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Title
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Permalink
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Journal
Frontiers of Biogeography, 14(1)

Authors
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Publication Date
2022

DOI
10.21425/F5FBG50928

Supplemental Material
https://escholarship.org/uc/item/2m2539gp#supplemental

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RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia

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This article is part of a Special Issue entitled Transboundary Conservation Under Climate Change, compiled by Mary E. Blair, Minh D. Le and Ming Xu

Abstract

Tortoises and freshwater turtles are among the most threatened taxa of vertebrates in the world due to consumption, urban development, agriculture, and land and water pollution. About 50% of the currently recognised chelonian species are considered threatened with extinction according to the IUCN Red List. Asia is an epicentre for the turtle and tortoise extinction crisis, containing the highest diversity of threatened species. In this study, we used species distribution models (SDMs) to assess the effectiveness of existing protected areas across Southeast and South Asia for the conservation of three large critically endangered freshwater turtles (*Batagur borneoensis*, *B. affinis,* and *Pelochelys cantorii*). We derived the models based on selected bioclimatic variables at the sites of known species records. Our SDMs showed that Indonesia is of particular importance in prioritising conservation for these three species, containing the largest areas of suitable habitat within protected areas. However, when considering water surface coverage, Thailand has the highest proportion of suitable areas under protection. Our results suggest that the present cover of protected network reserves seems inadequate in terms of size and should be expanded to sustain populations of the three target species. Therefore, we identified priority areas and reserves critical for further field surveys to guide the potential discovery of novel populations. To investigate the effect of climate change, we also projected potential distributions onto ensembles of four IPCC story lines. As a result, we found larger extralimital areas of suitable environment for all three species, particularly northwards and inland. However, high degrees of uncertainty in climate conditions indicate few reserves may provide long term protection. Lastly, we review the threats and propose recommendations for conservation of these poorly known freshwater turtles.

Highlights

- Species distribution models (SDMs) are useful tools to predict the distribution of rare species.
- We performed SDMs using bioclimatic variables and water surface cover to assess whether existing reserves are effective in the conservation of three critically endangered freshwater turtle species.
- Indonesia and Thailand are countries of major importance in preserving these threatened species, although current established reserves might be insufficient.
- We proposed several priority conservation areas where the species could potentially occur.
- Future projection models suggest an expansion of suitable habitat inland and northward in response to climate change, despite uncertainty due to extrapolation outside the training range of the models.

Keywords: climate change, conservation, endangered species, IUCN, protected areas, species distribution modelling, Testudines, water cover

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Introduction

Habitat loss due to land use changes is a significant factor leading to the decline of global biodiversity (Foley et al. 2005). South Asia and Southeast Asia have among the fastest rates of deforestation and habitat loss, with over 50% of native forest being depleted over the last two centuries (Sodhi et al. 2004). This, combined with poaching, illegal pet trade, and land degradation, has resulted in habitat fragmentation as well as other negative impacts on the native biodiversity.

Of the 356 species of turtles and tortoises recognised globally, about a quarter are found in Asia (Turtle Taxonomy Working Group [TTWG] 2017), making this region one of the species richness hotspots for turtles (Buhlmann et al. 2009, Ihlow et al. 2012, Mittermeier et al. 2015). However, the Asian continent is also a hotbed for turtles facing extinction since it harbours 17 of the 25 (68%) most threatened chelonian species (Turtle Conservation Coalition [TCC] 2018, Rhodin et al. 2018). Vietnam, India, and Indonesia are among the top five countries with the highest number of threatened chelonians. To date, seven species and three subspecies (2.1% of all modern turtle taxa) have already gone extinct (TTWG 2017, TCC 2018).

Predictions for future climate change from the Intergovernmental Panel on Climate Change (IPCC) suggested that 86% of all turtle species will be pushed out of their current realized niche by 2080 (Ihlow et al. 2012). In this study, we evaluated the availability of suitable habitats of three poorly known freshwater turtles. The large river turtles of the genus *Batagur* (Gray 1856) are one of the two most critically endangered turtle genera (next to Asian box turtles, *Cuora* [Gray 1856]), accounting for five of the Top 25 threatened species (TCC 2018).

The Painted Terrapin (*Batagur borneoensis* [Schlegel and Müller 1845]) is a large river turtle that was once widely distributed in the Sundaland region, occurring from southernmost Thailand southward through Peninsular Malaysia to the islands of Sumatra and Borneo (TTWG 2017). Once common, only three rivers in Peninsular Malaysia are believed to have more than 100 remaining nesting females, while a few other populations have less than 50. The species inhabits estuaries of medium to large rivers and mangrove swamps. Females tend to move from freshwater to oceanside beaches to nest (Dunson and Moll 1980).

The Southern River Terrapin (*Batagur affinis* [Cantor 1847]) was considered to be part of the species *Batagur baska* in South Asia until DNA sequence analysis demonstrated that the latter comprised at least these two genetically distinct species (Praschag et al. 2008). This recently described species is also a large river turtle found along the coasts of Peninsular Malaysia, eastern Sumatra, southernmost Thailand, and Cambodia, where a relic population persists (Platt et al. 2003, Moll et al. 2015). It has been suggested that *B. affinis* was historically distributed in all major rivers draining into the South China Sea (Moll et al. 2015). The species inhabits tidal regions of large rivers in coastal waters and estuaries, but unlike *B. borneoensis*, females prefer to migrate upriver to nest on sandbanks exposed after the monsoon season (Moll et al. 2015).

The Asian Giant Softshell Turtle (*Pelochelys cantorii* [Gray 1864]) has recently been provisionally assessed as critically endangered by the Tortoise and Freshwater Turtle Specialist Group (Rhodin et al. 2018). This species is a very large freshwater turtle with arguably the widest distribution of all non-marine turtles (Das 2008). It is remarkably widespread, occurring from southwestern Peninsular India to Southeast Asia and China and the western Indonesian and Philippine archipelagos. It was suggested by Taylor (1970) that its distribution might have been shaped by past human introductions as food during transportation, but this appears highly unlikely (Das 2008). Its widespread distribution along coastlines and across island archipelagos appears to be due to its tolerance of salt water. The species occurs in a variety of habitats, including lakes, rivers and seacoasts. Females are known to nest on sandbars alongside deep pools or ocean beaches (Das 2008).

Populations of these three turtle species have been severely depleted throughout their range and have disappeared from much of their former ranges (TCC 2018). *Batagur affinis* is considered to be extinct in the wild in Thailand, Vietnam and Singapore (Moll et al. 2015) while populations of *P. cantorii* appear to be locally extinct in China and Vietnam (Das 2008). Habitat destruction and alteration such as sand mining, hydropower dams, and urban construction have greatly affected nesting and feeding sites (Moll and Moll 2000, TCC 2018). Large scale agro-based plantations and the associated pollution have degraded the riparian vegetation on which these species rely. On top of that, trade in southeast Asian freshwater turtles has increased drastically in the past 30 years. They have been heavily exploited and exported for eggs and flesh for human consumption (Moll and Moll 2000, van Dijk 2000, CITES 2010). Wild *B. borneoensis* are also prized in the pet trade for their highly attractive colouration during the mating season (TCC 2018).

Established Protected Areas exist in many parts of southern and southeastern Asia. However, there is a lack of assessment of their effectiveness in sustaining viable populations of threatened turtle species. Species distribution modelling (SDM) based on the climatic niche of target species and land cover layers provides a reliable mechanism to assess the suitability and effectiveness of reserve networks (Araújo et al. 2004, 2007, Hannah et al. 2007, Ihlow et al. 2014). The survival of freshwater turtles largely depends on riparian habitats, including rivers, streams and estuaries (Moll and Moll 2004). We therefore assess the water surface cover to refine our predictions of where the three target species should thrive within protected reserves. Here, we sought to 1) compare the potential suitable habitat to each species' currently known historic range; 2) identify the areas of suitable habitat within current reserves; 3) based on water coverage, assess where the best areas are for prioritising future conservation efforts; and 4) assess the impact of climate change by using climate

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and socioeconomic projections for the year 2080 to project future changes in habitat suitability and in reserve areas from (3). We conclude by discussing whether current Protected Areas are sufficient to protect these critically endangered species.

Materials and Methods

Species records and climate data

Coauthors AGJR and JBI provided historic locality records for *Batagur borneoensis* (25), *B. affinis* (18), and *Pelochelys cantorii* (28), based on museum and literature records and unpublished data as well as their presumed historic indigenous distribution ranges (TTWG 2017, in press). We obtained information on current climate conditions from the Worldclim database, version 2.1, derived from climate conditions recorded for 1970-2000 with a spatial resolution of 2.5 arc minutes (Fick and Hijmans 2017, www.worldclim.org). We then computed a set of 19 bioclimatic variables derived from the monthly temperature and precipitation patterns. These variables, describing annual trends, seasonality and extreme environmental factors, are suggested to yield biologically meaningful results as they characterise the availability of water and energy throughout the year and thus are suitable predictors in SDMs (Busby 1991). We used a Mantel correlogram from the *ecospat* package v3.1 for R to determine potential spatial autocorrelation of environmental covariables within a set of occurrences as a function of distance (Broennimann et al. 2020). We further removed occurrences too close to each other using species occurrence thinning function from *spThin* package v0.2.0 for R (Aiello-Lammens et al. 2015). This is a robust function to reduce spatial biases and unevenness. We then used the remaining set of records (*B. borneoensis* [19], *B. affinis* [12], and *Pelochelys cantorii* [26]) after thinning for subsequent SDM computation.

To project future changes in distributions with respect to climate change, we used four shared socioeconomic pathways (SSPs: 126, 245, 370 and 585), which are emission scenarios driven by different socioeconomic assumptions. We chose the future period of 2081–2100, comprising an average of monthly values for the 19 bioclimatic variables. Due to uncertainty in forecasting future climate, we computed the average of eight global climate models (GCMs) that simulated the impact of climate scenarios: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0, downloaded from WorldClim at 2.5arc minute resolution to provide a non-biased future climate prediction.

Species distribution models

In interpreting a model, deciphering the driving variables is much simpler when variables have low correlation (Heikkinen et al. 2006). Therefore, using the *dismo* and *SDMtune* packages for R (Hijmans et al. 2017, Vignali et al. 2020), we assessed highly correlated variables and sequentially removed variables by performing a jackknife approach among correlated variables (based on Spearman rank correlations $|rs| \geq 0.7$) based on their percentage contribution to the model and TSS value. We repeated the process until the remaining variables had correlation coefficients less than 0.7. We then removed these resulting variables, which contributed less than 5% to initial SDMs when performing the models.

We used Maxent v3.4.1 (Phillips et al. 2006, 2017; available from http://biodiversityinformatics.amnh.org/open_source/maxent/) for SDM computation to assess the potential suitable habitats of the turtles. This program applies a machine-learning technique, which follows the principle of maximum entropy for modelling with presence-pseudoabsence data. It has been suggested that Maxent outperforms other established modelling methods such as generalised additive models and BIOCLIM, especially for low and biased sample sizes (Elith et al. 2006, Wisz et al. 2008, but see Peterson et al. 2007 on GARP). Results obtained from Maxent have been proven effective in predicting habitat suitability in poorly known species (Pearson et al. 2007), and reptiles and amphibians (Raxworthy et al. 2008, Ihlow et al. 2014).

Applying a bootstrap approach, we performed 100 replicates of Maxent runs with the standard settings (cloglog output format, 500 iterations, clamping) using the selected subset of climate variables. We used 90% of the records for model training and 10% for testing. To build models, we randomly created 10,000 pseudo-absences within a buffer of 200 km surrounding each species' presumed historic indigenous distribution range. These distributional areas were projected ranges based on GIS-defined hydrologic unit compartments (HUCs) with verified localities, and combined with HUCs that connected known point localities in the same watershed that had similar habitats and elevations as the verified HUCs (TTWG 2017, in press). They therefore provide suitable distribution backgrounds for these freshwater turtle species. The cloglog format creates potential suitable habitat values ranging from 0 (unsuitable) to 1 (optimal) along with the relative contribution of each bioclimatic variable as Maxent outputs.

To evaluate our models, we used Receiver Operating Characteristics (ROC) curves based on Area Under the Curve (AUC, Swets 1988). Values of AUC can range from 0.5 (when model predicts no better than random) to 1.0 (when model has perfect prediction). We also applied True Skill Statistics (TSS) to evaluate model performance (Shabani et al. 2018). TSS values ranges from -1 to +1, where +1 suggests perfect prediction, whereas values of zero or less suggest equal or lower performance than random. The minimum training presence threshold assumes that the lowest predicted suitability is the least suitable habitat in which the species may occur. Hence, for conservation purposes, we have chosen the minimum training presence threshold to assess suitability to avoid overprediction (Pearson et al. 2007). We subsequently used the average Maxent prediction across all 100 replicates as consensus map, which was reclassified using the

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minimum training presence as presence/absence threshold for further analyses.

The average model was projected on four different future scenarios, which were rescaled using the same threshold value. We performed multivariate environmental similarity surfaces (MESS; Elith et al. 2010) to identify the areas exceeding environmental training conditions under current and future scenarios within the projection layers.

Protected area network and water surface cover data

To assess the coverage of suitable turtle habitats with designated protected areas according to IUCN standard (criteria I, II, IV, V, VI), we downloaded polygons of protected areas from the World Database of Protected Areas (UNEP-WCMC and IUCN, 2020; https://www.protectedplanet.net/). These Protected Areas are clearly defined geographical areas, recognised, dedicated and managed to achieve long term conservation objectives and classified under the different objectives recognised by international bodies such as the United Nations as well as many national governments (Dudley 2008, IUCN 2020). We selected the following assigned categories: (Ia) Strict Nature Reserve, (Ib) Wilderness Area, (II) National Park, (III) National Feature, (IV) Habitat/ Species Management Area, (V) Protected Landscape/Seascape, (VI) Protected area with sustainable use of natural resources (more information available on https://www.iucn.org/). This assessment will help to identify future conservation areas and facilitate recommendations for improvements in existing reserve networks.

The incorporation of land cover data has been shown to perform better than using bioclimatic predictors alone (Cord and Rödder 2011). Freshwater turtles (especially our three target species) are strongly associated with water. We obtained high resolution (30-meter) water maps from Joint Research Centre Global Surface Water Mapping layers (Pekel et al. 2016; https://global-surface-water.appspot.com). The maps document the surface water present on the Earth's surface over 32 years using three million Landsat satellite images (Pekel et al. 2016). This presence of surface water (occurrence hereafter) gives the frequency of occurrence of water on land surface recorded in monthly time steps.

We then reclassified the original water occurrence to facilitate interpretation. We included only 100% occurrence (all monthly observations classified as water) and excluded other occurrences which were periodically under water or have never been under water. Since these turtles thrive in large meandering freshwater systems, we restricted our study to areas with only freshwater and land mass by cropping the coastline and using an inward buffer to exclude any uncertain seawater border strip of 90 m. Although *P. cantorii* appears to be tolerant of saltwater (Das 2008), a high-resolution salinity map was not available.

Using Maxent's output map as a base layer, we overlaid the water surface cover to exclude unsuitable areas lacking permanent water. Finally, we removed overlapping polygons of suitable areas in Protected Areas from the analysis to prevent computational redundancy. We conducted all spatial analyses with QGIS ver 3.12.2 (QGIS Development Team 2020) and R ver 4.0.2 (R Core Team 2020).

Results

We removed all auto-correlated occurrence records using spatial thinning in the radius of 20 km for both *Batagur borneoensis* and *B. affinis* and 50 km for *Pelochelys cantorii* based on the Mantel correlogram. The bootstrap of 100 Maxent models of the spatial extent gained good average AUC values for the three species (*B. borneoensis*: AUC_{test} = 0.9298, TSS = 0.6850; *B. affinis*: AUC_{test} = 0.7782, TSS = 0.3681; *P. cantorii*: AUC_{test} = 0.7305, TSS = 0.2606) (Table 1). AUC values suggest a high discrimination ability between suitable and unsuitable habitat. The minimum training presence threshold values in the training records of *B. borneoensis, B. affinis* and *P. cantorii* were 0.1473, 0.3541 and 0.2525, respectively (Table 1).

The variable contributions are presented in Table 1. In *B. borneoensis*, the environmental variable which contributed the most to the model (76%) was the "mean temperature of the driest quarter". The same pattern was also evident in *B. affinis* for the "minimum temperature of coldest month" (71.1%), followed by "annual mean temperature" (20.7%). In contrast, the "precipitation of driest quarter" (21.5%) and "temperature seasonality" (25.7%) contributed almost equally to the final model of *P. cantorii*, followed by "annual mean temperature" (16.2%), "mean temperature of warmest quarter"(12.5%), "mean diurnal range"(11.2%) and "precipitation of warmest quarter"(9.7%). We also provided Maxent lambda files for more details on the assessment of the variables used in the models (see Appendix S1).

Potential suitable habitats of *B. borneoensis* predicted by climate are mostly coastal areas comprising the estimated distribution by TTWG (2017) in Malaysia (Peninsular and Sarawak), Indonesia (Sumatra and Kalimantan) and a small area of southern Thailand. Other highly suitable habitats outside of the estimated distribution were identified in Sabah Malaysia and southern Sumatra, western Java, and the Philippines (Fig. 1b). However, only a small part of these potentially suitable habitats occurs within designated Protected Areas. The country with highest proportion of suitable surface area being protected is Indonesia (76%), followed by Malaysia (8%) and Thailand (7%) while the coverage is low (<5%) in other countries (Fig. 1c, Table 2). A ranking by water coverage in these suitable areas within reserves reveals that Thailand (65%) and Indonesia (26%) are of major importance compared to the other countries which contain less than 5% coverage (Table 3). Combining the estimated distribution of *B. borneoensis* and the water coverage of suitable habitat, highly important conservation areas applying IUCN standards were identified (Fig. 1d). These reserves include Selirong, Berakas Forest Reserves (both recreational and conservation) and Pulau Siarau Nature Reserve in

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Table 1. Results of the relative variable contribution in 100 Maxent models and the evaluation metric (AUC and TSS) values computed for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*. Environmental variables had a spatial resolution of 2.5 arc minutes. Study regions had an extent from 93°E to 120°E and from -8°N to 15°N for *Batagur* spp. and from 72°E to 129°E and from -8°N to 32°N for *Pelochelys cantorii*.

Variable contribution (%)	*B. borneoensis*		*B. affinis*		*P. cantorii*	
	Mean	SD	Mean	SD	Mean	SD
Precipitation Seasonality (Coefficient of Variation)	12.18	8.51	8.22	15.50		
Precipitation of Warmest Quarter	11.51	4.82			9.36	7.33
Mean Temperature of Driest Quarter	76.32	10.40				
Annual Mean Temperature			20.65	24.29	16.18	13.75
Min Temperature of Coldest Month			71.13	32.46		
Mean Temperature of Warmest Quarter					15.50	12.49
Precipitation of Driest Quarter					21.54	9.65
Mean Diurnal Range (Mean of monthly (max temp - min temp))					11.73	11.22
Temperature Seasonality (standard deviation ×100)					25.68	12.86
Minimum training presence cloglog threshold	0.15	0.09	0.35	0.12	0.25	0.11
AUC training	0.95	0.02	0.80	0.06	0.85	0.03
AUC test	0.93	0.09	0.78	0.21	0.73	0.18
TSS	0.69	0.28	0.37	0.30	0.26	0.26

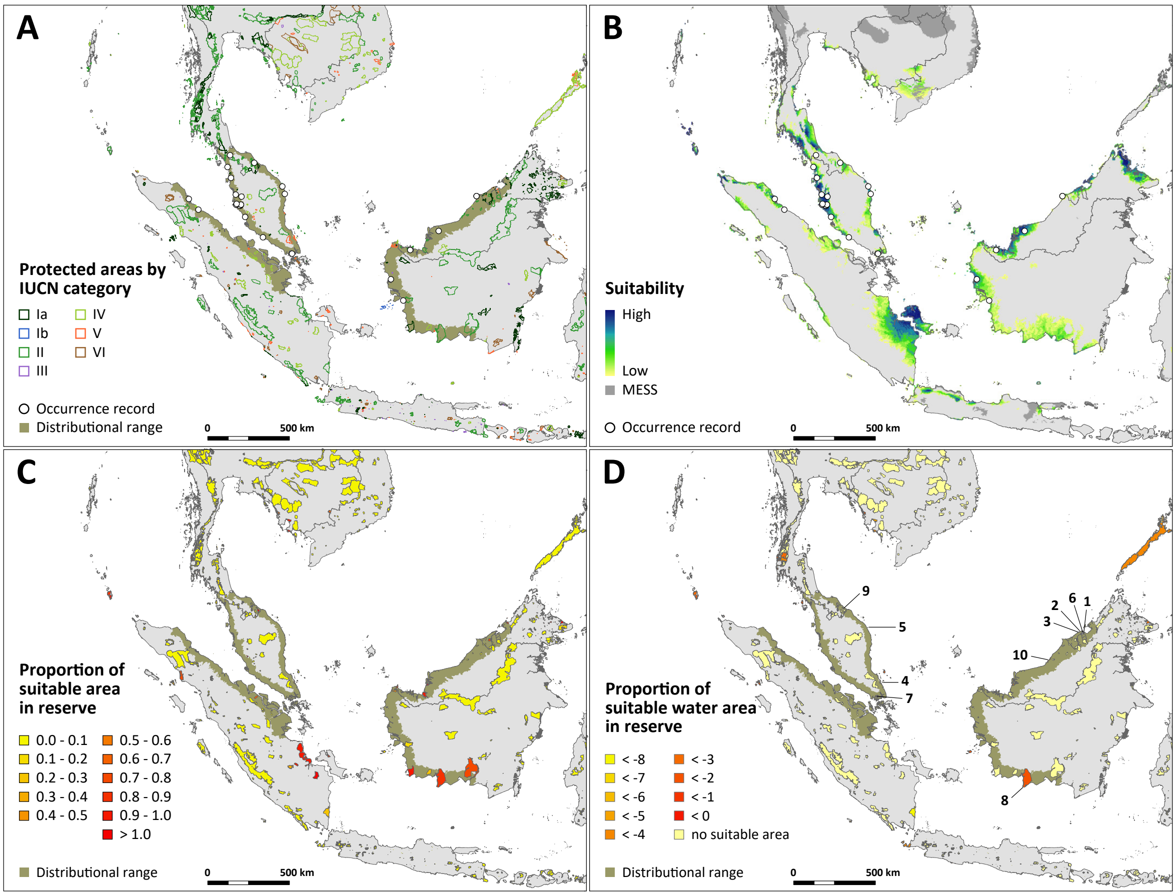

Figure 1. (A) The distribution of *Batagur borneoensis* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

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Table 2. Proportions of suitable habitat within designated protected areas per country for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*.

Species	Country	Current (%)	Future scenarios (%)			
			ssp126	***ssp245***	***ssp370***	***ssp585***
Batagur borneoensis	IDN	76.37	44.78	41.26	38.66	37.73
	MYS	7.53	8.87	10.85	10.50	9.87
	THA	6.76	16.91	15.58	16.35	18.41
	PHL	2.85	5.53	9.86	8.18	7.29
	KHM	2.73	17.13	15.80	19.90	20.38
	IND	2.17	0.24	0.48	0.37	0.32
	BRN	1.07	0.55	0.88	0.81	0.71
	VNM	0.52	3.29	2.11	1.92	2.04
	SGP	0.01	0.01	0.03	0.02	0.02
	LAO	0.00	1.88	2.24	2.27	2.15
	MMR	0.00	0.81	0.90	1.01	1.07
Batagur affinis	IDN	61.65	42.86	38.56	38.29	38.37
	PHL	22.65	10.54	8.34	7.31	6.76
	MYS	8.14	11.29	10.69	10.04	9.63
	THA	2.73	12.86	15.61	17.87	19.12
	BRN	1.72	1.01	0.83	0.72	0.67
	KHM	1.36	16.97	20.63	20.26	19.69
	VNM	0.87	1.30	2.24	2.33	2.46
	IND	0.84	0.51	0.38	0.32	0.29
	SGP	0.05	0.03	0.02	0.02	0.02
	LAO	0.00	2.40	2.43	2.23	2.11
	MMR	0.00	0.22	0.28	0.62	0.87
Pelochelys cantorii	IDN	24.00	22.60	20.35	18.95	18.96
	PHL	18.45	9.05	11.07	11.54	11.51
	THA	12.60	2.70	7.15	9.73	11.81
	KHM	9.65	2.61	5.89	6.84	6.89
	LKA	8.85	7.73	6.47	5.34	4.86
	IND	8.24	23.88	19.05	17.38	15.85
	MYS	6.52	1.65	4.17	4.81	4.89
	VNM	3.40	5.06	4.29	3.97	3.85
	LAO	2.61	1.96	4.74	7.28	8.04
	MMR	1.96	13.32	9.98	8.59	8.07
	BGD	1.16	1.83	1.23	0.91	0.80
	TWN	0.93	1.17	0.90	0.79	0.78
	NPL	0.85	4.66	3.12	2.36	2.16
	JPN	0.33	0.53	0.35	0.26	0.31
	BRN	0.25	0.07	0.32	0.37	0.38
	CHN	0.15	0.61	0.44	0.37	0.33
	BTN	0.02	0.52	0.47	0.48	0.49
	SGP	0.02	0.03	0.02	0.01	0.01
	GBR	0.01	0.01	0.01	0.00	0.00
	MDV	0.00	0.00	0.00	0.00	0.00

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Table 3. Proportions of suitable habitat containing water area cover existing within Protected Areas per country for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*.

Species	Country	Current (%)	Future scenarios (%)			
			ssp126	***ssp245***	***ssp370***	***ssp585***
Batagur borneoensis	THA	65.22	65.64	66.22	66.25	65.97
	IDN	25.84	14.25	14.15	14.15	14.09
	MYS	2.37	3.07	3.10	3.10	3.09
	KHM	2.06	0.82	0.82	0.82	0.82
	IND	1.76	0.70	0.71	0.70	0.70
	PHL	1.45	5.41	5.47	5.46	5.44
	BRN	1.31	0.52	0.52	0.52	0.52
	SGP	0.01	0.00	0.00	0.00	0.00
	MMR	0.00	5.43	5.49	5.48	5.46
	VNM	0.00	4.17	3.51	3.50	3.91
	LAO	0.00	0.00	0.00	0.00	0.00
Batagur affinis	THA	51.98	65.26	65.91	65.91	65.91
	IDN	27.85	14.56	14.08	14.08	14.08
	PHL	9.24	5.63	5.44	5.44	5.43
	MYS	5.99	3.19	3.08	3.08	3.08
	KHM	1.42	0.85	0.82	0.82	0.82
	VNM	1.41	3.61	4.00	4.00	4.00
	IND	1.21	0.73	0.70	0.70	0.70
	BRN	0.90	0.54	0.52	0.52	0.52
	SGP	0.00	0.00	0.00	0.00	0.00
	MMR	0.00	5.64	5.45	5.45	5.45
	LAO	0.00	0.00	0.00	0.00	0.00
Pelochelys cantorii	IDN	53.82	24.33	50.85	54.83	56.01
	IND	25.14	17.05	5.34	4.60	4.70
	PHL	10.65	27.14	31.07	29.41	28.42
	THA	6.26	19.82	8.09	7.17	7.03
	LKA	0.85	2.74	1.02	0.85	0.82
	JPN	0.74	2.76	0.86	0.74	0.71
	MMR	0.67	1.76	0.93	0.80	0.77
	VNM	0.59	1.00	0.37	0.34	0.33
	MYS	0.51	0.61	0.53	0.45	0.43
	GBR	0.35	1.45	0.45	0.39	0.37
	BGD	0.23	0.80	0.25	0.21	0.21
	KHM	0.11	0.45	0.14	0.12	0.12
	BRN	0.07	0.03	0.09	0.08	0.07
	MDV	0.01	0.05	0.02	0.01	0.01
	TWN	0.00	0.00	0.00	0.00	0.00
	SGP	0.00	0.00	0.00	0.00	0.00
	NPL	0.00	0.00	0.00	0.00	0.00
	BTN	0.00	0.00	0.00	0.00	0.00
	CHN	0.00	0.00	0.00	0.00	0.00
	LAO	0.00	0.00	0.00	0.00	0.00

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Table 4. Ranking of national and planned reserves of top conservation priority for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*. Reserves which are also found potentially important under climate change and outside their respective MESS ranges are listed under future scenarios (SSPs: 126, 245, 370, 585; NA: Not Available). More information on the IUCN categories can be found at https://www.iucn.org/.

Rank	Reserves	IUCN	Country	Status	Designation	Future scenarios (SSP)
Batagur borneoensis						
1	Selirong (Productive Production)	V	BRN	Designated	Forest Reserve	NA
2	Berakas (Recreation)	V	BRN	Designated	Forest Reserve	NA
3	Berakas (Conservation)	Ia	BRN	Designated	Forest Reserve	NA
4	Four Islands	IV	MYS	Designated	Wildlife Reserve	NA
5	Pulau Kapas	II	MYS	Designated	Marine Park	NA
6	Pulau Siarau Nature Reserve	Ia	BRN	Designated	Forest Reserve	NA
7	Sungei Buloh Wetland Reserve	Ib	SGP	Designated	Nature Reserve	NA
8	Tanjung Puting National Park	II	IDN	Designated	Ramsar Site, Wetland of International Importance	NA
9	Ao Manow-Khao Tan Yong	II	THA	Proposed	National Park	NA
10	Similajau	II	MYS	Designated	National Park	NA
B. affinis						
1	Thanh Phu	IV	VNM	Designated	Nature Reserve	126
2	Pulau Kapas	II	MYS	Designated	Marine Park	126
3	Sungei Buloh Wetland Reserve	Ib	SGP	Designated	Nature Reserve	126
4	Ao Manow-Khao Tan Yong	II	THA	Proposed	National Park	126
5	Dong Peng	VI	KHM	Designated	Multiple Use Management Area	126
6	Way Kambas	II	IDN	Designated	National Park	126, 245
Pelochelys cantorii						
1	Initao-Libertad	V	PHL	Designated	Protected Landscape and Seascape	NA
2	Sto. Niño-Basiawan	VI	PHL	Designated	Fish Sanctuary	NA
3	Naujan Lake	IV	PHL	Designated	National Park	NA
4	Sibuti	IV	MYS	Designated	Wildlife Sanctuary	NA
5	Turtle Islands Park	II	MYS	Designated	State Park	NA
6	Ao Phanganga	II	THA	Designated	Marine National Park	NA
7	Mu Ko Lanta	II	THA	Designated	Marine National Park	NA
8	Padada (Malalag)	VI	PHL	Designated	Fish Sanctuary	NA
9	Haliday Island	IV	IND	Designated	Sanctuary	126, 245
10	Had Vanakorn	II	THA	Designated	Marine National Park	126

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Brunei; Four Islands, Pulau Kapas, and Similajau in Malaysia; Sungai Buloh Wetland Reserve in Singapore; Tanjung Puting National Park in Indonesia, and Ao Manow-Khao Tan Yong Reserve in Thailand (Table 4).

Most of the distribution estimated by TTWG (2017) for *B. affinis* overlaps the potentially suitable habitats predicted by the model. In contrast to *B. borneoensis*, the potential distribution of the species inferred from climate data includes extensive inland areas, especially on Sumatra and Borneo (Fig. 2b). Other suitable habitats include Java in Indonesia, Palawan in the Philippines, eastern Thailand, and southern Vietnam and Cambodia. Note that although the species has not been reported there, the climate on Borneo and in the Philippines is predicted to be suitable for the species. Unfortunately, only a small part of the potentially suitable distribution is covered by Protected Areas. As for *B. borneoensis*, Indonesia has the highest proportion (62%) of potential distribution of *B. affinis* within protected reserves, followed by Philippines (23%), Malaysia (8%) and other countries (<5%) (Fig. 2c, Table 2). Figure 2d shows the reserves of major importance in terms of suitable areas with water surface cover, with the highest proportion in Thailand (52%), followed by Indonesia (28%), Philippines (9%) and Malaysia (6%), while coverage is low in other countries (<5%) (see also Table 3). Within the estimated distribution of *B. affinis*, several reserves with conservation priority were identified (Fig. 2d): Thanh Phu and Dong Peng (Cambodia), Pulau Kapas (Malaysia), Sungei Buloh Wetland Reserve (Singapore), Ao Manow-Khao Tan Yong (Thailand), and Way Kambas (Indonesia) (Table 4).

For the wide-ranging *P. cantorii*, the potential distribution predicted by climate covers a large part of the distribution estimated by TTWG (2017), which spans from peninsular India to Southeast Asia and China (Fig. 3b). Other suitable habitats were predicted in Sri Lanka, southern Myanmar, southern Cambodia, Java and Sulawesi in Indonesia, and the central Philippines. Ranking suitability of Protected Areas by country in Fig. 3c suggests that Indonesia

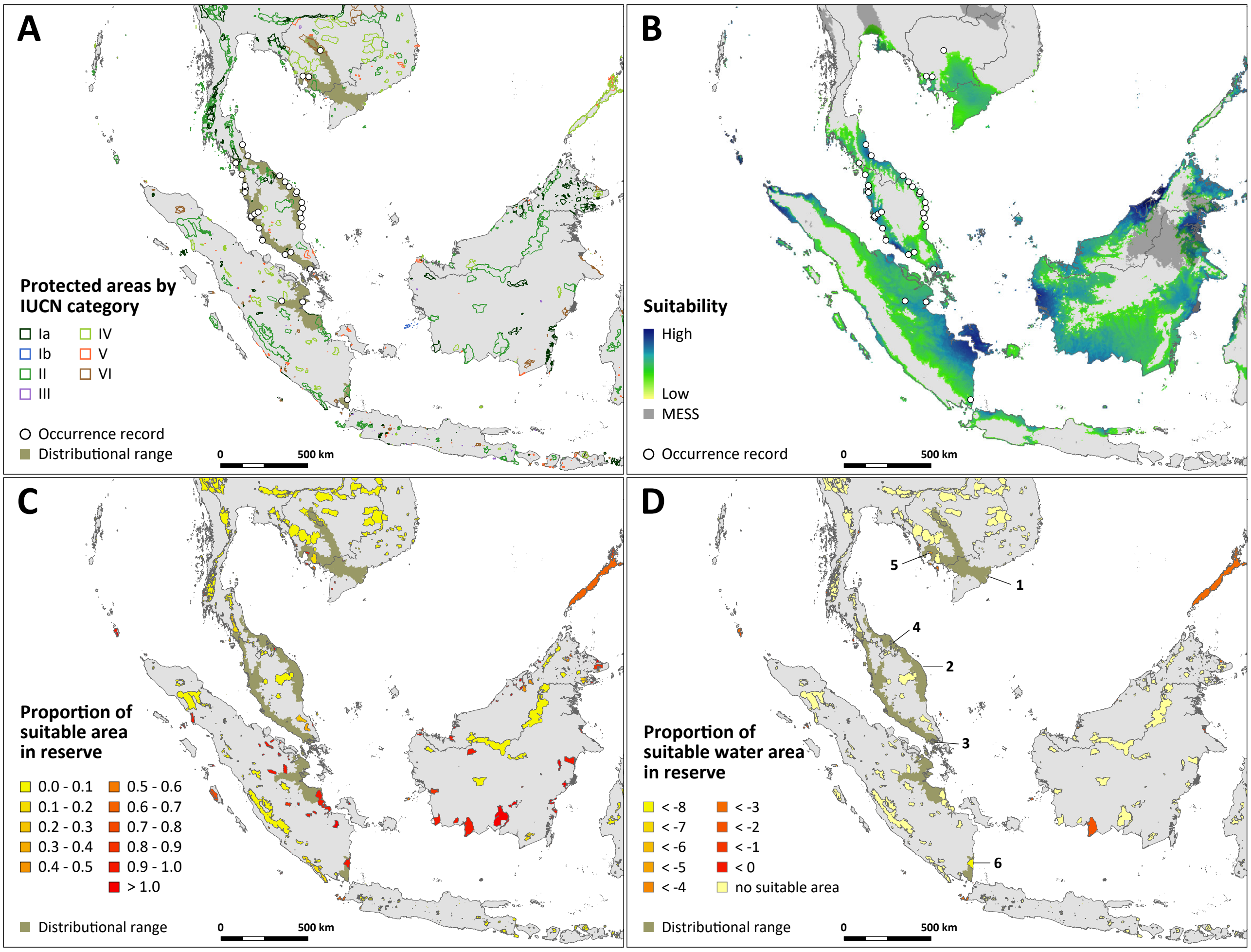

Figure 2. (A) The distribution of *Batagur affinis* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

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(24%) and Philippines (18%) are of major importance, while coverage is low in Thailand (13%), Cambodia (10%), Sri Lanka (9%), India (8%), Malaysia (6%), and other countries (<5%) (Table 2). The inclusion of water occurrence indicates that Indonesia (54%) represents the highest coverage of suitability, followed by India (25%), Philippines (11%) and Thailand (6%), whereas the coverage is less than 5% in other countries (Fig. 3d, Table 3). Several important Protected Areas providing major suitable water coverage for *P. cantorii* within the estimated distribution were identified: Initao-Libertad, Sto. Niño-Basiawan, Naujan Lake and Padada (Malalag) in Philippines; Sibuti and Turtle Islands Park in Malaysia; Ao Phanganga, Mu Ko Lanta and Had Vanakorn in Thailand, and Haliday Island in Indonesia (Table 4).

Future projections and potential distribution

Our models predicted future potential increases in the size of the geographic range for the three turtle species in all emission scenarios. Potential suitable habitats for *B. borneoensis* and *B. affinis* are predicted to move further north and inland as compared to current predictions (Fig. S1-S3). Large parts of Southeast Asia, including new areas, such as Myanmar and Laos are predicted to become suitable for both *Batagur* species (Fig. S1-S2). However, climate in mountainous regions seem to remain unsuitable. Surprisingly for *P. cantorii*, climate in coastal areas of Southeast Asia, peninsular India and Sri Lanka which are currently suitable are predicted to become less suitable than the current prediction (Fig. S3). The bioclimatic range of *P.cantorii* is predicted to increase northwards, especially into India, Myanmar, Vietnam, and China.

The four scenarios show that Indonesia still remains the country of the largest extent of designated Protected Areas with suitable habitat for all three species. The following countries of major importance in suitable Protected Areas are Cambodia, Thailand, Philippines, and Malaysia for all species, while Myanmar,

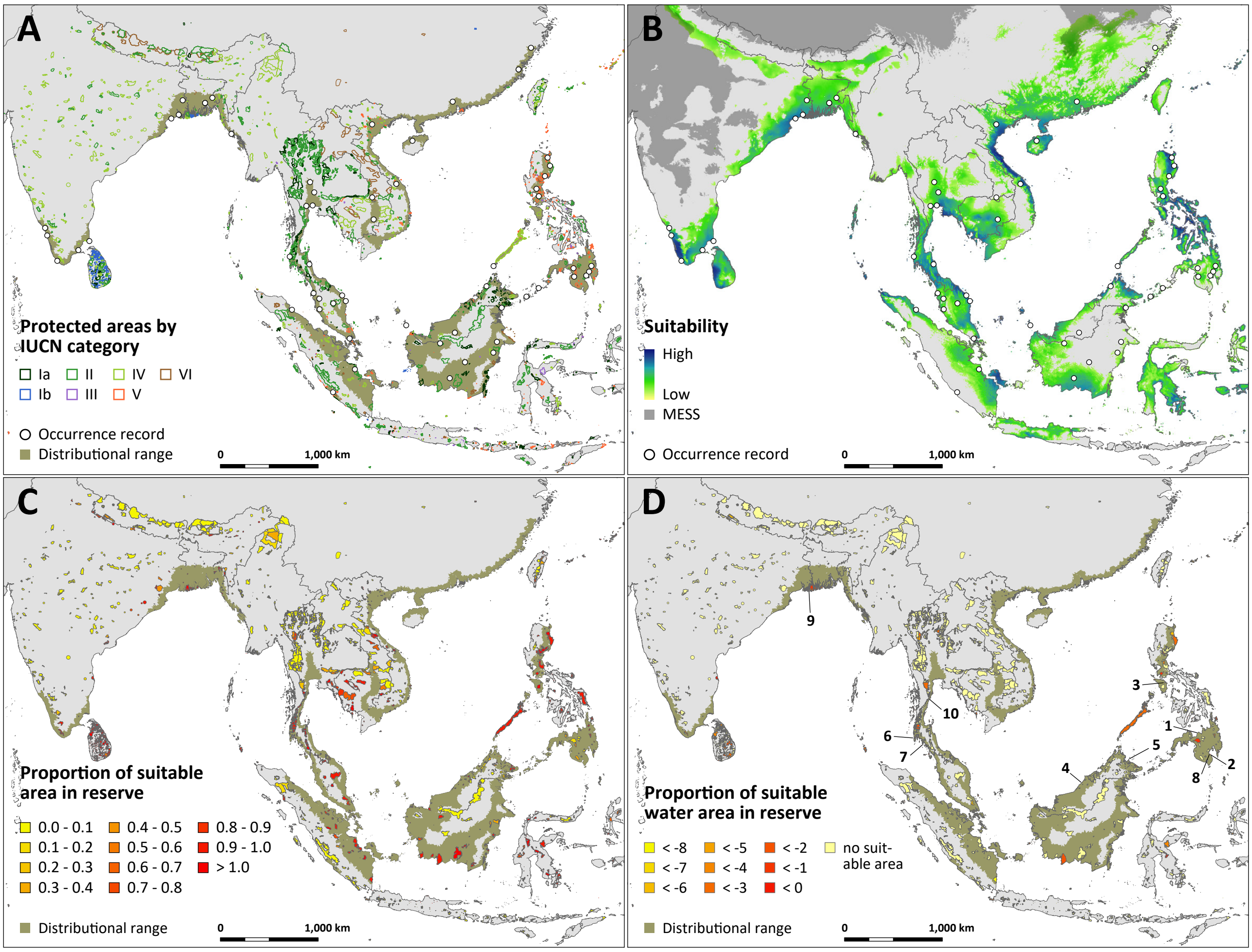

Figure 3. (A) The distribution of *Pelochelys cantorii* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

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Sri Lanka, and India are also important for *P. cantorii* (Table 2). Interestingly, Cambodia has the highest gain of potentially suitable habitat in Protected Areas in the future, up to 17% for *B. borneoensis* and 19% for *B. affinis*, while a similar pattern was also evident in Thailand (Table 2). Results of water coverage within reserves show that Thailand and Indonesia are predicted to remain highly suitable in all future scenarios of these two species (Table 3). For *P. cantorii*, the four scenarios show that water coverage located in reserves in the Philippines is predicted to increase by up to about 21%. Under the SSP126 scenario, this species is predicted to lose 20% of suitable water coverage in Indonesia while gaining 14% in Thailand. For all three species, we listed the future emission scenarios, containing the same predicted protected reserves found outside MESS area with the highest important water coverage as the current prediction, in Table 4.

Discussion

Our models may have a tendency for over-fitting. However, this should mean that they avoid over-prediction, which would be more problematic in the context of our study. As our goal is providing guidance for conservation, we prefer to have a robust assessment of those areas which are most suitable, avoiding predicting marginal habitats. The wide spatial extent of potentially suitable habitat for the three freshwater turtles detected by our models, compared to the distributions previously estimated by TTWG (2017), indicates that a number of potential undiscovered populations and/or anthropogenic exploitation of these populations may exist. The variables of highest contribution to the model (except for annual mean temperature and temperature seasonality) in this study correspond to those previously suggested to be of general importance to chelonian distributions (Ihlow et al. 2012). Although the incorporation of additional predictors of the three study species' habitat requirements and physiological data would improve the accuracy and performance of the models, current knowledge on their ecology is very limited. Our results suggest that based on Protected Areas designated under the IUCN standards, Indonesia appears to be of major importance for conservation priorities in all three species for current and future scenarios. However, Thailand has the highest ranked conservation areas with suitable water coverage for *Batagur borneoensis* and *B. affinis*. Even though no species records have been found on the small islands off the coast of the mainland, we did not exclude the possibility that these islands might harbour viable native or introduced populations.

Batagur borneoensis

Most of the potential distribution of *B. borneoensis* predicted by our model is restricted to coastal areas (see Fig. 1b). This corresponds to the species' habitat and nesting preferences. The species' presence is usually influenced by salinity level and availability of mangrove apples (*Sonneratia* spp.) in the mangrove forest biome, reflecting conditions which occur in the lower course of rivers (Hernawan et al. 2019). Also, females migrate as a group up to 20 km from the river mouth to find sandy areas as nesting sites (Dunson and Moll 1980). However, this species has been reported to have experienced a marked decline in the global population within the last century (Hernawan et al. 2019). On the east coast of Peninsular Malaysia, the largest known breeding populations are in the Paka and Setiu river systems, where two decades ago more than 100 breeding females possibly occurred (Sharma and Tisen 2000), but populations have since apparently continued to decline. Unfortunately, too few of these coastal areas are designated Protected Areas under the IUCN categories.

Because this species lives in close proximity to humans, its populations have been threatened by construction of beach front property and harvesting of adults and eggs for food (TCC 2018). Therefore, we strongly recommend the designation of additional reserves, applying IUCN standards, along the suitable coasts of Malaysia (e.g., Setiu Wetlands). In Indonesia, however, numerous designated and proposed reserves cover large parts of potential suitable habitat of *B. borneoensis*. Although highly suitable protected reserves with the highest proportion of water suitability are also found in Thailand and Brunei Darussalam (Table 4, Fig. 1d), limited evidence of sightings of *B. borneoensis* in these countries have been reported (TCC 2018). Further monitoring in these conservation priority areas is urgently needed to identify if they harbour viable populations of this endangered turtle species.

Batagur affinis

Once widespread in all major rivers draining into South China Sea, *B. affinis* is also a critically endangered species listed on the IUCN Red List, and its populations are declining or extirpated over most of its former range (Moll et al. 2015). The potential distribution of this species from our analysis showed that it might possibly be found further inland as compared to *B. borneoensis* (Fig. 2b), suggesting that *B. affinis* could be more of a generalist species. The inland preference could also be associated with movements of *B. affinis* up river with the rising tide in order to forage (Dunson and Moll 1980). Furthermore, this species migrates as much as 80 km upstream to riverine sand banks to nest during the dry season (Holloway 2003). Estuaries and tidal regions in large rivers (e.g., Perak and Setiu in Malaysia) are dominant habitats for this species where they feed on plant materials in water with salinities of not more than 20 ppt (Davenport et al. 1992). However, sand mining and dam construction have decimated suitable nesting areas in many areas. One example is the upstream dam construction on the Kedah River, which was built directly on the nesting beaches (Moll and Moll 2000, 2004). At the same time, this species has been locally exploited for its eggs and internationally for its meat from the vast demand for turtle consumption in China (Moll et al. 2015).

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Again, we propose the same recommendations as for *B. borneoensis,* to add additional designated reserves on the coasts of Malaysia, particularly in the states of Negeri Sembilan, Perak and Terengganu to prevent further habitat destruction and poaching. In the Sre Ambel River in Cambodia, a small population was rediscovered in 2001 (Platt et al. 2003) and currently is under the protection of the Dong Peng management area (Fig. 2d). Future conservation efforts should be focused in the river systems in southern Cambodia and the Mekong delta of Vietnam, where isolated populations represent important genetic variation within the species (Çilingir et al. 2019). A survey from a report by Mistar et al. (2012) [unpublished] to find wild *B. affinis* in Sumatra was futile (Moll et al. 2015, TCC 2018). However, a remnant population was found by local fishermen in the Indragiri River and mangrove swamps around Mumpa (Mistar et al. 2012 unpublished). Hence, we recommend further surveys for *B. affinis* populations in eastern and southeastern Sumatra (Fig. 2b) where a large part of the suitable area remains unprotected (Fig. 2c).

Pelochelys cantorii

Although it has a wide distribution, *P. cantorii* has disappeared from most of its former range, with only scattered individuals reported recently (TCC 2018). Our analysis confirmed the widespread habitat suitability of this species, with potential habitat matching closely with that estimated by TTWG (2017) (see Fig. 3a and 3b). This suggests that *P. cantorii* might be a generalist with a sparse geographical occurrence but with a wide range of habitat preferences (Das et al. 2008). Nesting habits on ocean beaches (Das et al. 2008) and tolerance of seawater are probably responsible for its occurrence along the coast. Therefore, despite having suitable climate, the potential inland occurrence along the Ganges and Brahmaputra basins shown in Fig. 3b is not possible due to the overwhelming distance from and lack of suitable connection to the sea.

Within recent decades, this species has often been caught for human consumption (Das 2008). Habitat destruction has also depleted and fragmented populations. For example, though protected as a national priority aquatic species, *P. cantorii* once occurred in large numbers in China, but is now presumed to essentially be extirpated there as a result of overcollection for food, urbanisation, water pollution, and overfishing (Lau and Shi 2000, Xiaoyou et al. 2019). Despite being a small country, Sri Lanka appears to have many suitable Protected Areas, although no sightings of *P. cantorii* have been observed there (Fig. 3c). In India, many individuals have been encountered in the suitable areas predicted in the peninsula and northern parts of the east coast (Rashid and Khan 2000), but there is a lack of designated or proposed reserves (Fig. 3c). A similar situation can be found in Bangladesh. In peninsular Malaysia, *P. cantorii* has been found in fair numbers (Sharma and Tisen 2000), with many suitable reserves far inland, even with an individual found in Taman Negara (TTWG 2017). However, the situation seems bleak in Thailand and Vietnam, where most populations are believed to be extirpated, leaving only one apparent viable population in the lower Mekong River in Cambodia (Touch et al. 2000). Indonesia currently holds the largest area suitable for conservation of *P. cantorii,* but breeding populations may be rare (TCC 2018). However, a fishery survey detected some collected specimens for trading in southern Sumatra (Oktaviani and Samedi 2017). The Philippines and Borneo seem to be the last strongholds, with suitable protected reserves which may support viable breeding populations. In Kalimantan Borneo, an individual was found as far as 200 km from the nearest coast (Fig. 3a). We thus urge further research and conservation efforts in these areas, particularly in the reserves with high suitability (Table 4).

Impact of climate change

Our initial results show that all three turtle species might benefit from climate change by 2080 in terms of potential increases in their suitable ranges. Not surprisingly, their ranges are predicted to expand northwards in mainland Asia and inland in southeast Asia due to more favourable climate conditions at higher elevations and latitudes. These patterns are consistent with the shift in species richness and in *Kinosternon* species predicted by Ihlow et al. (2012) and Butler et al. (2016), respectively.

However, many of these future potentially suitable areas of expanding range have uncertain predictabilities due to extrapolation (see MESS maps Fig. S1-S3). The MESS results suggest that climatic conditions in many areas, especially on the coasts, which are predicted to be suitable for these species, represent extrapolations beyond the training range of the models and hence might not be reliable. One stable suitable area for the future survivability of *P. cantorii* could exist in northern Vietnam and China under different scenarios (Fig. 3). Assuming the current water bodies and protected reserves remain, only *B. affinis* would be classifiable as 'least threatened' in scenario SSP 126, while in most other future scenarios, the long-term situation for the conservation of each of the three species appears bleak (Table 4). It is important to recognise that variance in future model prediction increases when only a small number of presence points are considered over large areas (Bean et al. 2012, Rej and Joyner 2018).

Loss of large suitable areas was also predicted by a similar climatic model for *B. borneoensis* in 2080 (Ihlow et al. 2012). Moreover, only up to a quarter of these areas were outside the extrapolation area (i.e., beyond training ranges) (MESS). However, the wide-ranging species *P. cantorii* was found to be least potentially impacted by climate change (Ihlow et al. 2012). The answer to the question of whether these turtle species can adjust to new climatic conditions generated by climate change, is still unclear. However, with the unavailability of stable suitable Protected Areas suggested by our models and assuming highly

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conservative climatic niches and low potential for rapid evolutionary adaptations in turtles (Stephens and Wiens 2009, Berriozabal-Islas et al. 2020), we would expect a severe decline in their populations in the future. In addition, synergistic effects from continued exploitation, habitat loss and degradation, economic development, agricultural pressures, and endemic plant species loss predicted by the year 2050 increase the uncertainty of long-term persistence of these turtles (Habel et al. 2019).

Conclusions

Although our Maxent models are derived from climate data and comparatively small numbers of occurrence records, they nevertheless provide a useful guideline to direct further surveys in areas of potentially unknown populations (Pearson et al. 2007). Urgent surveys and monitoring to detect and ensure adequate populations in Protected Areas throughout their ranges will be critical to the survival of these critically endangered turtles. As a result, having additional occurrence data from field surveys can be used to improve our current predictions. Continuing to collect ecological and physiological data and studying the genetic diversity, population structure and microhabitat preferences of these species will in turn help evaluate their future status. As our study area is currently a turtle diversity hotspot (Ihlow et al. 2012, Mittermeier et al. 2015), we might expect to find many other species in the Protected Areas included within the bounds of our study.

Our findings demonstrate that although these three endangered freshwater turtles are protected by several IUCN designated and proposed reserves, their populations are vulnerable as a result of extensive habitat loss and fragmentation in the present and expected to increase in the future (Sodhi et al. 2004, Habel et al. 2019). Despite being protected under national laws, many of these species are still relentlessly poached for eggs and meat and exported due to the lack of law enforcement (van Dijk et al. 2000, TCC 2018). Proposing new reserves may seem to be an easy direct approach to conserving these threatened species but insufficient funds in park management and monitoring remain a problem. Perhaps small-scale conservation efforts are more effective in preserving remaining specimens rather than allocation of new reserves in areas which are intensively degraded. In Peninsular Malaysia, captive breeding programs are currently operating in Terengganu and Melaka for *B. borneoensis* by the Fisheries Malaysia and WWF Malaysia, while similar hatcheries have long been established for *B. affinis* in the states of Perak and Kedah by the Department of Wildlife and National Parks (Duli 2009 unpublished). Several captive breeding centres in Guangdong and Yunnan China are starting to achieve some success in breeding and reintroducing *P. cantorii* (Xiaoyou et al. 2019). Van Dijk (2000) further recommended coordinating breeding programs between engaged countries. Successful conservation programs in the future will require cooperation from multiple countries in exchanging information and scientific knowledge. Lastly, awareness programs with community involvement and education are necessary in promoting the conservation of these turtles (Moll et al. 2015, TCC 2018).

Acknowledgements

W.C. Tan was financially supported through a stipend from the German Academic Exchange Service (DAAD). We thank M. Flecks for his invaluable technical assistance with the map figures.

Author Contributions

WCT and DR conceived the ideas, designed methodology and analysed the data. PG helped with data analyses and giving guidance in the models. WCT led the writing of the manuscript. AGJR and JBI provided locality and range data and added their expertise on the topic. All authors contributed to the drafts.

Data Accessibility

All locality data will be published in TTWG (in press) and are available from AGJR.

WorldClim: www.worldclim.org

World Database of Protected Areas: https://www.protectedplanet.net/

Water cover data: https://global-surface-water.appspot.com

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Figure S1. Future potential distribution of Batagur borneoensis by the year 2080 derived from the Maxent model.

Figure S2. Future potential distribution of Batagur affinis by the year 2080 derived from the Maxent model.

Figure S3. Future potential distribution of Pelochelys cantorii by the year 2080 derived from the Maxent model.

Appendix S1. Lambda files from Maxent models.

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Submitted: 21 November 2020
First decision: 13 January 2021
Accepted: 3 March 2021

Edited by Minh Le, Mary Blair and Robert J. Whittaker

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