



## Last chance to see? Iran and India as strongholds for the Mugger Crocodile (*Crocodylus palustris*)

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**Abstract.** Justified predictions of future changes in species distributions are necessary for defining adequate conservation plans over space and time. The Marsh or Mugger Crocodile (*Crocodylus palustris*) is native to freshwater habitats of the Indian subcontinent and in southeastern Iran. Habitat loss is currently the most important threat to crocodile dispersal and persistence, and climate change will likely exert increasing pressure on populations. This study used ecological niche modelling (maximum entropy) to predict the current distribution of this species and project it to future climatic conditions. For this purpose, 380 occurrence records were used for model computation and environmental data were obtained from Worldclim 2.0. Averages of eight global circulation model outputs, assuming four IPCC6 per story lines in 2081–2100, were used as future ensembles. Furthermore, future possible anthropogenic pressure was quantified using economic growth models. Temperature Annual Range was the climatic variable with the highest contribution to the modelling. Presently, most potential suitable habitats are located in Sri Lanka, in the southeastern peninsular of India, the tropical moist forest along the west coast of India, the border region between Nepal and India, and the south coasts of Iran and Pakistan. In the future, these suitable habitats are predicted to be further fragmented and to shift farther inland. Additional threats may arise from increased human/crocodile conflicts due to human population growth. Conservation should therefore focus on those areas that remain climatically comparatively stable with a low potential of human/crocodile conflicts. Key areas are located in the northern parts of India and at the westernmost range limits of this species in Iran.

**Key words.** Crocodylidae, biodiversity, global warming, habitat suitability, spatial conservation planning, species distribution modelling.

### Introduction

Justified concerns about the vulnerability of wildlife to the effects of climate change are increasing globally, and the potential response of species to such changes have been discussed widely (SEGAN et al. 2016, NEWBOLD et al. 2020). Likely impacts of climate change have been predicted for different species and their related ecosystems and well documented in different studies conducted on a variety of species

(NEWBOLD et al. 2020). Species may face direct and indirect impacts from climate change, which pushes them further to the brink of extinction (SEGAN et al. 2016). As such, predicting climate change effects on species has important impacts on conservation plans, as the magnitude of the threats that species and their habitat can be facing becomes clearer and alerts decision- and policy-makers (CARVALHO et al. 2010, BUTT et al. 2016). It follows that predicting the response of species to climate change is critical, as species may respond

in different ways, including changes in their behaviour, reproduction, lifecycle and migration (BELLARD et al. 2012). Dispersal may occur and species may actually expand their presently occupied habitats, or, on the contrary, experience significant range contractions. Ecological models can predict the responses of extant species distributions to rising temperatures (SUMMERS et al. 2012). In this context, species distribution models (SDMs) have the potential to predict current species distributions and their responses to climate change (EL-GABBAS & DORMANN 2018). SDMs have been widely used for different aims, including conservation and ecological research, and, since recently, predicting the effects of climate change on the future distribution patterns of species (ELITH et al. 2006, KAFASH et al. 2015).

Freshwater ecosystems provide essential services and functions, even though they cover less than one percent of the planet. Due to a variety of threats, including climate change effects, they are classified as one of the most threatened ecosystems worldwide. Furthermore, the freshwater species living in these ecosystems, which account for almost 10% of globally described species, are inevitably faced with severe climate change effects (BENATEAU et al. 2019).

As “Key Stone Species”, crocodilians are an important biodiversity component in their habitats, playing various ecological, commercial, cultural and livelihood roles. Most of the crocodilian species are globally threatened due to habitat destruction, overharvesting and climate change effects (GRIGG 2015). Due to their Temperature Dependent Sex Determination (TSD) reproduction strategy, crocodiles are highly vulnerable to increasing temperatures from global warming (MANNION et al. 2015). The Marsh or Mugger Crocodile (*Crocodylus palustris*) is native to freshwater habitats of the Indian subcontinent, with its westernmost population occurring in southeastern Iran (DA SILVA & LENIN 2010). As a globally threatened species, the Mugger Crocodile is categorized as Vulnerable in the IUCN Red List and mostly threatened by habitat loss. The total adult population of Mugger Crocodiles exceeds 2500 individuals across its entire range (DA SILVA & LENIN 2010). These populations are threatened by severe periodic droughts and floodings, which may be interpreted as consequences of climate change. Habitat destruction and modification exert pressures on crocodiles (MOBARAKI et al. 2015). Hunting, water pollution, sedimentation, food shortage, egg collection, seasonal fluctuation of water levels, and death from accidental capture in fishing nets are other threats for crocodiles (BHATT et al. 2012, CHANG et al. 2013, FELLOWS 2019). Predictions of climate change for southwestern Asia identifies this region as one of the world’s most vulnerable places to warming (PAL & ELTAHIR 2016). A study using Habitat Evaluation Procedure (HEP) to identify the best and most suitable habitats for crocodiles along the Sarbaz River, Iran, indicated that they prefer habitats with 2–4 m water depth, a mean vegetation cover of 35%, a mean slope of 25–35%, and a high density of fish and amphibians (AB-TIN 2012). Another study revealed that the main variables determining habitat suitability are climatic fluctuations and the amount of accessible water (MOBARAKI et al. 2018).

To date, there exists no study assessing the climatic suitability throughout the range of the Mugger Crocodile and the subsequent potential effects of climate change (see MOBARAKI et al. 2021). In this work we aim to: 1) identify the environmental factors most closely related with Mugger Crocodile occurrences in the range states; 2) model the potential distribution of the species; 3) predict the changes in future distribution of the species according to potential climate changes; and 4) identify priority areas for conservation given environmental niche stability and potential future human/crocodile conflicts. Modelling the potential effects of climate change on crocodiles allows us to predict their future distribution, which may in turn aid in proposing suitable conservation management actions.

## Material and methods

### Data preparation

To assess the potential distribution of the Mugger Crocodile, we obtained unique 636 occurrence records from GBIF covering the native range of the taxon based on preserved specimens and observations. Further, we georeferenced 84 occurrence records from our own fieldwork to increase the number of records in the westernmost parts of its range. We corrected the set of species records for potential sampling bias and spatial autocorrelation by a 10-km distance filtering using the thinning function in the *spThin* package for R (AIELLO-LAMMENS et al. 2015, R Core Team 2019). Finally, a set of 380 occurrence records was used for model computation.

Environmental data were obtained from Worldclim 2.0 ([www.worldclim.org](http://www.worldclim.org)). Based on monthly data, these 19 bioclimatic variables characterize average climatic conditions from 1970–2000 with a spatial resolution of 2.5 arc minutes (FICK & HIJMANS 2017). Multi-co-linearity of predicting variables was reduced by computing pairwise Spearman rank correlations and selecting only one variable in cases where  $R^2$  exceeded 0.75. The final variables selected for model computation comprised BIO1 = Annual Mean Temperature, BIO7 = Temperature Annual Range, BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, and BIO19 = Precipitation of Coldest Quarter.

To evaluate potential impacts of future climate change as can be expected in 2081–2100, we downloaded global circulation model (GCM) outputs assuming the IPCC6 story lines of *ssp126*, *245*, *370* and *585* from Worldclim.org (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC6, MIROC-ES2L, MRI-ESM2-0). Averages across all GCM simulations per story line were used as future ensembles.

## Species distribution modelling

To perform SDMs, we used Maxent ver. 3.4.4 and the R-packages: raster (HIJMANS et al. 2021a), dismo (HIJMANS et al. 2021b), and ENMeval (MUSCARELLA et al. 2014) were used for model optimization and processing. The available climate space was defined by a polygon provided by the IUCN Red List, representing a distribution range estimate based on expert opinion (Fig. 1). For model fitting, we tested several regularization multipliers (from 0.5 to 2.5 in steps of 0.25, plus 5 and 10) and feature classes (L, LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold). A total of 25 replicates were computed per combination of regularization multiplier and set of feature classes, wherein the species records were randomly selected each time via bootstrap with 80% used for model training and 20% used for model evaluation.

Based on the Maxent's raw output, we computed for each replicate the corrected Akaike Information Criterion [AICc, (WARREN & SEIFERT 2011)] and the difference between test and training AUC [= Area under the ROC curve (LOBO et al. 2008, PHILLIPS & DUDÍK 2008, ELITH & GRAHAM 2009)]. The best combination of settings was select-

ed by balancing the average predictive ability of the model ( $AUC > 0.8$ ), the smallest difference between  $AUC_{\text{training}}$  and  $AUC_{\text{test}}$  ( $AUC_{\text{delta}}$ ), as well as the lowest average AICc.

Using the best fitting model parameters (LPT, regularization parameter = 1,  $AICc = 2430.2$ ,  $AUC_{\text{Training}} = 0.833$ ,  $AUC_{\text{Test}} = 0.813$ ,  $AUC_{\text{delta}} = 0.019$ ), we finally computed 100 replicates, again using a bootstrap approach with an 80:20 split for model training and testing. The average predictions across the 100 replicates were projected onto current and future climatic conditions using the cloglog output format. Multivariate Environmental Similarity Surfaces (MESS [ELITH et al. 2010]) maps were used to assess potential uncertainties caused by extrapolation beyond the training range of the models. As the presence-absence threshold we selected the 10% training omission threshold, assuming that 10% of the species records may represent sink populations or georeferencing artefacts.

## Coverage with protected areas, habitat availability and anthropogenic pressure

Information on the distribution of protected areas within the range of the Mugger was obtained from the World Dic-

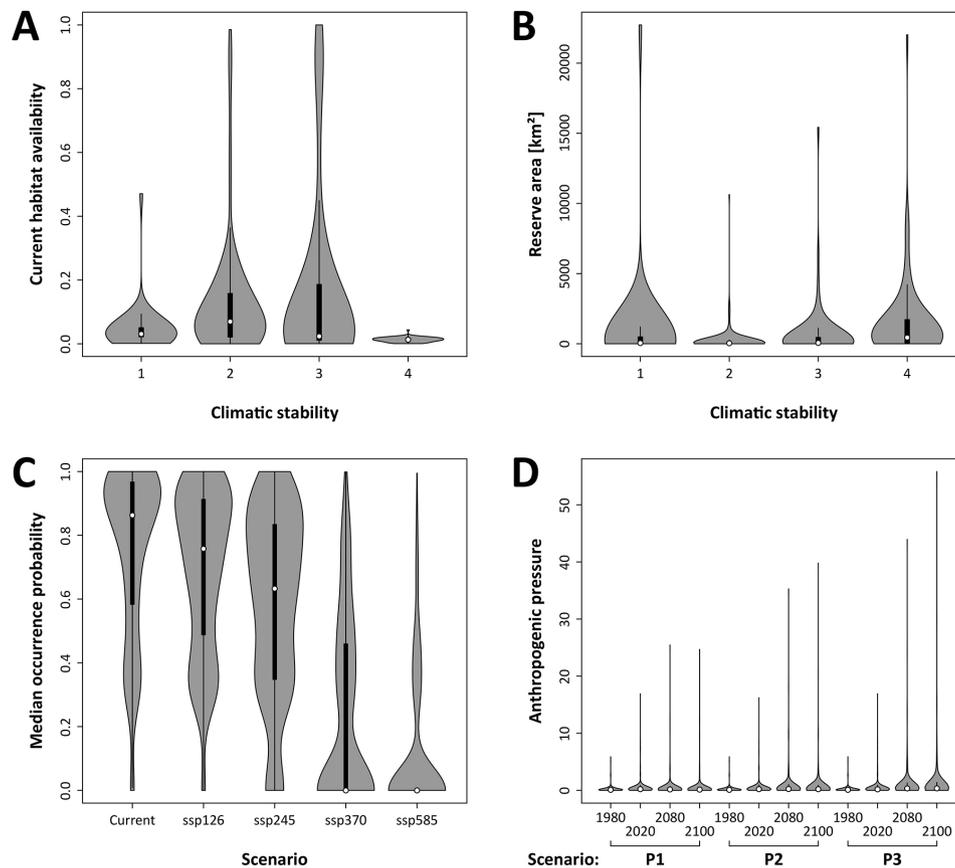


Figure 1. (A) Proportion of suitable habitat for, and (B) area of protected reserves holding the Mugger Crocodile at different degrees of climatic stability in future scenarios (1–4: stable climate in 1 to 4 of all scenarios). (C) Occurrence probability of the crocodile in current and future scenarios. (D) Anthropogenic pressures in time slices 1980, 2020, 2080 and 2100 across 3 storylines.

tionary of Protected Areas (<https://www.protectedplanet.net/en>), wherein only terrestrial, IUCN-categorized reserves of the categories Ia, Ib, II, III, IV, V and VI are included. To rank protected areas according to their conservation value for the Mугger, we assessed for each site their climatic suitability based on the SDMs, the availability of suitable microhabitats, and the potential anthropogenic pressure in current and future scenarios.

As microhabitat surrogates we used the recent assessment of tropical wetlands by GUMBRICHT et al. (2017). This data set has a spatial resolution of 232 m and is derived from biophysical indices related to wetland, i.e., a long-term water supply that exceeds atmospheric water demand; annually or seasonally water-logged soils; and a geomorphological position in which water is supplied and retained (GUMBRICHT et al. 2017). As river networks are missing from this data set but may represent valuable habitat for the Mугger, we added a high-resolution water layer as an additional category (GRDC 2020).

Expecting increasing potential conflicts between Mугgers and local human communities with increasing population densities of the latter, we obtained potential future scenarios of the ssp1-3 storylines with a spatial resolution of 0.5° from MURAKAMI & YAMAGATA (2019). The data set was downscaled to the resolution of our climate data with a nearest neighbour approach in R, and the time slices 1980, 2020, 2080 and 2100 were used for further processing.

For each protected area within the currently known range of the Mугger as suggested by the IUCN, we computed the factual area providing suitable microhabitats, the median environmental suitability across each reserve as expected in current and future scenarios, and the expected anthropogenic pressure. Our ranking of reserves was finally based on the proportion of suitable habitats and climatic stability throughout all future scenarios.

## Results

Across the 100 replicates we obtained good AUC values ( $AUC_{\text{training}} = 0.839$  and  $AUC_{\text{test}} = 0.827$ ), which indicates a good discrimination ability of our model and absence of overfitting. Temperature Annual Range (Bio7) made the highest contribution (42.9%), followed by Mean Temperature of Driest Quarter (Bio9, 10.7%), Annual Precipitation (Bio12, 10.5%), and Annual Mean Temperature (Bio1, 9.2%), Mean Temperature of Wettest Quarter (Bio8, 6.6%) and the other variables contributed less than 5% to the final model (Bio13 (4.8%), Bio18 (4.7%), Bio14 (3.6%), Bio16 (2.9%), Bio19 (2.6%) and Bio17 (1.4%)).

Potential suitable habitats of the Mугger Crocodile seem to be more fragmented than expected from the native distribution at present (Fig. 1B). Major suitable habitats are situated in Sri Lanka, in the southeastern peninsular of India, tropical moist forests along the west coast of India, the border region between Nepal and India, and lastly on the south coasts of Iran and Pakistan. In Iran, suitability decreases the farther the distance is from the coast, indicat-

ing a potential preference for coastal areas for the Iranian population. For the future, our models predicted a general reduction in potential suitability (except for the western parts of the distribution) in all story lines. When the MESS area is included, storylines ssp126 and ssp245 predict similar and only slightly smaller suitable habitats than is the case currently. More loss of suitable habitats was found in the other two storylines (ssp 370 and 585) (Figs 1C, 2E–F). However, when the MESS area is omitted, storylines ssp360 and ssp585 appear to contain ‘highly unsuitable’ in currently suitable areas, namely in Sri Lanka, southern India, and the coastal part of southern Iran. Potentially suitable habitats are predicted to shift farther inland (Fig. 3). Furthermore, we found that areas that are currently highly suitable do not appear to have a stable climate over time (see Figs 2B and 4A). In fact, there is little suitable habitat to be found in protected reserves with higher climatic stability, especially when the climate is stable in all four fu-

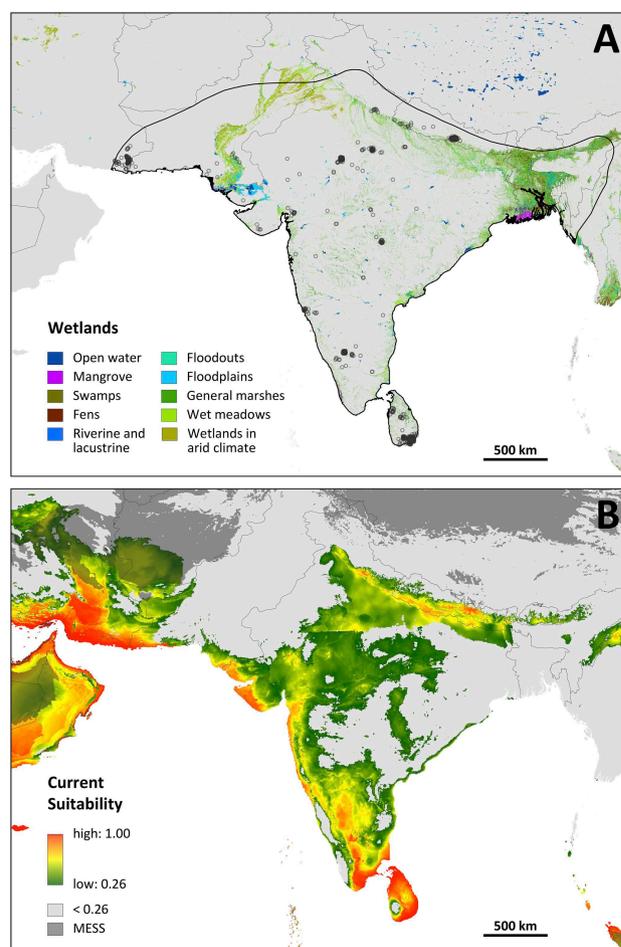


Figure 2. (A) Distribution of various types of wetlands and the Mугger Crocodile. The Global Range polygon for the species according to the IUCN Red List is indicated. (B) Predicted potential distribution of the Mугger Crocodile in the current climate. Warmer colours represent higher environmental suitability. Areas requiring extrapolation beyond the training range were identified via MESS and are indicated in grey.

ture scenarios (Fig. 1A). These stable climates seem to occur mainly in large reserves (Fig. 1B). There appears to be a large number of areas with suitable climate in all future scenarios, particularly along the Himalayan range and in tropical forest along the west coast of India as well as in neighbouring dry broadleaf forests, and more importantly, in the border region between Iran and Pakistan (Fig. 4A). In these areas, we identified reserves of top conservation priority based on overall stability and habitat percentage: Madinduwa, Seooyaka Samudra, Parapuduwa Nun's Island in Sri Lanka, Cut Muorki Chach, Marho Kotri, Keti Bunder South, Mirpur Sakro and Keti Bunder North in Pakistan, Mapangyong Cuo in China, and Thamihla Kyun Wildlife Sanctuary in Myanmar (Fig. 4B).

Potential future scenarios of anthropogenic pressures showed a general pattern of higher variability in later years, with the P3 storyline turning out the highest variability of anthropogenic pressure at the end of 2100 (Fig. 1D). The expected anthropogenic pressures seem to be prominent and increasing in many regions of India, Bangladesh and Pakistan by the year 2100 (Fig. 5).

## Discussion

This study identified the variables of highest contribution to the models and these agreed with previous findings from studies in other crocodiles (cf. RÖDDEK et al. 2010, IHLOW et al. 2015) or other habitat suitability studies on crocodiles. On the one hand, the annual temperature range between the coldest and warmest months of the year can be an important factor for the presence of crocodile prey (fish and amphibian species). On the other, mean temperature of the driest quarter and annual precipitation might determine vegetation cover but also the existence of shallow ponds, both of which are used by crocodiles (DA SILVA & LENIN 2010, ABTIN 2012). However, these crocodiles are known to use burrows as effective refuges from hot ambient temperatures. If habitats suitable for burrowing continue to exist, they could be favourable to the survival of the crocodiles (WHITAKER et al. 2007). Basking sites are important for thermoregulation for crocodiles, too (ATIGRE et al. 2015).

The surprisingly low spatial extent of potentially suitable habitats that is currently predicted suggests that Mug-

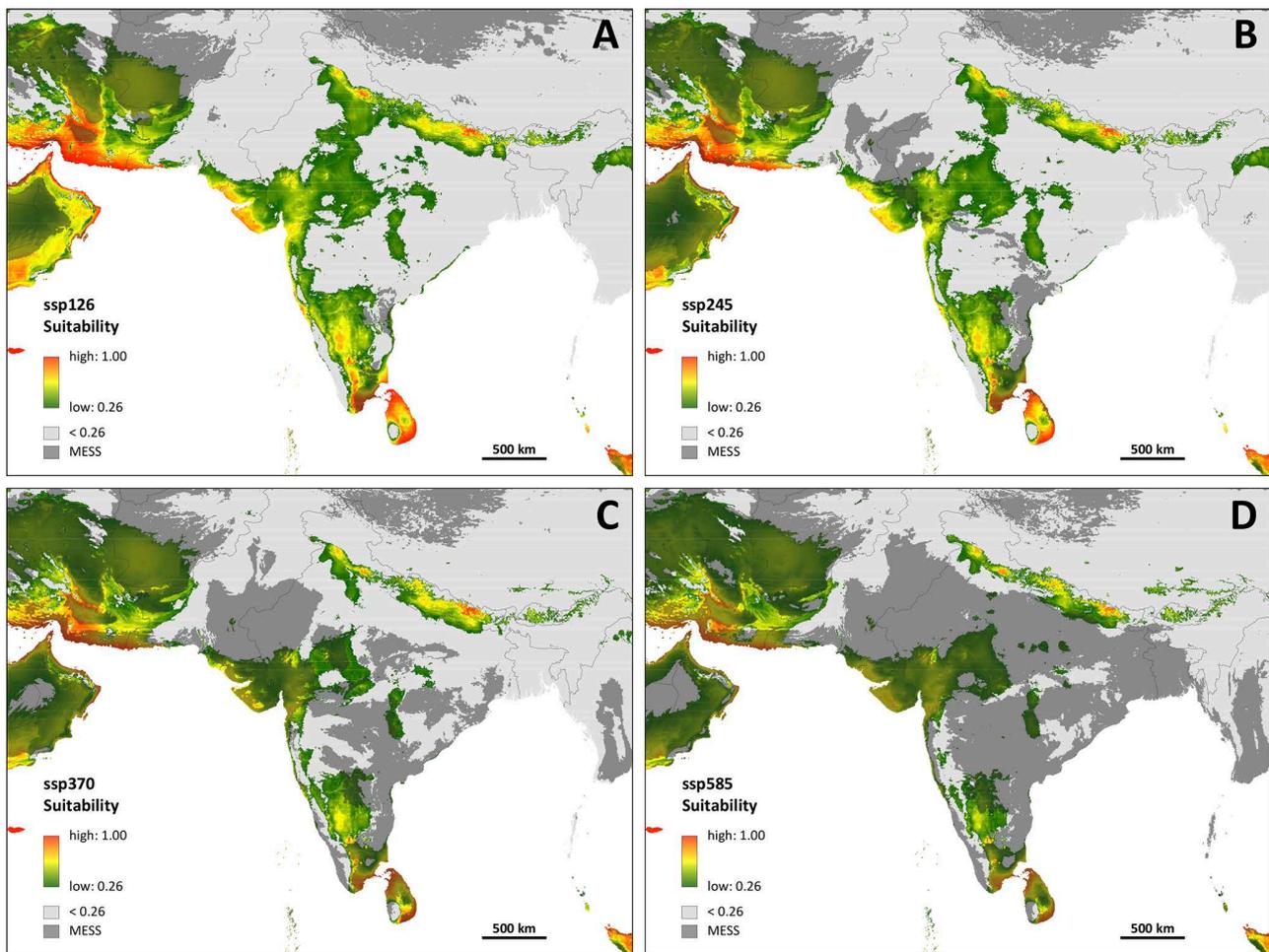


Figure 3. (A–D) Predicted potential distribution of the Mugger Crocodile in future climate change scenarios ssp126, ssp245, ssp370 and ssp585. Warmer colours represent higher environmental suitability. Areas requiring extrapolation beyond the training range were identified via MESS and are indicated in grey.

ger Crocodile populations are highly fragmented and degraded (Fig. 1). In fact, compared to their original distribution, these crocodiles do not have as much suitable habitat available as previously thought. One of the reasons explaining our results may be rapid urbanisation, especially in India with 5.33% growth between 2015 and 2020 (United Nations, Department of Economic and Social Affairs & Population Division 2019). Urbanisation is a form of habitat change that alters the entire environment from its native state (ELMQVIST et al. 2016).

All countries in the distribution range of this species are developing countries in which population growth and urbanization are evident (Fig. 5). In Iran, urbanization and related activities like land use modification and agricultural development are prominent, but the most serious problems arise from local human/crocodile conflicts with the Mugger posing a serious threat to local people close to water bodies due to the former losing their natural habitats, due to increasing water shortage, and the latter need-

ing water for daily living and agriculture (MOBARAKI et al. 2018, 2021, HILL et al. 2018). This conflict will continue to escalate as anthropogenic activities increase within and around the crocodiles' habitats (Fig. 5).

Our results suggest that Mugger Crocodiles will likely be affected by climate change in all future scenarios in the timeframe 2081–2100 (Fig. 1C), no matter whether the first scenario with the most optimistic situation for the future will apply or the fourth scenario with the worst situation in the future. There might be a similar trend where potentially suitable habitats are greatly reduced across their ranges, especially when uncertain predictability (MESS) areas are removed (Figs 2A–D). Such changes can be expected if temporary watercourses and ponds during the rainy season disappear as a result of rising global temperatures and intensive droughts become more frequent in the region. Loss of potentially suitable crocodile habitats in the coastal areas of Iran could be a major concern as most of the current Iranian populations are found near the coast. They are driven to the north and west where there are no water resources for the Mugger crocodile. Studies on other species such as the Asiatic black bear (*Selenarctus tibetanus*), Persian spider gecko (*Agamura persica*), Caucasian agama (*Paralaudakia caucasia*), and Iraqi Spiny-tailed Lizard (*Saara loricata*) in Iran reported similar results (KAFASH et al. 2015, YOUSEFKHANI et al. 2017, FARASHI & ERFANI 2018).

In terms of climate stability over time and possible future human/crocodile conflict, very few suitable areas (with large protected reserves) are found to be stable enough for the crocodiles in the future.

We therefore propose to focus future conservation efforts on the reserves with the highest rankings as shown in the results of this study (Fig. 4B). These reserves contain the best possible future refuges for the Mugger Crocodile. Two major areas are to be highlighted in this regard: a larger reserve in northern India (Nanda Devi National Park) and the westernmost area in Iran, especially within the Gando Reserve. Although climatically comparatively stable, the surroundings of the Nanda Devi National Park are expected to come under severe human pressure in the near future (Fig. 5), leaving the most important habitats in terms of conservation in Iran. These are located along two major rivers in the region, the Bahu-Kalat and Kaju. Here, crocodiles live in close contact with local people and conflicts are quite common (MOBARAKI et al. 2015), but these are predicted to remain comparatively stable in the near future because human population growth is expected to be rather low in this area (Fig. 5). In the isolated, western extension of its distribution, the Mugger Crocodile is restricted to limited freshwater habitats in Sistan and Baluchistan provinces. The population of this species is small here, estimated at more than 500 individuals, and fragmented into several scattered sub-populations (MOBARAKI et al. 2015, 2018) with only some level of intra-population connectivity (CAMPOS et al. 2018). Improving the connectivity of the meta-population network will be of utmost importance for the survival of the crocodiles in the near future.

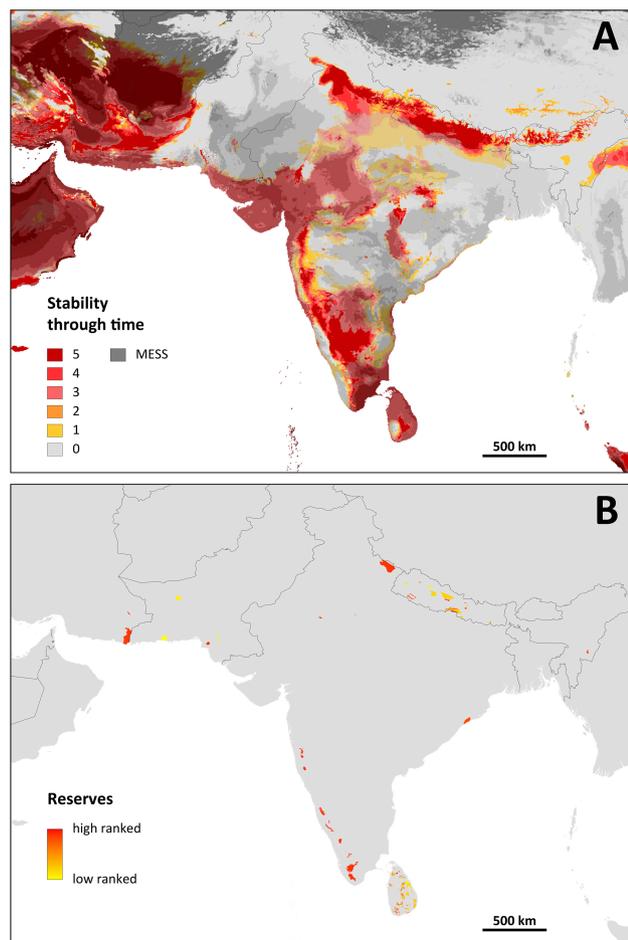


Figure 4. (A) Suitable areas that are stable at present and in the future scenarios. Numbers 0 to 5 indicate the number of scenarios (including current) that have a stable climate over time. (B) Ranking of protected reserves based on the proportion of suitable habitat and climate stability.

### Conclusion

Our findings provide first insights into habitat suitability for Mugger crocodiles (*C. palustris*) in the Indian subcontinent and West Asia derived from climate data. The future for this crocodile species appears to be uncertain and in despair due to the loss of suitable habitats with stable climate and ever-increasing anthropogenic pressures. New surveys are required to identify potentially undiscovered populations of Mugger Crocodiles in potentially suitable habitats as predicted by our suitability models. Studies focussing on the behaviour and physiology of the Mugger Crocodile are urgently needed to improve our knowledge of the ecology

of this species. These data would also be valuable for future niche models as well as the evaluation and management of current and future conservation areas for this species. Given the periodic water shortages and close contact with local people, human/crocodile conflicts may escalate and subsequently cause more problems from a conservation perspective. Defining sanctuaries and/or managing new suitable habitats would be beneficial to controlling those conflicts. Artificial ponds, irrigation drains, and reservoirs could be crucial to the survival of the crocodile in the face of ongoing climate change and urbanisation. Ex-situ conservation facilities would help in managing and conserving the Mugger Crocodile populations in the region.

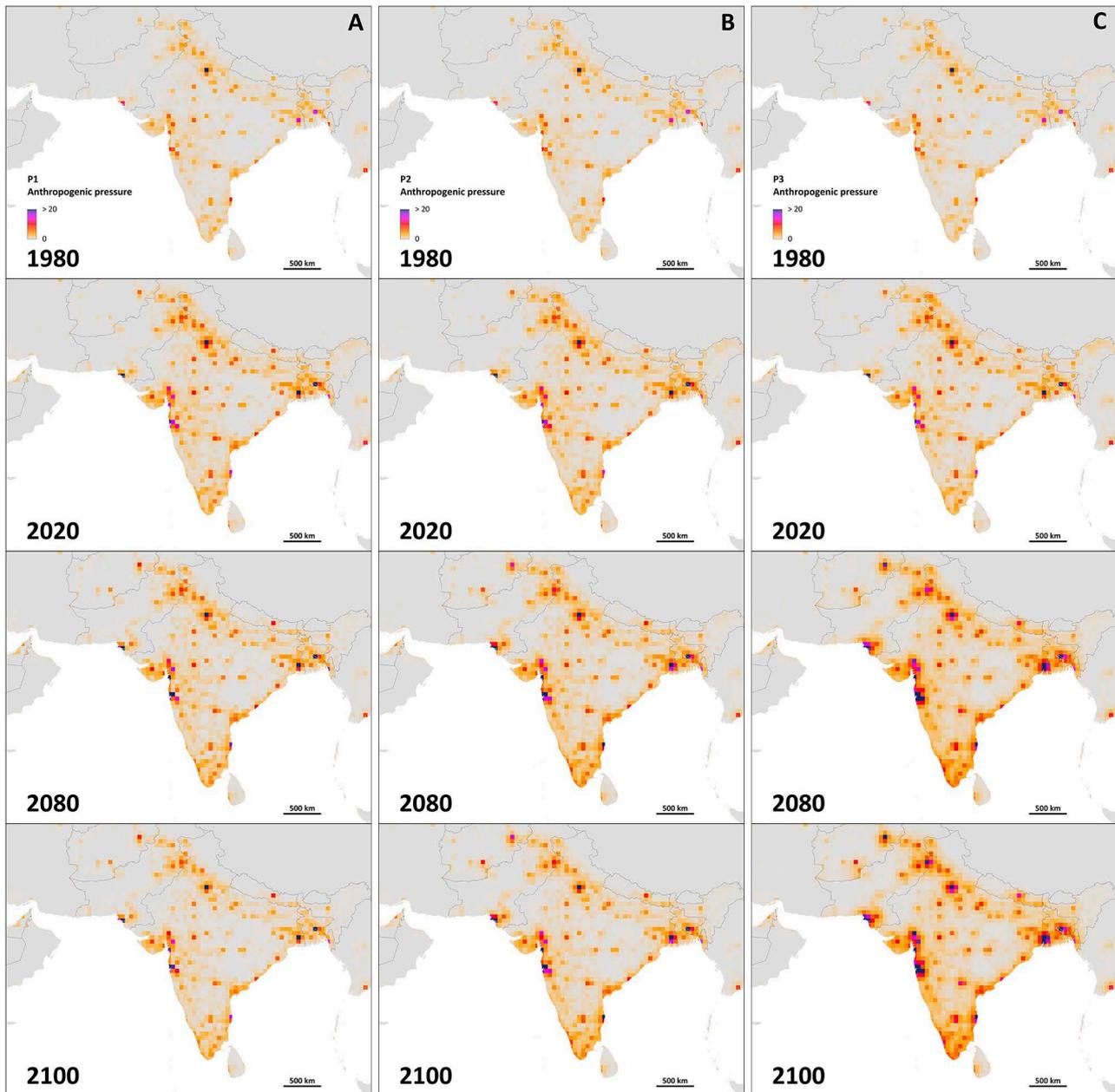


Figure 5. Distribution and intensity of anthropogenic pressures in the time slices 1980, 2020, 2080 and 2100 across 3 storylines.

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