

Varied projected changes in near-future climatically suitable areas for bats in South Asia

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Abstract

Aim We assessed the projected changes in climatically suitable areas for South Asian bats from current conditions (1970-2000) to the near future (2041-2060) in response to climate change scenarios, identifying hotspots of climatic suitability, and measuring the direction and zero-cost distance between climatically suitable areas in the present and the near future. **Location** South Asia **Time period** Present day and near future (2050) **Major taxa studied** South Asian bats **Methods** We used ensemble ecological niche modelling for 110 selected South Asian bat species with four algorithms (random forests, artificial neural networks, multivariate adaptive regression splines, and maximum entropy) to define climatically suitable areas under current conditions (1970–2000). We then predicted future (2041–2060) climatically suitable areas under four projected scenarios (combining two global climate models and two shared socioeconomic pathways, SSP2: middle-of-the-road and SSP5: fossil-fuelled development). **Results** Predicted future changes in climatic suitable areas varied across species but the majority were predicted to retain most of the current area or have small losses. When shifts occurred due to projected climate change, new areas were generally at higher latitudes (northward shift). Climatically suitable hotspots (suitable for >30% of species) were generally predicted to become smaller and more fragmented. **Main conclusions** Overall, climate change in the near future may not lead to dramatic shifts in the distribution of bat species in South Asia, but local hotspots of biodiversity may be lost. Our results offer insight into climate change effects in less studied areas and can inform conservation planning, motivating reappraisals of conservation priorities and strategies for bats in South Asia.

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Overall, climate change in the near future may not lead to dramatic shifts in the distribution of bat species in South Asia, but local hotspots of biodiversity may be lost. Our results offer insight into climate change effects in less studied areas and can inform conservation planning, motivating reappraisals of conservation priorities and strategies for bats in South Asia.

Data availability statement

Data used in this study is available on Dryad: https://datadryad.org/stash/share/83WgULbUmh_tIoXiSpo_kC5gVz3OqEy16PlQFUv4H4M

Introduction

Climate change is a major threat to biodiversity (Hughes et al., 2003; Araújo & Rahbek, 2006), and its impacts are predicted to accelerate towards the end of the century (Urban, 2015). The known consequences of climate change include modification of species biology, ecology, distribution, and ultimately, increased extinction risk across the world (Parmesan & Yohe, 2003; Thomas et al., 2004; Walther et al., 2005; Schmittner & Galbraith, 2008; Wolkovich et al., 2014). Loss of species diversity and reduced distribution ranges are expected in response to climate change (Malcom et al., 2006; Midgley et al., 2006; Jetz et al., 2007), particularly among taxa with behaviour and lifecycles closely influenced by climatic conditions (Brook, 2009; Sherwin et al., 2012). Climate change currently affects and will continue to impact many areas of the world including South Asia, which is considered one of the most vulnerable regions to climate change impacts (World Bank Group, 2022). This region hosts a wide and diverse range of biotic and abiotic conditions with spatial variation in climate and vegetation that have resulted in high degrees of diversity, richness, and endemism (Srinivasulu & Srinivasulu, 2016) and four recognized global biodiversity hotspots: Himalaya, Indo-Burma, Western Ghats & Sri Lanka, and Sundaland (Olson & Dinerstein, 1998; Myers et al., 2000). This biodiversity is likely to be threatened by climate change, but few studies have investigated the potential impacts of future climate scenarios in this region.

South Asia hosts over 500 species of mammals, of which 151 species, in nine families, are bats (Srinivasulu, 2018; Srinivasulu et al., 2023). Unfortunately, in most regions in South Asia, bats are often perceived negatively (Frembgen, 2006), and are not considered to be of conservation value - only six species are specifically protected by the Indian Wildlife (Protection) Act, 1972. Bats can be important as indicator species (Jones et al., 2009), ecological service providers, and keystone species (Kalka et al., 2008; Williams-Guillen et al., 2008; Altringham, 2011; Hughes et al., 2012; Raman et al., 2023). Globally bats have been identified as particularly susceptible to climate change (Sherwin et al., 2013; Festa et al., 2022) due to their high risk of dehydration caused by their high surface-to-volume ratios (as a result of their relatively smaller bodies and

larger wing and tail membranes; Korine et al., 2016; Salinas-Ramos et al., 2023), and their slower reproductive strategies (Frick et al., 2019). In addition, bat behaviour and ecology are often driven by climate-based cues (Bates & Harrison, 1997), and due to lacking an effective evaporative cooling body mechanism, bats are especially sensitive to heat (Salinas-Ramo et al., 2023). Climate extremes like heat waves, increasing in frequency due to anthropogenic climate change (Sippel et al., 2015; Vogel et al., 2019), are known to cause mass-mortality events in bats across the world (O'Shea et al., 2016). Overall, bats are likely to be impacted by predicted climate changes in South Asia; however, how changes could affect the current hotspots of bat diversity and species distribution ranges in this region remains unclear, and yet must be understood to develop much-needed conservation strategies.

Ecological niche modelling (ENM) is a set of techniques widely used to model potential climatic suitability in a spatial context by extrapolating from the abiotic and/or biotic ecological niche conditions present within a species' current distribution (Pearson & Dawson, 2003; Araújo et al., 2006) and define climatic suitability envelopes that approximate the fundamental niche (Soberón & Arroyo-Peña, 2017). This climatic suitability is subsequently used to evaluate changes in climatically suitable locations into the future based on modelled climate scenarios, as an assessment of the effect of climate change on the study species (Guisan & Thuiller, 2005). However, due to uncertainty in data acquisition and generation, modelling methodology, assumptions of statistical analyses, reproducibility of analytical methods, and other limitations, ENM requires careful consideration and application (Feng et al., 2019). This has resulted in the development of various robust statistical applications, algorithms, and frameworks for ENM (Hijmans et al., 2005; Pearson et al., 2006; Araújo & New, 2007; Elith et al., 2011; Drake, 2014; Breiner et al., 2018), and a rise in the use of these modelling methods in ecology, conservation, and policymaking (Araújo et al., 2019).

In this study, we investigate the predicted impact of climate change on bat species in South Asia using geographic occurrence data and bioclimatic variables describing current climates and four near future (2041-2060) scenarios. We used ensemble ENM and carefully constructed sets of simulated pseudoabsences that incorporate uncertainty in the data and considered biological and environmental factors. The consensus output was then evaluated to characterise changes in the size and location of climatically suitable areas for all studied bats and to identify hotspots of diversity based on climate suitability. These results provide information of value for conservation planning, prioritisation, and policymaking.

Methods

Study area

South Asia covers an area of approximately 3.75 million sq km, and comprises the countries of Afghanistan, Bangladesh, Bhutan, India, the Maldives, Nepal, Pakistan, and Sri Lanka (Figure 1). The region consists of four broad climate zones (Oliver, 2005): dry subtropical in the far North, equatorial in the far South, alpine in the mountainous regions, and tropical (with regional variations) in most of the rest of the subcontinent. According to the Koppen-Geiger climate classification system (Peel et al., 2007), the region comprises 15 different climatic subtypes, dominated by subtropical climates (humid summer, dry winter) in the north and the Indo-Gangetic plain, and tropical savanna climates (wet and dry) in the central, eastern, and peninsular regions. Most of the west and north-west of South Asia consists of arid and desert climates. Due to the large topographical variation in this region, the variety of elevations, soil types, and biomes in South Asia is very complex (Ramankutty et al., 2018). To avoid biases based on political boundaries, the focal area for the analysis was defined by a rectangular extent around the borders of South Asia (Figure 1). Due to the Himalayas and trans-Himalayan regions forming a barrier to bat movement and presence (Ruedi et al., 2008; Thapa et al., 2021), the regions of China that fell under this extent were removed, thus creating a dispersal boundary on the northern border of Nepal, which coincides with the Himalayas. Additionally, due to distance and isolation from most of the study area, a small region of Indonesia (Sumatra) within the study extent was removed (Figure 1). Three of the world's major biodiversity hotspots (Myers et al., 2000): Himalayas, Indo-Burma, and the Western Ghats and Sri Lanka, are located within the focal area for analysis.

Species distribution data

There are 151 recognized bat species in South Asia (Srinivasulu et al., 2023) but we *a priori* excluded the four species endemic to the Andaman and Nicobar Islands given the geographic isolation of the islands from the rest of the South Asian landmass. Species were identified based on current taxonomic information at the time of analysis (Srinivasulu et al., 2021). We also limited our study to species for which we could gather five or more occurrence localities across South Asia, with a minimum distance between occurrences of 5 km. Presence-only occurrence data for these species were collected from published (including but not limited to Bates & Harrison, 1997; Srinivasulu & Srinivasulu, 2012; Srinivasulu et al., 2021; Raman et al., 2023), unpublished sources (records collected during field surveys conducted in India between 2002 and 2022, and records communicated by collaborators and citizen scientists in the region confirmed by photographic or other evidence), and GBIF records [accessed July 2022]. Records of specimens housed in museums including the Natural History Museum (London, UK), Harrison Institute (Sevenoaks, United Kingdom), Field Museum of Natural History (Chicago, USA), Zoological Survey of India (Kolkata, India), and Natural History Museum, Osmania University (Hyderabad, India), were also included.

To define current localities, we omitted occurrence records collected before 1980 and only included records collected between 1980 and 1999 if presence was confirmed during field surveys conducted by the authors from 2000. In order to account for spatial bias in sampling and spatial autocorrelation between occurrences, points were spatially rarefied to the resolution of the climate data (2.5 arc-minutes). Duplicate records within the same cell were omitted from the analysis using random removal of nearest neighbours implemented in the *spThin* package (Aiello-Lammens et al., 2015) in R 4.3.0 (R Core Team, 2022). After processing, occurrence data were available for 110 bat species representing all nine families recognized in South Asia, for which we obtained a total of 5998 occurrence points. Data availability varied among species, with occurrences ranging from five points for six species (*Coelops frithii*, *Kerivoula lenis*, *K. malpasi*, *Murina leucogaster*, *M. pluvialis*, and *Myotis annectans*) to 439 points for *Pteropus medius*.

Bioclimatic variables

Yearly and seasonal patterns in temperature and precipitation are known to influence behaviour and life history in bats around the world (Conenna et al., 2019; Gorman et al., 2021; Kohyt et al., 2021; Weinberg et al., 2022). To capture these conditions and test the hypothesis that macroclimatic effects can determine occurrence of bats, the 19 standard current bioclimatic variables were sourced at 2.5 arc-minute resolution from the WorldClim v2.1 database for the period of 1970 to 2000 (Fick & Hijmans, 2017). We focused on this resolution (~4x4 km) considering, in the absence of detailed species-level information, that such distances are within the average foraging range and mobility of these species. Our study covers large taxonomic, spatial, and temporal scales that aim to capture broad environmental effects that are best detected using moderately coarse resolutions (Wiens et al., 2009). Finer resolutions are more suitable to detect smaller-scale behavioural effects (Pulliam, 2000) including movement, territoriality, and inter-species interactions in mixed colonies.

Four future climate predictions were obtained combining two different models and two different scenarios to capture uncertainty. We considered the Canadian Earth System Model 5 (CanESM5; Swart et al., 2019) and Hadley Centre Global Environment Model 3 (HadGEM3; Good, 2019; Good, 2020) available in the Coupled Model Intercomparison Project 6 (CMIP6) from which we obtained 2.5 arc-minute climate predictions for a near-future time (2050, averaged from 2041-2060). From each model, data were obtained for the shared socioeconomic pathways 2 and 5 (SSP2, equivalent to Representative Concentration Pathway RCP4.5; and SSP5, equivalent to Representative Concentration Pathway RCP8.5). These pathways, used by the International Panel on Climate Change, characterise an optimistic ‘middle of the road’ socioeconomic scenario representing an ideology towards sustainable development, and a pessimistic ‘fossil-fuelled development’ scenario of climate change based on development almost entirely based on fossil fuels in the future, and little development towards sustainability and an emphasis on resource- and energy-intensive lifestyles (Kriegler et al., 2017). The two CanESM5 models are hereafter referred to as Can2-45 for SSP2-RCP4.5 and Can5-85 for SSP5-RCP8.5, and the two HadGEM3 models as Had2-45 for SSP2-RCP4.5 and Had5-85 for SSP5-RCP8.5.

To allow for accuracy in model transfer and clarity in interpretation, bioclimatic variables in ENM models are usually selected *a priori* to avoid multicollinearity and variance inflation. The bioclimatic variables were first

filtered using an assessment of ecological relevance based on field knowledge and literature (Stones & Wiebers, 1965; Grindal et al., 1992; Bates & Harrison, 1997; Appel et al., 2019; Corro et al., 2021). Then the variables were further filtered based on collinearity - noting that available ENM algorithms are not greatly impacted or can account for correlation and interaction between variables (Muñoz & Felicísimo, 2004; Dormann et al., 2012; Junior & Nobrega, 2018; Feng et al., 2019), and in some cases, correlated variables may be used if they are considered ecologically relevant. An analysis of multicollinearity was conducted using a combined variance inflation factor (VIF) and pairwise correlation test in the *usdm* package (Naimi et al., 2014) in R. Variables with an absolute pairwise Pearson's $r < 0.85$ were selected for the analysis. When a variable pair had high correlation ($r \geq 0.85$), we removed the variable deemed to have least ecological relevance, but if both variables were considered ecologically relevant, the variable with the highest VIF was excluded instead. Additionally, collinearity shifts between current and future predictions were measured using paired t-tests of VIF scores for each variable, as these tend to impact model transferability (Feng et al., 2019). All climate data were cropped and masked to the extent of the study area defined above. A final set of 10 climate variables was selected for the analysis, which were considered ecologically relevant for South Asian bats, and showed no significant collinearity shifts between current and future scenarios (Supplementary Material 1). The same variables were used for all species for consistent interpretations.

Pseudoabsence generation

As the occurrence data available was presence-only, pseudoabsences were generated for use in the ensemble modelling. Broadly following recommendations from Barbet-Massin et al. (2012), 1000 pseudoabsences were specified as the minimum amount to be generated for each species. To balance sample sizes of presences and pseudoabsences for species with few occurrence localities, we generated multiple replicates of pseudoabsences where each replicate had equal number of presences and pseudoabsences. The number of replicates per species was calculated by dividing 1000 by the number of presences rounded up to the nearest integer. This ensured a minimum of 1000 pseudoabsence points for all species and integrated uncertainty in model results via replication for species with fewer presence localities. Pseudoabsences were generated randomly requiring a minimum distance of 2.5 km and a maximum distance of 1000 km away from occurrence localities. Because data availability varied among species, analyses included from 3 to 200 replicates (Supplementary Material 2).

Ensemble ecological niche modelling

Presence-pseudoabsence ensemble ecological niche models were generated for each species based on the current climatic data using the BIOMOD framework (Thuiller et al., 2009), implemented in the *biomod2* package (Thuiller et al., 2021) in R. The ensemble included four algorithms known to be robust and perform well across a range of distribution scales (Meller et al., 2014): multivariate adaptive regression splines (MARS), artificial neural networks (ANN), random forests (RF), and maximum entropy (MAXENT, implemented using *maxnet*; Phillips et al., 2017). This diversity in computational models provides low inter-correlation in model components, which is ideal for higher predictive performance in ensemble ENMs (Elith, 2019; Valavi et al., 2022). The models were calibrated according to the default parameters and parameterization processes in *biomod2*.

To validate model results we used five-fold cross-validation, dividing the occurrence data into five subsets, and testing each subset against a model calibrated on the remaining four subsets. Hold-out validation, where a small subset of the data is used only for evaluation, while the remaining data are used for calibration-validation, was unsuitable due to the small sample size of occurrences in several species. Model performance was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) and the true skill statistic (TSS). Variable contributions were calculated by performing five permutations for each algorithm, each involving removal of the focal variable from the model to calculate the difference in performance. We report the average permutation importance.

The individual models with a final TSS value > 0.7 were then combined into ensemble consensus models for each species which we used with future climate data to predict the future climatically suitable areas.

Predicted suitability was reclassified into binary suitable-unsuitable predictions using the threshold at which TSS was maximised (values above this threshold represent climatic suitability). These binary maps were used to characterise changes in climatically suitable areas from current to future climatic scenarios using four metrics: the relative change in climatically suitable areas (% change), the percentage of the current area retained into the future, and the distance and azimuth (angle of direction) between centroids of current and future suitable areas. Change and retention were calculated respectively as:

$$\text{Change} = \frac{\text{Current suitable area} - \text{Future suitable area}}{\text{Current suitable area}} * 100$$

$$\text{Retention} = \frac{\text{Current suitable area} \cap \text{Future suitable area}}{\text{Current suitable area}} * 100$$

To estimate distance and azimuth we first defined distinct fragments within suitable areas. Fragments represent connected suitable cells from the binary maps, estimated by first applying morphological dilation using a buffer of radius 2.5 km, followed by a morphological erosion using a negative buffer of the same radius. As a result of this process, suitable areas within 2.5 km of each other were connected to reflect the assumption that bats can move easily within this distance. The resulting number of fragments varied among species depending on the configuration of the suitable area. For all fragments we then identified centroids and the shortest straight paths between each centroid in the current scenario and its nearest neighbour in the future scenario, assuming zero movement costs. The length and azimuth of that path was used to estimate distances and angles of direction. For each species we calculated a mean distance and mean azimuth. Azimuths were classified into cardinal and intercardinal directions based on angle, assuming North to be 0 and 360. All centroid-based calculations were performed using the *geosphere* package (Hijmans, 2022) in R.

Summary models of climatically suitable areas were generated for all species together by creating a map of species richness for each time period. All binary models for each time period were summed together into a model that ranged from 0 to 110, representing the number of species for which a cell is climatically suitable according to their binary models. This model was then rescaled to a 0 to 1 scale for consistent comparison and converted into a binary map using a threshold of 0.3, such that in the final binary models for current and future, the positive cells represented suitability hotspots - areas that were climatically suitable for [?] 30% (more than 33) of the study species. Certainty in projected models was calculated as a continuous model by first averaging individual replicates within a species to assess model agreement, and then averaging these species models into a final model ranging from 0 to 1, which can be interpreted as high certainty of climatic unsuitability through uncertainty to high certainty of climatic suitability.

Results

Impact of future climate change

The expected climatic conditions by the mid-21st century are likely to result in smaller climatically suitable areas for bats in South Asia (average reduction >8%), but with large portions of the current areas expected to remain suitable (average retention >59%. Figure 2). However, these average impacts hide considerable variation among species resulting partly from different climatic variables being important across species and models (Supplementary Material 1). In all scenarios there were potential winners and losers, with some species predicted to have no climatically suitable areas in the future while for others the area could double, and retention varied from nearly 0 to 99.8% (Figure 2). These ‘losing’ and ‘winning’ species were more common in some taxonomic groups, with species in the family *Miniopteridae* being consistently among the highest losers, and species in *Rhinopomatidae* and *Pteropodidae* predicted to be among the most affected in the CanESM5 model scenarios and the HadGEM3 model scenarios, respectively. On the other hand, *Molossidae* and *Emballonuridae* showed the highest gain in suitable areas under the CanESM5 model and the HadGEM3 scenarios, respectively. Nevertheless, in nearly all scenarios even winning families generally had species projected to lose suitable area (Supplementary Material 2). In the CanESM5 scenarios *Molossidae* showed the highest projected retention of suitable areas in the future for any family (73.5% in Can2-45 and

71.2% in Can5-85), while Hipposideridae was projected to retain the highest amount of suitable area in the HadGEM3 scenarios (80.7% in Had2-45 and 76.8% in Had5-85; Figure 2; Supplementary Material 2).

Overall patterns were largely consistent among the four future climate change scenarios explored, with smaller impacts predicted under ‘middle of the road’ SSP2-RCP4.5 socioeconomic scenarios than in the pessimistic ‘fossil-fuelled development’ SSP5-RCP8.5 scenarios (Figure 2). Many species show consistent losses, like *Kerivoula malpasi*, known from five localities, with predicted losses of 66% to 84% in climatically suitable area across scenarios; while others showed consistent gains, including *Myotis hasseltii* that was projected to increase the area of suitable climate by more than 60% and *Saccolaimus saccolaimus* which is projected to gain 106% of its current suitable area (Figure 2; Supplementary Material 2). For some individual species projected impacts were highly dependent on the scenario - for example, *Myotis csorbai*, known from seven localities, was projected to lose 100% of climatically suitable areas in the future in CanESM5 scenarios, but had losses around 47% in the HadGEM3 scenarios. *Pteropus medius*, with 439 occurrences, and *Cynopterus sphinx*, with 312 occurrences showed moderate projected retention of suitable areas (25.9 – 57.1% in *P. medius*, 30.8 – 44.8% in *C. sphinx*; Supplementary Material 2), with varied degrees of projected losses in all scenarios (18 – 61.7% in *P. medius*, 37.9 – 60.7% in *C. sphinx*; Supplementary Material 2).

Across all climate scenarios and species, and including all projected spatial changes, future climatically suitable areas were on average 216 km from current climatically suitable areas. However, distances also varied between scenarios and species. For example, *Murina pluvialis*’ climatic suitable area was projected to shift by an average of 4.5 km in the future, the smallest distance in the CanESM5 scenarios; however, in the HadGEM3 scenarios the average distance between current and future areas was 128 km (Supplementary Material 2). For some species, the disparity in projected suitable areas between socioeconomic scenarios led to extremely large differences in distance between current and future. For example, *Rhinolophus subbadius*, in the SSP2-RCP4.5 scenarios for both climate models, had a projected distance of 28 km from current to future; however, in SSP5-RCP8.5, the distance increased to 2202 km. Most future suitable areas were located northward from current suitable areas with a trend for more north-eastern shifts under SSP2-RCP4.5 socioeconomic scenarios and more north-western shifts under the more pessimistic SSP5-RCP8.5 scenarios (Figure 3; Supplementary Material 2).

Suitability hotspots

The most suitable areas under current climate conditions were projected to host up to 64 of the 110 study species, with 11.9% of the total study area (446,686 km²) projected to be suitable for at least 30% of the study species (i.e., 33 species; Figure 4). We detected four contiguous hotspots in all climate models: the lower Himalayas of north and northeast India, northeastern Pakistan, Nepal, northern Myanmar, and Bangladesh; the Andaman and Nicobar islands and southernmost coast of Myanmar; Sri Lanka, covering the entirety of the island; and south India, in the Western Ghats and along the coasts of central and southern Maharashtra, Karnataka, and Kerala, and fragmented regions of southern Karnataka and southern Tamil Nadu, extending to the southern Nilgiris and Coromandel coast of Tamil Nadu. Additional smaller hotspots appear in the Ballari-Vijayapura-Hubli region of Karnataka, India, an area characterised by unique geography and isolated geology and climate; the highlands west of the Indus valley in northern Pakistan and eastern Afghanistan; and regions including and immediately north of Gir National Park, southern Gujarat, India (Figure 4).

Most of these hotspots were projected to remain climatically suitable for many species by the mid-21st century in all scenarios, although their extent was generally reduced, particularly in the lower Himalayas and the Western Ghats hotspots, and projections suggested northward shifts in the Himalayan regions (Figure 4). In northern India and northern Pakistan, projected changes reduced contiguity in projected suitability hotspots (particularly under the CanESM5 scenarios). In the Western Ghats, declines particularly affected central Maharashtra and Tamil Nadu. Additionally, the small distinct hotspots in Ballari-Vijayapura-Hubli were projected to disappear, while hotspots west of the Indus valley and north of Gir were projected to expand (Figure 4). Although both climate change models predicted similar changes, under both HadGEM3 scenarios a marked northward increase in suitable area in southern Myanmar was projected. Analysis of model certainty showed a moderate degree of uncertainty around the projected suitability hotspots in all

scenarios, combined with some areas of high certainty of suitability in the Himalayas and northeastern India, and in southern India and central-southwestern Sri Lanka (Supplementary Material 3).

Model evaluation

We found variation in performance of the four algorithms used, with some models having TSS < 0.7 for several species. RF was utilised for all 110 species, while MARS, MAXENT, and ANN were limited to 93, 90, and 89 species respectively. For 17 species (*Cynopterus sphinx*, *Hipposideros fulvus*, *Lyroderma lyra*, *Pipistrellus ceylonicus*, *P. coromandra*, *P. tenuis*, *Pteropus medius*, *Rhinolophus lepidus*, *Rhinopoma hardwickii*, *R. microphyllum*, *Rousettus leschenaultii*, *Scotophilus heathii*, *S. kuhlii*, *Scotozous dormeri*, *Sphaerias blanfordi*, *Taphozous longimanus*, and *T. nudiventris*) RF was the only algorithm represented in the final ensemble. There was a significant negative correlation between the number of occurrence points and the number of models used in the final ensemble (Pearson's $r = -0.791$; $p < 0.001$). RF was the only model represented in the final ensemble for most species with more than 120 occurrences; *Taphozous nudiventris* and *Sphaerias blanfordi* were the two exceptions to this, with 97 and 17 occurrences respectively. RF models also had the highest mean AUC and TSS scores across all species (AUC: 0.998 ± 0.001 [0.991 - 1.000]; TSS: 0.980 ± 0.014 [0.940 - 1.000]), followed by MARS (AUC: 0.970 ± 0.016 [0.920 - 0.997]; TSS: 0.897 ± 0.055 [0.761 - 0.995]), MAXENT (AUC: 0.958 ± 0.019 [0.904 - 0.994]; TSS: 0.859 ± 0.052 [0.754 - 0.978]), and ANN (AUC: 0.955 ± 0.024 [0.887 - 1.000]; TSS: 0.869 ± 0.059 [0.750 - 0.999]).

Discussion

Our analyses of the effects of projected near-future climate change on bats in South Asia show a general pattern of moderate potential loss in all scenarios with relatively high degrees of retention in climatic suitable areas. As expected, smaller losses were projected under the 'middle-of-the-road' SSP2-RCP4.5 scenarios compared to the more pessimistic 'fossil-fuelled development' SSP5-RCP8.5 scenarios, reinforcing the need for changing behaviour and avoiding business as usual (Peters et al., 2013). While loss was moderate, our results also revealed variability among species and scenarios with winners and losers. For example, *Myotis csorbai*, a species restricted to Nepal, was projected to lose all its current suitable area in some scenarios, while *Saccolaimus saccolaimus*, a species with a very wide but fragmented distribution in South and Southeast Asia, was projected to double its current suitable area in some scenarios. Previous work has also reported varied responses of bats to climate change including negative impacts (Rebelo et al., 2010; Hughes et al., 2012; Bellard et al., 2013; Thapa et al., 2021), no or limited effects (Bandara et al. 2022), and positive effects (Costa et al., 2018; Hayes & Piaggio et al., 2018; Thapa et al., 2021). This variation likely reflects differences in niche plasticity, robustness to changing conditions, and migratory propensity among species. Additionally, variation can occur due to data limitations and modelling choices. Indeed, our results showed uncertainty in projections for some species: many species involved small (< 30 occurrences) sample sizes, and the minimum sample size of five occurrences has been used before but may not be fully reliable (Pearson et al., 2007). However, most advanced ENM algorithms, especially techniques such as MAXENT, can account for fewer occurrences in species with low prevalence and narrow ranges (Pearson et al., 2007; van Proosdij et al., 2016; Morales et al., 2017), and ensemble modelling can provide higher predictive accuracy by accounting for inter-model variation. Capturing and reporting this variation by considering various scenarios, scales, and algorithms is important to ensure conservation and management recommendations are not misguided due to over- or under-fitting and a lack of reliability in results.

Similar to other studies on bats (in Europe by Rebelo et al., 2010; in Southeast Asia by Hughes et al., 2012; in Nepal by Thapa et al., 2021), we also found a trend for likely shifts towards higher latitudes in climatically suitable areas. In SSP2-45 scenarios, suitable areas for most species were projected to be located north-northeast or northwest from current areas; in SSP5-85 scenarios the shift was more generally northeast. Overall, climate change is expected to lead to latitudinal shifts towards polar regions, but arguably, our projected shifts could also reflect the geographic configuration in our study area, where the Southern region is mostly coastal. However, this is unlikely the reason for the observed trend, as for species currently in northern and central areas we also did not generally find projected southward shifts. Future suitable areas were also usually not located far from current suitable areas, and it is likely bats could track changes in

climatic suitable in many cases. However, there are several barriers that could limit shifts, including the Himalayas in the north and northeast, the Thar Desert and the Great Rann of Kutch in central India, and the hill ranges of south and central India. Similarly, moving across large tracts of water may prevent tracking of climatically suitable areas in some species. Importantly, even if there are no strong geographical barriers, movement may be prevented due to lack of other abiotic and biotic resources or variation in dispersal behaviour.

Combining information from individual species we identified current and future suitability hotspots - areas of climatic suitability for >30% of study species. The current hotspots aligned with the four biodiversity hotspots in the region defined by Myers et al. (2000), but representation varied. While a large proportion of the current suitability hotspots were projected to be retained into the future, projected losses outweighed areas of projected gain. In the Himalaya and Indo-Burma hotspots, projected losses would lead to high fragmentation and isolation between hotspots (especially under the SSP2-RCP4.5 scenarios). Movement corridors and continuous protected area networks are likely to be critical to allow movement and occupation of new suitable areas. Interestingly, new suitable areas were consistently identified nearby rivers, around the northern regions of the Indus valley, northwestern Pakistan, and southern Gujarat. The small areas of suitability in southern Myanmar were projected to increase only in the HadGEM3 scenarios, and in Had5-85 there were a few additional isolated fragments of projected gain in suitability in Bangladesh and northeast India, regions with typically moist deciduous and wet evergreen habitats (Champion & Seth, 1968; Olson et al., 2001), quite similarly to southern Myanmar. The Western Ghats suitability hotspot was mostly retained and contiguous across all scenarios, and increases were restricted to small areas on the margins, showing that the Western Ghats are likely to remain stable as a suitability hotspot into the near future. Decreases were consistently seen in the Nilgiri hills and in northern Maharashtra - both regions with unique vegetation and habitat structures, ranging from semi-arid scrublands in the north of the Western Ghats to tropical moist deciduous forests in the Nilgiris. Many regions in peninsular India which are known to be specific in geography and habitat consistently showed patterns of projected loss in suitable areas. Combined with a growing understanding of the effects of climate change in the Himalayas and Western Ghats, and how it impacts biodiversity (Srinivasulu et al., 2021; Thapa et al., 2022), our results showing high degrees of retention combined with severe losses and minimal gains further support the importance of these regions.

We evaluated projected impacts of climate change using ensemble ecological niche modelling, an approach with good predictive accuracy that captures uncertainty from algorithm choice (Hao et al., 2020). However, this method has some limitations. First, ensemble ENM requires considering the balance between selecting many algorithms and the increased computational time and resources. Generally, the suggestion is that if a smaller number of algorithms is used, the ones with higher predictive accuracy and robustness are selected, as done here (Drake, 2014). A second limitation is the challenge to generate suitable pseudoabsences for presence-only occurrence data (Engler et al., 2004; Lütolf et al., 2006; Barbet-Massin et al., 2012). Our method for generating pseudoabsences incorporates random sampling within geographic limits based on spatial resolution and scale of the analysis and estimated foraging distances of study species. We aimed to balance statistical rigour and ecological realism while working with the constraints of lacking accurate species-level data on bat ranging and movement in South Asia. Further analyses for species with available data could incorporate information on ecological distance and environmental profiling as additional limiting factors to pseudoabsence generation (Iturbide et al., 2015). Model certainty is also an issue with ENM that greatly impacts the reliability and interpretability of these results. For instance, our analysis showed high certainty of climatic unsuitability in most of the study area (Supplementary Material 3). However, it is important to note that per-species results are much more informative and broad interpretations must be very cautious. Finally, another limitation of ENM is the need to carefully select variables to balance ecological importance, methodological constraints including the effects that multicollinearity and collinearity shift have on different algorithms, and model transferability (Feng et al., 2019). Here, we also considered this balance selecting robust methods, reducing variables to avoid high collinearity while prioritising ecologically relevant information.

Understanding species responses to rapid climate change is vital in conservation planning, especially in

regions with high biodiversity and rates of endemism (Warren et al., 2008; Quintero & Wiens, 2013; Raman et al., 2023). This study is an initial assessment of potential effects of near-future climate change on bat species in South Asia, offering reasons for concern but also some hope. While climatically suitable areas may be reduced, many currently suitable areas are likely to remain, and shifts may be within the dispersal potential of many species. Nonetheless, retention of suitable areas and moderate loss does not necessarily ensure population persistence. Our initial assessment of impacts focuses on abiotic climate effects, but climate change may influence habitat and food resources differently and may result in climatically suitable areas being effectively unable to support healthy bat populations. Analysing climate effects alone ignores the potential combined effects of climatic and ecogeographic impacts on species distributions (Newbold, 2018), but it is a first step to understand potential changes in areas where climate and ecogeographic data may not be of the same quality, interpretability, or accessibility, possibly biasing ecological interpretations. Future climatically suitable areas may also be unsuitable due to geology and topography, factors linked to human activities including human land use, human population densities, and proximity to various infrastructures and developed areas. However, while it is possible to model both types of factors together (e.g. Hughes et al., 2012; Simões & Peterson, 2018; Raman et al., 2023), the lack of accurate data on their interactions when it comes to bats in this region could lead to overfitting, erroneous predictions, and misinterpretations across highly diverse species and functional groups (Araújo et al., 2007; Peterson et al., 2011; Fordham et al., 2012; Newbold, 2018; Simões & Peterson, 2018). It is important to analyse the effects of climate (and future climate change) and ecogeography independently as well as together, and also study their interactions, in order to truly understand the drivers of suitability for each species. Future work that considers these additional factors and the current intactness of future suitable areas would be important to inform conservation actions for climate change mitigation. In addition, it is important to consider that climatic niche modelling based on data from current occupied areas may not reflect the full climatic limits or niche of a species or its capacity to adapt (Hoffmann & Sgrò, 2011). Our results offer a first evaluation that highlights the need to further study climate change impacts in megadiverse regions such as South Asia and to develop robust conservation plans that integrate this information. Effective conservation requires the integrated study of species responses to climate, biotic, geographic, and anthropogenic factors, and effective communication with and outreach to policymakers and stakeholders at all levels.

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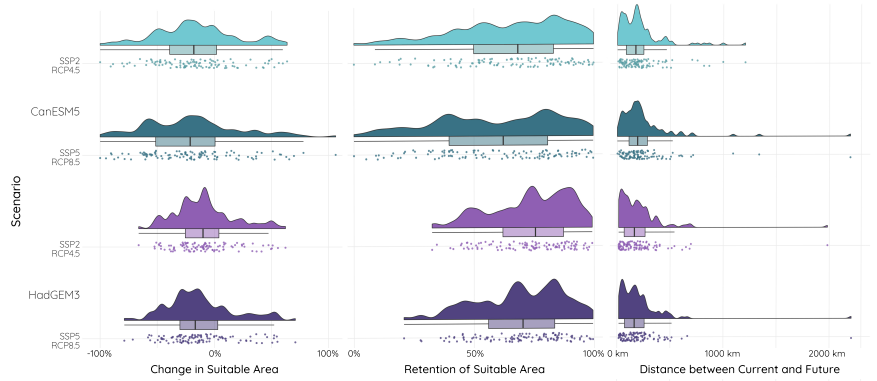
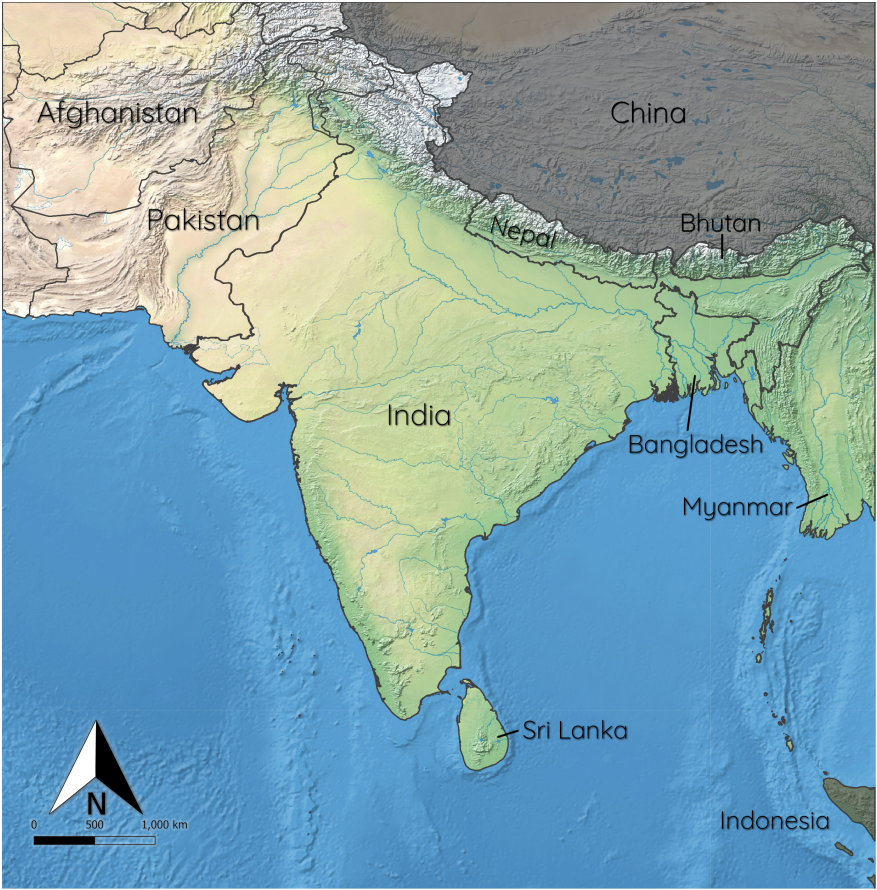
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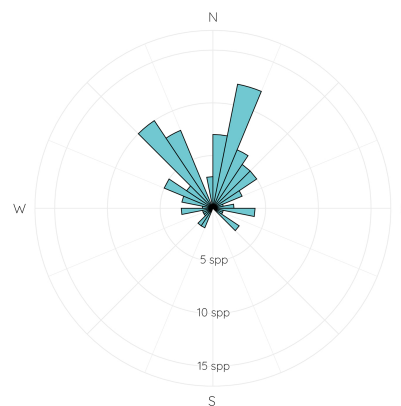
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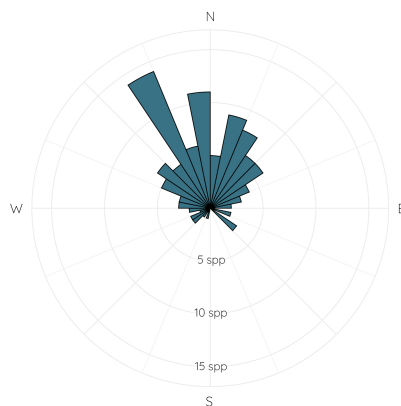
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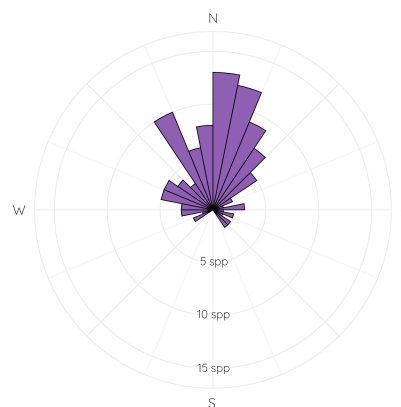




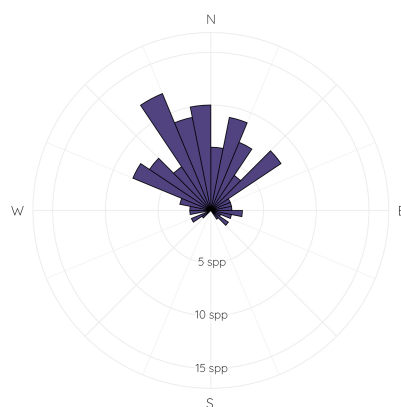
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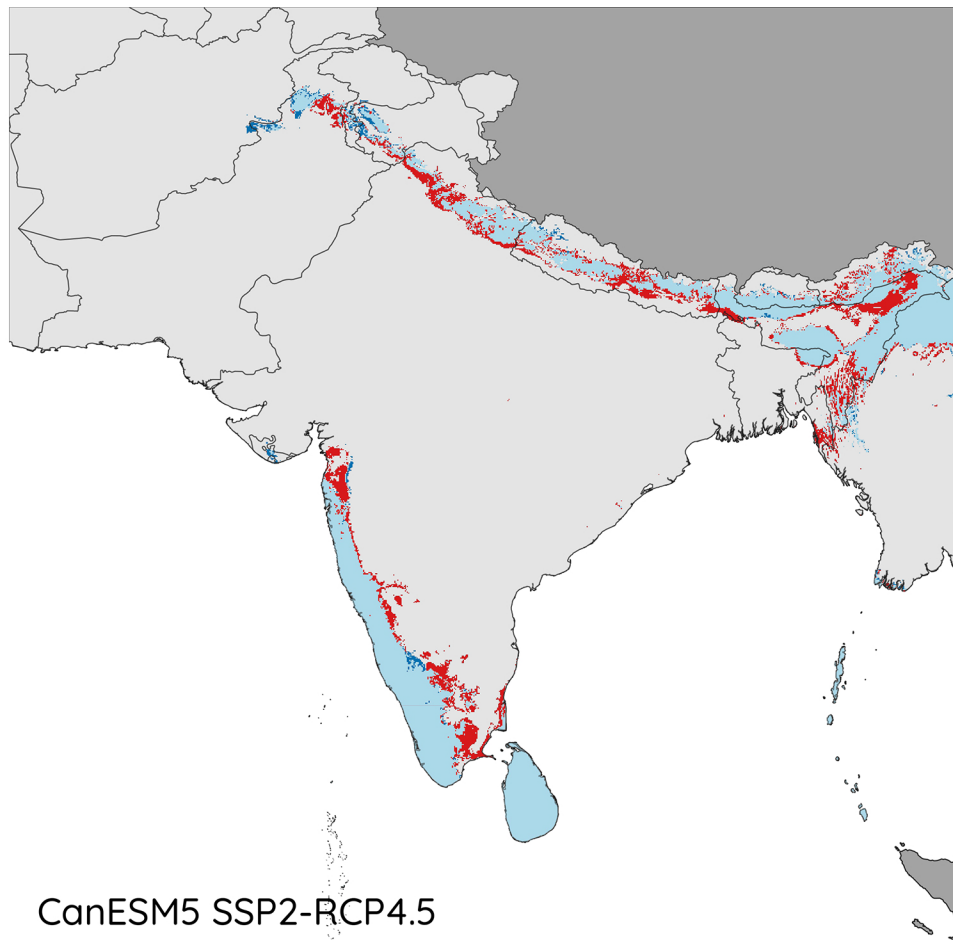
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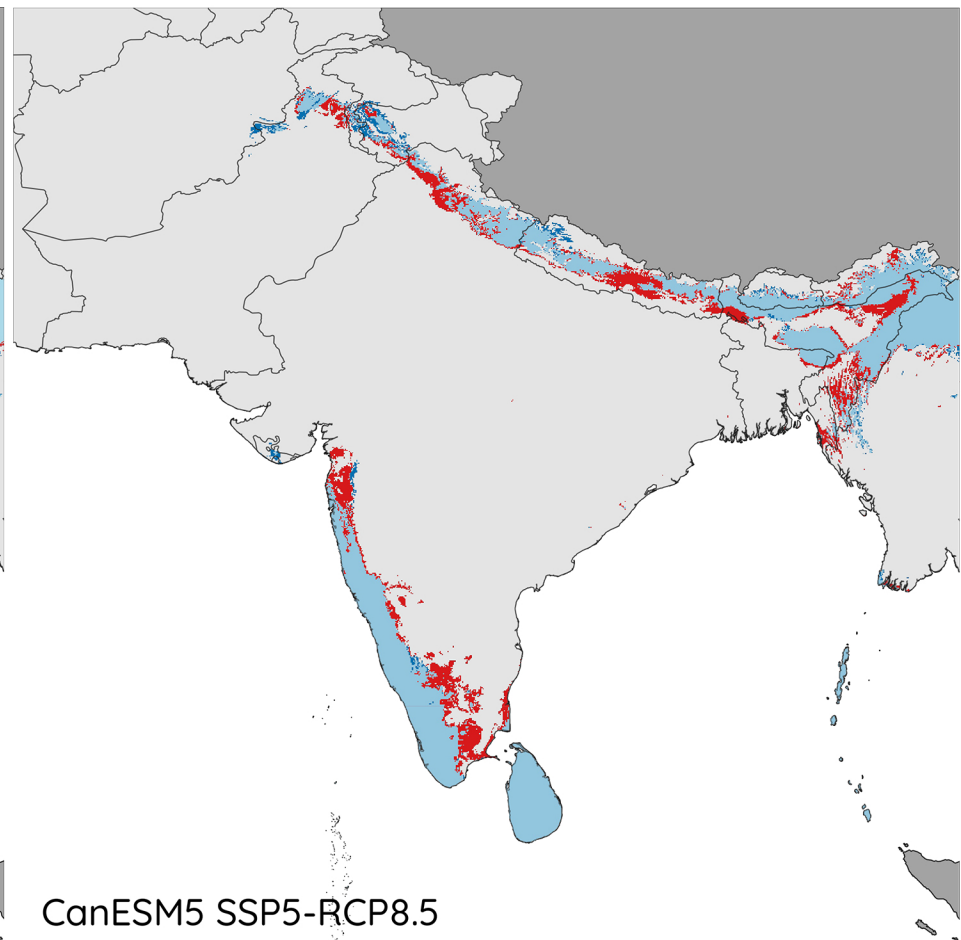
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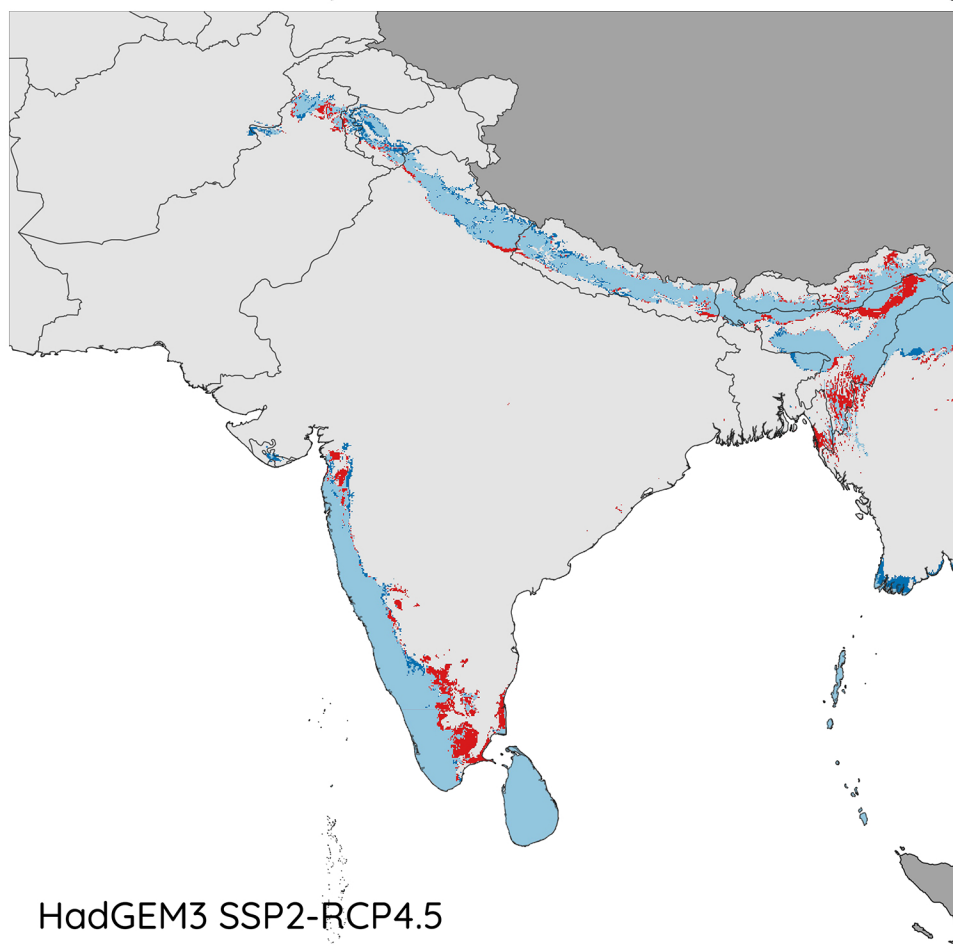
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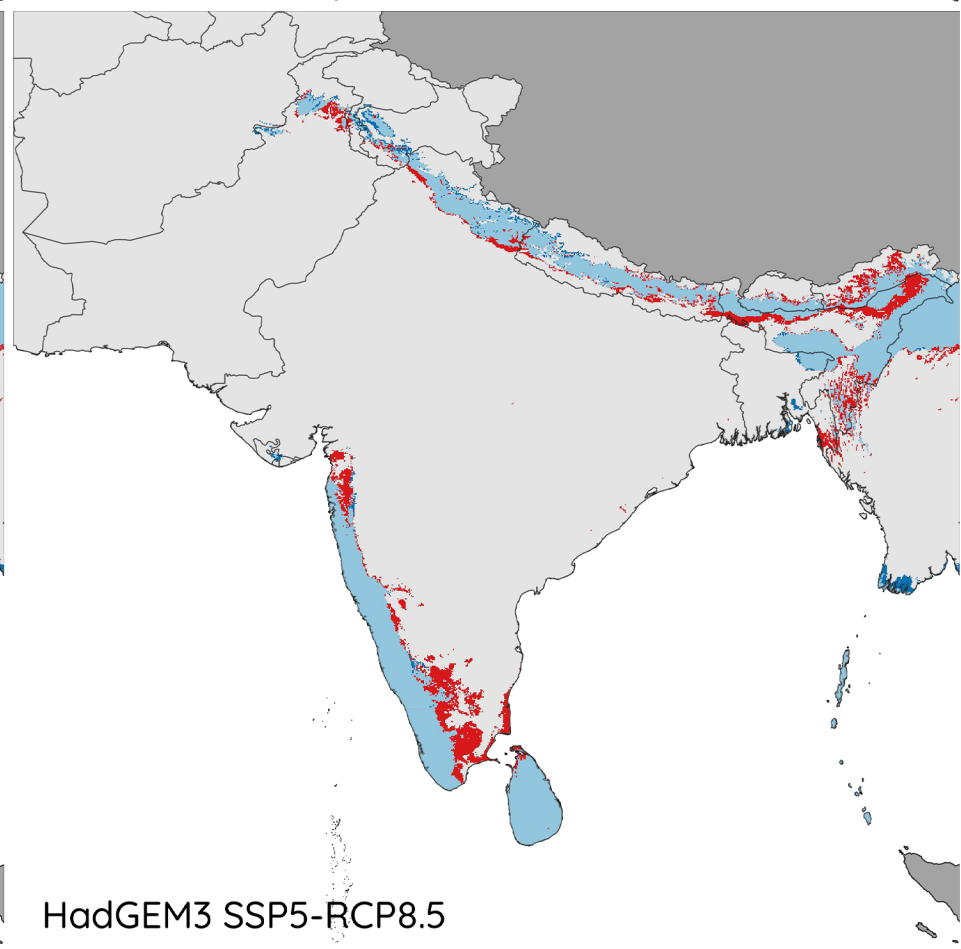
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