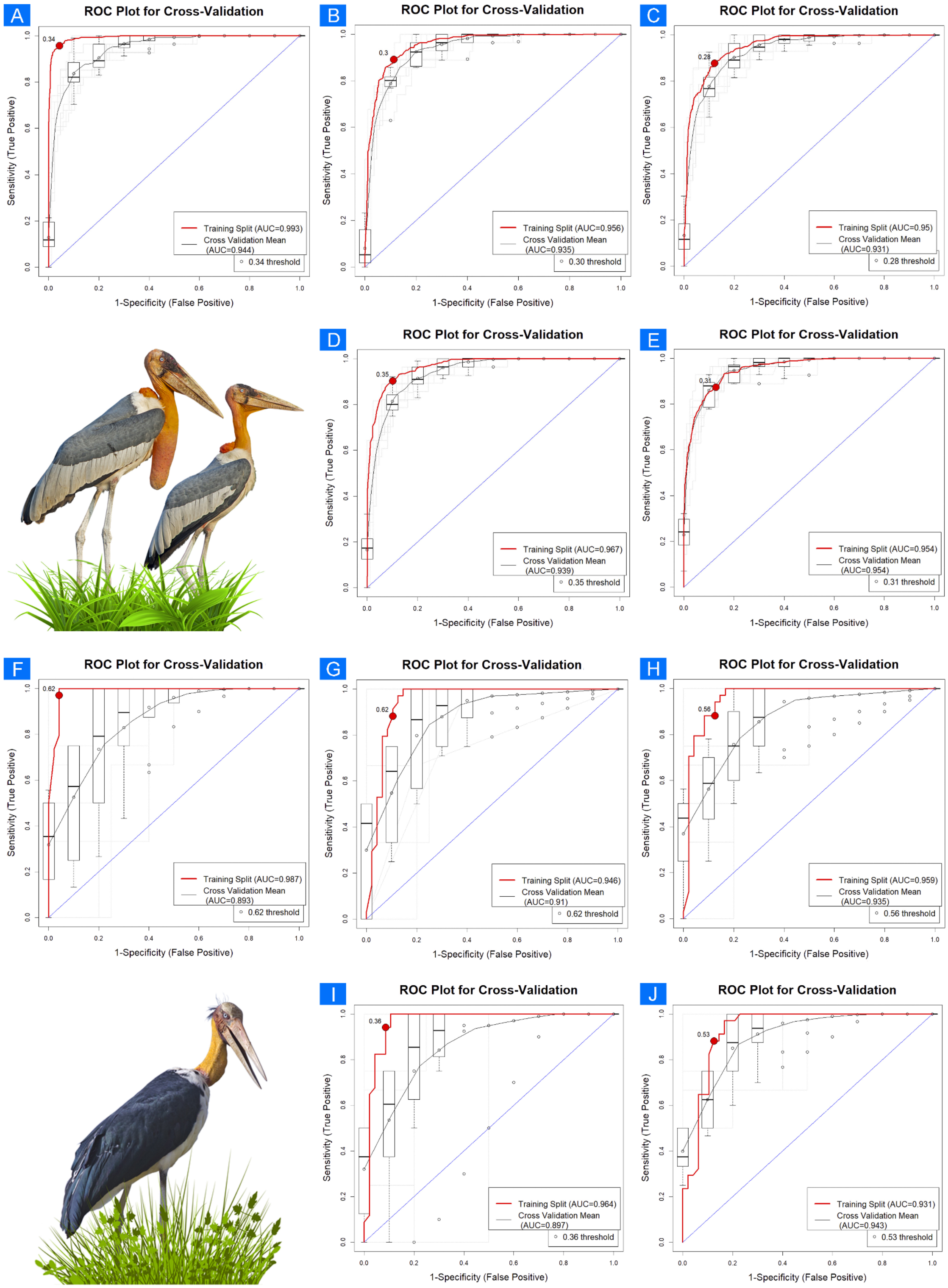

Fig. 3. Model evaluation plot, showing the average training ROC of both training and cross-validation (CV) for the replicate runs under five models of *Leptoptilos dubius* and *Leptoptilos javanicus*. For, *L. dubius*: (**A**) showing ROC plot of boosted regression tree (BRT), (**B**) generalized linear model (GLM), (**C**) multivariate adaptive regression spines (MARS), (**D**) Maximum entropy (MaxEnt), and (**E**). Random Forest (RF). For *L. javanicus*: (**F**) showing ROC plot of boosted regression tree (BRT), (**G**) generalized linear model (GLM), (**H**) multivariate adaptive regression spines (MARS), (**I**) Maximum entropy (MaxEnt), and (**J**) Random Forest (RF). The graphs were generated by the SAHM (Software for Assisted Habitat Modelling) package within the VisTrails software. Species photographs were taken by Dhritiman Mukherjee and edited manually in Adobe Photoshop CS 8.0.

Species	Model	Dataset	AUC	ΔAUC	PCC	TSS	Kappa	Specificity	Sensitivity
L. dubius	BRT	Train	0.993	0.049	95.7	0.91	0.887	0.958	0.957
		CV	0.944		88	0.739	0.692	0.89	0.849
	GLM	Train	0.956	0.021	88.9	0.779	0.719	0.887	0.892
		CV	0.935		85.8	0.704	0.645	0.863	0.841
	MARS	Train	0.95	0.019	87.8	0.756	0.694	0.878	0.877
		CV	0.931		85.8	0.712	0.647	0.86	0.852
	MaxEnt	Train	0.967	0.028	90	0.801	0.745	0.899	0.903
		CV	0.939		88.1	0.746	0.697	0.887	0.859
	RF	Train	0.954	0.001	87.3	0.746	0.682	0.873	0.874
		CV	0.953		90.2	0.719	0.728	0.94	0.779
L. javanicus	BRT	Train	0.987	0.094	96.3	0.929	0.925	0.958	0.971
		CV	0.893		84.2	0.692	0.681	0.850	0.842
	GLM	Train	0.946	0.036	89.0	0.778	0.775	0.896	0.882
		CV	0.910		85.3	0.700	0.699	0.850	0.850
	MARS	Train	0.959	0.024	87.8	0.757	0.751	0.875	0.882
		CV	0.935		84.4	0.678	0.672	0.870	0.808
	MaxEnt	Train	0.964	0.067	92.6	0.856	0.849	0.915	0.941
		CV	0.897		85.5	0.702	0.700	0.885	0.817
	RF	Train	0.931	0.012	87.8	0.757	0.751	0.875	0.882
		CV	0.943		83.0	0.655	0.653	0.830	0.825

Table 1. Model fit metrics for each of the participating modelling methods and for the final ensemble model for estimation of habitat suitability of *Leptoptilos dubius* and *Leptoptilos javanicus*. A total of five model algorithms were used with the threshold of < 0.75 AUC score. The models were maximum Entropy (MaxEnt), Random Forest (RF), boosted regression tree (BRT), generalized Linear Model (GLM), and Multivariate Adaptive Regression splines (MARS). AUC: area under curve, ΔAUC: change in Area under curve (training – Cross Validation), PCC: proportion correctly classified, TSS: true skill statistic.

Assessment of predictive variable efficacy in predicting distribution

The ensemble model for *L. dubius* revealed that, on average (μ) across the five models, the predominant contributor was the habitat variable Wetlands/Waterbodies (euc_water), constituting 26.63% of the model's influence, while Mean Temperature of Driest Quarter (bio_9) emerged as the most significant bioclimatic variable, accounting for 23.99% (Table 2). Among the topographic variables, aspect (asp) made the highest contribution at 0.73%, and the anthropogenic variable Cropland (euc_40) contributed 0.45% to the model. The least influential variable among all was slope (slp), with a contribution of 0.01%. Additionally, the ensemble model for *L. javanicus* identified distinct variables. In this case, builtup/urban (euc_built) emerged as the most significant contributor, representing 13.47% of the overall contribution. The leading bioclimatic variable was Isothermality (bio_3), accounting for 17.97% of the contribution. Within the habitat variables, euc_124 exhibited the highest contribution at 12.99%, while elevation (elv) emerged as the primary contributor among the topographic variables (0.29%). Among all the selected variables, the topographical variable aspect (asp) made the smallest contribution, at 0.01% (Table 2).

Forecast of suitable habitat suitability extent trajectories

The IUCN Red List recognizes a total extent of approximately 6,53,610 km² for *L. dubius*, of which the model identified only 38,686 km² (5.91%) as currently suitable (Fig. 4, Supplementary Table S3). Similarly, for *L. javanicus*, out of the total IUCN Red List extent of 10,60,056 km², only 22.59% (02,39,490 km²) was considered suitable by the model (Fig. 5, Supplementary Table S3). The future climate change projections yielded alarming outcomes across all scenarios, with *L. dubius* facing a projected reduction of more than 90% in suitable areas, while *L. javanicus* is anticipated to experience a decline ranging from 20 to 28% (Figs. 6 and 7A,B). In particular, within the SSP245 scenario, habitat declines for *L. dubius* were estimated at 93.60% and 98.96% during the periods of 2041–2060 and 2061–2080, respectively (Fig. 6, Supplementary Table S3). Similarly, extent declines for *L. javanicus* ranged between 20.63% and 22.96% during the same periods (Fig. 7, Supplementary Table S3). Additionally, under the high emission scenario SSP585, even more severe habitat reductions were indicated, with declines of 98.48% and 99.30% for *L. dubius* during the same time intervals compared to the present scenario (Fig. 7, Supplementary Table 1). Furthermore, the reduction in suitable areas for *L. javanicus* during the same timeframe was 22.36% and 28.60%, respectively (Fig. 8, Supplementary Table 1). The analysis of centroid shifts from the present to future scenarios revealed distinct patterns for the two species (Fig. 8C,D). Specifically for *L. dubius*, the centroid shifted westward, with a range of 121° to 269° from its current position. In contrast, for *L. javanicus*, the centroid shifted towards Southeast Asia, with a range of 306° to 314° from the present centroid.

Species	Predictors	Predictors Abbreviations	BRT	GLM	MARS	MaxEnt	RF	μ(Mean)	μ(Mean) %
L. dubius	Aspect	asp	0.00000	0.01832	0.00000	0.00000	0.00000	0.00366	0.73
	Annual Precipitation	bio_12	0.00030	0.00000	0.07600	0.00638	0.01478	0.01949	3.89
	Precipitation of Driest Month	bio_14	0.00000	0.08126	0.01668	0.05828	0.00100	0.03144	6.27
	Precipitation Seasonality	bio_15	0.00000	0.23520	0.02460	0.01410	0.00198	0.05518	11.01
	Isothermality	bio_3	0.00510	0.00000	0.04824	0.04870	0.00100	0.02061	4.11
	Mean Temperature of Driest Quarter	bio_9	0.01652	0.29674	0.24014	0.03196	0.01576	0.12022	23.99
	Elevation	elev	0.00000	0.00958	0.00346	0.00206	0.00050	0.00312	0.62
	Euclidean distance to Evergreen Forest	euc_122	0.00000	0.26464	0.00000	0.02034	0.00100	0.05720	11.41
	Euclidean distance to Deciduous Forest	euc_124	0.00012	0.23106	0.00000	0.03284	0.00100	0.05300	10.58
	Euclidean distance to Cropland/ Agricultural Land	euc_40	0.00002	0.00000	0.00004	0.00978	0.00148	0.00226	0.45
	Euclidean distance to Builtup/Urban	euc_built	0.00000	0.00000	0.00000	0.00136	0.00050	0.00037	0.07
	Euclidean distance to Waterbodies	euc_water	0.04928	0.28814	0.21192	0.10348	0.01456	0.13348	26.63
	Normalized difference vegetation index	ndvi	0.00000	0.00000	0.00000	0.00106	0.00250	0.00071	0.14
	Slope	slp	0.00000	0.00000	0.00000	0.00018	0.00000	0.00004	0.01
L. javanicus	Aspect	asp	0.00000	0.00000	0.00000	0.00020	0.00000	0.00004	0.01
	Annual Precipitation	bio_12	0.04376	0.00000	0.05202	0.03992	0.01696	0.03053	8.11
	Precipitation of Driest Month	bio_14	0.00000	0.00000	0.01358	0.00222	0.00000	0.00316	0.84
	Precipitation Seasonality	bio_15	0.00000	0.03836	0.00358	0.00498	0.00000	0.00938	2.49
	Isothermality	bio_3	0.03716	0.10038	0.07120	0.12688	0.00240	0.06760	17.97
	Mean Temperature of Driest Quarter	bio_9	0.01166	0.24204	0.05872	0.00708	0.00062	0.06402	17.02
	Elevation	elev	0.00000	0.00278	0.00000	0.00276	0.00000	0.00111	0.29
	Euclidean distance to Evergreen Forest	euc_122	0.00000	0.03548	0.08046	0.02274	0.00014	0.02776	7.38
	Euclidean distance to Deciduous Forest	euc_124	0.02708	0.08608	0.10498	0.02604	0.00022	0.04888	12.99
	Euclidean distance to Cropland/Agricultural Land	euc_40	0.00000	0.12052	0.01656	0.02756	0.00096	0.03312	8.80
	Euclidean distance to Builtup/Urban	euc_built	0.02420	0.16634	0.02086	0.03908	0.00296	0.05069	13.47
	Euclidean distance to Waterbodies	euc_water	0.03674	0.08828	0.00394	0.06288	0.00232	0.03883	10.32
	Normalized difference vegetation index	ndvi	0.00000	0.00000	0.00000	0.00440	0.00000	0.00088	0.23
	Slope	slp	0.00000	0.00000	0.00000	0.00112	0.00008	0.00024	0.06

Table 2. The mean percentage contribution of each covariate generated from the final ensemble model for both *Leptoptilos dubius* and *Leptoptilos javanicus*.

National-scale habitat suitability dynamics in South and Southeast Asia

A detailed assessment of habitat suitability was undertaken on a nationwide scale to aid in the construction of an effective conservation action plan, as each country has a distinct legislative framework (Table 3). The model identified ten countries (India, Cambodia, Thailand, Vietnam, Laos, Bangladesh, Myanmar, Nepal, Bhutan, and Pakistan) within the distribution range of *L. dubius* as harboring suitable areas, while fourteen countries (India, Cambodia, Thailand, Vietnam, Laos, Bangladesh, Myanmar, Nepal, Bhutan, Sri Lanka, Malaysia, Indonesia, China, and Singapore) were identified as suitable for *L. javanicus* within its extent in South and Southeast Asia. This extensive assessment highlights the diverse geographic distribution of suitable habitats for these species across the region. Among the nations evaluated for *L. dubius*, notable levels of suitability were observed in India (0.795), Bangladesh (0.618), and Cambodia (0.284) within the species extent. Similarly, LA displayed high suitability in Bangladesh (0.819), Sri Lanka (0.659), and Cambodia (0.606) within its distribution range. Interestingly, India, Bangladesh, and Cambodia emerged as significant hosts for suitable habitats for both *L. dubius* and *L. javanicus* across the South and Southeast Asian regions. This observation underscores the importance of these countries in conservation efforts for these adjutant species.

However, rapid climatic changes have profoundly impacted these nations and both species. For example, India is expected to experience declines ranging from 20 to 49% in all future climate change scenarios concerning the suitable extent of *L. dubius*. Similar declines are projected in Bangladesh (34–51%) and Cambodia (60–63%) in future climatic scenarios. Interestingly, Bhutan stands out as the only country where suitability for *L. dubius* is projected to increase by 2–11% in future climate projections. Additionally, within the distribution range of *L. javanicus*, there is a significant shift towards Southeast Asian countries, with many southeastern countries experiencing gains in suitability for *L. javanicus*. Notably, Indonesia exhibits the highest gain, with suitability increasing by over 50% in all future projections. Conversely, declines are predominantly observed in the Indian Subcontinent, with countries like India (13–22%), Sri Lanka (9–23%), and Bangladesh (12–18%) showing substantial decreases in habitat suitability in future climate change scenarios (Table 3).

Integrated assessment of habitat shape and niche overlap dynamics

Given the substantial decrease in viable habitats for both species, considerable changes in their geometry have occurred, resulting in high habitat fragmentation (Table 4). Specifically, within the habitat extent of *L. dubius*, the

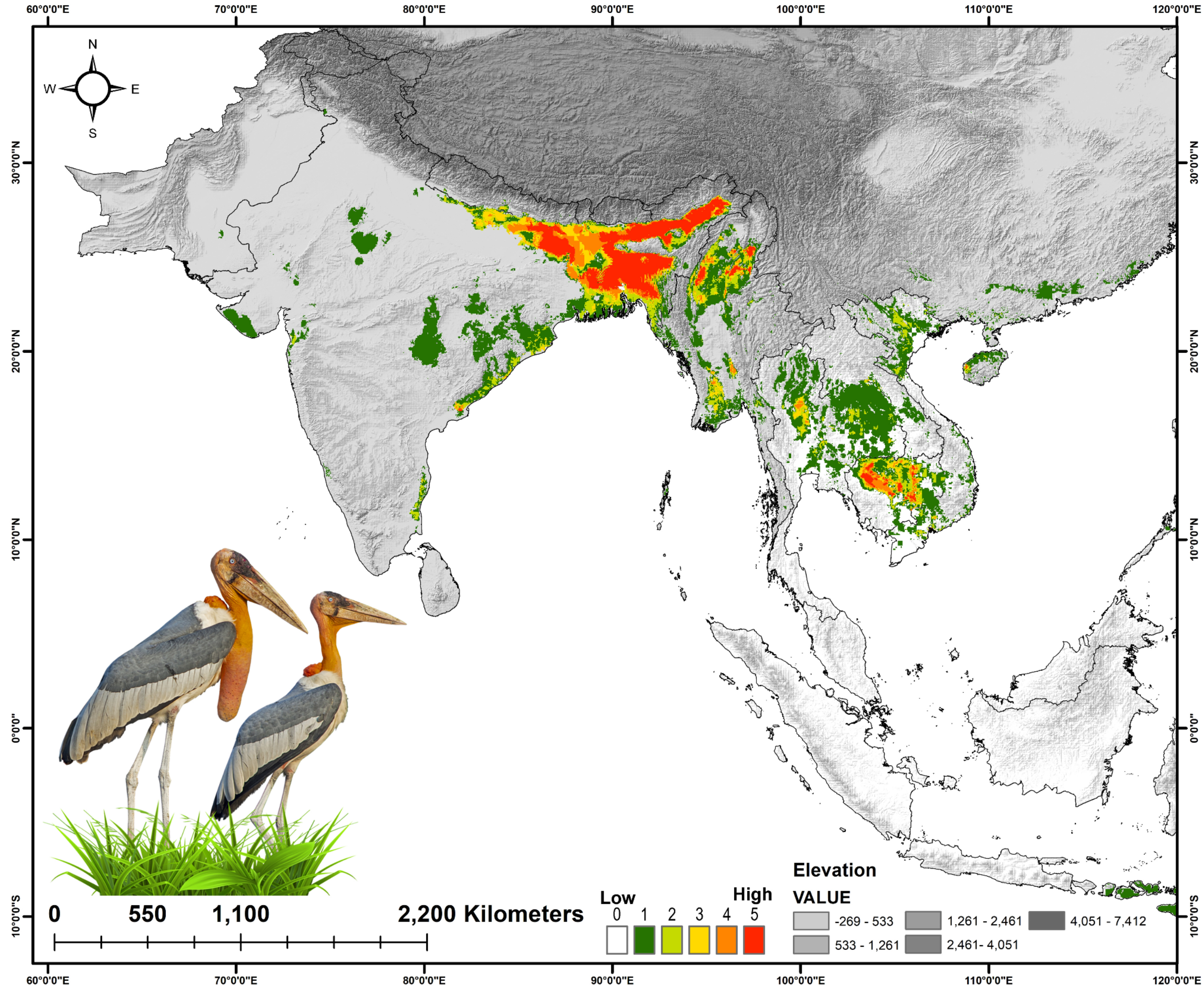

Fig. 4. The suitable habitat extent in present scenario for *Leptoptilos dubius* in South and Southeast Asia. The five classes (1–5) defined in the map shows the five model arguments used in the present study. The class-5 means 'highest suitability', whereas class-0 means 'no suitability'. The map was generated by using ArcGIS version 10.6. The species photograph was taken by Dhritiman Mukherjee and edited manually in Adobe Photoshop CS 8.0.

NP is projected to decrease by up to 88% in the future. This decline in NP has directly resulted in a reduction in PD, decreasing from 65.7 to 97%. Moreover, the reduction in NP has also impacted edge metrics such as TE (by 79–98%) and ED (more than 80%), which are also expected to decline in future climate change scenarios. The reduction in suitable areas has further influenced the size of suitable patches, as LPI also experiences a significant decline, exceeding 96%. Additionally, these patches exhibit simpler shapes and are more dispersed, reflected in LSI and AI decreasing to a considerable extent in *L. dubius*.

In contrast to *L. dubius*, habitat fragmentation is more pronounced in *L. javanicus*. There is a significant increase in NP from 28 to 31% in future climatic projections. This increase in NP has resulted in a corresponding rise in PD of over 28%. The elevation of both NP and PD has consequently led to an increase in edge metrics, with TE increasing by more than 4% and ED by over 3% in future climate change scenarios. Additionally, habitat fragmentation is also evident through an increase in shape complexity, as indicated by LSI, and a reduction in patch proximity, as revealed by AI, in the future extent of *L. javanicus* (Table 4).

In the present scenario, the entirety of the *L. dubius* range coincides with the suitable extent of the *L. javanicus*, yielding a Schoener's D niche overlap value of 0.370 (Table 5). However, as per projections for the future, this overlap is anticipated to decline significantly. The projected decline in niche overlap ranges from 54 to 80% in future climate change scenarios. This indicates a potential shift in habitat preferences or distributions for one or both species as environmental conditions change over time.

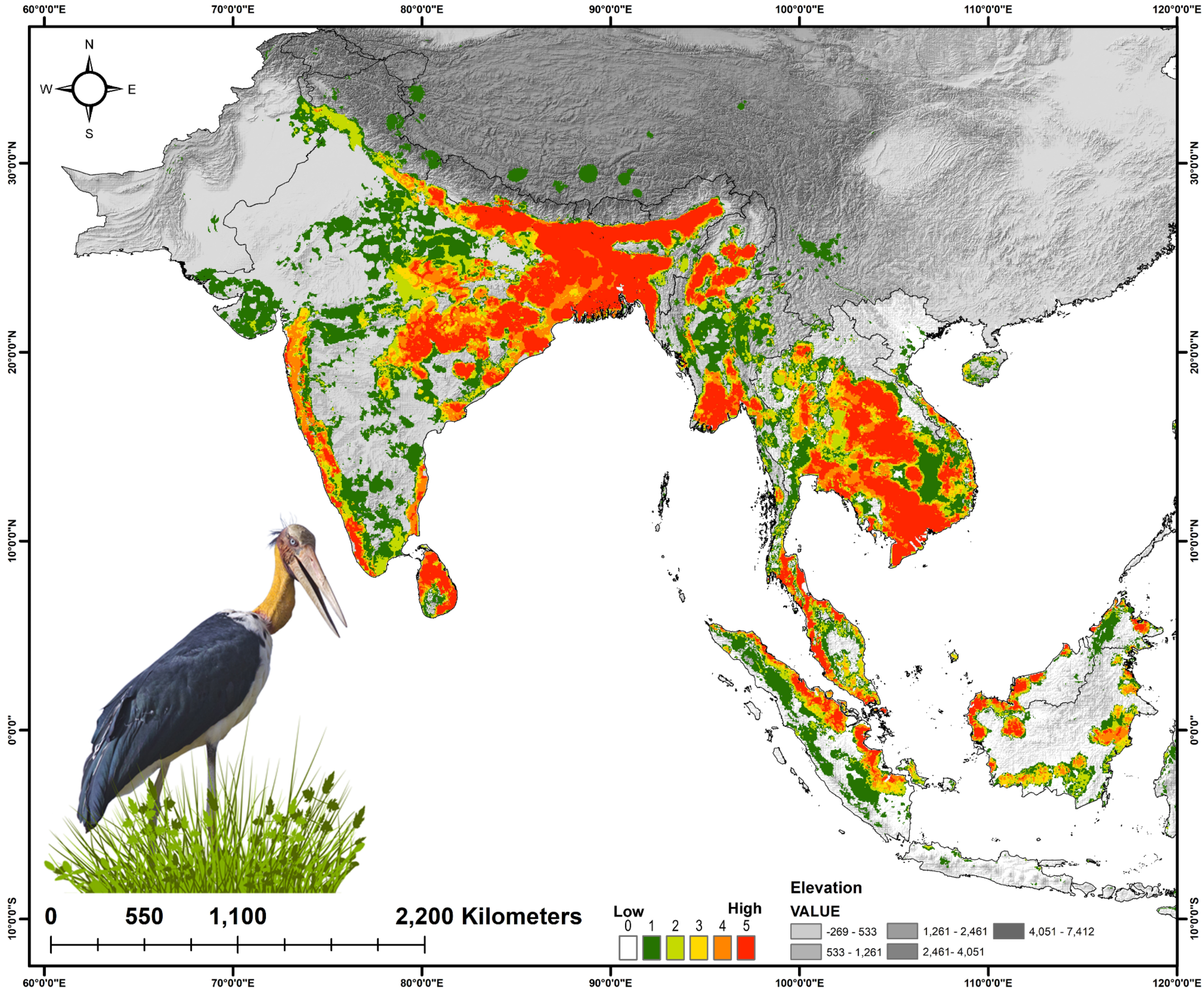

Fig. 5. The suitable habitat extent in present scenario for *Leptoptilos javanicus* in South and Southeast Asia. The five classes (1–5) defined in the map shows the five model arguments used in the present study. The class-5 means 'highest suitability', whereas class-0 means 'no suitability'. The map was generated by using ArcGIS version 10.6. The species photograph was taken by Dhritiman Mukherjee and edited manually in Adobe Photoshop CS 8.0.

Discussion

In recent decades, accelerated climate change and the direct destruction of natural habitats by human activities have emerged as significant threats to global terrestrial biodiversity, resulting in considerable range contractions and extinctions in bird populations[66–71]. Climate change is projected to have severe impacts on biodiversity, particularly in tropical regions where ongoing land-use changes may intensify species loss in the near future[66,72,73]. Therefore, understanding the current and projected impacts of climate change on birds is crucial for evaluating the effectiveness of ongoing conservation practices and formulating management strategies to mitigate future species decline and extinction risks[74]. This is also warranted by the Kunming-Montreal Global Biodiversity Framework under the Convention on Biological Diversity (CBD), which aims to integrate biodiversity considerations into climate change mitigation and adaptation strategies further acknowledges the critical interplay between climate change, biodiversity, and wildlife conservation, setting forth targeted actions by 2050 to address these interconnected challenges[75]. However, the storks have historically received relatively less attention in the integration of climatic studies assessing the effects of climate and habitat fragmentation[8,74,76,77]. Thus, the integration of climatic effects, both present and future, alongside considerations of habitat fragmentation and species ecology, is imperative and requires urgent attention[74]. The present study on the climatic aspect can be integrated with the ecological studies for better-informed conservation strategies. This endeavor is further warranted by recommendations from the IUCN for conservation measures aimed at both *L. dubius* and *L. javanicus*[12,13].

The current study reveals alarming trends concerning both adjutants inhabiting the Asian continent. The availability of suitable habitats within the IUCN extent is notably scarce, accounting for a mere 5.91% for *L.*

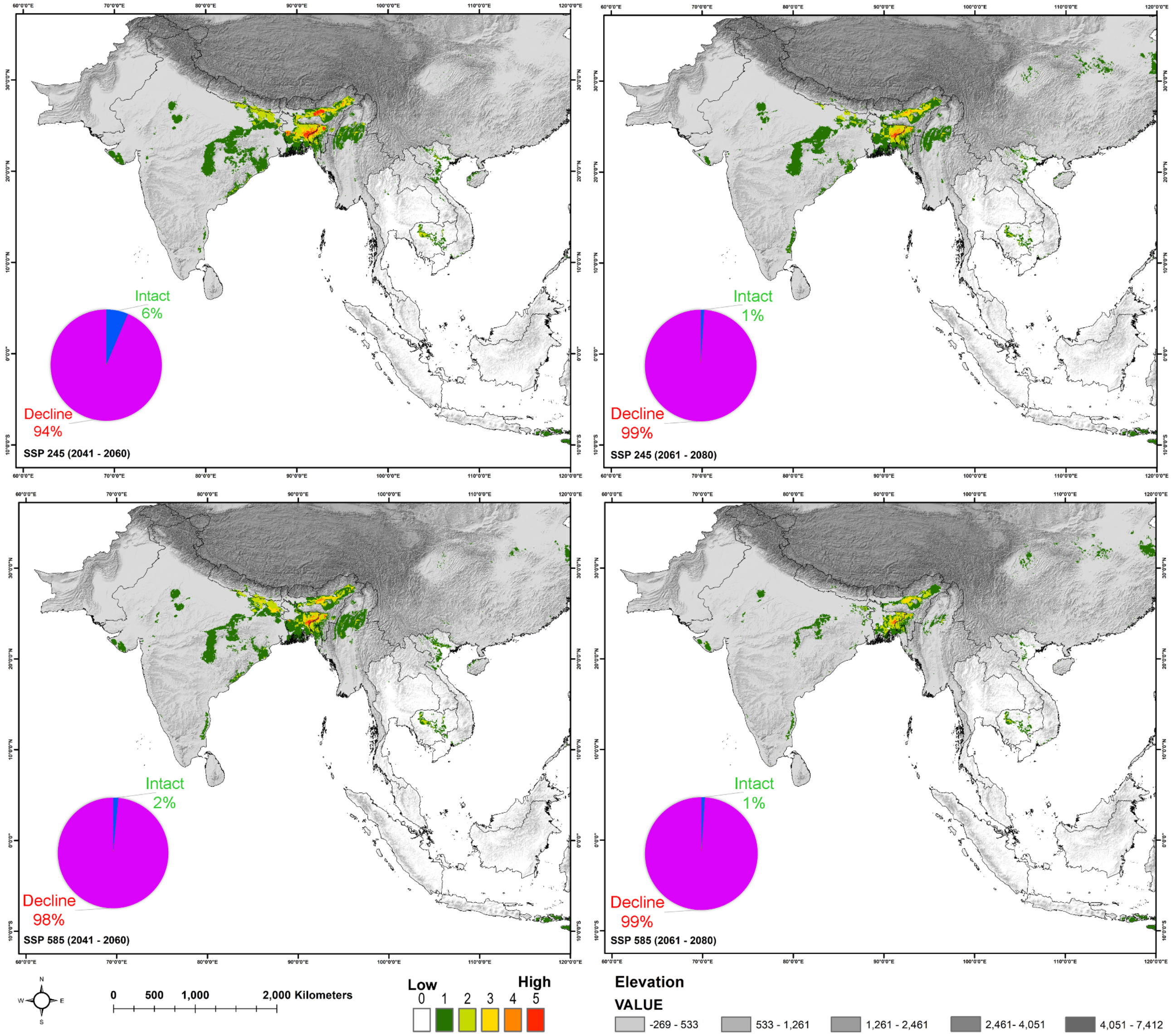

Fig. 6. The suitable habitat extent in future scenarios (two SSPs and two Timeframes) for *Leptoptilos dubius* in South and Southeast Asia. The five classes (1–5) defined in the map shows the five model arguments used in the present study. The class-5 means 'highest suitability', whereas class-0 means 'no suitability'. The pie charts determine the intact and decline area percentage in the future scenarios. The maps were generated by using ArcGIS version 10.6 and pie charts were generated by Microsoft Excel and edited manually in Adobe Photoshop CS 8.0.

dubius and 22% for *L. javanicus*. Such circumstances might have resulted in their evaluation being considered threatened for an extended duration in previous studies[9,14,78]. The projected declines due to climate change are even more disconcerting in all the future projected scenarios, with *L. dubius* facing a decline of over 95% and *L. javanicus* experiencing a decline of over 20%. These findings align with existing studies indicating that Ciconiiformes, including South and Southeast Asian adjutants, require escalated conservation efforts due to habitat loss induced by climatic changes[79,80]. Moreover, the present study on *L. dubius* and *L. javanicus*, holds congruent outcomes with other threatened stork species in Asia, namely the Oriental Stork, *Ciconia boyciana* and the Black Stork, *Ciconia nigra*[25,27,77]. Both species (*C. boyciana* and *C. nigra*) are also projected to undergo rapid habitat declines in the future due to climate change[27,77]. This is demonstrated by the importance of bioclimatic variables, such as the Mean Temperature of the Driest Quarter (bio_9), which contributed 23.99% to the habitat suitability for *L. dubius*, and Isothermality (bio_3), which contributed 17.97% to the habitat suitability for *L. javanicus*. Furthermore, evergreen forests (11.41% for *L. dubius*; 7.38% for *L. javanicus*) and deciduous forests (10.58% for *L. dubius*; 12.99% for *L. javanicus*) were also determined as important variables influencing the habitat suitability of both stork species. Hence, the conversion of these natural habitats into agricultural land serves as an additional factor driving the decline of these species[25,27,77]. Furthermore, the proliferation of agricultural fields predominantly occurs in proximity to waterbodies, leading to water degradation due to

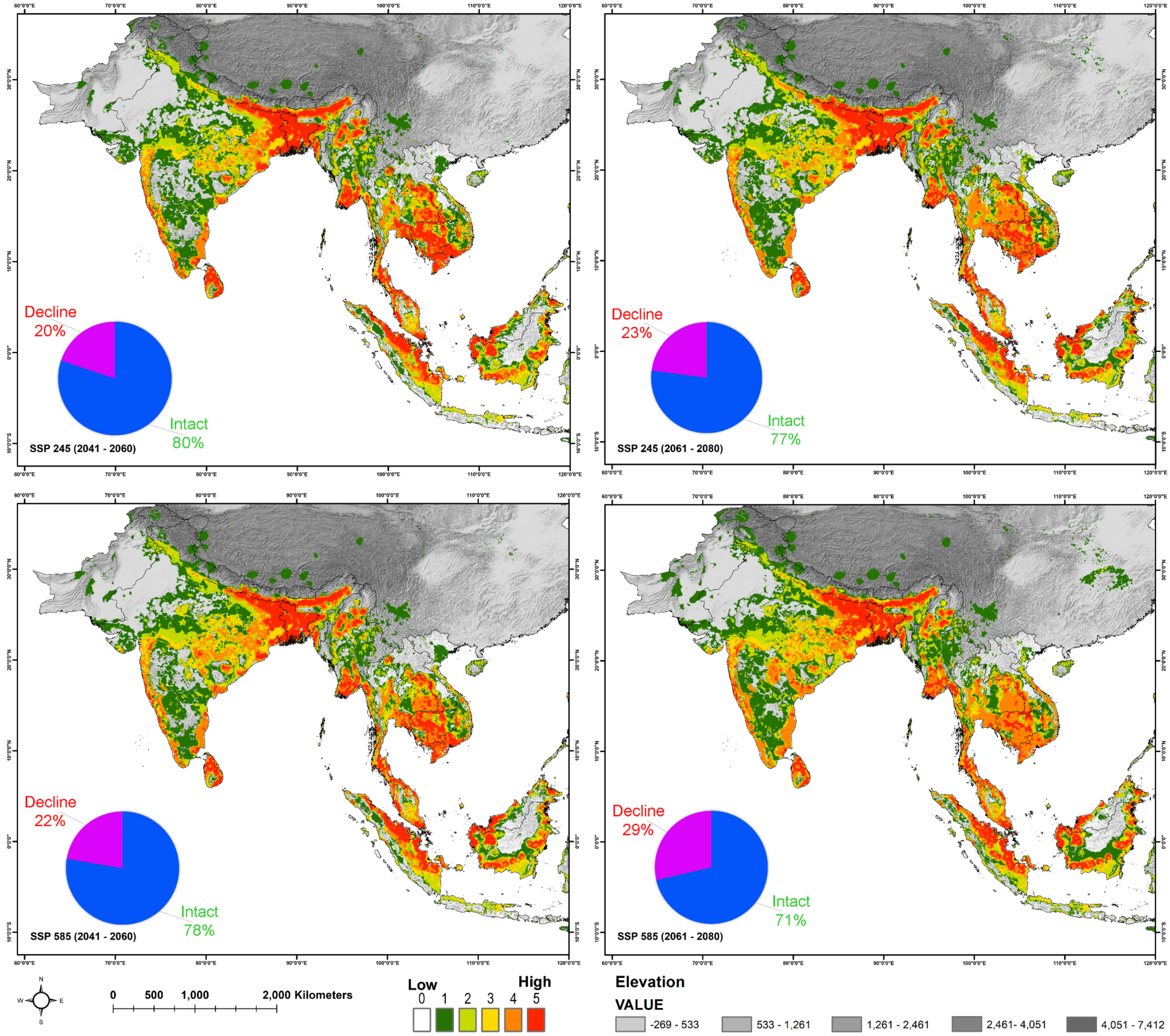

Fig. 7. The suitable habitat extent in future scenarios (Two SSPs and Two Timeframes) for *Leptoptilos javanicus* in South and Southeast Asia. The five classes (1–5) defined in the map shows the five model arguments used in the present study. The class-5 means 'highest suitability', whereas class-0 means 'no suitability'. The pie charts determine the intact and decline area percentage in the future scenarios. The maps were generated by using ArcGIS version 10.6 and pie charts were generated by Microsoft Excel and edited manually in Adobe Photoshop CS 8.0.

nutrient runoff[81]. This is a great concern for the adjutant species as well as other wetland birds. The present study highlights waterbodies (euc_water) as one of the primary contributing factors (26.63% contribution for *L. dubius*; 10.32% for *L. javanicus*) for both species, emphasizing the conversion into anthropogenic land use near waterbodies as a major threat. Furthermore, the *L. dubius* has been observed foraging in garbage dumps adjacent to waterbodies, particularly in Deepor Beel in Guwahati, as these dumps offer a consistent food source for this carnivorous/scavenger species[82]. The shift in foraging habitats from shallow water bodies to landfill sites may be influenced by the drying of these water bodies, which subsequently leads to a scarcity of fish food resources. Furthermore, there have been instances of *L. dubius* fatalities reported due to the ingestion of non-biodegradable waste and polluted water from the nearby waterbody, resulting from runoff from the garbage dumps. These factors have significantly impacted the nesting success of *L. dubius* near the city of Guwahati, Assam[78]. Moreover, for *L. javanicus*, cropland (8.80% contribution) and built-up (13.47% contribution) were identified as influential factors impacting its distribution. The *L. javanicus* utilizes agricultural landscapes for foraging and breeding, showcasing a degree of adaptability to these environmental alterations amidst extensive land conversion[83,85].

The findings also highlight a notable divergence between *L. javanicus* and *L. dubius* in their spatial distribution, with *L. dubius* experiences a pronounced decline whereas *L. javanicus* experiences a comparatively

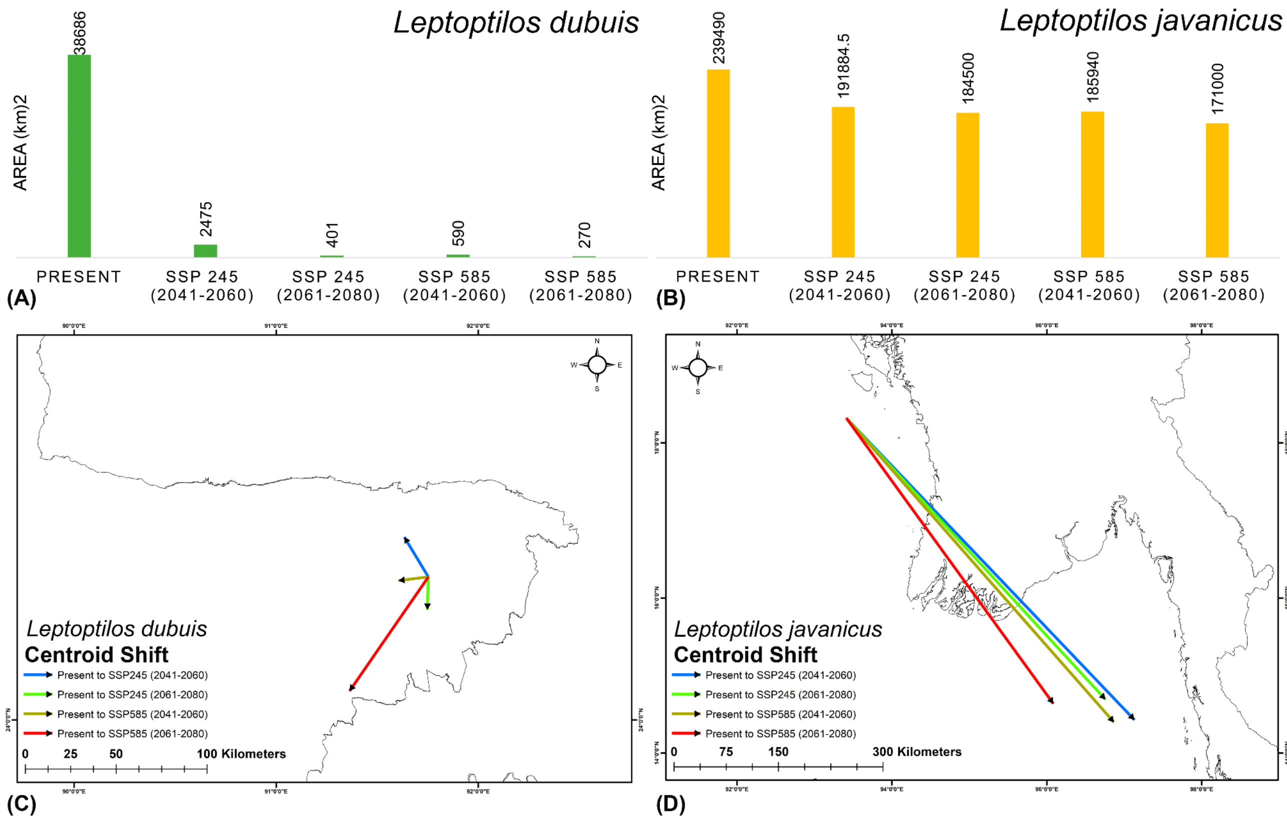

Fig. 8. The figure illustrates the suitable habitats and centroid shifts for two species, *Leptoptilos dubius* and *Leptoptilos javanicus*, under present and future SSP scenarios. Panels (**A**) and (**B**) display bar graphs representing the suitable habitat areas for *L. dubius* and *L. javanicus*, respectively. Panels (**C**) and (**D**) Maps showing the direction of centroid shifts for *L. dubius* and *L. javanicus* from the present to future SSP scenarios.

less decline and displaying a shift towards Southeast Asia. This divergence in distribution patterns may be attributed to the *L. javanicus* adaptability to cropland, as evidenced in previous studies[84]. Additionally, this range shift may be influenced by *L. javanicus* resilience to changing climatic conditions, particularly the climatic shift towards Southeast Asia, coupled with its extensive geographic range[86]. Nevertheless, the range shift remains absent in the *L. dubius*, leaving it notably vulnerable due to its constrained climate resilience and potentially low adaptability to cropland—a factor recognized as a significant threat by the IUCN[12]. This absence of adaptability of *L. dubius* in agricultural land may have contributed to its pronounced decline, as observed in this study. This circumstance can also be attributed to the outcomes of habitat fragmentation, as they present divergent findings for both adjutants. The decrease in NP along with other edge and shape metrics (PD, TE, ED, LSI) for *L. dubius* is linked to the substantial loss of suitable habitats, leading to the complete disappearance of many viable patches. Conversely, the NP for *L. dubius* exhibits an increase, indicating high degree of fragmentation within its extensive geographic range. This divergence is attributed to the slower pace of decline in suitable habitats for *L. dubius* compared to *L. dubius*. Furthermore, the suitable patches within the geographic range of *L. javanicus* disintegrate and separate into smaller, discrete units. This fragmentation phenomenon is corroborated by the increased count of NP alongside the reduction in LPI and AI. Moreover, the distribution range of *L. dubius* completely overlaps with that of *L. javanicus*, as they predominantly inhabit similar habitat types, which is also supported by the niche overlap results of the current study[12,13]. However, the niche overlap is projected to decrease in the future, likely due to declines in suitable habitat areas and observed range shifts in both species. This decline in niche overlap is particularly concerning for *L. dubius*, considering the potential for interspecific competition, which could exacerbate threats as one species may outcompete the other for living resources[87,89]. Hence, greater attention must be directed towards preserving the habitat extent of *L. dubius*. Furthermore, the study categorized particular nations according to their suitability for both species. However, the habitat suitability of *L. dubius* has decreased in the majority of countries due to climate change, thus necessitating immediate targeted conservation actions. Meanwhile, *L. javanicus* had a few exceptions where habitat suitability increased, such as Southeast Asian countries like Indonesia, Malaysia, and Vietnam. These geographic regions witnessing an expansion in suitability for *L. javanicus*, may also need to heighten conservation efforts.

The recent IUCN assessment has reclassified both species (*L. dubius* and *L. javanicus*) as 'Near-Threatened', switching *L. dubius* from 'Endangered' and *L. javanicus* from 'Vulnerable' category. Specifically, the IUCN status of *L. dubius* has been switched due to the increase in population and ongoing conservation efforts locally. However, the population of *L. dubius* is still relatively low (~ 1,500) compared to other threatened bird species

Species	Country	Present	SSP 245 (2041–2060)	% change from Present	SSP 245 (2061–2080)	% change from Present	SSP 585 (2041–2060)	% change from Present	SSP 585 (2061–2080)	% change from Present
L. dubius	India	0.795	0.605	-23.93	0.528	-33.53	0.569	-28.35	0.405	-49.02
	Bangladesh	0.618	0.408	-34.01	0.380	-38.54	0.376	-39.11	0.301	-51.25
	Cambodia	0.284	0.113	-60.17	0.106	-62.85	0.111	-60.84	0.105	-63.19
	Thailand	0.146	0.045	-68.94	0.047	-67.46	0.044	-69.86	0.039	-73.05
	Myanmar	0.132	0.079	-39.72	0.072	-45.01	0.077	-41.25	0.050	-61.87
	Vietnam	0.127	0.072	-43.13	0.067	-46.97	0.072	-43.41	0.055	-56.25
	Nepal	0.081	0.059	-26.90	0.051	-37.00	0.056	-31.18	0.043	-46.25
	Laos	0.064	0.030	-52.80	0.029	-55.14	0.030	-52.75	0.026	-59.15
	Bhutan	0.023	0.023	+ 2.17	0.025	+ 9.50	0.024	+ 4.11	0.026	+ 11.65
	Pakistan	0.010	0.006	-38.46	0.006	-38.27	0.006	-42.53	0.005	-50.35
L. javanicus	Bangladesh	0.819	0.720	-12.10	0.700	-14.55	0.695	-15.16	0.667	-18.57
	Sri Lanka	0.659	0.595	-9.78	0.528	-19.86	0.576	-12.59	0.504	-23.52
	Cambodia	0.606	0.653	+ 7.81	0.667	+ 10.08	0.660	+ 9.04	0.664	+ 9.60
	Thailand	0.537	0.528	-1.79	0.543	+ 1.00	0.513	-4.46	0.517	-3.73
	Vietnam	0.380	0.399	+ 4.85	0.406	+ 6.83	0.393	+ 3.40	0.405	+ 6.44
	Myanmar	0.366	0.380	+ 3.75	0.395	+ 8.04	0.384	+ 5.05	0.406	+ 10.87
	India	0.351	0.303	-13.89	0.300	-14.61	0.291	-17.18	0.271	-22.77
	Malaysia	0.336	0.441	+ 31.15	0.451	+ 34.03	0.453	+ 34.83	0.460	+ 36.94
	Laos	0.303	0.291	-3.74	0.289	-4.60	0.280	-7.62	0.275	-9.23
	Nepal	0.222	0.246	+ 10.89	0.265	+ 19.58	0.254	+ 14.38	0.273	+ 23.30
	Indonesia	0.210	0.320	+ 52.65	0.334	+ 59.15	0.335	+ 59.36	0.353	+ 68.04
	Bhutan	0.043	0.053	+ 21.29	0.059	+ 37.09	0.056	+ 28.84	0.064	+ 48.00
	Singapore	0.014	0.015	+ 10.49	0.018	+ 28.38	0.016	+ 17.02	0.021	+ 50.94
	China	0.012	0.015	+ 28.87	0.018	+ 49.74	0.016	+ 36.49	0.021	+ 76.05

Table 3. The table represents the national-scale habitat suitability dynamics in South and Southeast Asia for *Leptoptilos dubius* and *Leptoptilos javanicus* in descending order for present and future climate change scenarios along with the percentage change in each future climate scenarios from the present. The loss of mean habitat suitability is denoted by '-', whereas the increase/gain is denoted by '+'.

Species	Scenarios	NP	PD	LPI	TE	ED	LSI	AI
L. dubius	Present	70	39103.8	0.6343	141.288	789.27	9.0753	91.1689
	SSP 245 (2041–2060)	24	13410.9	0.0253	28.56	159.59	7.234	72.1747
	SSP 245 (2061–2080)	13	7264.23	0.004	6.888	38.4893	4.3158	60.3774
	SSP 585 (2041–2060)	15	8381.81	0.006	9.324	52.1013	4.8261	63.1799
	SSP 585 (2061–2080)	8	1117.57	0.002	1.764	9.857	2.1	65.625
L. javanicus	Present	463	258,644	2.0141	885.99	4949.38	24.8658	89.596
	SSP 245 (2041–2060)	597	333,601	1.2931	931.61	5094.03	28.8015	86.4709
	SSP 245 (2061–2080)	611	341,424	1.1081	942.236	5153.41	29.4142	85.9924
	SSP 585 (2041–2060)	567	339,747	1.1178	927.654	5183.68	29.5819	85.8944
	SSP 585 (2061–2080)	608	316,837	1.0007	921.732	5150.59	30.3214	84.9453

Table 4. Assessment of Habitat quality and shape geometry of *Leptoptilos dubius* and *Leptoptilos javanicus* in present and future scenarios. NP: no. Of patches, PD: Patch Density, LPI: Largest Patch Index, ED: Edge Density, TE: total edge, LSI: Landscape shape index; AI: Aggregation Index.

listed in EDGE and IUCN Red list (Critically Endangered *Gyps bengalensis* = 4,000 to 6,000 and *Sarcogyps calvus* = 2,500 to 9,999; Endangered *Aquila nipalensis* = 50,000 to 75,000, *Platalea minor* = 2250, *Ciconia boyciana* = 1,000 to 2,499, and *Haliaeetus leucoryphus* = 1,000 to 2,499; Vulnerable *Aquila rapax* = 1,00,000 to 4,99,999, *Buceros bicornis* = 13,000 to 27,000, *Aceros nipalensis* = 7,000 to 10,000, *Aquila heliaca* = 2,500 to 9,999, and *Grus antigone* = 13,000 to 15,000). Moreover, the IUCN assessment did not account for climatic changes or habitat fragmentation in the present or future scenarios, although they emphasized the importance of conservation dependence for the survival of these adjutants. Due to extreme threat faced by the *L. dubius*, intensified conservation measures were undertaken to revive the population in wild. These efforts have prioritized integrated community development, education, and outreach, particularly aiming to instill pride

Scenarios	Niche overlap	% Change from present
Present	0.370	0.000
SSP 245 (2041–2060)	0.167	-54.767
SSP 245 (2061–2080)	0.132	-64.3919
SSP 585 (2041–2060)	0.157	-57.5582
SSP 585 (2061–2080)	0.072	-80.6287

Table 5. The assessment of niche overlap of both species (*Leptoptilos dubius* and *Leptoptilos javanicus*) in present and future scenarios in the South and Southeast Asian Landscape. The decline of niche overlap is denoted by '-'.

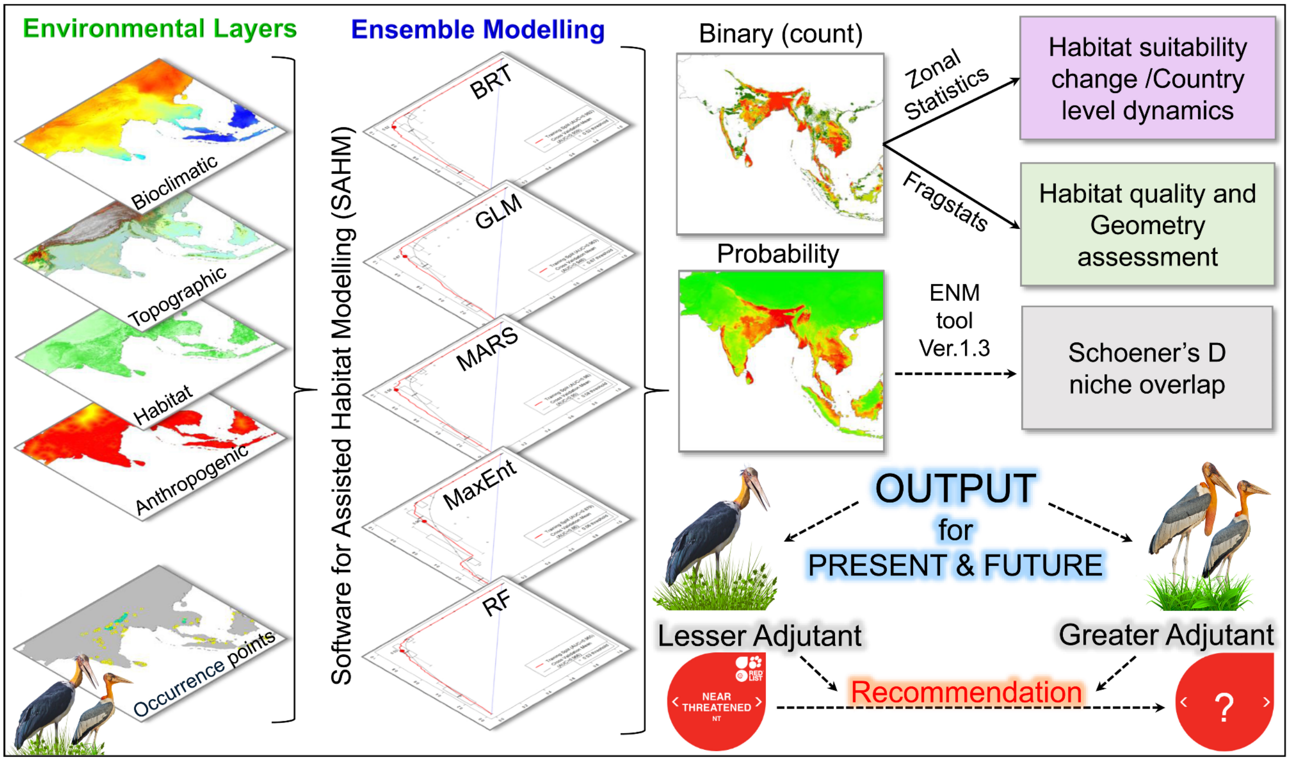

Fig. 9. The figure presents a schematic flowchart outlining the overall study and recommendations for the conservation of two adjutant stork species in South and Southeast Asia.

and ownership of storks among local villagers[12,14]. In Kamrup District of Assam, awareness campaigns have been conducted to address negative perceptions of *L. dubius*, which are often viewed as bad omen due to their scavenging behavior and nest-building habits. Multiple initiatives have also targeted influential village groups to encourage the preservation of nest trees for *L. dubius*[12,14]. Moreover, efforts have also engaged youth, women, and respected community members to foster a sense of ownership of nesting trees and support for *L. dubius* conservation. The establishment of the '*Hargila Army*', a rural women's group, aims to empower women in stork conservation through livelihood tools and biodiversity education. Furthermore, to mitigate the high mortality rate of young *L. dubius* chicks due to falling from trees, nylon nets have been strategically placed beneath their nests to prevent such accidents[12,14]. Additionally, a number of nesting locations within protected areas have been found for enhanced protection of *L. javanicus*[13]. Moreover, extensive engagement from local NGOs, governmental departments, and community members underscores the collaborative effort in conservation initiatives with the support from different international funds.

Given the commencement of conservation efforts for both adjutant species in Asia, the present study advocates for further conservation initiatives in light of the acknowledged impacts of climate change. The present study recommends the IUCN Stork, Ibis, and Spoonbill Specialist Group (SIS-SG) to reevaluate the IUCN Red List status of both species based on the insights gained from this research (Fig. 9). This assessment would facilitate the implementation of more targeted and effective long-term conservation measures. Moreover, the expansion of agricultural land near significant water bodies in adjutant habitats should be regulated, and existing croplands should undergo assessments to ensure the responsible use of pesticides. Additionally, it is advised to refrain from dumping waste near water bodies to prevent potential water pollution. Given their scavenging nature, waste disposal areas should be segregated for non-degradable and degradable waste, with strict policies for the immediate burial of animal carcasses suspected of poisoning. Furthermore, it is imperative to raise awareness among villagers, cattle owners, tea garden workers, farmers, and other relevant stakeholders about the hazards of using poisoning as retaliation against dogs, as it poses a significant risk to adjutants when they scavenge on such carcasses. Moreover, during the breeding season, adjutants typically nest in tall trees, emphasizing the necessity of safeguarding such trees, particularly those adjacent to Protected Areas and National Highways. In particular, the ongoing conservation efforts for *L. dubius* in Kamrup district should be extended to other high-abundance regions such as Sivsagar, Jorhat, and Tinsukia in Northeast India, while considering the socio-political issues. In conclusion, this study offers critical insights that can enhance conservation strategies for adjutants and other Ciconiiformes, particularly in South and Southeast Asia. While there are inherent limitations in predicting future land-use changes alongside projected climate change impacts, these challenges can be mitigated by integrating projections from both climate-habitat and climate-only models. This integrative approach provides a more comprehensive framework for conservation planning, enabling more precise species distribution modeling tailored to specific target species.

Data availability

Data used for the analysis were sourced from open-access resources. The records of field survey occurrences used for the model can be made available upon request to the corresponding author (S.K.).

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References

1. Slikas, B. Phylogeny of the avian family ciconiidae (Storks) based on cytochrome b sequences and DNA–DNA hybridization distances. *Mol. Phylogenetics Evol.* **8**, 275–300 (1997).
2. Winkler, D.W., Billerman, S.M. & Lovette, I.J. Storks (Ciconiidae), version 1.0. Birds of the World. (2020).
3. Ericson, P. G. P. et al. Diversification of Neoaves: Integration of molecular sequence data and fossils. *Biol. Lett.* **2**, 543–547 (2006).
4. Gibb, G. C., Kennedy, M. & Penny, D. Beyond phylogeny: Pelecaniform and ciconiiform birds, and long-term niche stability. *Mol. Phylogenetics Evol.* **68**, 229–238 (2013).
5. Hackett, S. J. et al. A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768 (2008).
6. Van Tuinen, M., Butvill, D. B., Kirsch, J. A. W. & Hedges, S. B. Convergence and divergence in the evolution of aquatic birds. *Proc. Roy. Soc. London, Ser. B Biol. Sci.* **268**, 1345 (2001).
7. Gula, J., Sundar, K. S. G., Willows-Munro, S. & Downs, C. T. The state of stork research globally: A systematic review. *Biol. Conserv.* **280**, 109969 (2023).
8. Luthin, C. S. Status of and conservation priorities for the world's stork species. *Col. Waterbird.* **10**, 181 (1987).
9. Rahmani, A. R., Narayan, G. & Rosalind, L. Status of the greater adjutant (*Leptoptilos dubius*) in the Indian subcontinent. *Col. Waterbirds.* **13**, 139–142 (1990).
10. Singha, H., Rahmani, A. R., Coulter, M. C. & Javed, S. Nesting ecology of the greater adjutant stork in Assam, India. *Waterbirds* **25**, 214–220 (2002).
11. BirdLife International. 2016. *Leptoptilos crumenifer*. The IUCN Red List of Threatened Species 2016: e.T22697716A93633034. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22697716A93633034.en. Accessed on 15 April 2024.
12. BirdLife International. 2023. *Leptoptilos dubius*. The IUCN Red List of Threatened Species 2023: e.T22697721A229597779. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T22697721A229597779.en. Accessed on 15 April 2024.
13. BirdLife International. 2023. *Leptoptilos javanicus*. The IUCN Red List of Threatened Species 2023: e.T22697713A232128569. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T22697713A232128569.en. Accessed on 15 April 2024.
14. Barman, P. D. et al. Saving the greater adjutant stork by changing perceptions and linking to Assamese traditions in India. *Ethnobiol. Lett.* **11**, 20–29 (2020).
15. Jetz, W. et al. Global distribution and conservation of evolutionary distinctness in birds. *Curr. Biol.* **24**, 919–930 (2014).
16. Singha, H., Rahmani, A. R., Coulter, M. C. & Javed, S. Surveys for greater adjutant *Leptoptilos dubius* in the Brahmaputra valley, Assam, India during 1994–1996. *Forktail* **19**, 146–148 (2003).
17. Elliott, A. & Kirwan, G.M. Greater Adjutant (*Leptoptilos dubius*), version 1.0. Birds of the World. (2020).
18. BirdLife International. Threatened Birds of Asia: The Birdlife International Red Data Book. *BirdLife International*, Cambridge, United Kingdom, (2001).
19. Perennou, C., Mundkur, T., Scott, D.A., Follestad, A. & Kvenild, L. The Asian Waterfowl Census 1987–91: Distribution and Status of Asian Waterfowl. Kuala Lumpur: Asian Wetland Bureau Publication No. 86. International Waterfowl and Wetlands Research Bureau Publication No. 24. Kuala Lumpur, Malaysia and Slimbridge, United Kingdom. (1994).
20. Choudhary, D. N., Mandal, J. & Rohitashwa, R. Distribution, and potential breeding records, of Lesser- *Leptoptilos javanicus* and Greater- *L. dubius* Adjutant-Stork in Bihar, India. *Indian Birds* **7**, 38–40 (2011).
21. Campbell, I. C., Poole, C., Giesen, W. & Valbo-Jorgensen, J. Species diversity and ecology of Tonle Sap Great Lake. *Cambodia. Aquat. Sci.* **68**, 355–373 (2006).
22. Hancock, J. A., Kushlan, J. A. & Kahl, M. P. *Storks, ibises and spoonbills of the world* (Academic Press, 1992).
23. Choudhury, A. *The birds of Assam* (Gibbon Books and WWF-India, 2000).
24. Zöckler, C., Zaw Naing, T., Moses, S., Nou Soe, R. & Htin Hla, T. The importance of the Myanmar coast for water birds. *Stilt* **66**, 37–51 (2014).
25. Cheng, L., Zhou, L., Yu, C., Wei, Z. & Li, C. Nest habitat distribution and spatio-temporal dynamics based on multi-scale modeling: Implications for the endangered Oriental Storks (*Ciconia boyciana*) conservation in China. *Glob. Ecol. Conserv.* **43**, e02439 (2023).
26. Hao, T., Elith, J., Lahoz-Monfort, J. J. & Guillera-Arroita, G. Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography* **43**, 549–558 (2020).
27. Zheng, H. et al. Efficacy of conservation strategies for endangered oriental white storks (*Ciconia boyciana*) under climate change in Northeast China. *Biol. Conserv.* **204**, 367–377 (2016).
28. Abedin, I. et al. Unraveling the unknown: Adaptive spatial planning to enhance climate resilience for the endangered Swamp Grass-babbler (*Laticilla cinerascens*) with habitat connectivity and complexity approach. *Heliyon* **10**, e30273 (2024).
29. Beerens, J. M., Noonburg, E. G. & Gawlik, D. E. Linking dynamic habitat selection with wading bird foraging distributions across resource gradients. *PLoS One* **10**, 0128182 (2015).
30. Kundu, S. et al. Matrilineal phylogeny and habitat suitability of the endangered spotted pond turtle (*Geoclemys hamiltonii*; Testudines: Geoemydidae): A two-dimensional approach to forecasting future conservation consequences. *PeerJ.* **11**, e15975 (2023).

31. Wei, Z. H. et al. Patterns of change in the population and spatial distribution of oriental white storks (*Ciconia boyciana*) wintering in Poyang Lake. *Zool. Res.* **37**, 338–346 (2016).
32. GBIF.org (Accessed on 15 April 2024) GBIF Occurrence Download https://doi.org/10.15468/dl.v76qg9.
33. GBIF.org (Accessed on 15 April 2024) GBIF Occurrence Download https://doi.org/10.15468/dl.mez97a.
34. Brown, J. L., Bennett, J. R. & French, C. M. SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ.* **5**, e4095 (2017).
35. Bladon, A. J. et al. Climatic change and extinction risk of two globally threatened Ethiopian endemic bird species. *PLoS One* **16**, e0249633 (2021).
36. Buchhorn, M. et al. Copernicus global land service: Land Cover 100m: Version 3 Globe 2015–2019: Algorithm theoretical basis document. (2020).
37. Abedin, I. et al. Distribution model reveals rapid decline in habitat extent for endangered hispid hare: Implications for wildlife management and conservation planning in future climate change scenarios. *Biology* **13**, 198 (2024).
38. Kundu, S. et al. Mitochondrial DNA and distribution modelling evidenced the lost genetic diversity and wild-residence of star tortoise, *Geochelone elegans* (Testudines: Testudinidae) in India. *Animals* **13**, 150 (2023).
39. Morisette, J. T. et al. VisTrails SAHM: Visualization and workflow management for species habitat modeling. *Ecography* **36**, 129–135 (2013).
40. Warren, D. L., Glor, R. E. & Turelli, M. ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* **33**, 607–611 (2010).
41. Mukherjee, T. et al. Adaptive spatial planning of protected area network for conserving the Himalayan brown bear. *Sci. Tot. Environ.* **754**, 142416 (2021).
42. Elith, J. & Leathwick, J. R. Species distribution models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697 (2009).
43. Guisan, A. et al. What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics?. *Ecol. Monogr.* **77**, 615–630 (2007).
44. Miller, J. Species distribution modeling. *Geogr. Comp.* **4**, 490–509 (2010).
45. Talbert, C.B. & Talbert, M.K. User Manual for SAHM package for VisTrails. (2012).
46. Hayes, M. A., Cryan, P. M. & Wunder, M. B. Seasonally-dynamic presence-only species distribution models for a cryptic migratory bat impacted by wind energy development. *PLoS One* **10**, e0132599 (2015).
47. Lavazza, L., Morasca, S. & Rotoloni, G. On the Reliability of the Area under the ROC curve in empirical software engineering. *ACM International Conference Proceeding Series*, 93–100 (2023).
48. Salas, E. A. L., Valdez, R., Michel, S. & Boykin, K. G. Habitat assessment of Marco Polo sheep (*Ovis ammon polii*) in Eastern Tajikistan: Modeling the effects of climate change. *Ecol. Evol.* **8**, 5124–5138 (2018).
49. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223–1232 (2006).
50. Cohen, J. Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit. *Psychol. Bull.* **70**, 213–220 (1968).
51. Jiménez-Valverde, A., Acevedo, P., Barbosa, A. M., Lobo, J. M. & Real, R. Discrimination capacity in species distribution models depends on the representativeness of the environmental domain. *Glob. Ecol. Biogeogr.* **22**, 508–516 (2013).
52. Phillips, S. J. & Elith, J. POC plots: Calibrating species distribution models with presence-only data. *Ecology* **91**, 2476–2484 (2010).
53. Illán, J. G., Gutiérrez, D. & Wilson, R. J. The contributions of top climate and land cover to species distributions and abundance: Fine-resolution tests for a mountain butterfly fauna. *Glob. Ecol. Biogeogr.* **19**, 159–173 (2010).
54. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259 (2006).
55. Pearson, R. G. Species' distribution modeling for conservation educators and practitioners. Synthesis. New York: *Am. Mus. Natl. Hist*, http://ncep.amnh.org (2007).
56. Grenouillet, G. L., Buisson, L., Casajus, N. & Lek, S. Ensemble modelling of species distribution: The effects of geographical and environmental ranges. *Ecography* **34**, 9–17 (2011).
57. Andrews, M. B. et al. Historical Simulations with HadGEM3-GC31 for CMIP6. *J. Adv. Model. Earth. Sy.* **12**, e2019MS001995 (2020).
58. Desmet, Q. & Ngo-Duc, T. A novel method for ranking CMIP6 global climate models over the southeast Asian region. *Int. J. Climatol.* **42**, 97–117 (2022).
59. Norgate, M., Tiwari, P. R., Das, S. & Kumar, D. On the heat waves over India and their future projections under different SSP scenarios from CMIP6 models. *Int. J. Climatol.* **44**, 973–995 (2024).
60. Atsawawaranunt, K., Whibley, A., Cain, K. E., Major, R. E. & Santure, A. W. Projecting the current and potential future distribution of New Zealand's invasive sturnids. *Biol. Invasions.* **26**, 1345–1366 (2024).
61. McGarigal, K. & Marks, B.J. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. **351**, 122 (1995).
62. Barwicka, S. et al. The use of selected landscape metrics to evaluate the transformation of the rural landscape as a result of the development of the mining function—A case study of the Puchaczów commune. *Sustainability* **13**, 12279 (2021).
63. Midha, N. & Mathur, P. K. Assessment of forest fragmentation in the conservation priority Dudhwa landscape, India using FRAGSTATS computed class level metrics. *J. Indian Soc. Remote Sens.* **38**, 487–500 (2010).
64. Hosseinian Yousefkhani, S. S., Rastegar-Pouyani, E. & Aliabadian, M. Ecological niche differentiation and taxonomic distinction between *Eremias strauchi strauchi* and *Eremias strauchi kopetdaghica* (Squamata: Lacertidae) on the Iranian Plateau based on ecological niche modeling. *Ital. J. Zool.* **83**, 408–416 (2016).
65. Schoener, T. W. & Gorman, G. C. Some Niche Differences in Three Lesser Antillean Lizards of the Genus *Anolis*. *Ecology.* **49**, 819–830 (1968).
66. Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected impacts of climate and land-use change on the global diversity of birds. *PLOS Biol.* **5**, e157 (2007).
67. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
68. Pimm, S. L. & Raven, P. Biodiversity. Extinction by numbers. *Nature* **403**, 843–845 (2000).
69. Root, T. L. et al. Fingerprints of global warming on wild animals and plants. *Nature.* **421**, 57–60 (2003).
70. Walther, G. R. et al. Ecological responses to recent climate change. *Nature.* **416**, 389–395 (2002).
71. Warren, M. S. et al. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature.* **414**, 65–69 (2001).
72. Arneth, A. et al. Post - 2020 biodiversity targets need to embrace climate change. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 30882–30891 (2020).
73. Watson, J. E. M. & Brodie, J. F. Human responses to climate change will likely determine the fate of biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2205512120 (2023).
74. Şekercioĝlu, Ç. H., Primack, R. B. & Wormworth, J. The effects of climate change on tropical birds. *Biol. Conserv.* **148**, 1–18 (2012).
75. Convention on Biological Diversity (CBD). (2024). https://www.cbd.int/. Accessed on 15 April 2024.

76. Harris, J. B. C. et al. The tropical frontier in avian climate impact research. *IBIS* **153**, 877–882 (2011).
77. Tuohetahong, Y. et al. Modeling the wintering habitat distribution of the black stork in Shaanxi, China: A hierarchical integration of climate and land use/land cover data. *Animals* **13**, 2726 (2023).
78. Choudhury, A. Counting large gatherings of globally threatened greater adjutant *Leptoptilos dubius*. *Indian Birds* **4**, 133–135 (2009).
79. Maleki, S. et al. Habitat mapping as a tool for water birds conservation planning in an arid zone wetland: The case study Hamun wetland. *Ecol. Eng.* **95**, 594–603 (2016).
80. Maleki, S., Baghdadi, N. & Rahdari, V. Which water bird groups need greater habitat conservation measures in a wetland ecosystem?. *Ecol. Eng.* **143**, 105677 (2020).
81. Chimwanza, B., Mumba, P. P., Moyo, B. H. Z. & Kadewa, W. The impact of farming on river banks on water quality of the rivers. *Int. J. Environ. Sci. Technol.* **2**, 353–358 (2006).
82. Mandal, J., Bhaduri, R. & Sharma, N. The struggle of existence for scavenging greater adjutants *Leptoptilos dubius*. *Imperiled: Encyclopedia Conserv.* **1**, 77–87 (2022).
83. Karki, S. & Thapa, T. B. Translating Knowledge into Actions Conservation Science Population status, nesting habitat selection and conservation threats of lesser adjutant stork (*Leptoptilos javanicus*) in the eastern lowlands of Nepal. *Conserv. Sci.* **1**, 27–35 (2013).
84. Katuwal, H. B. et al. Factors affecting the breeding ecology of the globally threatened Lesser Adjutant (*Leptoptilos javanicus*) in agricultural landscapes of Nepal. *Avian Conserv. Ecol.* **17**, 15 (2022).
85. Subaraj, R. & Lok, A. F. S. L. Status of the lesser adjutant stork (*Leptoptilos javanicus*). *Nat. Singapore* **2**, 107–113 (2009).
86. Sentian, J., Payus, C. M., Herman, F. & Kong, V. W. Y. Climate change scenarios over Southeast Asia. *APN Sci. Bull.* **12**, 102–122 (2022).
87. Drury, J. P., Cowen, M. C. & Grether, G. F. Competition and hybridization drive interspecific territoriality in birds. *Proc. Natl. Acad. Sci. USA* **117**, 12923–12930 (2020).
88. Thomas, B. T. Coexistence and behavior differences among the three western hemisphere storks. *Ornithol. Monogr.* **36**, 921–931 (1985).
89. Udvardy, M. D. F. The significance of interspecific competition in bird life. *Oikos* **3**, 98 (1951).

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Author contributions
I.A, T.M., and S.K. conceived the study and assisted with the study design; I.A., T.M., Y.G., and H.E.K., were responsible for the data collection and analysis; I.A., T.M., H.S., and S.K. wrote the original draft; H.S., H.W.K., and S.K. critically reviewed the manuscript and ensured the accuracy of the findings; H.E.K., and H.W.K. were responsible for the project administration and funding acquisition; All authors engaged in discussions regarding the findings and made valuable contributions to the final manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

Ethical approval
The adjutant storks studied in this research are classified as 'Near Threatened' on the IUCN Red List of Threatened Species. The study did not involve any direct sampling. Instead, occurrence points were gathered through observations, photographic records, and publicly available secondary sources. Hence, the study did not require any special permissions or approval from an ethical committee. However, the study design was developed with the approval (No. Zoo/Corr/2025/05 dated 3rd Feb 2025) of the host institution involved in the research.

Additional information
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