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Disappearing archosaurs – an assessment of established protected areas in the Philippines to save the critically endangered, endemic Philippine Crocodile (*Crocodylus mindorensis*)

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Abstract. Once distributed all over the Philippines, the endemic Philippine Crocodile (*Crocodylus mindorensis*) is nowadays threatened with extinction. It is estimated that less than 140 mature individuals live in the wild. Human activities like fishing and poaching, as well as land-use change and habitat conversion cause a continuing threat to the remaining populations. Therefore, designated protected areas (PAs) were evaluated with species distribution models (SDMs) and also to see if most suitable areas are covered by PAs in order to improve future conservation efforts. For this purpose, the existing IUCN-reserves were analysed for potential habitat suitability (combining bioclimatic and remote sensing variables), wetland occurrences and the human footprint index by using MaxEnt and QGIS. Based on species records, our final SDM showed high performance and revealed the climatically most suitable areas for the species, which were mostly on Luzon and Mindanao. However, only small parts of the climatically suitable wetlands are currently covered by reserves (0.3–46.3%). In addition, none of the species' records was located within a PA. The anthropogenic pressures in the reserves measured by human footprint index (considering eight variables i.e. 'population density', 'navigable waterways', 'crop lands' and 'roads') were diverse and varied between a low and moderate level. Most of the records were found in areas with a moderate human footprint. Considering the three criteria, 'Lake Lanao Watershed Reservation', 'Angat Watershed Forest Reserve District (Metro Water District)', 'Northern Sierra Madre Natural Park', 'Talaytay Protected Landscape' and 'Agusan Marsh Wildlife Sanctuary' revealed to be the most suitable conservation areas for *C. mindorensis*, whereas suitable areas outside PAs are highly recommended for further surveys. We recommend to declare Ligawasan Marsh, Mindanao as a PA as this area harbours a large population of *C. mindorensis*. The declaration of more climatically suitable areas with low level of human footprint to PAs is a necessary step for the long-term conservation of this endemic crocodile species. The current network of existing PAs needs improvement in order to provide well-suited and long-term protection for *C. mindorensis.* More surveys are also necessary to find hidden, so far overlooked populations and to assess *C. mindorensis* tolerance level for human impacts.

Key words. Crocodylia, species distribution modelling, human footprint index, wetlands, IUCN, MaxEnt, conservation, reptiles.

Introduction

The Philippines are one of the 20 global megadiverse countries and a major biodiversity hotspot in Southeast Asia due to its isolated location and diverse topography (CBD 2018, Peria 2014, UNDP 2021, von Rintelen et al. 2017). These megadiverse countries are home to about 70–80% of the plant and animal species on the planet, of which more than 20,000 are endemic (Ambal et al. 2012, FPE 2013). Almost half of the terrestrial animals occurring in the Philippines are also endemic to the country and in the case of reptiles, ~ 70% (244 of the 352 known species in 2017) of native species are endemic (PSA 2019). According to the categories of the International Union for Conservation of

Nature's (IUCN) Red List of Threatened Species, 652 native species of animals and plants are classified as 'Vulnerable', 542 as 'Endangered', 309 as 'Critically Endangered' and 15 of those (all members of the fish genus *Barbodes*) are already extinct (IUCN 2021a).

The Philippine Crocodile *Crocodylus mindorensis* Schmidt, 1935 has been classified as 'Critically Endangered' on the IUCN Red List since 1996, while the latest assessment was in 2012 (van Weerd 2016). Unlike the Indo-Pacific Crocodile, *Crocodylus porosus* Schneider, 1801, also known as Saltwater Crocodile, which is native to the Philippines but extends as far as South Asia, Southeast Asia and Australia (Uetz 2021), the Philippine Crocodile is endemic to the Philippines (van de Ven et al. 2017). Originally, *C. mindorensis* was distributed over almost the entire archipelago and inhabited islands of Mindoro, Masbate, Samar, Negros, Busuanga, Luzon and Mindanao (Ross 1982, Ross & Alcala 1983). Since the late 1990s and in the 2000s, more surveys have been conducted, but information on the actual distributional range of the crocodile remains scarce. Although it is protected by law since 2001, there are only about 92–137 estimated mature individuals left in the wild to date (van Weerd 2016), and populations are estimated to decline. These are highly fragmented populations in 'Dalupiri Island', 'Northern Luzon' and 'Ligawasan Marsh' on Mindanao (Manalo et al. 2013, Manalo et al. 2015, van Weerd 2016).

The habitats of the relatively small Philippine Crocodile are wetlands with freshwater occurrences such as creeks, ponds, man-made water reservoirs, mangrove areas and marshes, but also fast-flowing rivers with caves made from limestone cliffs (van de Ven et al. 2017). These caves are used as hiding places just as the ones in sandy and clay river banks. Similar behaviour has also been documented with the introduced population of the species in Paghungawan Marsh, Siargao Island which was part of the government's effort to repopulate the species in the wild (Binaday et al. 2020). The species' altitudinal range extends from the favoured inland wetlands up to 850 m (sea level vs. Cordillera Mountains on Luzon) (Manalo 2007).

The Philippines face several environmental problems like deforestation and forest degradation, water pollution, poaching and illicit wildlife trade (USAID 2021). The national desire for more sustainability, environmental protection and species conservation is often contrasted by the poor income situation of local communities (Adams et al. 2004, Jaisankar et al. 2018). Furthermore, large parts of protected areas (PAs) overlap with the ancestral domains (Perez 2018). Local communities living close to or even within these areas rely on the local resources and will be socio-economically harmed by strict environmental regulations, especially if there are no alternative livelihoods (Adams et al. 2004). In fact, some of the greatest threats for the Critically Endangered *C. mindorensis* is the use of its natural habitat by rural people, as well as habitat destruction. In addition, the crocodiles are often persecuted and their nests destroyed or plundered by humans. Fishing is also considered a danger to these crocodiles as they are likely caught in fishing nets as bycatch (Akmad & Pomares 2008, van Weerd 2016).

As early as 1992, the Philippine government committed itself to the international goals of the Convention on Biological Diversity (CBD). This resulted in several national environmental laws such as the National Integrated Protected Area System (NIPAS) Act of 1992 and the Wildlife Resources Conservation and Protection Act (2001), which are intended to protect the country's natural resources in the long term (DENR-BMB 2021). Currently, 248 areas have been recognised by the Philippine government as PAs, covering a cumulative area of 7.8 million ha (DENR-BMB 2020). However, it is currently unknown if these PAs provide climatically suitable habitats for the Philippine Crocodile. Species distribution models (SDMs) have been widely used and proven to be very useful in habitat analyses of other species and are used for prioritisation in conservation planning (Binaday et al. 2020, Fois et al. 2018, Ihlow et al. 2015, Rödder et al. 2010, Tan et al. 2022, Tsuyama et al. 2015). SDMs attempt to predict potentially environmentally suitable habitat by linking documented presence records of species to environmental variables and spatial characteristics such as human footprint and availability of surface water based on the species' ecological niche. In this study, it was investigated whether the existing PAs (1) provide suitable wetland habitats and (2) are climatically suitable for the Philippine Crocodile. Furthermore, we (3) included anthropogenic impact measured as human footprint index to identify these PAs where low anthropogenic pressure occurs.

Methods

For the evaluation of suitable PAs for the species, the 248 current PAs, availability of wetland areas, the climatic suitability and anthropogenic pressure were considered. Since the first two criteria are decisive for the basic survival of the ectothermic species, the final ranking involved three steps. In the first step, the wetlands were evaluated. In a second step, the climatically suitable areas of the remaining 117 sites were identified. Anthropogenic pressure to the remaining 114 sites was assessed in the third step. A final ranking was calculated based on the combined proportions of suitable wetland area and climate suitability ('wet-sdm-ranking') and anthropogenic pressures ('hfp-ranking'), which were multiplied with each other. Below we describe our workflow in detail.

PAs and wetlands data

As it is easier to implement *in situ* conservation measures of *C. mindorensis* in areas that are subject to minor anthropogenic influence, the coverage of the species range with PAs was assessed in addition to the assessment of available potential habitats. PAs are defined as geographical areas and classified by IUCN standards (categories I–

VI) to achieve the long-term conservation of nature and the corresponding ecosystems (IUCN 2021b). The World Database of Protected Areas (WDPA) polygon shapefiles were obtained from UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC; UNEP-WCMC & IUCN 2021).

The importance of wetlands was evaluated based on assessed tropical and subtropical wetlands with a resolution of 232 meters downloaded from the Global Wetlands Map (https://www2.cifor.org/global-wetlands/) (Manalo et al. 2018, van Weerd & van der Ploeg 2012). Gumbricht et al. (2017) developed a mapping method combining different data sources and methods, and classified wetlands into three key biophysical attributes: 'long-term water supply', 'annually or seasonally water-logged soils' and 'a geomorphological position where water can be supplied and retained'. Seven categories were selected for *C. mindorensis*: 'open water', 'mangrove', 'riverine', 'floodplains', 'marshes', 'swamps' and 'fens'. Furthermore, an additional category was added by importing a high-resolution water layer from the Global Runoff Data Centre (GRDC) to assess the suitability of river networks for the crocodile (GRDC 2020).

Species records and predictor variables

Species occurrence records were collected by JWB and RM between 2003 and 2021. The dataset was examined for outliers in QGIS, ver. 3.16.3 with GRASS 7.8.5 (QGIS.org 2021), but not corrected for potential spatial autocorrelation due to the few occurrence records. Habitat suitability was predicted using SDMs based on a combination of 46 environmental variables (Supplementary Table S2; Cord & Rödder 2011). The 19 bioclimatic variables were obtained from Worldclim database, ver. 1.4 and contain interpolated elements from different climate conditions collected over a period of 30 years (1960–1990) with a resolution of 30 arc seconds (Hijmans et al. 2005). The remaining 27 environmental predictors were derived from Moderate Resolution Imaging Spectroradiometer (MODIS) sensors of two NASA satellites. The spatial resolution of the pre-processed remote sensing variables amounts to 30 arc seconds and the temporal resolutions are 8-day averages (MOD11A2) and 16-day averages (MCD43B4) (Mu et al. 2007, Scharlemann et al. 2008). Since SDMs are sensitive to multicollinearity of predictors (De Marco & Nóbrega 2018, Merow et al. 2013), we calculated Variance Inflation Factor (VIF) in R (ver. 4.0.3; 'usdm package') (Naimi et al. 2014, R Core Team 2020) to exclude highly correlated variables, when one of them exceeded the value of 10. The final variables were temperature ranges, precipitation and isothermality (Supplementary Table S2).

Species distribution modelling

For SDM, MaxEnt was chosen as this machine-learning programme (Phillips et al. 2006, Phillips et al. 2016) is shown to be more reliable than other modelling tools especially when dealing with small sample sizes (Elith et al. 2006). As the historic distributional range of *C. mindorensis* covers large parts of the Philippines (Uetz 2021), the whole country was chosen as background area. In addition, the records used for SDM construction were reduced to one per grid cell to reduce sampling bias (Phillips et al. 2009).

Model fitting and selection followed the procedure described in Ginal et al. (2022) and is based on testing multiple regularisation multipliers (0.5 to 2.5 in steps of 0.1, as well as 5 and 10) and feature classes (LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold)). MaxEnt's raw output format was used for further processing and model selection, and the averaged AICc [corrected Akaike Information Criterion (Warren & Seifert 2011)] and AUC (Elith & Graham 2009, Lobo et al. 2008, Phillips & Dudík 2008) were calculated across ten replicates. Further, AUC was used as an evaluation of the model performance (Elith et al. 2010). For AUC calculation, the presence data were randomly divided for model training (80%) and testing (20%) using the bootstrap approach. For model selection, the lowest average AICc and an AUC_{Test} above 0.7 were used (Phillips & Dudík 2008, Warren & Seifert 2011). The final model was replicated 100 times, again with an 80:20 split for training and testing. Finally, the average over the 100 replicates was calculated and evaluated using a combination of AUC (Elith et al. 2006) and True Skills Statistics (TSS) (Allouche et al. 2006, Shabani et al. 2018). For the final model, cloglog format was used as output. Considering the limited number of available occurrence records and the historical distribution of the species, the 'minimum training presence'-threshold was chosen for presence/absence.

The above mentioned wetland shapefile was overlaid with the reclassified MaxEnt-output (settings '0 – threshold = NA; ≥ threshold = 1') and then analysed together with PAs using the 'zonal.histogram'-raster function in QGIS (QGIS.org 2021). The obtained numbers of grid cells per category were summed up per reserve in proportion to the total area of the reserve.

To obtain sums and counts from the final model, the MaxEnt output was subjected to a second but separate classification in a first step (settings '0 – threshold = NA'). Then this reclassified MaxEnt output was rescaled within the range 0–1 before it was analysed with the shapefile generated in the 'zonal.histogram-analysis' using the 'zonal.statistics'-raster function in QGIS. The generated data provided information on how well the habitat is suited for the Philippine Crocodile in terms of climatic conditions ('sum'). Furthermore, it was possible to calculate the area of suitable habitat within a PA using 'count', which calculates the number of grid cells of the suitable area. The sum values were ranked in descending order. Since the resolutions of the MaxEnt-map (~ 1000 m) and the wetlands map (232 m) differ, both rankings were multiplied and a new combined ranking was assigned ('wet-sdm-ranking', ascending order).

Table 1. Results of the ten best MaxEnt models used for model selection, ranked by the mean AICc values and with information on the regularisation multipliers, feature classes, number of parameters, AICc, AUC_{Train} and AUC_{Test}. The final model used for the following processes is shown in bold.

Regularisation	Features	nParameters	AICc	AUC_{Train}	AUC_{Test}
0.6	**LPT**	**7.5**	**253.40**	**0.92**	**0.86**
0.9	L	6.5	256.08	0.90	0.83
1.0	LP	6.5	260.48	0.93	0.89
0.8	LP	6	265.08	0.88	0.89
1.2	LPT	5.5	266.02	0.88	0.86
1.1	LPT	6	266.06	0.86	0.84
1.0	LT	7	266.30	0.90	0.87
1.1	L	5.5	266.67	0.87	0.83
1.0	L	6.5	266.94	0.88	0.83
1.3	LT	5	267.03	0.90	0.85

Anthropogenic pressure

To assess the potential effect of anthropogenic pressure on the crocodiles, the 2018 release of human footprint was obtained from SEDAC (NASA Socioeconomic Data and Applications Center) and added to our analyses. These maps comprise eight variables (i. e. 'population density', 'navigable waterways', 'crop lands' and 'roads') to measure the direct and indirect human pressure (Venter et al. 2018). The human footprint-ranking ('hfp-ranking') was computed based on means of the 'zonal.statistics'-raster function of the combined map of "wildareas v3 2009 human footprint" and previously mentioned PAs shapefile.

Results

Species distribution modelling

For model fitting, MaxEnt computed 3450 models in total (23 regularisation multipliers × 15 feature class combinations × 10 replicates) of which the ten best performing models were ranked according to the lowest average AICc (Table 1). The ten models revealed high AUC values [AUC_{Train} 0.86 – 0.93, AUC_{Test} 0.83 – 0.89]. The values of the final model, which was replicated 100 times, were: regularisation multiplier 0.6, feature classes LPT, AUC_{Train} 0.92, AUC_{Test} 0.86 and TSS 0.45 ± 0.18. 'Mean diurnal range of temperature' had the highest contribution to the final SDM (36.4%), followed by 'isothermality' (16.8%), 'seasonality' (8.5%), 'precipitation of coldest quarter' (8.4%) and 'annual range of NDVI' (7.9%). The remaining variables contributed only less to the model performance (Table 2).

Availability of wetlands, climatic suitability and anthropogenic pressure

Only 57 of the 248 national PAs are currently designated by the IUCN. The areas of the 248 PAs strongly differed and ranged from 0.04 km² ('HinuluganTaktak Protected Landscape', Luzon) to 10,881.81 km² ('Palawan Game Refuge and Bird Sanctuary', Luzon). In the first step of ranking, 131 PAs were excluded from further evaluation due to the lack of habitat availability (Supplementary Material S1). In the second step another three areas were excluded as they did not provide suitable climatic conditions. The remaining 114 PAs were included in the final ranking.

Considering the results of the 'sdm-ranking', the PAs 'Northern Sierra Madre Natural Park' (North Luzon),

Table 2. MaxEnt variable contribution of the final species distribution model for *Crocodylus mindorensis*.

Variable	Abbreviation	Derived variable	Variable contribution [%]
V39	ED15078_bio2	Mean Diurnal Range of Temperature	36.4
V40	ED15078_bio3	Isothermality (Bio2/Bio7) (*100)	16.8
V41	ED15078_bio4	Seasonality	8.5
V19	bio_19	Precipitation of Coldest Quarter	8.4
V26	ED1514_bio7	Annual Range of NDVI	7.9
V37	ED1515_bio11	Mean EVI of Coldest Quarter	5.2
V14	bio_14	Precipitation of Driest Month	4.2
V18	bio_18	Precipitation of Warmest Quarter	3.9
V35	ED1515_bio7	Annual Range of EVI	3.8
V27	ED1514_bio10	Mean NDVI of Warmest Quarter	2.9
V13	bio_13	Precipitation of Wettest Month	1.9
V43	ED15078_bio6	Min Temperature of Coldest Month	0.1
V31	ED1515_bio3	Isothermaility (BIO2/BIO7) (*100) of EVI	0.0
V30	ED1515_bio2	Mean Diurnal Range of EVI	0.0
V22	ED1514_bio3	Isothermaility (BIO2/BIO7) (*100) of NDVI	0.0
V21	ED1514_bio2	Mean Diurnal Range of NDVI	0.0

Table 3. Top 5 reserves suitable for the Philippine Crocodile: reserve name, reserve category (assignment according to IUCN), reserve area, climatically suitable area [relative to reserve area in %], climatically suitable wetland area [relative to reserve area in %], and ranks according to the wet-sdm-ranking, hfp-ranking, and final-ranking.

Name	Reserve category	IUCN	reserve area [km²]	climatically suitable area [km²]	wetland area [km²]	wet-sdm-ranking	hfp-ranking	final-ranking
Lake Lanao Watershed Reservation	Watershed Reservation	not assigned	1712.93	946.87 [55.3%]	113.82 [6.6%]	2	34	1
Angat Watershed Forest Reserve District (Metro Water District)	Watershed Forest Reserve	not assigned	545.74	191.96 [35.2%]	2.83 [0.5%]	38	2	2
Northern Sierra Madre Natural Park	Natural Park	II	3569.69	1664.39 [46.6%]	96.22 [2.7%]	1	86	3
Talaytay Protected Landscape	Protected Landscape	V	35.98	1.44 [4.0%]	0.09 [0.3%]	100	1	4
Agusan Marsh Wildlife Sanctuary	Wildlife Sanctuary	IV	409.41	247.32 [60.4%]	189.43 [46.3%]	3	37	5

'Lake Lanao Watershed Reservation' (West Mindanao), 'Quirino Protected Landscape' (Luzon), 'Allah Valley Watershed Forest Reserve' (South Mindanao) and 'Upper Agno River Basin Resource Reserve' (Luzon) revealed the highest scores with climatically suitable areas between 549.29 and 1,664.39 km² (Table 3, Supplementary Material S1).

According to the 'wet-sdm ranking', the top five reserves with the highest scores were 'Northern Sierra Madre Natural Park' (North Luzon), 'Lake Lanao Watershed Reservation' (West Mindanao), 'Agusan Marsh Wildlife Sanctuary' (East Mindanao), 'Mindoro Island's Mangrove Swamp Forest Reserves as per Presidential Proclamation 2152' (South Luzon) and 'Allah Valley Watershed Forest Reserve' (South Mindanao). This coincided with the distribution of the species records, which were also identified on the Northern portion of Luzon Island and Mindanao Island (Figs 1 and 2). However, none of the species' occurrence records laid inside the top five reserves. Only two records were located on the edge or close to a reserve ('Northern Sierra Madre Natural Park'). Following the IUCN categories, three PAs were not assigned to any IUCN category ('Lake Lanao Watershed Reservation', 'Mindoro Island's Mangrove Swamp Forest Reserves' and 'Allah Valley Watershed Forest Reserve'), while 'Agusan Marsh Wildlife Sanctuary' belongs to category IV 'habitat/species management area', and 'Northern Sierra Madre Natural Park' is classified as 'national park' (category II). 'Lake Lanao Watershed Reservation' and 'Allah Valley Watershed Forest Reserve' are two reserves proclaimed by the national government through Presidential Proclamations No. 871 and 2455, respectively. Governance and management of these reserves are also covered by the NIPAS Act of 1992. Meanwhile, the Presidential Proclamation 2152 declares several mangrove areas throughout the country as 'Mangrove Swamp Forest Reserves', this includes the mangroves areas of Mindoro Island mentioned in this study. Our analysis showed that there are generally few areas with low anthropogenic pressure except for the mountain ranges on Luzon (Fig. 3). Not surprisingly, high human activity was found around the capital Manila. On the main island of Palawan, the human footprint was low, whereas in the Visayas, except for 'Samar Island', there were only a few contiguous areas with low human footprint. Mindanao, meanwhile, has a very homogeneous pattern distributing between high and low anthropogenic pressure. The reserves with the lowest human footprint were 'Talaytay Protected Landscape' (Central Luzon, IUCN category V = 'protected landscape/seascape'), 'Angat Watershed Forest Reserve District (Metro Water District)' (Luzon, not assigned), 'Mt. Mantalingahan Protected Landscape' (Luzon, IUCN category V), 'Amro River Protected Landscape' (Central Luzon, IUCN category V) and 'Mt. Pulag Protected Landscape' (Luzon, not assigned) (Supplementary Material S1).

Considering the availability of wetlands, the climatic suitability and the anthropogenic pressure, the final ranking revealed 'Lake Lanao Watershed Reservation' (West Mindanao, not assigned), 'Angat Watershed Forest Reserve District (Metro Water District)' (Luzon, not assigned), 'Northern Sierra Madre Natural Park' (North Luzon, IUCN category II), 'Talaytay Protected Landscape' (Central Luzon, IUCN category V) and 'Agusan Marsh Wildlife Sanctuary' (East Mindanao, IUCN category IV) as most suitable reserves for the Philippine Crocodile. The reserves covered a total area of between 35.98 km² and 3,569.69 km², with climatically suitable areas of between 1.44 km² and 1,664.39 km², and finally consisted of between 0.09 km² and 189.43 km² climatically suitable wetland habitats. The anthropogenic pressure strongly varied between low (ranks 1, 2, 34 and 37 in the 'hfp-ranking') and moderately high (ranks 86; Tables 3 and S1).

Discussion

General results

The assessed PAs strongly differ in size, IUCN/reserve category, climatic suitability, habitat availability and anthropogenic pressure, and therefore a trade-off is necessary to identify the most suitable PAs to protect the Philippine Crocodile *in situ*. Our SDMs indicated an average daily temperature range (36.4%), temperature fluctuations during the course of the day and year (16.8%), and seasonality (8.5%) to be most relevant climatic parameters for the Philippine Crocodile (Table 2). Ambient temperature influences the nest temperatures for reproduction and long-term maintenance for the species (Akmad & Pomares 2008). The amount of precipitation in the coldest quarter was also found important for the crocodiles (Table 2). Specific weather or climatic events such as floods can cause mortality to juveniles when they are still vulnerable (van de Ven et al. 2009, van de Ven et al. 2017). Furthermore, prolonged dry periods limit food resources and are therefore a threat for all age groups (Mazzotti et al. 2009).

Assessment of top five PAs and recommendations to establish new reserves

'Lake Lanao Watershed Reservation' (not assigned) is a watershed reservation located in the province of Lanao del

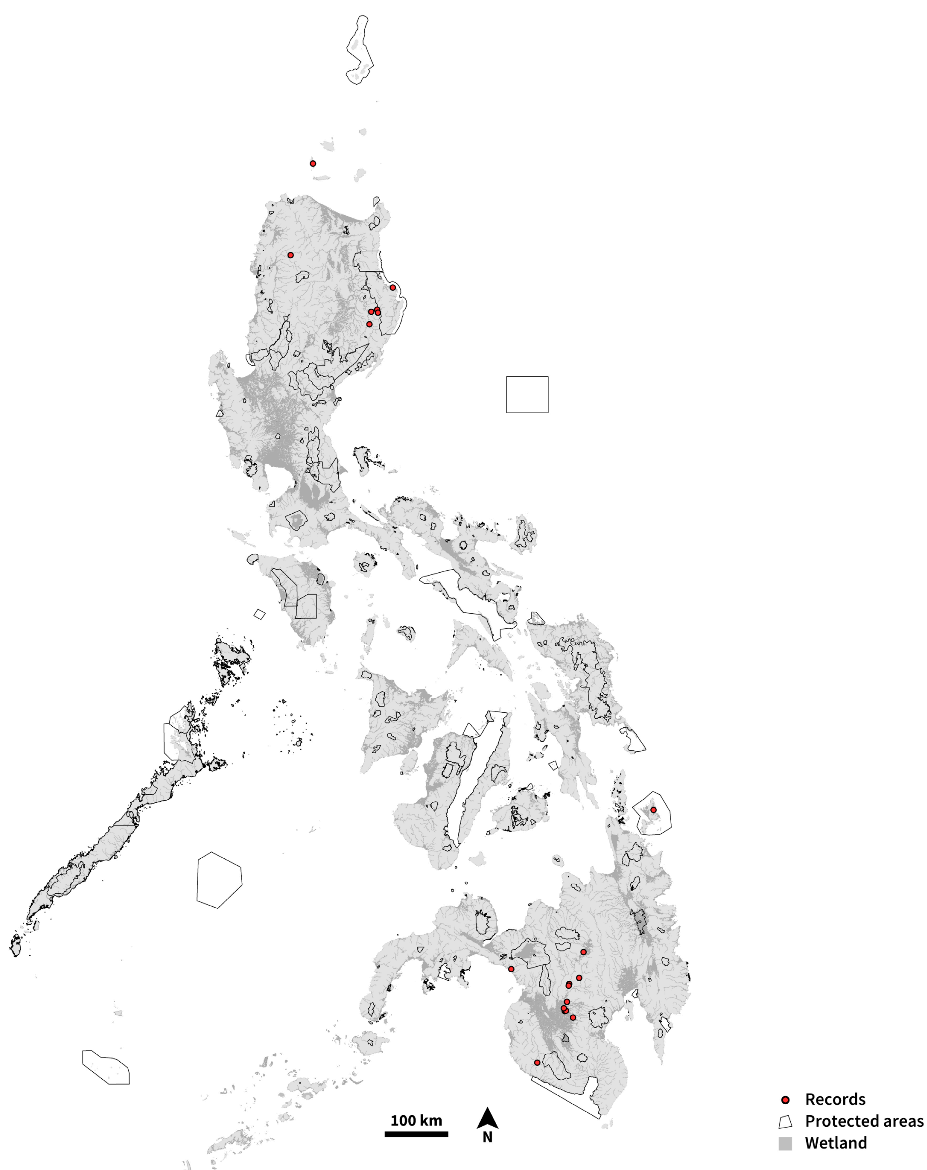

Figure 1. Map of the Philippines including species records of the Philippine Crocodile (*Crocodylus mindorensis*), wetland habitats, and national PAs.

Sur of the Bangsamoro Autonomous Region in Muslim Mindanao (BARMM) on the island of Mindanao. With a total reserve area of 1,712.93 km², covering 113.82 km² of climatically suitable wetland habitats, it is the second largest of the top five. Lake Lanao is Mindanao's largest lake (36.300 ha) and has five watersheds with rivers and major tributaries stretching over a total length of 431 km (DENR 2023). Its wetlands border the lake to the east for the most part and mainly consist of general marshes (39%), swamps (26%), fens (16%) and rivers (14%). The hydropower plant built along the lake and the Agus River is responsible for a significant contribution to Mindanao's electricity supply (70%) (DENR 2023), which also reflected by high anthropogenic pressure. The PA is also recognised as key biodiversity area (KBA) by IUCN and is therefore of crucial global importance. The lake is home to 18 endemic freshwater fish and supports a large number of waterfowl and other birds such as *Halcyon chloris* (White Collared Kingfisher) (DENR 2023). Moreover, a healthy population of *C. mindorensis* is inferred to be thriving in the rivers of Miundas, Maladi and Matling in Lanao del Sur with a recent discovery of individuals in 2019 and affirmation of its presence by the local community (Manalo et al. 2019). The headwaters of these three rivers are located in the vicinity of Lake Lanao.

The 'Angat Watershed Forest Reserve District (Metro Water District)' (not assigned to IUCN categories) protects the watershed of the Southern Sierra Madre north of Manila, where surface water flows into the Angat River and its tributaries. The rivers hold a proportion of 74% of the total wetlands in the PA. The reserve covers an area of 545.74 km² in the eastern part of Bulacan Province and the northern portion of Rizal Province at elevations between 490 to 1,206 metres a.s.l. The PA extends to the provinces of Nueva Ecija and Quezon and is centred on an artificial lake created by the Angat Dam which, together with the Ipo Dam (7.5 km downstream), supplies the majority of Metro Manila's water requirements. Despite this fact,

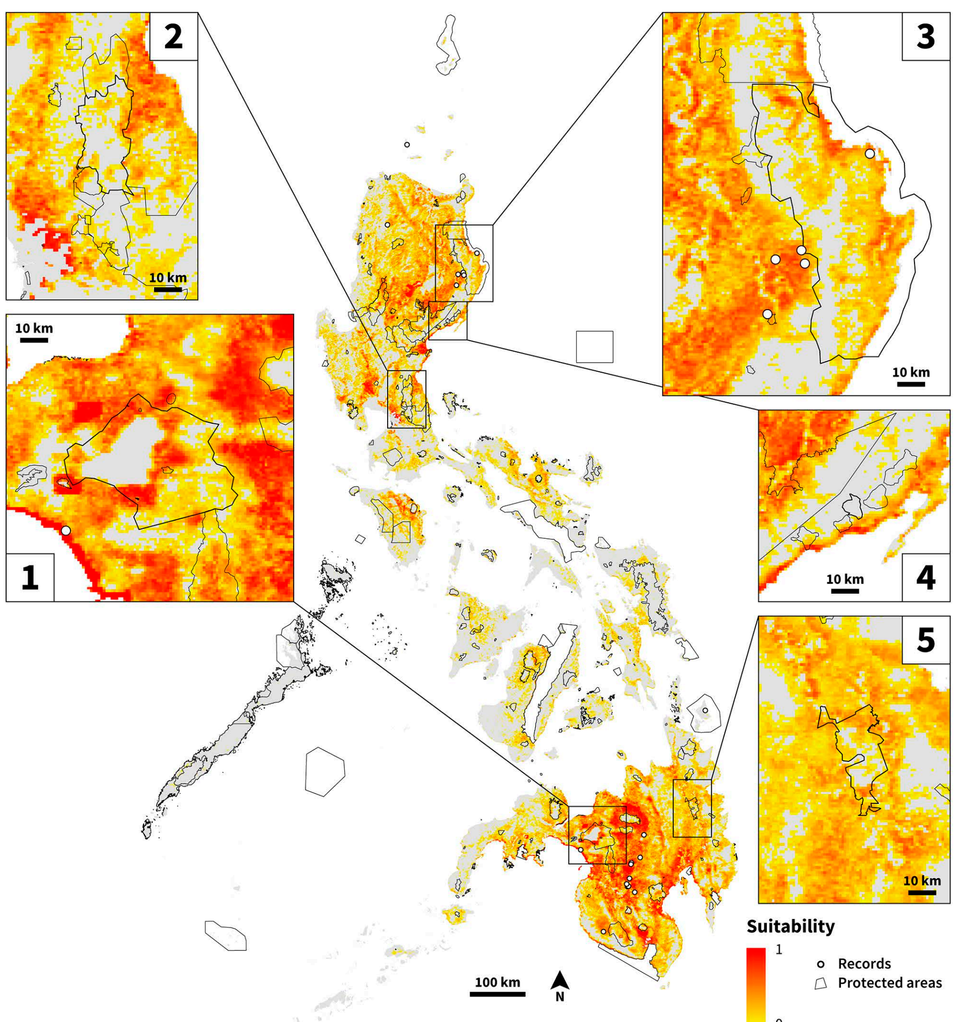

Figure 2. Suitable climatic space for the Philippine Crocodile *(Crocodylus mindorensis)* according to the results of our species distribution model as well as species records and national PAs. The five best suitable PAs according to our final ranking are highlighted.

the PA has a homogenous low human footprint. The watershed is a popular birdwatching site and a biodiversity hotspot, containing most of the remaining closed canopy forests in Central Luzon. A herpetofaunal survey conducted by McLeod et al. (2011) documented 19 frog, 22 lizard, two turtle, and 20 snake species within the PA, but survey efforts were mostly focused on low elevation sites (200–600 m a.s.l.). However, the presence of *C. mindorensis* in this PA is still unknown and needs further surveys. Although the area is highly suitable for the crocodile, large dams may restrict movement of the animals and the separation of populations would have a detrimental effect on the long-term conservation of the species (McAllister et al. 2001) or would require management or assisted migration. Nevertheless, the Philippine Crocodile has been documented to be able to climb steep slopes (Binaday et al. 2020) and studies are yet to be done on whether such infrastructures will have a significant impact on the species' population.

'Northern Sierra Madre Natural Park', a large national park, covers 3,569.69 km² of the north-east coast of Luzon. About 21.02% of the park is highly suitable. The wetland area, covering 17 km², is mainly consisting of rivers, swamps and marshes. The areas of the Sierra Madre Mountains on the east coast and the Cordillera Mountains on the middle-west side are exposed to little or no anthropogenic pressure. Only the settlements and human activities along the branches of the Palanan River possess medium to high human footprint. In the east of San Mariano, there are already several crocodile sanctuaries for this species (Manalo et al. 2018, van de Ven et al. 2017). However, the sanctuaries are currently located outside the PA where three of the species occurrences were found (Fig. 1). We highly recommend the extension of the designated reserve to cover areas surrounding the sanctuaries and especially the area north along the foothills of the Dicatian River as a potential reserve, where there is high climatic suitability and low human footprint (Figs 2 and 3). This park contains

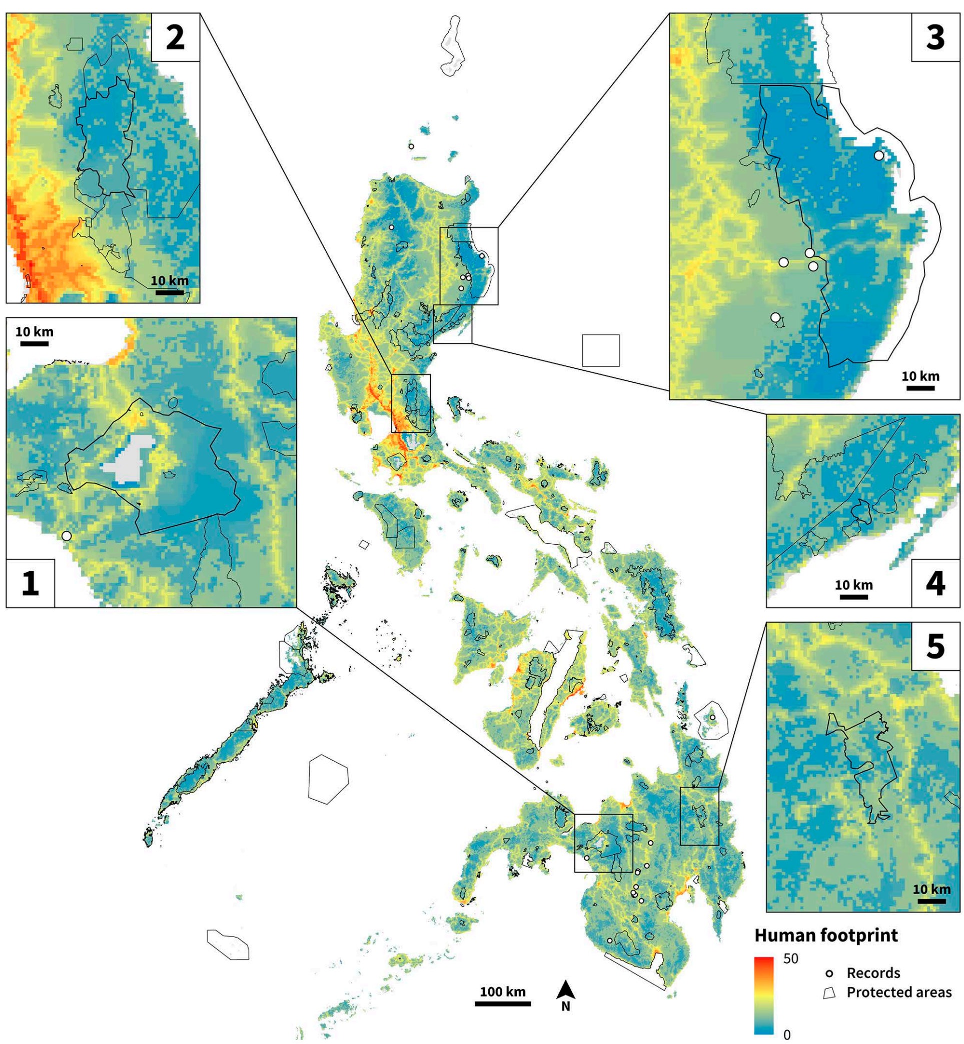

Figure 3. Anthropogeneic pressure in the Philippines measured as human footprint index as well as species records of the Philippine Crocodile (*Crocodylus mindorensis*) and national PAs. The five best suitable PAs according to our final ranking are highlighted.

the highest species richness of the Philippines, a wide variety of habitats (DENR 2015) and is home to many indigenous people (CEPF 2001). Among the Philippine endemic species, about 30% of all bird species and 62% of all mammal species are found here. It is also home to 35 threatened species (van der Ploeg et al. 2011), including *C. mindorensis*, Philippine Eagle (*Pithecophaga jefferyi*), Isabela Oriole (*Oriolus isabellae*) and Sierra Madre Forest Monitor (*Varanus bitatawa*) (DENR 2015). A herpetofaunal survey was conducted by Brown et al. (2013) in the PA and documented a total of 101 species of amphibians and reptiles, including the two species of crocodiles in the Philippines – *Crocodylus mindorensis* and *C. porosus*. Although much of the PA is covered by forest, it is reducing by about 1,400 ha per year (DENR 2015). Van der Ploeg et al. (2011) estimated that between 20,000–35,000 m^2 disappear from the national park each year due to illegal timber logging, but little action has been taken against this so far.

'Talaytay Protected Landscape' is located in northern Aurora (province) and covers the Talaytay River watershed in the Sierra Madre range of the island of Luzon. The PA comprises an area of 35.98 km^2, making it the smallest of the top five PAs, but like 'Lake Lanao Watershed Reservation' it is a KBA. This Protected Landscape (IUCN category V) stretches from the rugged interior including the source region of the Talaytay River to its mouth at the lowlands of the municipality of Dinalungan. Some important bird and mammal species are native to this PA, such as *Penelopides panini* (Tarictic Hornbill) or *Macaca fascicularis philippensis* (Philippine Long-Tailed Macaque). The wetlands there consist exclusively of rivers, and anthropogenic pressure is low. 'Northern Sierra Madre Natural Park' and 'Talaytay Protected Landscape' are PAs that are close to the coast or include parts of it. These habitats might also be suitable for the much larger *C. porosus*, which might outcompete the Philippine Crocodile for food, nesting sites or basking sites. Furthermore, hybrids between both species are known from captivity, which should be considered for conservation actions in these areas.

Almost 60% of Agusan area are climatally suitable of climatically suitable area and has 189.43 km^2 of suitable wetland habitat. The main parts of the wetlands are marshes, swamps and flood-outs. The persistence of wetlands is essential as they store atmospheric carbon in the plant roots and filter upstream pollutants, thus protecting coral reefs by holding back sediments (Gibbens 2021, Kumar et al. 2017). The Agusan River is accessible by small boats and therefore shows high anthropogenic pressure from northwest to southeast portion of the marsh (Gibbens 2021). The conversion of nearby areas along the river into fish ponds, rice fields, and/or settlements by the indigenous Manobo people result to areas with slightly increased anthropogenic pressure (Fig. 3) (Ramsar Sites Information Service 1999). The remaining part of the PA is exposed to low to moderate human pressure. In fact, it is even known to be the 'least disturbed freshwater wetland' in the Philippines (ASEAN CHM-ACB 2022). Having low human pressure and high suitability, the surrounding areas of Lake Mambagongon appear to be a hotspot for crocodiles and the lake is already known as a crocodile reproduction site (Tomas et al. 2009, van Weerd 2010). This PA is also a significant transit point for wild birds in Asia (DENR 2022) and home for 197 bird species as well as 53 reptile and 240 vascular plant species (ASEAN CHM-ACB 2022). Among the threatened species native to the area are the two crocodile species, the Philippine Duck (*Anas luzonica*), Golden-Crowned Flying Fox (*Acerodon jubatus*) and Philippine Sailfin Lizard (*Hydrosaurus pustulatus*) (DENR 2022). Philippine Crocodile populations were reported to occur in this PA but actually this revealed to be a *C. porosus* locality (Ross 2008). The coexistence of both species in the Agusan Marsh is still uncertain (Manalo et al. 2012).

Legislated PAs offer a large natural habitat for the species with the absence or minimal presence of anthropogenic pressures. The governance of such reserves is through the Protected Area Management Board (PAMB) whose members include several stakeholders from public and private sectors. This management board ensures that activities that will be conducted within the PA's boundaries abide with the national laws, particularly with the NIPAS Act. The strict regulation of anthropogenic activities within these reserves provide a safeguard for these habitats to remain intact and ensure its ecological integrity. Moreover, legislated PAs have allocated government funds for their management and protection. Additionally to the top five reserves, we recommend Ligawasan Marsh Game Refuge and Bird Sanctuary on Mindanao for the establishment of a new reserve, which is not a declared PA yet, but in reality there is a large population of *C. mindorensis* present. The area also shows high climatic suitability and low level of human footprint. The declaration as a PA is highly important for the conservation and existence of the Critically Endangered Philippine Crocodile.

Most of the species occurrence records in this study were outside declared and legislated PAs. Establishment of these habitats into PAs would entail a large sum of funds and efforts, which usually takes years to be established. Under the Philippine Wildlife Resources Conservation and Protection Act of 2001, public and privately owned areas outside PAs which serve as a habitat for threatened species can be declared as a Critical Habitat. Similar to legislated PAs, the declaration provides a layer of protection through a management board which regulates activities within the Critical Habitat, but takes shorter time to establish.

Crocodiles role in the ecosystem and human-wildlife conflicts

Crocodiles may serve as umbrella species for their ecosystems, which enables the protection of other threatened species and entire ecosystems. In the case of the Philippine Crocodile, there are many other wetland-dependent species with threatened status that would benefit from the expansion of existing PAs or the establishment of new ones in order to better protect crocodiles, including Philippine natives or even endemics such as *Pelochelys cantorii* which is Critically Endangered (Brown et al. 2013), *Anas luzonica, Hydrosaurus pustulatus, Limnonectes parvus, Platymantis sierramadrensis, Sanguirana tipanan* (Brown et al. 2013, Sanguila et al. 2016), which are Vulnerable, as well as diverse migratory birds.

Bucol et al. (2020) and Corvera et al. (2017) have shown that crocodile species native to the Philippines might have positive impact on the fish stocks. Brown et al. (2021) suggests *C. mindorensis* as a potential natural pest control agent based on analyses of the digestive tract. Invasive species such as *Pomacea canaliculata* (Golden Apple Snail) or *Rattus tanezumi* (Asian House Rat) are agricultural nuisances which are preyed by *C. mindorensis*.

The increase of protected reserves suitable for the Philippine Crocodile is also necessary to prevent future extinction of the species in the wild. Unfortunately, the main threat for *C. mindorensis* concerns its habitat, particularly fragmentation, use and destruction. The human footprint index can be a useful indicator of anthropogenic expansion and habitat loss, even if it is assessed remotely and can slightly differ from a local scale. Our results reveal that many protected reserves also have larger proportions with moderate to high human footprint (Fig. 3). The expansion of agricultural land for aquaculture or for the cultivation of rice and sugar cane, human-settlement growth, energy production and lucrative mining are destroying the habitats of this species (Corvera et al. 2017, Manalo et al. 2018, Sarmiento 2022, van Weerd & van der Ploeg 2012). Deforestation deprives them of shelter and prey resources (van Weerd & van der Ploeg 2012), which is intensified by fishing activities and can have a particularly negative impact on hatchling survival (Manalo et al. 2015, Somaweera et al. 2018). As a result, crocodiles are being displaced from their former habitats. They are now found more frequently in rice fields and near settlements, increasing the risk of human-crocodile conflicts (Corvera et al. 2017). Therefore, home ranges observed in studies by van Weerd et al. (2006) and van de Ven et al. (2017) should be taken into account when selecting areas for in situ conservation measures and appropriate buffer zones. More space is necessary than is available now to deescalate the aggressive intraspecific, territorial behaviour in particular of young Philippine Crocodiles (Mauger et al. 2017, van Weerd 2010, van Weerd & van der Ploeg 2012).

Unlike the larger and more aggressive species *Crocodylus porosus*, there has only been a single record of human–crocodile conflict in *C. mindorensis* in the country (Corvera et al. 2017). For the Critically Endangered *C. mindorensis*, repopulating the species in the wild can be considered a priority conservation action. Nevertheless, regardless of the species, crocodiles are generally feared by most Filipinos which is a major problem for introducing crocodiles in suitable habitats in the country. This makes the conservation introduction programs for the species highly complex involving political aspects and gathering the communities' support (Manalo et al. 2015). Such complexities would still arise if a decision has been made to introduce the species in suitable habitats within the identified PAs. On the other hand, the low human footprint in PAs makes them ideal as introduction sites with fewer human-crocodile interactions. In spite of such difficulties, there have been two conservation release programs already for the species (Manalo et al. 2015, van de Ven et al. 2009) which proves that it is not impossible to introduce and repopulate the species in the wild.

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Supplementary data

The following data are available online:

Supplementary Table S1. Final ranking containing detailed information on all 248 PAs including wetland categories, lower rankings, and further statistical values.

Supplementary Table S2. List of pre-processed variables obtained from WorldClim and MODIS before calculating multi-collinearity.