Setting the priorities straight - Species distribution models assist to prioritize conservation targets for the mangroves

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HIGHLIGHTS

- Habitat suitability for ten mangroves in the Indo-West Pacific was mapped.
- We used ensemble of eight models to map species distribution across temporal scale.
- Range expansion in future was predicted for six out of ten species.
- Suitable areas for high species richness were predicted to decrease in future.
- Priority conservation areas and species were identified and characterized.

GRAPHICAL ABSTRACT
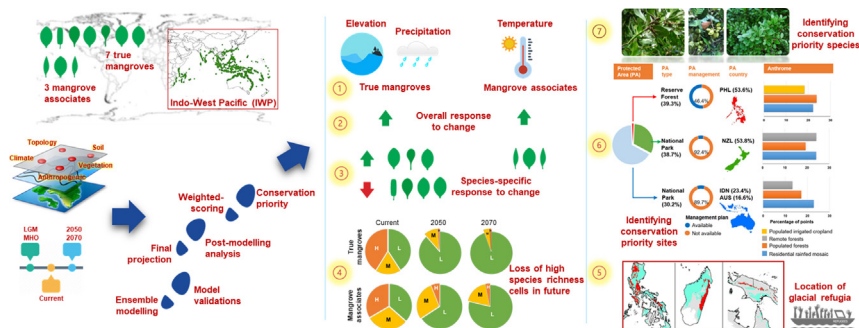
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ABSTRACT

Mangrove forests provide a wide range of ecosystem services, yet they are declining rapidly due to climate change and human activities. Identification of conservation priority targets across spatial and temporal scales may assist in planning and decision making, especially in areas having rich mangrove diversity but with limited response capacity.

In this study, we aimed to identify the species and areas which should be prioritized for conservation in the Indo-West Pacific (IWP) region, one of the two global hotspots of mangroves. We used an ensemble species distribution modelling framework to map the potential distribution of ten species, including true mangroves and mangrove associates, in current, past, and future environmental conditions. The priority targets were then identified through a weighted-scoring approach with the current distribution and the modelled outputs.

Our study revealed that precipitation and surface elevation could influence the distribution of the true mangroves, while the temperature was the important variable for the mangrove associates. Although suitable habitat for the mangroves is predicted to increase in future, primarily due to the northward range expansion of six species, areas with high species richness would decrease. We found 7.09% and 4.16% areas of the IWP should be prioritized for conservation of the true mangroves and mangrove associates, respectively. The characteristics of these priority sites indicated that the inclusion of the anthropogenic component in the conservation framework and species-targeted management plans in the protected areas are required for the effective implementation of conservation actions. Five of the studied species, namely *Acanthus ilicifolius*, *Dolichandrone spathacea*, *Heritiera littoralis*, *Pemphis acidula* and *Xylocarpus granatum*, were found to have the highest priority score for conservation. The glacial refugia of the species, mostly distributed in the Philippines, New Guinea, southern India and Madagascar, should be explored further for species-specific conservation actions.

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1. Introduction

The tropical and subtropical intertidal plant communities are dominated by mangroves, which provide a range of essential ecosystem services and have a direct impact on the coastal human livelihood (Friess, 2016). The loss of these valuable ecosystem service providers has been substantial due to both climate change and human activity. Indeed, analysing species-specific traits of 70 mangroves, Polidoro et al. (2010) found that 11 of these species were at elevated threat of extinction. So severe was the decline that 'a world without mangroves' was predicted in absence of conservation measures (Duke et al., 2007). Recent studies, however, have highlighted that the global loss rate of mangrove forests have been reduced in the 21st century with the increased public and government recognition of ecosystem services provided by the mangroves (Friess et al., 2020). However, conservation success is regionally variable, and mangrove hotspots, especially in the developing countries with limited response capacity, are at the same or even higher risk of loss (Friess et al., 2020).

Species distribution model (SDM) is increasingly used in decision making for the conservation of threatened taxa (Spiers et al., 2018) and developing ecosystem-specific management strategies (Pecchi et al., 2019). SDM is a powerful tool to identify areas that are environmentally suitable for the establishment of the concerned taxa (Elith and Leathwick, 2009). Numerous studies have used this tool to extrapolate the relationship between known occurrences and environmental covariates, both spatially and temporally, and generated the potential distribution of the focal species under novel situations [e.g., (Fois et al., 2018; Gilani et al., 2020)].

For mangroves, SDM has been used to map the restoration potential of mangrove forests in China (Hu et al., 2020) and identifying the environmental variables in determining mangroves distribution in Mexico (Rodríguez-Medina et al., 2020). However, the inherent physiological differences between species may influence species-specific responses to the environmental variables, and therefore, 'a single model fits all' approach, like the one adopted by Hu et al. (2020), may not provide the complete picture. Besides, both these studies lack the temporal scale of investigation, which would be important, especially for long term conservation planning (Das et al., 2019). Specifically, the glacial refugia, where the species overwintered the cold and dry glacial periods, often act as centres of plant diversity and endemism (Selwood and Zimmer, 2020). In addition, the high genetic diversity of species residing in these refugia may allow them to cope with changing environments in the future. Therefore, identification of the glacial refugia along with the refugia from modern climate change (which would predictively remain suitable for a set of environmental variables in future), may provide important insights into conservation planning. The global scale study, which used SDM to predict responses of 30 mangrove species to future climate conditions (Record et al., 2013), lacks the information of species projections in the past and the resolution of translating the SDM-outputs to conservation actions. Besides, the climate change projections of environmental variables vary between the two regions of global mangrove distributions - the Indo-West Pacific (IWP) and Atlantic East Pacific (AEP). For example, annual precipitation is forecasted to decrease in the AEP, while it will increase by more than 50% in the IWP region under the Community Climate System Model (CCSM) (Record et al., 2013). Therefore, using SDM for species with restricted distribution in either of these two regions may provide finer predictive resolution.

In this study, we focused on the Indo-West Pacific (IWP), the region which hosts 54 mangrove species (Duke, 2017). The deforestation activities in this region, particularly in Southeast Asia and West Africa, have threatened the survival of mangrove ecosystems. The loss rate of mangrove forests in countries like Myanmar and Malaysia exceeds the global average, thereby suggesting reconsideration of the conservation optimism for these species (Friess et al., 2020). In this context, we aimed to – 1) map the potential distribution of mangroves at both spatial and temporal scales, and 2) use this information for prioritizing conservation targets. To achieve these objectives, we considered ten species, including true mangroves and mangrove associates, and used an ensemble modelling framework to map their potential distribution in the IWP in current, future, and past environmental conditions. We chose a set of species having varied habitat preferences within the IWP biogeographic region to test the hypothesis that species-specific responses to a set of environmental variables will influence their distribution and extent in the IWP. Finally, we used a weighted-scoring approach for the SDM outputs to identify species and areas which should be prioritized for conservation actions.

2. Materials and methods

We selected seven true mangroves and three mangrove-associates for modelling distributions in the Indo-West Pacific (IWP) region (Table 1). Selection of species was conducted based on three criteria:

i) Family – the species belonging to different families. Within the same family, species having the widest distribution in the IWP has been selected. For example, within the family Combretaceae, *Lumnitzera racemosa* was chosen over *L. littorea* since the former is distributed in East Africa, Indo-Malesia and Australasia, whereas *L. littorea* is restricted in Indo-Malesia and Australasia (Duke, 2017).

ii) Biogeography – genus-level distribution is restricted to the IWP, i.e., species belonging to the genera *Avicennia* and *Rhizophora* were not considered since they have species distributed in the Atlantic East Pacific, e.g., *A. germinans* and *R. mangle* in Southeast USA and Central/South America (Kathiresan and Bingham, 2001).

iii) Habitat – the selected species pool having varied preferences for estuary locations (downstream-intermediate-upstream) and intertidal positions (low-mid-high) (Duke, 2017).

Based on these criteria, *Acanthus ilicifolius* L., *Aegiceras corniculatum* (L.) Blanco, *Ceriops tagal* (Perr.) C.B.Rob., *Excoecaria agallocha* L., *Lumnitzera racemosa* Willd., *Sonneratia alba* Sm., and *Xylocarpus granatum* J.Koenig were selected as true mangrove species, whereas *Dolichandrone spathacea* (L.f.) Seem., *Heritiera littoralis* Aiton, and *Pemphis acidula* J.R.Forst. & G.Forst. were selected as mangrove associate species. The categorization of the selected species as true mangrove and mangrove associate was based on their distribution, morphological and physiological characteristics, and taxonomic information following Tomlinson (2016): i) the true mangroves occur only in mangrove environment (tidal swamps), while the mangrove associates are mainly distributed in terrestrial or aquatic habitat but can also occur in the mangrove ecosystem; ii) true mangroves possess specialized morphological features (aerial roots, vivipary of the embryo) and physiological mechanism for salt exclusion and/or excretion; and iii) true mangroves are systematically separated from their terrestrial level (at generic, subfamily or family level).

The modelling activities in our study included three major steps – 1) preparation of occurrence data and environmental variables, 2) model development and validation, and 3) post-modelling analyses. The modelling framework has been provided in Fig. 1, and the tools used in each of the modelling steps have been mentioned in Table A.1.

2.1. Data preparation

### 2.1.1. Occurrence data

Occurrence records of the selected species were downloaded from the Global Biodiversity Information Facility (GBIF) database (GBIF.org (27 April 2021) https://doi.org/10.15468/dl.swsh6m). The GBIF data (n = 12,101) was supplemented with occurrence data collected opportunistically in our previous field surveys (n = 310). Occurrence records

Table 1
Details of the seven true mangroves and three mangrove associate species considered in this study.

Species	Code	Family	No. of occurrences	Biogeographic regions	Common habitat	
					Estuary location	Intertidal position
True mangroves						
Aegiceras corniculatum (L.) Blanco	AC	Primulaceae	810	Indo-Malesia Australasia	Intermediate, upstream	Low
Acanthus ilicifolius L.	AI	Acanthaceae	292	Indo-Malesia Australasia	Intermediate, upstream	Middle, high
Ceriops tagal (Perr.) C.B.Rob.	CT	Rhizophoraceae	733	East Africa Indo-Malesia Australasia	Downstream, intermediate	Middle, high
Excoecaria agallocha L.	EA	Euphorbiaceae	745	Indo-Malesia Australasia	Downstream, intermediate, upstream	Middle, high
Lumnitzera racemosa Willd.	LR	Combretaceae	574	East Africa Indo-Malesia Australasia	Downstream	Middle, high
Sonneratia alba Sm.	SA	Lythraceae	424	East Africa Indo-Malesia Australasia	Downstream	Low
Xylocarpus granatum J.Koenig	XG	Meliaceae	362	East Africa Indo-Malesia Australasia	Intermediate	Middle, high
Mangrove associates						
Dolichandrone spathacea (L.f.) Seem.	DS	Bignoniaceae	105	Indo-Malesia Australasia	Upstream	Middle
Heritiera littoralis Aiton	HL	Malvaceae	379	East Africa Indo-Malesia Australasia	Intermediate	High
Pemphis acidula J.R. Forst. & G. Forst.	PA	Lythraceae	392	East Africa Indo-Malesia Australasia	Downstream	High

Note: The species codes have been generated from the first letters of genus and species names. These codes have been used in Figs. 2, 3 and 6.
The species and family names have been standardized using the World Flora Online (http://www.worldfloraonline.org; Accessed on: 27 April 2021).
Information on biogeographic regions and common habitat of each species was curated from Duke, 2017.
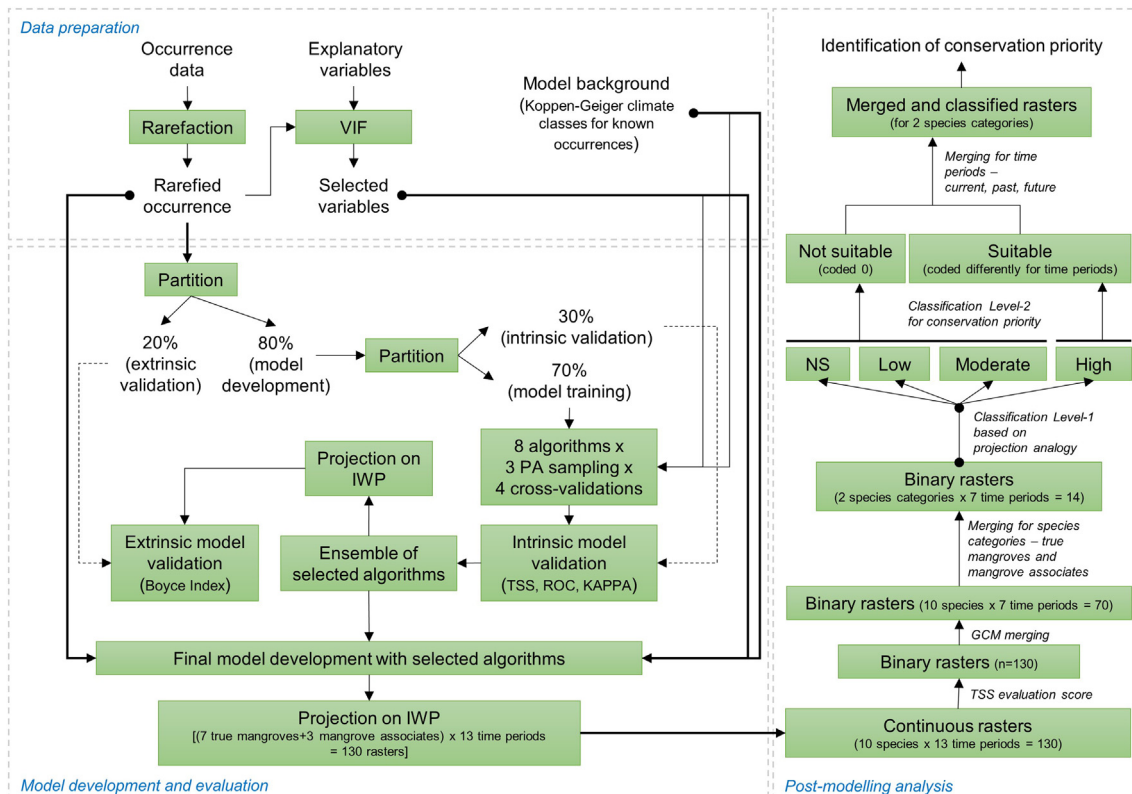
Fig. 1. General scheme of the modelling framework used in the study.

were screened for duplicates. To avoid model overfitting and ensure the validity of statistical analyses, occurrence records were spatially rarefied (using SDMtoolbox 2.3 in ArcMap 10.2.1) by selecting a single point per grid cell (cell size = 5 km) (Brown, 2014). The size of the grid cell was chosen in accordance with the cell size of the environmental variables (see Section 2.1.2). The occurrence records for individual species were further checked for possible outliers. The climate classes were identified by spatially intersecting the occurrences with the Köppen–Geiger climate raster layer (available from CliMond database, https://www.climond.org/Koppen.aspx; accessed on 30 April 2021), and the outliers were identified based on the interquartile range of data distribution across the climate classes. Finally, we were left with a total of 4816 occurrences for the selected mangroves and mangrove associate species (Table 1).

2.1.2. Environmental variables

We considered 30 environmental variables in this study, the detailed information (source, resolution, date of access, and reason for choosing) of which has been provided in Table A.2. Briefly, we downloaded 19 bioclimatic variables (averaged over 1970–2000 period) and altitude data (elevation above sea level) from the WorldClim database version 2 (Fick and Hijmans, 2017), at a spatial resolution of 2.5 arc minutes. Eight soil parameters, namely, bulk density of the fine earth fraction, cation exchange capacity, proportion of clay particles, total nitrogen, soil pH, proportion of sand particles, proportion of silt particles, and soil organic carbon content, were downloaded from the SoilGrids™ database version 2.0 (De Sousa et al., 2020). The human influence index data was retrieved from the Global Human Footprint Dataset of the Last of the Wild Project version 2 (Wildlife Conservation Society - WCS and Center for International Earth Science Information Network - CIESIN - Columbia University, 2005). We resampled the raster files using the nearest neighbour assignment technique, as implemented in ArcMap version 10.2.1, to have a uniform spatial resolution (2.5 arc minutes) and processing extent for all the variables.

For past and future projections, we selected two general circulation models (GCMs) – the Community Climate System Model (CCSM4) and an earth system model (MIROC-ESM). The bioclimatic variables were downloaded from the WorldClim database version 1.4 (http://worldclim.com/version1) (Hijmans et al., 2005). We used the Last Glacial Maximum (LGM) and Mid-Holocene (MHO) for paleoclimate projections, whereas, for future climate projections, we used two IPCC greenhouse gas concentration pathways (i.e., representative concentration pathways; RCPs) – RCP 4.5 and RCP 6.0, for two future periods – 2050 (average for 2041–2060) and 2070 (average for 2061–2080). The two GCMs were chosen based on – 1) data availability of the bioclimatic variables for both past and future climate conditions, and 2) their consensus predictions of increased annual temperature and precipitation in the IWP in the future (Tangang et al., 2020; Ullah et al., 2020). The RCP 4.5 and RCP 6.0 were selected because these RCPs provide two intermediate pathways to explore the climate system response to stabilizing the anthropogenic components of radiative forcing.

2.2. Model development and validation

To avoid the negative impact of correlated variables on SDM performance (Beaumont et al., 2005), we selected variance inflation factor (VIF) = 7 as a threshold to determine collinearity among variables. The variables having VIF below this threshold were included in the modelling framework (Table A.3). We used the *usdm* package (Naimi et al., 2014) in R to do the VIF analysis for variable selection. Spatial transfer of the models from reference to projection domains is uncertain if the available climate data is non-analogous between the two, both in univariate and multivariate spaces (Guisan et al., 2014). Therefore, before modelling, we assessed the environmental analogy between two ranges using an extrapolation detection tool called ExDet version 1.1

(Mesgaran et al., 2014). Specifically, we identified two types of novelty (non-analogous environment) between the reference (background) and projection (IWP region) ranges for: i) individual covariates (type 1 novelty; NT1), and ii) novel combinations between covariates (type 2 novelty; NT2). The analysis revealed that the majority of the IWP is within the univariate range of the selected variables for individual species (green in Fig. A.1). The NT1 component (type 1 novelty, marked red in Fig. A.1), although varies between species, is restricted to the northern part of the IWP. These findings are indicative of model transferability in geographic space.

The potential distribution of each species was estimated by contrasting probability densities of environmental covariates of the species' known occurrences to that of randomly selected points (referred to as pseudo-absence points) across the user-defined model background. Three fundamental processes can influence species distribution, namely biotic interactions (B), abiotic conditions (A) and migration or dispersal (M) (the BAM framework; (Soberón and Nakamura, 2009)). In this study, we considered the abiotically suitable area in the IWP as the model background where the species can exist given unlimited dispersal (Barve et al., 2011). To generate this background, we first spatially intersected the occurrence points with the Köppen–Geiger climate layer to identify currently occupied climate classes by the species and restrained the model background to include only those areas having these climate classes.

We performed species distribution modelling using eight different algorithms implemented in the *biomod2* package (Thuiller et al., 2009) in R. Multiple statistical models of different complexities and properties provide several possible projections, and an ensemble of the selected models based on a set of evaluation criteria has often been found to improve model transferability through time (Guisan et al., 2017). In this study, we considered models based on regression methods [GAM: general additive model (Hastie and Tibshirani, 1990), GLM: general linear model (McCullagh and Nelder, 1989)]; machine learning methods [GBM: generalized boosting model (Ridgeway, 1999), MAXENT: Maximum Entropy (Phillips et al., 2006), RF: random forest (Breiman, 2001)], classification methods [CTA: classification tree analysis (Breiman, 1984), FDA: flexible discriminant analysis (Hastie et al., 1994)] and one envelope model [SRE: Surface Range Envelop (Busby, 1991)]. To meet the criteria of having absence (or pseudo-absence) data for most of these models (except SRE), we generated three equalsized (to the true presence records; n = 4816) sets of random pseudo-absence points across the model background.

Individual model performance was assessed by both intrinsic and extrinsic validation methods following the recommendation of Guisan et al. (2017). First, occurrence data of individual species were randomly split into 80% for model training and 20% for model testing (extrinsic evaluation) (Fig. 1). For intrinsic model evaluation, the models were calibrated using 70% of randomly selected data while keeping 30% data for model evaluation. The modelling process was replicated four times, thus generating a total of 96 models (8 algorithms × 3 PA datasets × 4 crossvalidation runs) for each species. The performance of the individual algorithm was evaluated using three metrics – true skill statistic (TSS), the area under the curve of receiver operating characteristics (ROC), and Cohen's Kappa (KAPPA). The metric values were averaged for 12 runs (3 PA datasets × 4 cross-validation runs) for each algorithm. For extrinsic evaluation, the algorithms with high predictive intrinsic accuracy (TSS, ROC, KAPPA >0.75) were used to build an ensemble model with a weighted mean approach. We used the ensemble forecast method of the *biomod2* package to map the potential distribution of the species in the IWP. The individual projection was then validated using Boyce index (BI) values for 20% data which were kept aside for model testing at the first step. Threshold-independent BI ranges from −1 to 1 and provides an assessment of the degree to which model predictions differ from random expectation (Boyce et al., 2002). We used the *ecospat* package (Broennimann et al., 2018) in R to estimate the BI.

2.3. Mapping potential distribution

Finally, full occurrence datasets were used to generate the potential distribution of the individual species in the IWP, under current environmental conditions. The complete occurrence datasets were used to allow the modelling framework to use all available information to ensure better projection. For past and future projections, we focused on the bioclimatic variables only since global datasets of bioclimatic indicators are available for a large set of both past and future climate change models. For a comparative assessment of range change of the species across the time periods, we conducted the VIF analysis of the bioclimatic variables for the current, past and future modelling projections. The ensemble modelling framework was then used with the selected bioclimatic variables and the complete occurrence dataset to generate potential distribution maps of the individual species. The number of rasters generated in this process and used hereafter in post-modelling analyses has been explained in Table A.4.

2.4. Post-modelling analyses

The continuous projections generated from the ensemble models were converted to binary projections (suitable/unsuitable). The value of the optimum threshold is commonly determined by finding the particular threshold that maximizes the value of a given skill score (Allouche et al., 2006). Here, we first determined the threshold value that maximized the TSS evaluation score for individual species. The threshold value was then used to classify the pixels into suitable (above the break) and unsuitable (below the break) categories. Ensembling of individual GCM outputs are often preferred to avoid inherent errors and account for uncertainties (Hughes et al., 2014). Therefore, we merged the binary rasters of individual species for two GCMs (CCSM4 and MIROC-ESM) under past and future climate projections. The binary rasters were merged for the true mangroves and mangrove associates separately for each of the seven time periods. The merged rasters were classified based on prediction analogy – not suitable, low species richness (0.3 quantile of prediction analogy), moderate species richness (>0.3 to 0.5 quantile of prediction analogy) and high species richness (>0.5 quantile of prediction analogy). In absence of any biotic interaction component in our modelling framework, species richness should be considered as species co-occurrence (Stephens et al., 2020), which is an essential but not sufficient condition for biotic interaction to occur. Therefore, the sites predicted suitable for more than one species simply designate the areas where these species can co-occur.

2.4.1. Identification of areas for conservation priority

To identify the areas for conservation priority, the merged rasters were categorized into binary forms – cells predicted suitable only for high species richness and the rest (including cells predicted suitable for low and moderate species richness and unsuitable cells). We only considered the high species richness cells to prioritize conservation areas since we observed loss of these cells in future climate conditions (see Section 3.2). The binary rasters were then merged for the true mangroves and mangrove associates separately. We ranked the individual cell based on their suitability under current, past, and future climate conditions. The cells found suitable in both current and future climate conditions designate areas that are expected to remain intact for a long time. These cells were ranked as the highest priority (rank 1) for conserving species diversity. The glacial refugia generally harbour high genetic diversity, which may allow species to cope with changing environments in the future. Therefore, the cells identified as climate refugia under the past environmental conditions were ranked as the higher priority (rank 2) for conservation of the environmental conditions and species diversity. Finally, the environment of the areas predicted suitable for the species in the current climate condition should be conserved with high priority (rank 3) to safeguard species diversity and prevent further loss.

These three priority groups were characterized in terms of the anthropogenic biomes (Ellis and Ramankutty, 2008), designated protected areas (PA), ecoregions and habitats (Olson et al., 2001). The detailed data source and logic for choosing these variables to characterize the conservation priority sites have been provided in Table A.2. Briefly, the global raster of the anthropogenic biomes version 1.0 was downloaded from the NASA Socioeconomic Data and Applications Centre. The polygons (boundaries) and point locations of PAs were retrieved from the World Database of Protected Areas (WDPA). The polygons of the ecoregions and habitats were downloaded from the geospatial database of The Nature Conservancy (TNC).

The binary rasters were first converted to vectors (points) by identifying the centroids of each cell. The values of each of these centroids were then extracted from the anthropogenic biome raster to identify the anthrome classes. The centroids were further intersected with the PA and ecoregion polygons to provide the PA, ecoregion and habitat characteristics to the three priority groups. These operations were carried out in ArcMap version 10.2.1, and the specific functions have been mentioned in Table A.1.

2.4.2. Identification of taxa for conservation priority

We designated each species a rank corresponding to conservation priority based on their niche characteristics and potential distribution estimates. Environmental niches of the ten species were characterized by the first two axes of a Principal Component Analysis (PCA) conducted on the entire environmental space of the IWP. By applying a kernel density function, the occurrence points were converted to smoothed densities of occurrences and plotted in the gridded environmental space. Observed niche overlap between the species was estimated using Schoener's index of niche breadth (D) and modified Hellinger metric (I). The null hypothesis of random expectation of niche similarity and equivalency between species was evaluated using niche similarity test and niche equivalency test (Warren et al., 2008) based on a 95% confidence interval. These analyses were performed using the *ecospat* package version 3.0 (Broennimann et al., 2012) in R. Since all species were found to occupy a specific part of the IWP environmental space and exhibited a significant amount of overlap (see Section 3.3), we combined the occurrence records of all species and conducted another PCA to highlight the relationship between the species occurrences and environmental combinations. We used the *FactomineR* package (Lê et al., 2008) to compute the PCA and the *factoextra* package in R for extracting and visualizing the results.

Based on the variables' contribution along the two PCA axes (see Section 3.3), we defined thermal and hydric niche traits (breadth and position) for each of the ten species. Since annual mean temperature (bio1) and precipitation (bio12) were found to be the most contributing variables (see Section 3.3), we considered the variables which can capture the extremes of temperature (bio5 and bio6) and precipitation (bio13 and bio14) values to have a finer resolution of these two niche traits. We extracted values of the selected variables for the occurrence records of each species. The thermal niche breadth (TNB) was calculated by subtracting the minimum bio6 value from the maximum bio5 value, and the hydric niche breadth (HNB) was calculated by subtracting the minimum bio14 value from the maximum bio13 value. The niche positions (TNP and HNP) were defined as the distance between the average environmental niche of a species and the average environmental niche of the IWP:

$$TNP = \left(\frac{max(bio5) + min(bio6)}{2} - IWP\left(\frac{max(bio5) + min(bio6)}{2}\right)\right) \quad (1)$$

$$HNP = \left(\frac{max(bio13) + min(bio14)}{2} - IWP\left(\frac{max(bio13) + min(bio14)}{2}\right)\right) \quad (2)$$

The niche traits (breadth and position) were standardized following:

$$\frac{(NT_i - aNT)}{\sigma NT},$$ (3)

where NT is the niche trait, aNT is the average niche trait estimated for 10 species, σNT is the standard error of NT. Based on the standardized NT values, we created a two-dimensional niche space divided into four quadrants.

We adopted a weighted-scoring approach to rank the species based on their position in the niche spaces as well as their potential distribution estimates under current and future climate conditions. First, the highest weight (1) was assigned to the species belonging to quadrant 1 (NB and NP negative) and the lowest (0.25) to species in quadrant 3 (NB and NP positive). The scoring was done for the thermal and hydric niche spaces separately. Secondly, we estimated the median potential distribution area of 10 species under current climate condition. Maximum weight (1) was assigned to the species having potential distribution lower than this median value, whereas the rest of the species were scored with 0.5. Thirdly, the median of changes (loss or gain) in potential distribution areas in future was estimated. The species were scored as - more than median loss (1), less than median loss (0.75), less than

median gain (0.5), and more than median gain (0.25). Based on the summation of all scores, the species were ranked as - highest priority, higher priority and high priority.

3. Results

3.1. Variable contribution and model evaluation

The VIF analysis revealed that 12–15 variables can influence mangrove and mangrove associate distribution in the IWP (Fig. 2A; Table A.3). Four bioclimatic variables, namely mean diurnal range (bio2), precipitation of wettest month (bio13), precipitation of warmest quarter (bio18), and precipitation of coldest quarter (bio19), were common for all species. In addition to climate, five variables also influenced species distribution: elevation, human footprint, and among soil parameters, bulk density, organic carbon content, and proportion of sand particles (except *P. acidula*). Assessment of the average variable contribution (averaged for eight algorithms) revealed that precipitation related variables and elevation influenced the distribution of the true mangroves, whereas the mean diurnal range of temperature (bio2) primarily determined the mangrove associates' distribution in the IWP (Fig. 2A).
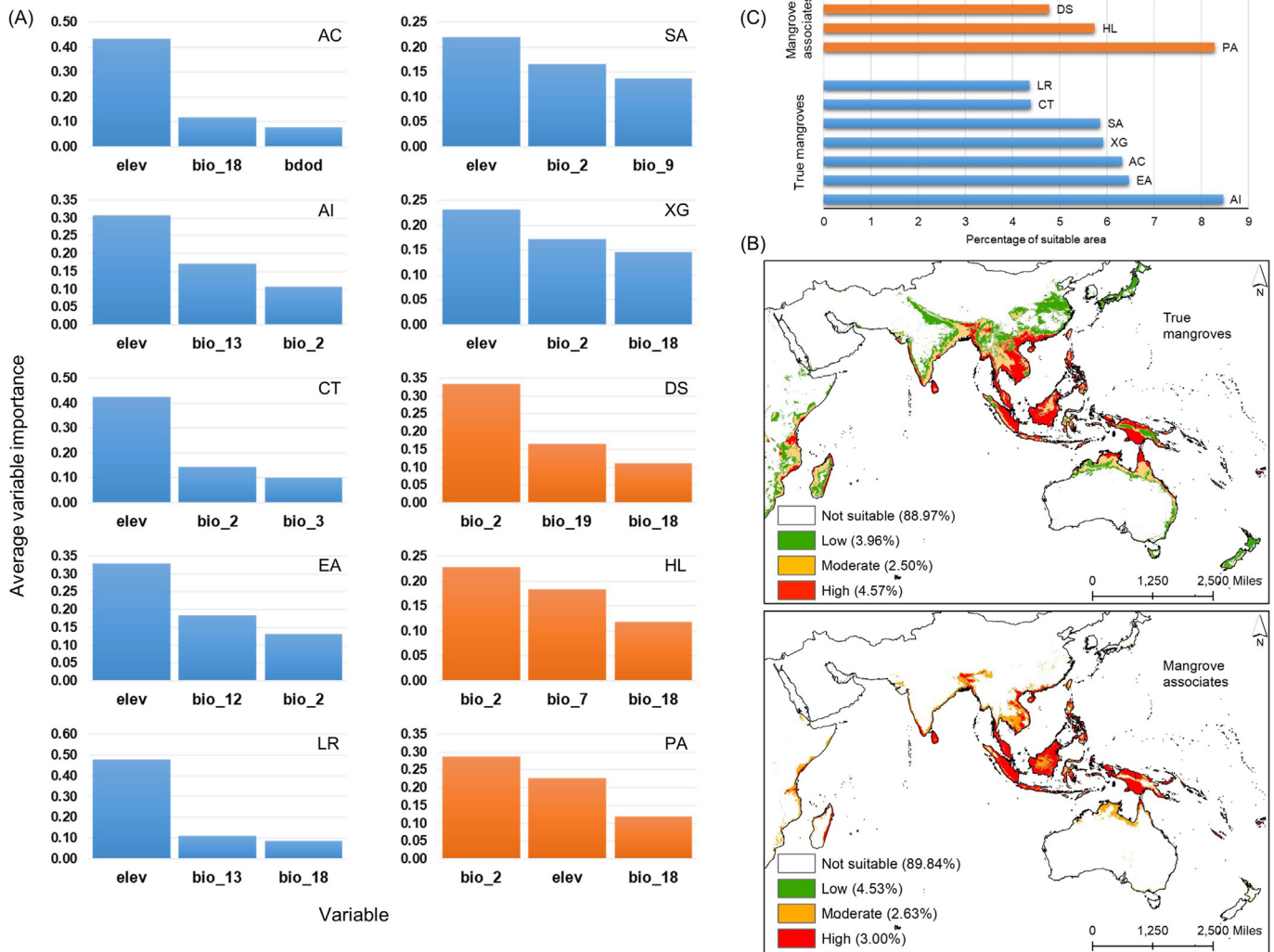
Fig. 2. Projected distribution of mangroves in the Indo-West Pacific (IWP) – (A) average contribution of the three most important variables (averaged for eight algorithms) for the distribution of the true mangroves and mangrove associates; (B) classified maps showing suitable areas in the IWP for the true mangroves (top) and mangrove associates (bottom), figure legends depict four suitability classes based on prediction analogy of individual species; (C) percentage of areas in the IWP predicted suitable for the seven true mangroves and three mangrove associates. The abbreviated species names and the environmental variables have been given in Tables 1 and A.2, respectively.

The intrinsic model evaluation of the individual modelling algorithm based on three metrics (ROC, TSS, and KAPPA) revealed that predictive accuracy was maximum for the RF model for all species (Fig. A.2). The intrinsic evaluation score (averaged for ten species) of the three metrics (ROC, TSS, and KAPPA) for the ensemble models were found to be 0.989 ($\pm$0.002) for ROC, 0.93 ($\pm$0.011) for TSS, and 0.921 ($\pm$0.014) for KAPPA (Table A.5), suggesting predictive accuracy. The extrinsic model evaluation of the ensemble forecast outputs (weighted mean) revealed positive BI values, ranging from 0.761 (for *E. agallocha*) to 0.955 (for *D. spathacea*).

3.2. Potential distribution

The potential distribution maps, generated using the selected environmental variables, revealed that 11.03% and 10.16% area of the IWP are suitable for true mangroves and mangrove associates, respectively (Fig. 2B). Considering the species individually, *A. ilicifolius* has been found to have the maximum suitable area (8.46%) followed by *E. agallocha* (6.47%) and *A. corniculatum* (6.32%) (Fig. 2C). Among the mangrove associates, maximum potential distribution has been observed for *P. acidula* (8.28%) (Fig. 2C).

The bioclimatic variables were used to compare the potential distribution of the mangroves between the three time periods. Under the current climate condition, 15.87% area of the IWP is suitable for the true mangroves, out of which 6.53% is suitable for high species richness (Fig. 3A). For mangrove associates, 9.57% area of the IWP is suitable,

out of which 3.19% area is suitable for high species richness (Fig. 3B). Compared to the current distribution, the potential area for the true mangroves and mangrove associates would increase in future climate conditions. In 2050, 16.05% (RCP 4.5) and 22.09% (RCP 6.0) area will remain suitable for the true mangroves. In 2070, the area will marginally decrease in RCP 4.5 (15.26%) but will increase in RCP 6.0 (20.37%). The overall increase in suitable areas in future was found to be driven by the increase in low species richness cells; however, a sharp decrease was observed for high and moderate species richness cells in both the RCPs in 2050 and 2070 (Fig. 3C). These high and moderate species richness cells will be restricted to the east coast of Madagascar, southern India, Myanmar, Vietnam, the Philippines, PNG, and the northeast coast of Australia and New Zealand (Fig. 3D and F). In the case of the mangrove associates, 15.39% (RCP 4.5) and 14.59% (RCP 6.0) of the area will remain suitable in 2050. In 2070, the area will increase in RCP 4.5 (25.32%) but will decrease in RCP 6.0 (25.22%). The high species richness cells were found to be lost in future climate conditions (Fig. 3C). These high species richness cells will be restricted to northeast India, Vietnam, Taiwan and PNG (Fig. 3E and G). In future, an increase in suitable area was observed for three true mangroves (*A. corniculatum*, *L. racemosa*, and *X. granatum*) and three mangrove associates (*D. spathacea*, *H. littoralis* and *P. acidula*) (Fig. 3H). Four true mangroves (*A. ilicifolius, C. tagal, E. agallocha,* and *S. alba*) were found to lose suitable habitats in future.

The ensemble projections of the two GCMs revealed that during the LGM, 20.38% and 20.18% area of the IWP were climatically suitable for
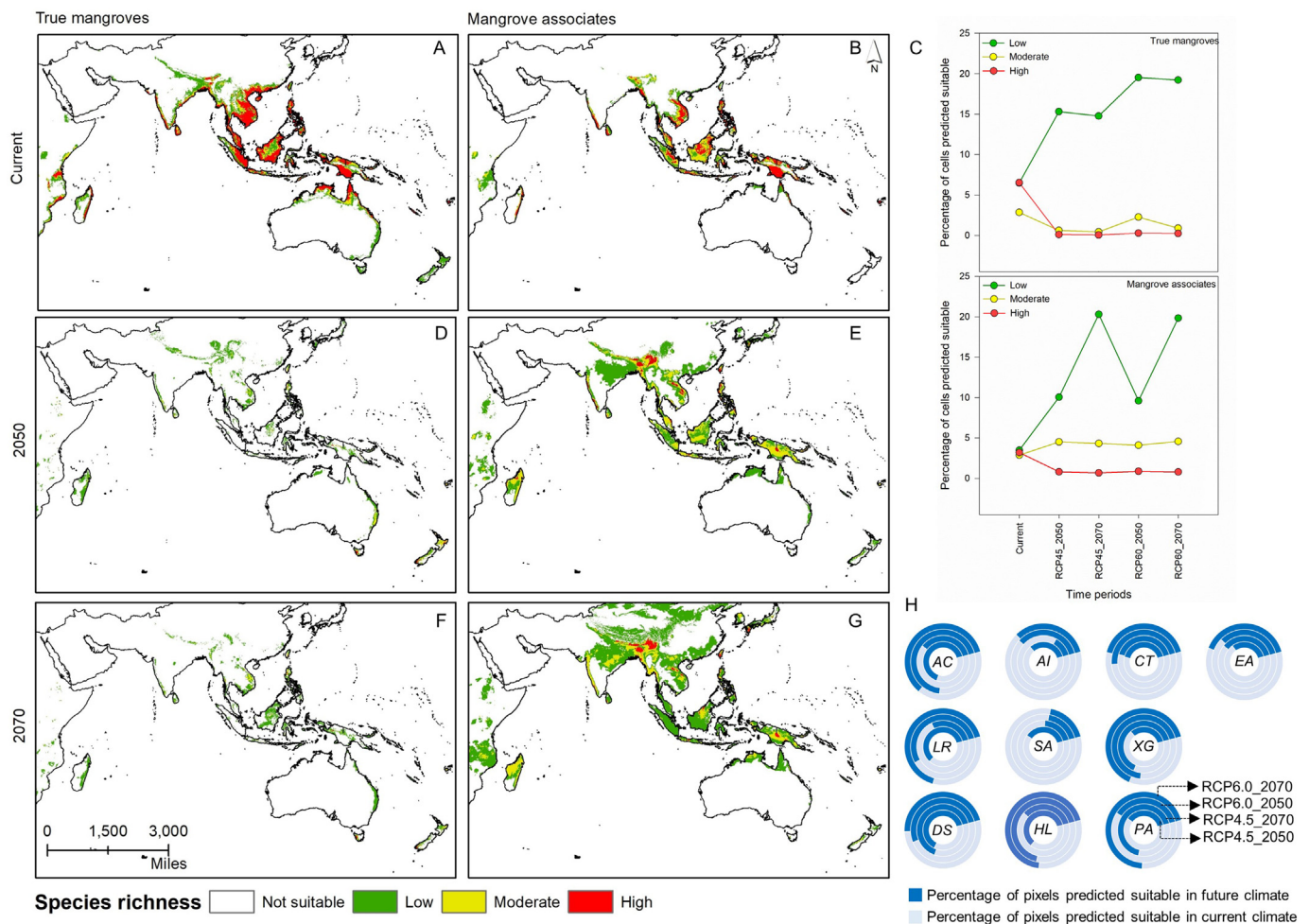
Fig. 3. Comparative assessment of projected distribution across time based on bioclimatic variables - true mangroves in current (A) and future (D and F), and mangrove associates in current (B) and future (E and G) climate conditions; change in percentage of cells predicted suitable across time periods for - (C) true mangroves and mangrove associates, and (H) individual species. The abbreviated species names have been given in Table 1.

the true mangroves and mangrove associates, respectively. Climatically suitable areas increased in the MHO for both the true mangroves (22.01%) and the mangrove associates (24.58%). Combining the individual projections revealed that high species richness cells during the LGM were restricted in parts of Papua New Guinea and northern New Zealand (marked in red in Fig. 4A). In addition to these locations, the Philippines, the east coast of Madagascar, southwest India and Sri Lanka became climatically suitable in the MHO (Fig. 4B). In the case of the mangrove associates, high species richness cells were found in parts of Bangladesh and northeast India, Taiwan, west Philippines, east Madagascar, southwest India and Sri Lanka, and a few scattered locations of Thailand during the LGM (Fig. 4C). During the MHO, more inland areas became climatically suitable for these species (Fig. 4D).

3.3. Identification of conservation targets

Priority ranking of the high species richness cells revealed that 7.086% and 4.162% areas of the IWP should be prioritized for conservation of the true mangroves (Fig. 5A) and mangrove associates (Fig. 5B), respectively. The priority conservation sites for the true mangroves are distributed among 1475 PAs (17 for highest priority, 475 for higher priority and 983 for high priority). The majority of these PAs were found to be national parks and reserve forests, and management plans are not available for more than 85% of them (except the reserve forest for the highest priority conservation). These PAs are mostly distributed in the Philippines, New Zealand, Indonesia and Australia. Most of the priority conservation sites for the true mangroves belonged to the residential

populated forest (highest), remote forest (higher) and rainfed mosaic (high) anthromes. A total of 718 PAs contained the priority sites for the mangrove associates. The majority of these PAs were found to be national parks and wildlife sanctuaries. More than 50% of these PAs have not reported any management plan. Most of these PAs are distributed in Laos, Madagascar, Myanmar and Indonesia. The priority conservation sites for the mangrove associates can be characterized by residential rainfed mosaic (highest and higher) and populated forest (high) anthromes.

The first two axes of the PCA revealed that all species occupied a specific and nearly identical part of the IWP environmental space (Fig. 6A). A high degree of overlap of environmental niches between the species was observed, as evident from the average ($\pm$SE) values of the two metrics (D = 0.69 $\pm$ 0.021; I = 0.979 $\pm$ 0.018) (Table A.6). Maximum values of D and I were observed between *C. tagal* and *P. acidula*, and *A. ilicifolius* and *E. agallocha*, respectively. Minimum overlap (D and I) was observed between *D. spathacea* and L. *racemosa*. Two variables, namely, the annual mean temperature (bio1) and annual precipitation (bio12), were found to be the most contributing variables along the first and second PCA axes, respectively (Fig. 6B). In the two-dimensional niche spaces, two species, namely *H. littoralis* and *X. granatum*, are in quadrant 1 for both thermal (Fig. 6C) and hydric (Fig. 6D) niche spaces. In the weighted-scoring approach, these two species, along with *A. ilicifolius*, *D. spathacea*, and *P. acidula*, are categorized as rank 1, corresponding to the highest priority for conservation. The rest of the species were categorized as rank 2 (higher priority), whereas *A. corniculatum*, having positive niche breadth (NB) and
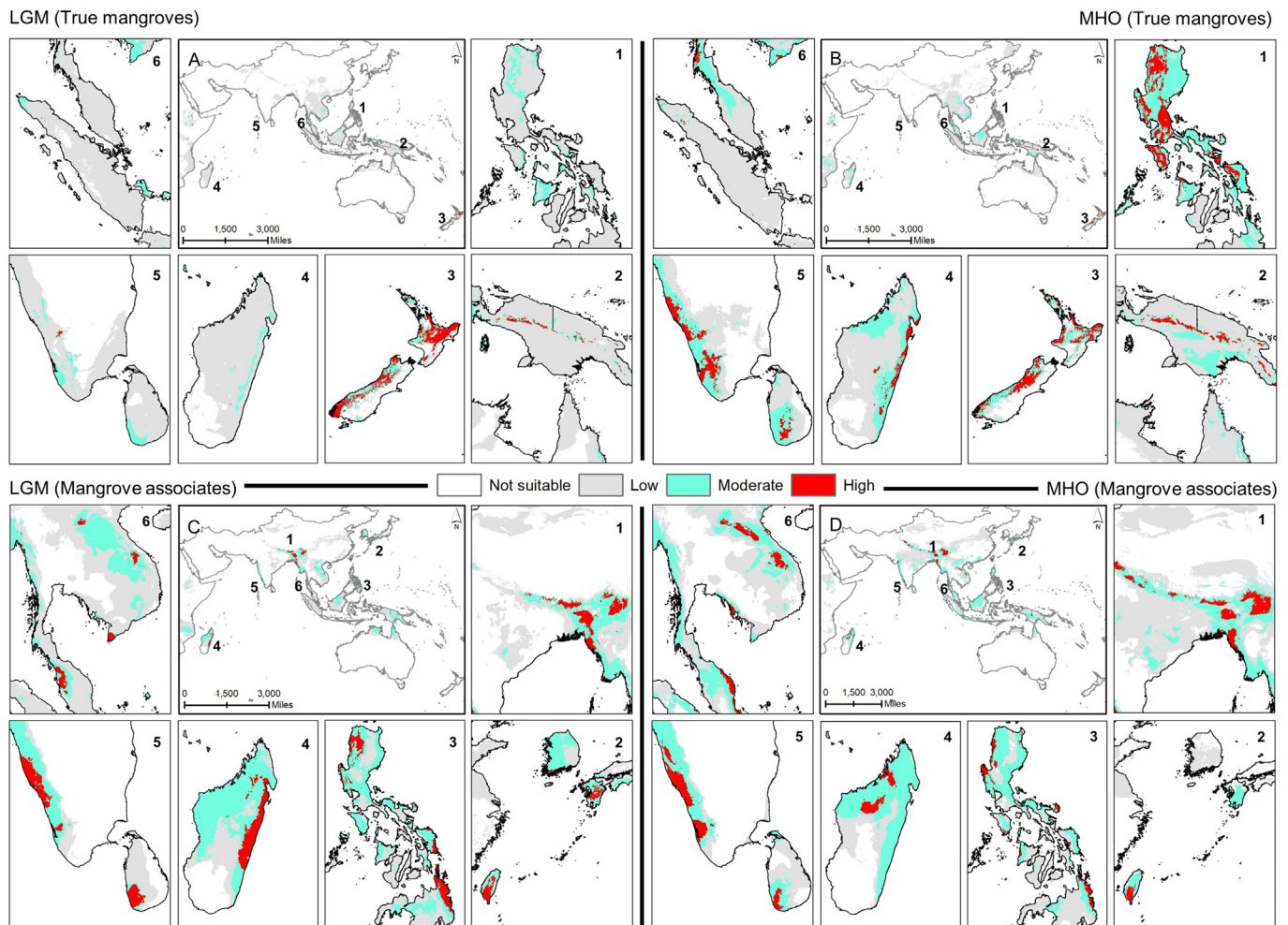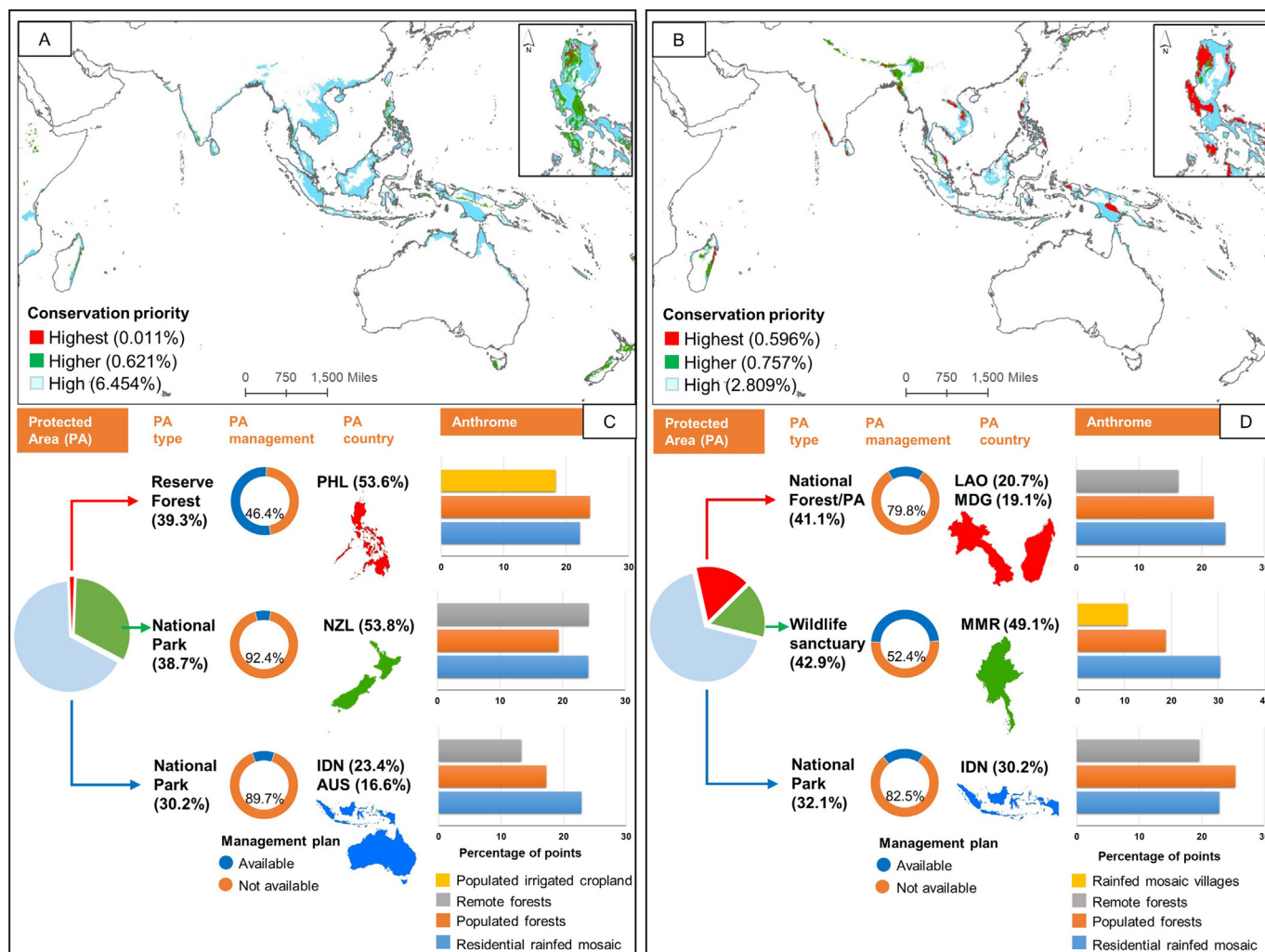

Fig. 4. Identification of glacial refugia for the true mangroves (A and B) and mangrove associates (C and D) during the Last Glacial Maxima (LGM) and Mid-Holocene (MHO) in the Indo-West Pacific.

Fig. 5. Identification of conservation priority sites for – A) true mangroves, B) mangrove associates; characterization of these priority sites in terms of protected areas (PAs) [number (pie charts), type, management plan (doughnut plots), country having >30% of these PAs] and anthropogenic biomes (bar plot showing top three biomes) for - C) true mangroves and D) mangrove associates. The country names are following International Standards Organization (ISO) 3-digit alphabetic codes.

niche position (NP) in both niche spaces, were categorized as the high priority for conservation (rank 3).

4. Discussion

To the best of our knowledge, this is the first study that mapped the dynamics of mangroves' distribution in the IWP across spatial and temporal scales. Here, we followed the standard protocol for reporting SDMs (Zurell et al., 2020), and used the SDM outputs to prioritize species- and region-specific conservation targets in the IWP.

4.1. Current distribution

Our study revealed that temperature and precipitation related variables, along with elevation, influenced the current distribution of all the studied species, being concurrent with the pattern observed at global (Simard et al., 2019a) and regional (Hoguane et al., 1999) scales. However, a comparison of the variables' contribution to the potential distribution of these species revealed that different sets of variables influenced true mangroves and mangrove associate distribution in the IWP.

Precipitation has been found more influential than the temperature for driving true mangrove distribution. The three mangrove species showed maximum potential distribution in the IWP - *A. ilicifolius*, *E. agallocha* and *A. corniculatum*. Precipitation related variables

contributed most to these species' distribution – bio13 for *A. ilicifolius*, bio12 for *E. agallocha* and bio18 for *A. corniculatum*, probably because greater rainfall is often associated with longer soil inundation periods, an optimum habitat requirement for the mangrove ecosystem. A similar inference was drawn at a global scale, where precipitation was found to be significantly correlated with mangrove carbon stocks in 17 ecosystems distributed mostly in Indo-Pacific and Australasia (Sanders et al., 2016). However, this finding contradicts Hu et al. (2020), who found temperature as the most important variable for determining mangrove distribution at the country scale. Our study also revealed the influence of elevation on the current distribution of the true mangroves. The elevation is intricately linked with the tidal inundation, one of the key environmental gradients of the mangrove ecosystem, and therefore, has often been found as the determining factor for mangrove species distribution (Leong et al., 2018). For the mangrove associates, the mean diurnal range of temperature (bio2), was found to be the most contributing variable. This finding can be explained since the mangrove associates occur at the landward edge of the mangrove ecosystem (Tomlinson, 2016), the areas which have a higher diurnal range of temperature compared to the coastal areas (Scheitlin, 2013).

Among the soil parameters, our study found that the soil organic carbon, bulk density and proportion of sand particles had important roles in mangrove distribution. The positive association between the soil organic carbon and mangrove species distribution, as revealed by the correlation circle (dimension 1), is expected since mangrove sediment can
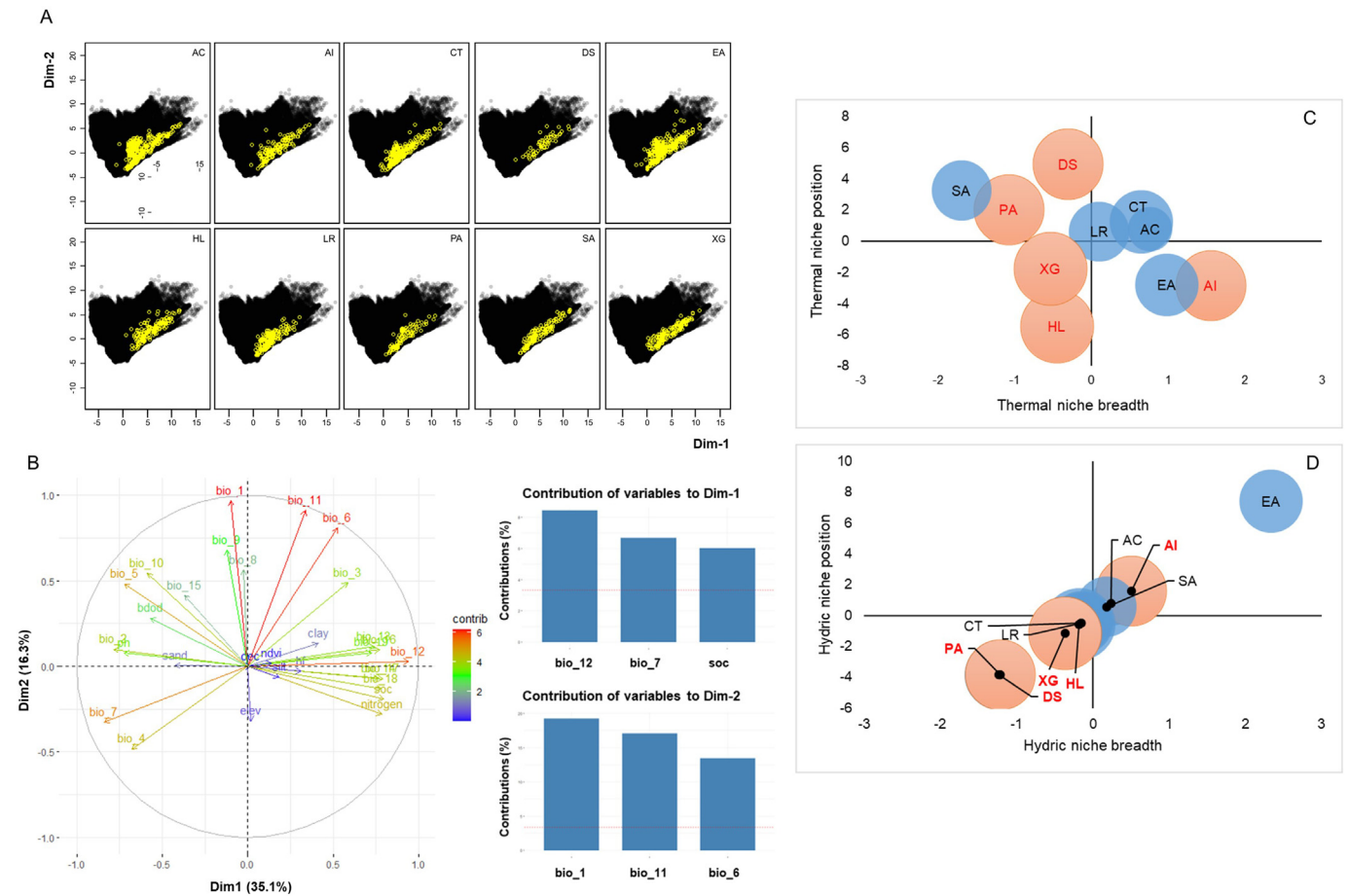
Fig. 6. Identification of conservation priority at the species level – (A) results of the Principal Component Analysis (PCA) showing the position of individual species in the two-dimensional niche spaces of the Indo-West Pacific, B) correlation circle showing variables' contribution along the two PCA axes for all species and the bar plots showing three most contributing variables along the two PCA axes; the position of the individual species in the two-dimensional thermal (C) and hydric (D) niche spaces, the bubble size depicts priority score with the five species having >75% quartile of score range have been marked in red. The abbreviated species names and the environmental variables have been given in Tables 1 and A.2, respectively.

sequester a large amount of organic carbon due to the high primary productivity, periodic submersion, and slow decomposition of the organic material in the water-logged anaerobic soil environment of the mangrove ecosystems (Liu et al., 2020). Besides, the proximity of mangrove habitats to the seawater entrance, where water flow is more intense and waters are richer in nutrients, increases the accumulation of organic matter in the soil (Ferreira et al., 2010). Our findings, therefore, further strengthen the previous observations that mangroves play an important role in global carbon cycling and sequestration [e.g., (Alongi, 2014)]. High soil bulk density has been found to increase mangrove productivity by increasing root biomass and diameter (Ola et al., 2019; Ola et al., 2018), which can explain the observed positive association of the bulk density and mangrove species distribution (dimension 2 of the correlation circle) in this study. The influence of the proportion of sand particles in the soil on the distribution of the mangroves is consistent with the observed pattern of particle-size distribution in the mangrove forests at a regional scale (Ferreira et al., 2010). However, particle-size distribution varies at a global scale, with clay percentage dominating over sand and silt (Shih, 2020). Understanding coastal evolution processes along the geological timescale may provide deeper insights into the sedimentation conditions and particle-size distribution in the IWP.

Overall, the potential distribution of the true mangroves and mangrove associates under current environmental conditions revealed by this study closely matches with the global baseline map of mangrove extent produced by using remote sensing data (Bunting et al., 2018). Most of the suitable habitats for the true mangroves and mangrove associates were found in Indonesia followed by Australia, being consistent

with the global dataset of mangrove distribution (Simard et al., 2019b). It is important to note here that our models identified areas in the IWP which are environmentally suitable for these species, and therefore, should not be compared with the estimates based on in situ field observation. Several factors may limit the species' presence in the areas, even if the environment is favourable for the species occurrence. For example, mangroves may be absent from environmentally suitable areas because of human-mediated removal. Indeed, the human influence index was found as an important variable influencing the distribution of the species studied here. Besides, other environmental variables not considered in this study (e.g., tidal dynamics, species interactions, coastal erosion, species dispersal) and the stochastic processes involved in species responses to the environmental factors (Gaston and He, 2002), may also influence local and regional distributions of these species.

4.2. Impacts of climate change

In the face of climate change, coastal areas were found to be impacted more, suggesting either loss of suitable habitat (range contraction) or landward migration of the species (range expansion and/or range shift). More importantly, we found species-specific responses to future climate and resultant variation in range size changes. The hypothesis of range contraction of individual species under future climate conditions (Ellison, 1994) was found to be valid for four mangroves (*A. ilicifolius*, *C. tagal*, *E. agallocha* and *S. alba*). For the rest of the three mangroves and three mangrove associates, we found northward range expansion, in accordance with the observations that mangroves are

expanding towards salt marshes in temperate zones around the world (Cavanaugh et al., 2019).

Precipitation, being the most important variable to influence the true mangrove distribution in the IWP, is predicted to increase in the two GCMs considered in this study. Changes in precipitation can influence mangrove distribution by altering soil salinity, mineral concentration in the soil, and sedimentation of the mangrove ecosystem. Therefore, species having a wide range of salinity tolerance are expected to gain suitable habitats in future. Previous studies have found that viviparous mangrove *A. corniculatum* has high salt tolerance (Ye et al., 2005). Besides, the species was found to have a large niche breadth, as evident from its position in the two-dimensional niche spaces. Therefore, it is not surprising that maximum gain of suitable habitats was observed for *A. corniculatum* in this study. Precipitation related variables, namely, precipitation of the wettest month (bio13), was found to influence the distribution of L. *racemosa*. Therefore, an increase in precipitation may positively influence the distribution of this species, as observed in this study and elsewhere (Record et al., 2013). Mean diurnal range of temperature has also been found to influence the current distribution of some mangroves (e.g., *X. granatum*) and mangrove associates (e.g., *D. spathacea*) in the IWP. An increase in temperature, as predicted in the two GCMs, may also help these species to expand their range into salt marsh communities at higher latitudes.

Future changes in climate conditions may negatively impact some of these species, as evident from our study. Notable is the case of *A. ilicifolius* (true mangrove) and *P. acidula* (mangrove associate), which showed maximum potential distribution in the current climate among the studied species, and in future, there is a predicted decrease in suitable habitat for the species. Increases in the frequency and intensity of precipitation can result in persistent inundation and sedimentation, and prolonged flood events (Asbridge et al., 2015), which may restrict the distribution and extent of some mangroves. Previous studies have found that prolonged inundation delays seed germination and decreases the germination rate in *A. ilicifolius* (Yang et al., 2015). Availability of suitable habitat for colonization, especially in future climate conditions, may be another limiting factor for species distribution. For example, calcareous rocky habitats are suitable for *P. acidula* distribution (Goutham-Bharathi et al., 2015). The VIF analysis in this study also found that the proportion of sand particles in the soil is not an important variable for this species' distribution. In the two-dimensional niche space, the positive TNP value of this species indicates that it may have reached the boundary of its potential distribution in the IWP, and the negative TNB is indicative of its inability to occupy a broad range of environmental conditions. Therefore, availability of novel and suitable habitats for colonization and the ability of the species to colonize them, might restrict its distribution in future climate condition.

It is important to take caution while interpreting our results since we could not consider variables other than climate for future projections, primarily due to the unavailability of such data at a large spatiotemporal scale. Although the major influence of temperature and precipitation related variables on the current distribution of the selected species addressed this concern here to some extent, integration of such data along with the dispersal ability of these species in future modelling frameworks may further clarify the impacts of habitat loss. In addition, there are other factors than climate which can influence mangroves distribution in future. For example, in the case of landward expansion due to rising sea levels, coastal terrain features can be a limiting factor leading to mass mortality or confinement of mangroves in narrow fringes (Asbridge et al., 2015). Notably, our modelling framework considered the realized niche of the species. Availability of information on fundamental niches of these species from fossil records, controlled experiments and genetic analyses may improve the predictive resolution. Given that the environmental conditions may vary at a finer scale, especially in coastal and estuarine environments, the predictive resolution can further be enhanced through modelling at multiple spatial scales and integrating variable information from field

observations. Finally, our estimates will be influenced by the choice of threshold to convert continuous projections to binary. Using TSS as the threshold in this study minimizes the sum of commission and omission errors by providing equal weights to these errors. A threshold that favours sensitivity over specificity might be a better approach but would also result in large commission errors (Das et al., 2019).

4.3. Conservation priorities

The loss of high species richness cells in future emphasizes the need for the conservation of habitats that are environmentally suitable for a large number of mangroves and mangrove associates. Previous studies have found that mangrove species diversity has a positive effect on soil carbon storage (Bai et al., 2021). The highest priority for conservation should be given to the locations which are currently suitable for these species and will remain so in future climate conditions. These areas are mostly distributed in the populated forest and residential rainfed mosaic anthromes, which have been characterized by having substantial human populations (Ellis and Ramankutty, 2008). Therefore, conservation planning for these areas should include the anthropogenic component in the framework to avoid future conflict of interest and effective management implementation. The areas of undisturbed mangroves are likely to be more in the developed countries (e.g., Australia, New Zealand), due to having vast uninhabited areas and a strong legislative framework. In the developing countries (e.g., India, China), the mangroves free from anthropogenic influence are mainly restricted in the PAs, which can provide greater protection to these species (Asbridge et al., 2015). However, our study found that most of these PAs have reported no management plan, or the plan is simply not existing. Moreover, the majority of the PAs having the highest priority conservation sites are located in the Philippines, Laos, and Madagascar, suggesting that management plans for the PAs located in developing countries should be formulated and implemented with priority. It is worth mentioning here that we estimated the species richness and identified the conservation priority sites by summation of the binary rasters for individual species. While this approach has been widely used in multispecies modelling studies [e.g., (McKerrow et al., 2018)], it did not account for biotic interactions (such as facilitation and competition), which may lead to over-or underestimation of species richness. Therefore, the conservation priority targets identified by our simple species-level modelling approach can change if the biotic interactions between species are included in the more complex community-level modelling framework (Dormann et al., 2018).

The areas identified as glacial refugia should also be prioritized for conservation. The LGM has been characterized as a period of high aridity, increased evapotranspiration and cooler temperatures as well as lowering of sea level (Woodroffe and Grindrod, 1991). These geoclimatic changes caused extensive range contraction of the mangroves and constrained them at lower latitudes (Kennedy et al., 2016), as also evident from our study. During the MHO, the temperature and precipitation increased considerably, which helped the species to start expanding their range to their potentially broadest extent in the current climate. The probable refugial locations identified in this study closely matches the distribution of glacial refugia for the coastal mangrove swamp in Sundaland (Cannon et al., 2009). In addition, the pollen sediment of mangrove plants in the continental slope of the SCS, as revealed by the paleopalynology studies (Sun and Li, 1999), also supported the presence of glacial refugia in areas of the Philippines and Taiwan. Our study revealed that very few of these refugial locations remain suitable for the true mangroves under the current climate condition and are restricted to parts of Indonesia. These findings are in accordance with Cannon et al. (2009), who observed that coastal mangrove and swamp forests underwent a complete and major biogeographic relocation during deglaciations. It is important to note here that these areas have climatic suitability to support high species richness. If we consider areas suitable (both in past and current climate condition) for individual

species (result not shown), a larger area has been found that remain suitable since the LGM to the present.

Our study revealed a significant overlap of the environmental niche among the selected species, thereby suggesting conservation actions targeted for specific habitats may benefit more than one species and maintain an integrated coastal ecosystem functioning. However, species like *A. ilicifolius* and *P. acidula* need more attention, as the distributions of these species have been predicted to decrease in future. In addition, the weighted-scoring approach in this study identified three more species, which should be prioritized for conservation actions despite showing potential range expansion in future. Notable is the case for *D. spathacea*. The average niche overlap (both D and I metrics) of *D. spathacea* with other species was found to be the lowest, which indicated that this species may have unique environmental requirements and might explain the narrow and fragmented distribution of this tree species (Patil et al., 2015). Having the negative niche breadth and niche position, *D. spathacea* may face a high risk of regional extinction (Peng et al., 2016), especially in the face of climate change.

Similar is the case for *H. littoralis*, which received the maximum conservation priority score. Indeed, the species was found to have negative niche traits, which may restrict its current distribution in the IWP, and make this species more susceptible to climate change-related effects more than the other species. Comparative studies involving *H. littoralis* to environmental change have revealed that photosynthesis and survival rates of the species decline with increasing salinity and prolonged inundation (Mangora, 2016). An increase in temperature (leading to increased salinity) and precipitation (leading to prolonged inundation) may therefore negatively impact the species extent in future climate. Species ecology could be an additional factor to determine how the species can respond to climate change (Asbridge et al., 2015). For example, the poor reproductive capacity of *H. littoralis* and low rate of germination and transformation of juvenile to adult (Jian et al., 2010), can further restrict the species distribution in future. The conservation actions for this species should also consider the anthropogenic influence. Comparing the uses and trade information, as recognized by the IUCN, between the studied species, we found the maximum number of uses for *H. littoralis* (n = 7; (Duke et al., 2010)). Extinction of *H. littoralis* due to anthropogenic activities has been reported from India (Kripa et al., 2020), and the species is currently restricted in protected areas across its distribution range in the IWP (Banerjee et al., 2020).

5. Conclusion

Our study revealed that precipitation and surface elevation could influence the distribution of the true mangroves, while temperature influenced the mangrove associates. Due to species-specific responses, the areas with high species richness are predicted to decrease in future. Rising sea levels and anthropogenic activities may further reduce the available habitats for these species. We identified the areas and the species which should be prioritized for conservation in the IWP. With the increasing number of international conservation programs for mangroves, these findings should assist in decision making to prioritize conservation targets.

CRediT authorship contribution statement

Achyut Kumar Banerjee: Conceptualization, Investigation, Methodology, Writing – original draft, Visualization, Supervision, Funding acquisition. **Hui Feng:** Investigation, Software, Writing – review & editing, Visualization. **Yuting Lin:** Investigation, Data curation, Writing – review & editing. **Xinru Liang:** Software, Data curation, Writing – review & editing, Visualization. **Jiakai Wang:** Software, Data curation, Writing – review & editing. **Yelin Huang:** Conceptualization, Resources, Writing – review & editing, Project administration, Funding acquisition.

Declaration of competing interest

Acknowledgement

Funding

Data availability

The occurrence data and estimates of the predicted distribution of all species, as well as the characteristics of conservation priority sites and areas, have been submitted to the Figshare repository and can be accessed through the DOI: https://doi.org/10.6084/m9.figshare.14992356. The environmental variables can be accessed through their respective websites (see Table A.2 for details).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150937.

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