Ecological Indicators 129 (2021) 107960

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Mapping the seagrass conservation and restoration priorities: Coupling habitat suitability and anthropogenic pressures

Wenjia Hu [a,b], Dian Zhang [a], Bin Chen [a,b], Xinming Liu [c], Xiaomin Ye [d], Qutu Jiang [e], Xinqing Zheng [a,b], Jianguo Du [a,b,*], Shiquan Chen [f,*]

[a] Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China
[b] Fujian Provincial Key Laboratory of Marine Ecological Conservation and Restoration, Xiamen 361005, China
[c] Institute of Marine Drugs, Guangxi University of Chinese Medicine, Nanning 530200, China
[d] Key Laboratory of Space Ocean Remote Sensing and Application, National Satellite Ocean Application Service, Ministry of Natural Resources, Beijing 100081, China
[e] Institute of Islands and Coastal Ecosystems, Ocean College, Zhejiang University, Zhoushan 316021, China
[f] Hainan Academy of Ocean and Fisheries Sciences, Haikou 570125, China

ARTICLE INFO

Keywords:
Seagrass conservation
Exposure assessment
Habitat sustainability
Conservation and restoration planning

ABSTRACT

Seagrass meadows provide important ecosystem services, but are among the least conserved marine ecosystems. The Southern bioregion of China has the nation's largest seagrass distribution. However, lack of information on the distribution of seagrasses and the threats they face pose a significant obstacle to their conservation and restoration. Accordingly, a framework for prioritizing conservation and restoration objectives was proposed in the present study. First, we modeled the suitable habitats with MaxEnt, random forest (RF), and ensemble models to obtain a reliable basis map of seagrass distribution. A potentially suitable area of approximately 3,536–4,852 km^2 was mapped in the coastal sea of South China, with the greatest area occurring between 18 °N and 22 °N. The anthropogenic pressures on the seagrass habitat were then estimated using an integrated exposure index consisting of four indicators, namely, population density, fishery economy, aquaculture, and shipping. The results indicated 48% of the coastal seas were under intensive anthropogenic pressures, with a higher exposure in the north than the south. The current conservation status suggests that there is a large seagrass conservation gap. By coupling the two dimensions of habitat suitability and integrated exposure, priority sites for seagrass management in South China were identified for the first time. Our work will not only provide basic information for coastal ecosystem management, but also serve as a tool to support the conservation and restoration planning of seagrass, thus, ultimately promoting the sustainability of seagrasses habitats.

1. Introduction

Seagrasses are marine flowering plants constituting some of the most productive ecosystems on earth (Waycott et al., 2009). They have successfully colonized a very wide range of marine habitats between subarctic and tropical latitudes (Orth et al., 2006). Seagrass meadows not only provide nursery and foraging grounds for fishes and invertebrates of subsistence and commercial value (Du et al., 2020; Heck Hay et al., 2003; Reynolds et al., 2018; Unsworth et al., 2019a,b), but are also important habitats for threatened species (Fedrizzi et al., 2015; Hearne et al., 2019). Moreover, they support important ecological processes (Duarte, 2002; Lamb et al., 2017; Lotze et al., 2006). It has been recognized in recent years that seagrasses contribute to climate change mitigation through large organic carbon sinks within their ecosystems (Stankovic et al., 2021).

However, during the past decades, large-scale losses have been reported in seagrass meadows worldwide. Seagrasses and the services they provide are threatened by the immediate impacts of coastal development and growing human populations, as well as by the impacts of climate change and ecological degradation (Hotaling-Hagan et al., 2017; Orth et al., 2006; Short and Wyllie-Echeverria, 1996; Waycott et al., 2009). Nearly one third of seagrass coverage has been lost since seagrass distribution was first recorded in 1879. Since 1990, the rate of decline in seagrass area has accelerated to 7% annually (Waycott et al., 2009). Notably, only 26% of recorded seagrass meadows fall within marine protected areas (MPAs), placing seagrass habitats among the least

* Corresponding authors at: Third Institute of Oceanography, Ministry of Natural Resources, PRC, 178 Daxue Road, Xiamen 361005, China (J. Du).
E-mail addresses: dujianguo@tio.org.cn (J. Du), chensq@hnhky.cn (S. Chen).

https://doi.org/10.1016/j.ecolind.2021.107960
Received 27 May 2021; Received in revised form 5 July 2021; Accepted 6 July 2021
Available online 12 July 2021

conserved marine ecosystems (UNEP, 2020). Considering that seagrass management is implemented as a practical scheme of nature-based solutions for climate change mitigation (Shilland et al., 2021; Stankovic et al., 2021), there is a growing need for the efficient protection and conservation of seagrass meadows worldwide (Downie et al., 2013; Orth et al., 2006).

Seagrass is distributed along the temperate and tropical coastlines of China, covering a recorded area of approximately 9,000 ha (Zheng et al., 2013). However, these seagrass habitats have been degrading with their range rapidly declining over the past decades. For example, the seagrass meadows in Yingluo Harbor, Guangxi province have nearly disappeared (Deng, 2002; Li et al., 2010). Specifically, the seagrasses along the south and east coast of Hainan Island have rapidly declined in the past ten years (Chen et al., 2015; Yin and Zhong, 2018). Additionally, the anthropogenic pressures on seagrass meadows have not yet been fully assessed. Thus, a major concern is that various seagrass meadows will silently vanish before they are discovered and recorded, owing to rapid economic development and urbanization (Jiang et al., 2017).

Due to long-term degradation, China's seagrass meadows have shrunken to small patches scattered along the coast instead of large continuous distributions (Zheng et al., 2013). In addition, since the seagrass meadows in China are generally distributed in the low-intertidal or subtidal zone with a depth of approximately 4 m, they are not readily accessible by foot or boat (Huang, 2019). These conditions often make data collection costly and relatively inefficient. Therefore, although the surveys on seagrasses in China began in the 1980 s, most have only focused on select bays, with almost no distribution information of seagrass in other areas (Yang, 2017; Xu et al., 2021). This causes a substantial lack of information required for the seagrass conservation and restoration planning (Jiang et al., 2017).

Spatially explicit seagrass data are lacking in China and other regions. For example, the tropical Indo-Pacific bioregion (including South China) has the largest documented seagrass area (52%). However, data for 42 countries within this bioregion are lacking (Unsworth et al., 2019a, 2019b). This knowledge gap hinders the effective management and protection of seagrass habitats worldwide (Downie et al., 2013). Therefore, coastal managers have focused their efforts and resources on mapping the possible distribution of seagrasses (Bittner et al., 2020; Short et al., 2011). In a study investigating carbon sinks, the global seagrass distribution was estimated to be between 300,000 km^2 and 600,000 km^2 (Duarte et al., 2010). An updated map providing a representation of large-scale seagrass distribution across approximately 800,000 km^2 was released in 2020 (UNEP-WCMC and Short, 2020). Another global seagrass meadow distribution map was produced using species distribution modeling (SDM), which predicted a much greater coverage than that predicted by previous studies (1,646,789 km^2) (Jayathilake and Costello, 2018). Within these global maps, however, the mapped distribution in the region of China remains quite inadequate or differs from the actual distribution, which may be caused by insufficient mapping and modeling data.

SDMs are often used to plot species distribution maps and assess habitat suitability, especially regarding species for which it is difficult to obtain records. This approach associates field observations with environmental predictor variables to predict the abundance of taxa and their likelihood of existing in a given area, while characterizing the underlying environmental drivers of their geographic distribution (Georgian et al., 2019). Hence, the use of SDMs has recently increased significantly in marine ecosystem applications (Melo-Merino et al., 2020). The most frequently studied marine taxa are fishes and mollusks, while seagrasses are among the least studied groups (Melo-Merino et al., 2020).

Recently, machine learning methods have become the most popular modeling methods; among these, the maximum entropy model (MaxEnt) is the most widely used (Anderson et al., 2016b; Bittner et al., 2020; Downie et al., 2013; Melo-Merino et al., 2020). Meanwhile, some studies found that tree-based classification algorithms perform better than others in terms of predicting seagrass habitats, with random forest model (RF) being the most effective (Effrosynidis et al., 2018; Stankovic et al., 2019). In addition to a single model, an ensemble of multi-algorithms was also used to obtain a reliable prediction (Araújo and New, 2007).

Using these approaches, regional-scale seagrass distribution studies have been conducted in Europe (Beca-Carretero et al., 2020; Downie et al., 2013; Effrosynidis et al., 2018; Valle et al., 2011), North America (Bittner et al., 2020), and Southeast Asia (Hashim et al., 2017; Stankovic et al., 2019). Based on known or predicted distributions, human activity and regional threats have been further analyzed to aid site selection for seagrass conservation and restoration efforts (Hotaling-Hagan et al., 2017; Stankovic et al., 2019). Moreover, expert questionnaires, vulnerability assessments, and superimposed ranking maps have been employed to identify potential priority areas (Hotaling-Hagan et al., 2017; Unsworth et al., 2018). However, to the best of our knowledge, no such studies have been reported from China or East Asia.

In the present study, we mapped the environmental areas considered conducive to seagrass conservation and restoration and established priorities for these objectives along the coast of Southern China. To this end, we implemented three models to produce a reliable seagrass habitat suitability map. We also evaluated the anthropogenic pressure in the seagrass distribution area. The present study aimed to: (i) Test and compare the performance of MaxEnt, RF, and the ensemble model in predicting seagrass habitat suitability (ii) Plot a map of seagrass meadow distribution in the coastal area of South China and help prioritize locations for future surveys (iii) Quantify the exposure of seagrass habitats to anthropogenic pressure (iv) Provide new insights into future seagrass habitat conservation and restoration measures.

2. Methods

2.1. Study area

The seagrasses in China are primarily distributed in the Southern (South China Sea) and Northern (Yellow Sea-Bohai Sea) bioregions (Xiao et al., 2020). Over 90% of all seagrass meadows in China are distributed in the Southern bioregion (Yang, 2017; Zheng et al., 2013) belonging to the tropical Indo-Pacific bioregion of global seagrass distribution (Short et al., 2007). The study area covered the south coast of mainland China including the Hainan, Guangxi, and Guangdong Provinces, Hong Kong, and part of Fujian Province (Fig. 1). Nearly 200 million people live in these administrative areas with nine seagrass genera and 15 seagrass species identified in this bioregion (Zheng et al., 2013). The northern boundary of the study area was located at Quanzhou in Fujian Province (approximately 150 km north of the Tropic of Cancer) and the southern boundary was set as the southern coast of Hainan Island. Internal seawaters and 12 nautical miles of territorial sea were also included to map the anthropogenic pressure. The latitude range was approximately 17 °57′ N–24 °55′ N and the coastline was more than 13,000 km long, including island coastlines.

2.2. Methodological framework

Fig. 2 shows a flowchart depicting the methodology of the present study. SDMs and an exposure index were combined in the methodology framework. First, MaxEnt and RF models were applied using seagrass occurrence data and environmental variables. An ensemble model was then generated according to the performance of the two SDMs, and seagrass distribution and habitat suitability were mapped. Subsequently, an exposure index integrating four indices was proposed to evaluate anthropogenic pressures in the study area. Finally, the spatial pattern of pressures and conservation were superimposed with the modeled distribution to interpret the conservation and restoration priorities.

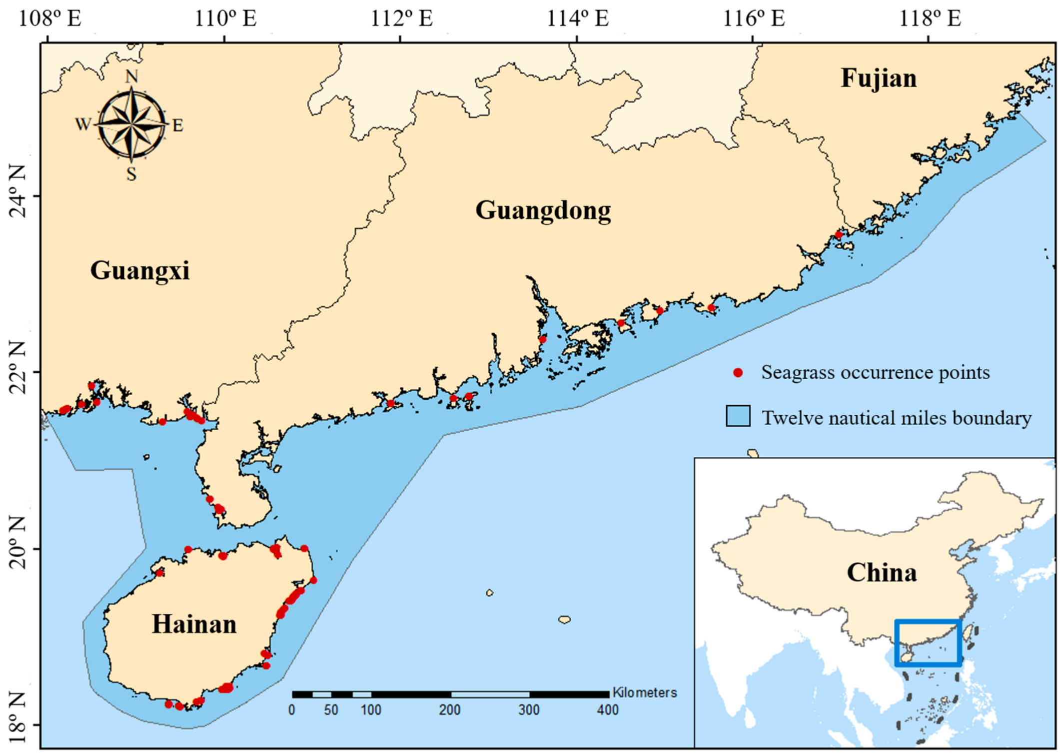

Fig. 1. Study area and seagrass presence records used in modeling.

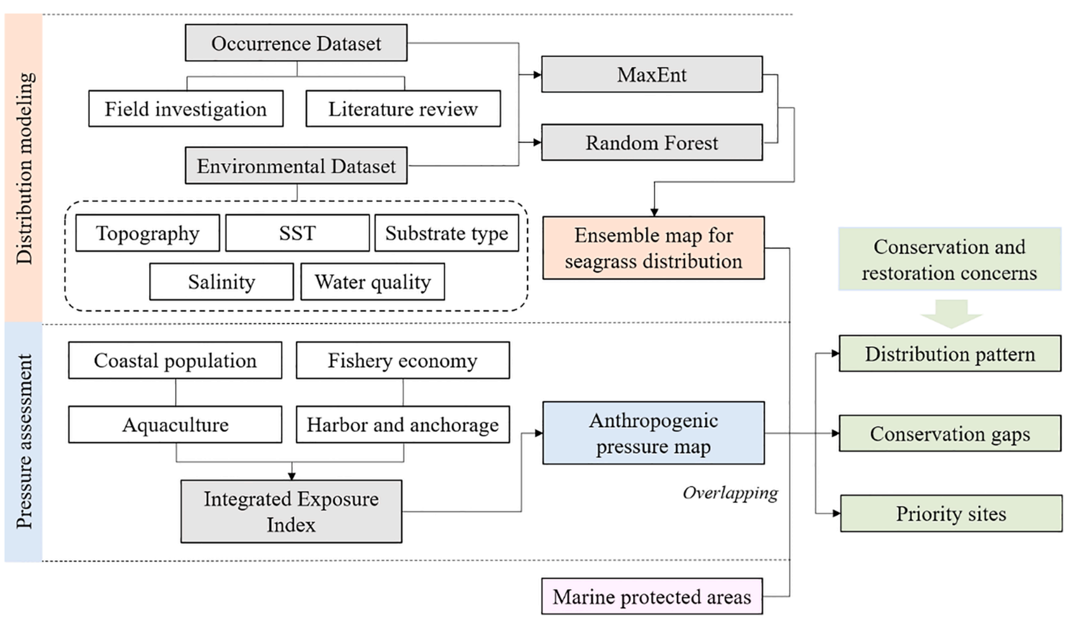

Fig. 2. Methodology flowchart.

2.3. SDM dataset preparation

2.3.1. Seagrass occurrence dataset

Species distribution modeling was based on target species' occurrence records. Since seagrass research along the large coastlines of China is relatively limited (Xiao et al., 2020), there is no publicly available seagrass dataset for the study area. In addition, due to the large variation in water quality in the near-shore of mainland China, seagrass distribution can be hardly extracted from remote sensing data (Yang, 2017), which can often be used as an alternative data source in other regions. Therefore, in this study we compiled records from field surveys and literature reviews to generate an occurrence dataset. Surveys were performed annually in Hainan in August from 2004 to 2020, and in Guangxi in May and June from 2014 to 2020. Surveys were conducted in Guangdong and Fujian in May and November 2020. All surveys were carried out during low tide to increase the probability of observing seagrass meadows. An underwater census was also conducted in deep waters. Section and sample frame surveys were carried out based on the method advocated by previous studies and survey guidelines (Short and Coles, 2001; SOA, 2005). Environmental conditions at various seagrass sites were compared, and those with identical environmental variables were excluded. There were 125 and seven occurrence points extracted from the survey data and the literature (Huang et al., 2010), respectively, all of which served as presence records and covered most areas where seagrass meadows are known to concentrate (Fig. 1).

The MaxEnt model was trained with presence-only data, whereas both presence and absence data were required to train the RF model. We obtained 73 absence records from the survey. Additionally, a set of artificial absence records was created in the background of the study area based on certain rules (Effrosynidis et al., 2018; Udyawer et al., 2020). Around each occurrence point, a 50 km buffer zone was established that had environmental conditions similar to those of the occurrence points and could be suitable for seagrasses. Hence, these areas were excluded from the background used to generate pseudo-absences. Random sampling was then performed in the background generating 5,000 pseudo-absence records. Latitudes and longitudes of all presence-absence points were converted to CSV format, yielding a seagrass distribution dataset.

2.3.2. Environmental dataset

Critical environmental factors controlling seagrass distribution and physiological processes include temperature, salinity, light, and substrate type and depth (Adams et al., 2020; Collier and Waycott, 2014; Dennison, 2009; Downie et al., 2013; Green et al., 2003; McMahon et al., 2013). Water quality variables such as pH, suspended solids, and chlorophyll, nitrogen, and phosphorous concentrations are strongly correlated with seagrass distribution (Bittner et al., 2020), whereas eutrophication is a major driver of global seagrass loss (Thomsen et al., 2020). Therefore, 18 environmental variables, directly or indirectly affecting seagrass distribution were selected and grouped according to topography, sea surface temperature (SST), sea surface salinity (SSS), substrate type, and water quality (Table 1).

Most environmental data were obtained from different global databases or remote sensing data products. Some topographic variables were calculated from elevation data using the spatial analysis tools of ArcGIS 10.7. As the resolution of pH and nutrient concentration data was low in the global database, we extracted near-shore survey records from State Oceanic Administration investigations and interpolated them to the study area. All variables were interpolated to a 30 arcsec resolution (~1 km grid cell) for further analysis.

Table 1
Environmental variables used in the models.

Data type	Variable	Unit	Source
Topography	Distance from shore	m	Data from globalfishingwatch.org
	Elevation	m	ETOPO1 data from NOAA
	Compound topographic Index	–	A function of slope and upstream area per unit of orthogonal width contributing to flow direction (Moore et al., 1993; Gessler et al., 1995), calculated in ArcGIS 10.7 and based on elevation data
	Local deviation from global	–	Calculated by Local Deviation from Global tool in ArcGIS 10.7 based on elevation data to indicate the landform process
SST	SST of the coldest quarter	°C	NASA MODIS-Aqua L3 products (http://oceancolor.gsfc.nasa.gov)
	SST of the warmest quarter	°C	NASA MODIS-Aqua L3 products (http://oceancolor.gsfc.nasa.gov)
	SST of the driest quarter	°C	NASA MODIS-Aqua L3 products (http://oceancolor.gsfc.nasa.gov)
	Annual mean SST	°C	NASA MODIS-Aqua L3 products (http://oceancolor.gsfc.nasa.gov)
	Annual SST range	°C	NASA MODIS-Aqua L3 products (http://oceancolor.gsfc.nasa.gov)
SSS	Annual mean SSS	‰	Bio-ORACLE data (Tyberghein et al., 2012; Assis et al., 2017)
	Annual SSS range	‰	Bio-ORACLE data (Tyberghein et al., 2012; Assis et al., 2017)
Substrate type	Substrate type	–	2018 AHO S57 map
Water quality	pH	–	Spatial interpolation based on 861 sites (Survey conducted in 2015 by the State Oceanic Administration)
	Phosphate	mg/L	Space-time phosphate concentration prediction (Jiang et al., 2019)
	Nitrate	mg/L	Space-time nitrate concentration prediction (Jiang et al., 2019)
	Transparency	m	NASA MODIS-Aqua products (http://oceancolor.gsfc.nasa.gov), using retrieval algorithms developed by Lee et al. (2015)
	Suspended solids	mg/L	NASA MODIS-Aqua products (http://oceancolor.gsfc.nasa.gov), using retrieval algorithms developed by Tassan (1994) and He et al. (2013)
	Chlorophyll α	mg/m^3	NASA MODIS-Aqua products (http://oceancolor.gsfc.nasa.gov), using retrieval algorithms developed by John et al. (2019)

2.4. Model construction and evaluation

2.4.1. Modeling process

MaxEnt is among the most highly recommended models for species distribution predictions (Melo-Merino et al., 2020), while the RF model has been shown to perform best for seagrass in some cases (Effrosynidis et al., 2018; Stankovic et al., 2019). Recently, the use of an ensemble modeling approach was promoted, as it can reduce uncertainty over single algorithms and improve model robustness (Araújo and New, 2007; Kaky et al., 2020; Marmion et al., 2009). Therefore, we selected MaxEnt, RF, and an ensemble model to determine seagrass meadow habitat suitability, and to test and compare methods for predicting seagrass distribution.

MaxEnt estimates the probability of the presence of any species by randomly generating background points and finding the maximum entropy of the species distribution based on input presence data (Elith et al., 2011; Phillips et al., 2006). RF is an algorithm that was developed out of classification and regression trees and bagging approaches (Breiman, 2001; Evans et al., 2011). Each tree is trained by selecting a random set of variables and a random sample from the training dataset (Vincenzi et al., 2011). The final classification prediction is a majority vote based on predictions for all the trees in the collection (Breiman, 2001; Effrosynidis et al., 2018).

In both MaxEnt and RF, 75% of the distribution data was randomly selected to train the models, while the remaining 25% was used to test the models. The MaxEnt model was developed in MaxEnt version 3.4.1. The recommended default parameters for the convergence threshold (10–5), maximum number of iterations (500), and maximum number of background points (10,000) were used and repeated 10 × with bootstrap resampling. The randomForest package (Liaw and Wiener, 2002) in R version 4.0.2 (R Development Core Team, 2009) was used to train the RF model. The two main user-defined parameters in the RF model were the number of variables to test at each node (mtry) and the number of trees in the forest (ntree). We pre-tested the models using various mtry and ntree values in order to identify the optimal settings and estimated the model errors. The model performance was relatively stable, and the error was relatively low when mtry = 10 and ntree = 1,000. Therefore, these values were used in the RF model settings. To minimize the stochasticity that is inherent in RF, the model was replicated 30×, and the average of the best ten runs served as the final output. After the aforementioned models were constructed separately, an average consensus method was used to generate the ensemble model (Marmion et al., 2009; Crimmins et al., 2013).

All model outputs were plotted as grid maps with a 30-arcsec resolution (approximately 1 km). The value of each grid cell represented the distribution probability in floating-point format ranging from 0 to 1.

Grid maps with continuous values were simplified into binary maps and classified as either suitable (1) or unsuitable (0) for further analysis. The lowest presence threshold (Pearson et al., 2007), which is the lowest predicted value associated with any real presence points (Udyawer et al., 2020), was adopted as the threshold level to produce the binary maps.

2.4.2. Model evaluation

The area under the receiver operating curve (AUC) and the true skill statistic (TSS) were used to evaluate the predictive performance and accuracy of all models (Fourcade et al., 2018; Phillips et al., 2006). The AUC value is in the 0–1 range and indicates the degree of agreement between the model projection and actual occurrence data (Elith and Graham, 2009). The model was considered usable when AUC was greater than 0.75. AUC values between 0.90 and 1.0 indicated excellent model performance (Fourcade et al., 2018). TSS is a threshold-dependent model evaluation metric that accounts for both model omission and commission errors. TSS ranges from -1.0 to $+1.0$, where $+1.0$ represents perfect performance and ≤ 0 indicates a performance worse than random prediction (Allouche et al., 2006). For both MaxEnt and RF, mean AUC and TSS values across the ten replicates per algorithm were used to assess the overall model performance (Kaky et al., 2020; Udyawer et al., 2020).

2.5. Pressure assessment

Compared to natural disturbances, human population expansion is now the most serious cause of seagrass habitat loss; more specifically, increasing anthropogenic input to the coastal oceans is primarily responsible for the worldwide seagrass decline (Short and Wyllie-Echeverria, 1996). In rapidly developing regions, seagrass loss is correlated with coastline urbanization (Effrosynidis et al., 2018). Additionally, human activities, such as land reclamation, harbor construction, aquaculture, boating, anchoring, and certain fishing practices have caused seagrass damage (Duarte, 2002; Herbeck et al., 2014; Hotaling-Hagan et al., 2017; Short and Wyllie-Echeverria, 1996; Thomsen et al., 2020).

The southeastern coast of China is the most densely populated and economically developed region in the country. Thus, the seagrass meadows of the area are subjected to anthropogenic pressure (Xiao et al., 2020). A geospatial approach was proposed to rapidly estimate the magnitude of this pressure. The study area was divided into 1 km grids with the same resolution as the SDMs. For each grid cell, human pressure intensity was quantified considering the types of pressure and the distance from their sources (Parravicini et al., 2012). The direct/indirect pressures included population density, fishery economy, aquaculture, and shipping (Table 2). An integrated exposure index was developed to calculate the total exposure:

$$E = \sum_{i=1}^{n} W_i \times Z_i \quad (1)$$

where E is the integrated exposure index, $Z_i$is the value of pressure i, W_i is the weight of pressure i, and n represents the number of pressures. Previous studies suggest that aquaculture is the most serious source of seagrass meadow disturbance in China (Han, 2016; Short et al., 2011; Thomsen et al., 2020; Zheng et al., 2013). Hence, the weight of aquaculture was set to 0.4, and the weights of the other three indices were set to 0.2.

Table 2
Pressure indicators and data sources.

Indicator	Data Source
Population density	Grid dataset of China's population distribution (http://www.resdc.cn/) (Xu et al., 2017a)
Aquaculture	2019 coastal survey data of the Ministry of Natural Resources
Fishery economy	Grid dataset of China's GDP distribution (http://www.resdc.cn/) (Xu et al., 2017b); China fishery statistical data (MARA of PRC, 2016)
Shipping	2018 IHO S-57/Electronic Nautical Charts

Population density and fishery economy pressures were calculated based on 1 km grid 2015 population and GDP maps of China. Coastal settlements were extracted according to population density. The ratio of the gross fishery output to the total GDP was calculated for each coastal province, while the GDP map grid values were adjusted to represent only the fishery output values. Coastal aquaculture and shipping areas were extracted from surveys and nautical charts (Table 2). The Euclidean distance tool in ArcGIS version 10.7 was then used to calculate the distance from each pressure. To facilitate calculation and comparison, the grid values in each pressure layer were standardized to a range of 0–1 as follows:

$$Zj = \frac{max(x) - xj}{max(x) - min(x)} \quad (2)$$

where Zj is the standardized value of grid j Xi is the original value of grid j, max(X) is the maximum value of the grids within the study area, and min(X) is the minimum value of the grids within the study area.

2.6. Conservation and restoration prioritization

To identify the potential areas that could pose the greatest threats to seagrass or with the highest conservation priority, we superimposed the pressure map to the distribution map. A conceptual two-dimensional framework was proposed to help identify conservation and restoration priorities (Fig. 3). Areas with high seagrass habitat suitability and low anthropogenic pressure were the most conducive to seagrass habitat maintenance. At the same time, low-intensity human activity reduced the conservation costs. Therefore, theoretically, these areas could be classified as conservation priorities. However, seagrass is prone to degradation in suitable areas with high anthropogenic pressure. Areas with moderate anthropogenic pressure constitute restoration priorities, while those under severe anthropogenic pressure are poor candidate sites for seagrass restoration owing to the high maintenance costs (Hotaling-Hagan et al., 2017). Based on the framework, the two dimensions of suitability and pressure were then projected into a bivariate choropleth map to determine the locations of conservation and restoration priorities. Furthermore, we overlaid the existing MPAs (Hu et al., 2020) on the seagrass distribution map, and analyzed the potential conservation gaps.

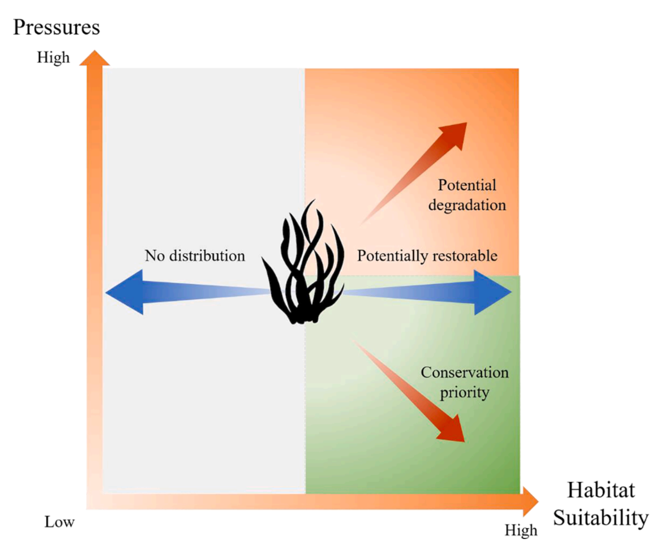

Fig. 3. Conceptual framework for identifying potential conservation and degradation areas.

3. Results

3.1. Model performances and predictors

The AUC values for the MaxEnt, RF, and ensemble models were 0.99, 0.92, and 0.91, respectively, while their TSS values were 0.65, 0.85, and 0.82, respectively. The AUC values indicated that all three models had excellent performance. Nevertheless, the RF and ensemble models had higher TSS than the MaxEnt model. The statistical tests showed that all the three models were highly reliable at simulating potential seagrass habitat suitability.

The relative importance of the environmental variables was interpreted by percent contribution in the MaxEnt model and mean decrease accuracy (MDA) in the RF model. Among the 18 environmental predictors, the main contributors were distance from shore, annual mean SSS, and nitrate content, which ranked in the top 30% according to both the percent contribution and the MDA (Fig. 4). The best suitable ranges of the main predictors were distance from shore < 885 m, annual mean SSS in the 33.09–33.17‰ range, and nitrate content in the 0.01–0.06 mg/L range. Considering that the distribution of tropical Indo-Pacific seagrasses is often limited by temperature, the best suitable range of annual mean SST was also calculated as 27.2–32.7 °C.

3.2. Potential habitat and suitability

Each model predicted the potential seagrass distribution area differently. For RF, MaxEnt, and the ensemble models, it was 4,851.56 km^2, 4,417.69 km^2, and 3,536.41 km^2, respectively (Table 2). The lowest presence thresholds used to produce the binary maps were 0.13, 0.09, and 0.15 for the RF, MaxEnt, and ensemble models, respectively. The overall model agreement was high, and all models predicted similar areas as being suitable seagrass habitats, both in the vicinity of known seagrass locations and in unsampled areas (Fig. 5a-c).

The results predicted by the MaxEnt, and RF models were similar for southern regions, such as Hainan Province (Fig. 5a, b). Suitable seagrass habitats were nearly continuously distributed around Hainan Island, with the exception of its southwest coast. The suitable seagrass habitats in Hainan accounted for approximately 50% of the total estimated suitable area in the three models and covered the largest area among all four provinces. MaxEnt provided a marginally more conservative estimate than RF for the northern region. In Fujian Province, the suitable areas predicted by MaxEnt were concentrated at the junction of Fujian and Guangdong, near the Tropic of Cancer. The habitats predicted by RF were distributed intermittently to the northern boundary of the entire study area. Overall, the seagrass distribution area predicted by all three models decreased with increasing latitude.

The theoretical seagrass habitat suitability decreased along the latitude gradient. High suitability values occurred between 18 °N and 22 °N, a zone characterized by tropical climate (Fig. 5a-c). In all three models, the most suitable habitats appeared along the east coast of Hainan Island. MaxEnt and RF predicted similar suitability values within the same provincial geographic range (Table 3).

3.3. Spatial pressure patterns

The spatial patterns of the four exposure indices differed (Fig. 6a-d). The population density pressure was higher in the north than the south. The coastal areas of Xiamen and Shantou were under the highest population density pressure while that along the southwestern coast of Hainan was the lowest. Although areas under high fishery pressure occurred along the coasts of all four provinces, they were most concentrated in northern Guangdong and southern Fujian. The map of aquaculture activities indicated widely spreading pressures along the southeast coast of China, while the pressures in Guangxi and west Hainan were relatively low. The patterns for shipping pressure resembled those for aquaculture pressure. Large ports were widely distributed along the coastline of the study area except for the southeastern corner of Hainan Island and the western coast of Leizhou Peninsula.

The integrated exposure index was calculated based on the four indices (Fig. 6e). Within South China, 48% of the coastal seas were

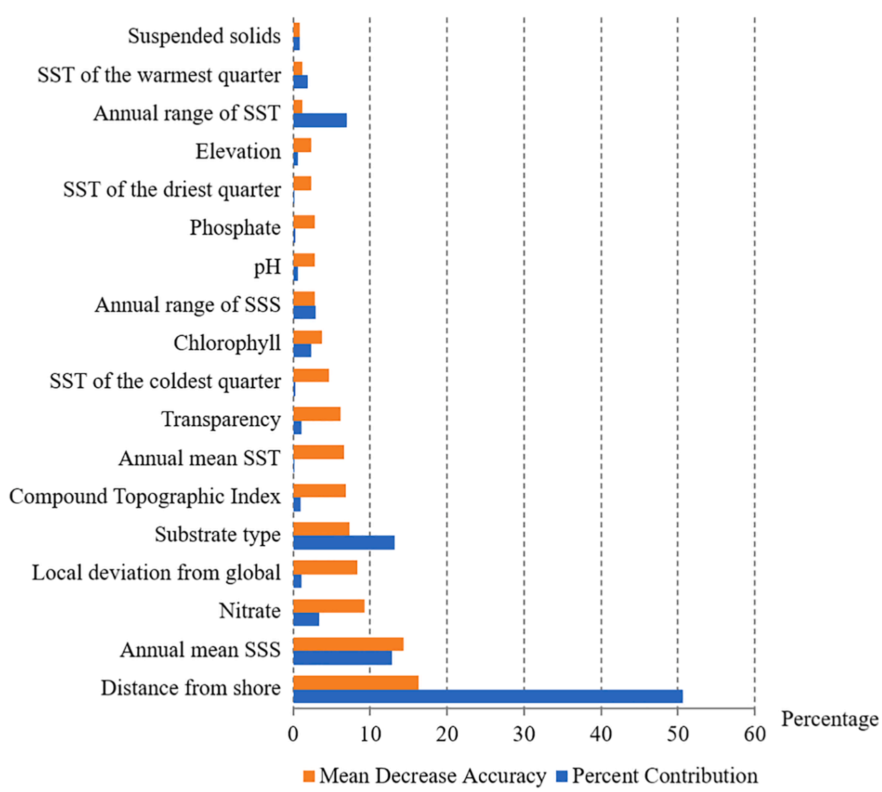

Fig. 4. Contribution of environmental variables.

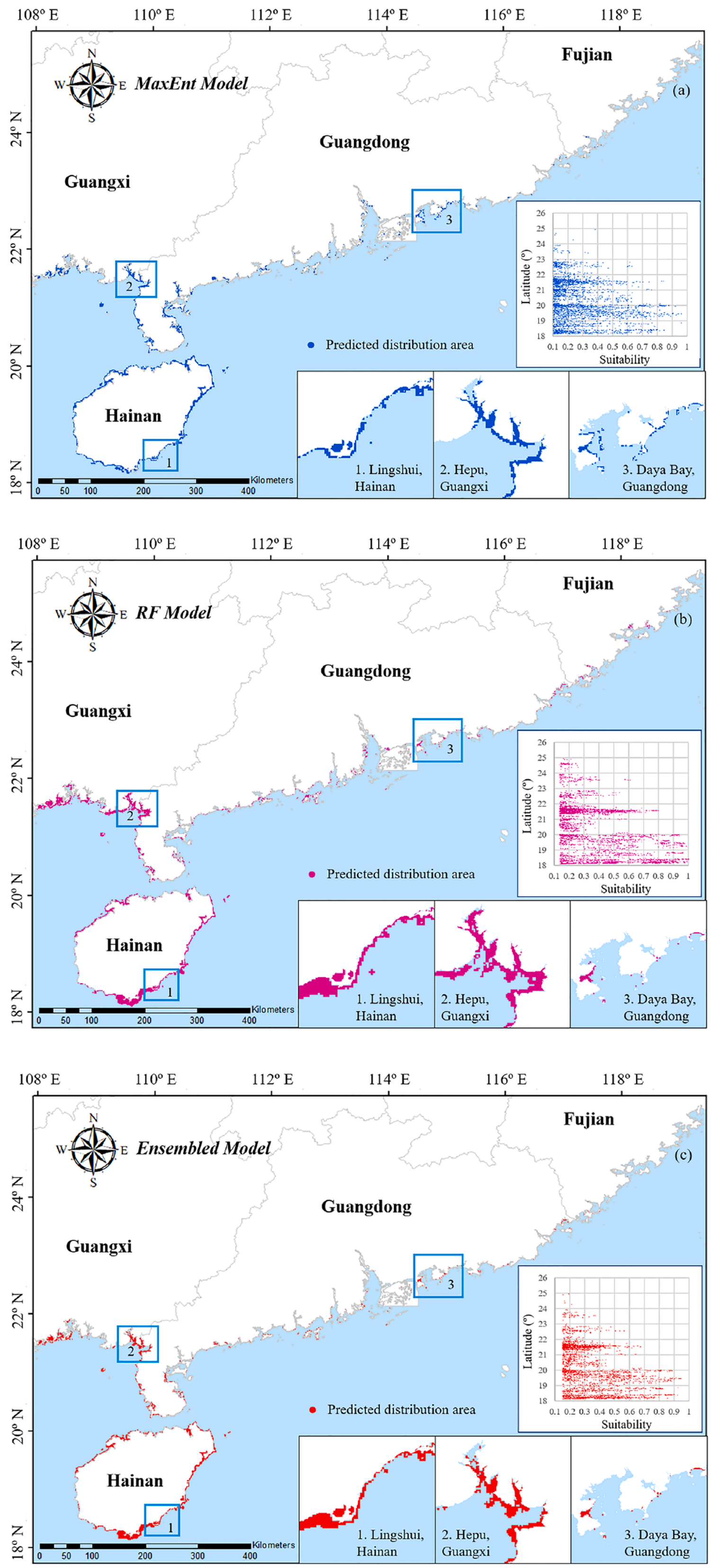

Fig. 5. Suitable seagrass habitat distribution in the coastal sea of South China (Predicted by a. MaxEnt model, b. RF model, and c. ensemble model).

Table 3
Area and suitability of potential habitats for seagrasses in the coastal sea of South China.

Province	Latitude extent	Area (km^2)			Maximum suitability		
		MaxEnt	RF	Ensemble	MaxEnt	RF	Ensemble
Hainan	17°57′N–20°07′N	2,239.57	2,288.21	2,078.19	0.96	1.00	0.94
Guangdong	20°07′N–23°37′N	1,592.09	1,169.33	830.91	0.67	0.69	0.61
Guangxi	21°26′N–21°56′N	557.60	1,255.54	608.97	0.84	0.80	0.67
Fujian	23°37′N–24°55′N	28.43	138.48	18.34	0.38	0.38	0.24
Total		4,417.69	4,851.56	3,536.41	–	–	–

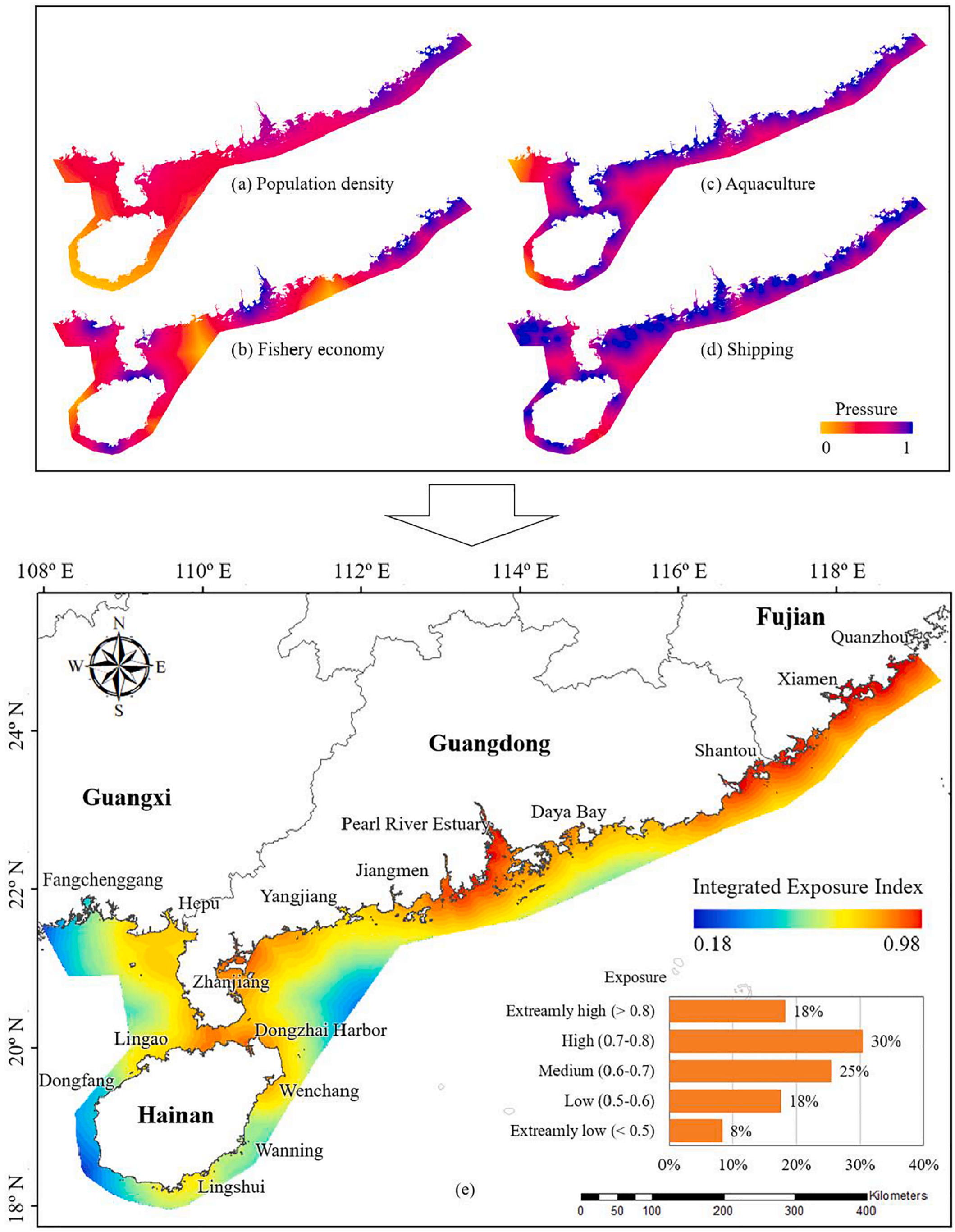

Fig. 6. Anthropogenic pressures in coastal areas and in 12 nautical miles of territorial sea.

under high or extremely high pressures. The results indicated a higher exposure trend in the north and a lower exposure trend in the south, taking the Pearl River Estuary as a demarcation mark. The pressure in southern Fujian, northern Guangdong, and the Pearl River Estuary was high and the extent of the impact was broad. In contrast, exposures were relatively low in the coastal areas of Hainan and Guangxi.

3.4. Spatial analysis for conservation and restoration concerns

We summarized the distribution of MPAs along the mainland coast of South China and found that until 2018, there were 46 national and provincial MPAs, of which only two were designated for seagrass. One county-level MPA in Guangdong Province assigned seagrass as its protection object (Fig. 7). The total area of the three MPAs was only 409.53 ha. However, the total recorded area for all seagrass meadows in South China was ~ 7,555.4 ha (Zheng et al., 2013), with a predicted potential distribution much larger than this number. Therefore, the seagrass habitat conservation rate is extremely low (<5%), indicating the existence of a large conservation gap.

We then superimposed the exposure map onto suitable habitat plots to identify priority areas for seagrass conservation and restoration. These areas were marked using a color continuum based on the suitability-pressure framework (Fig. 8). The results indicated that most high-pressure areas did not correspond to the highly suitable seagrass habitats. The seagrass distribution hotspots were situated between 18 °N and 22 °N south of the Pearl River Estuary, whereas the high-pressure areas were concentrated to the north of the Pearl River Estuary. Hence, seagrass bed refuges were more likely to exist in southern regions, such as Hainan and Guangxi. There may be endangered seagrass meadows in sites where high suitability and high pressure occur simultaneously, e.g., in Dongzhai Harbor in Hainan and Daya Bay in Guangdong. Areas with high suitability and moderate pressure, such as Lingshui, Lingao, and Hepu, were identified as possible restoration priorities. Meanwhile, areas with high suitability combined with low pressure, such as Dongfang, Wanning, and Fangchenggang, could be considered as conservation priorities.

4. Discussion

4.1. Environmental drivers of distribution

Seagrass distribution is influenced by many environmental variables. Different studies have chosen different variable combinations to model seagrass distribution. The most commonly used variables were SST, salinity, bathymetry, distance from shore or coastal cities, phosphate content, nitrate content, and light conditions (Bittner et al., 2020; Effrosynidis et al., 2018; Stankovic et al., 2019). Among the variables, we found that the most important drivers of seagrass distribution in South China were distance from shore, salinity, and nitrate content. Onshore development often negatively impacts water clarity in shallow coastal waters (Waycott et al., 2009), causing high sediment input that increases turbidity and leads to a decrease in the available light for the growth of seagrasses (Hotaling-Hagan et al., 2017). Salinity affects seagrass physiology, biochemistry, and ultimate survival (Munns, 2002). The growth of *Thalassia hemprichii* (one of the dominant seagrass species in South China) was retarded when the salinity fell to 22‰ (Jiang et al., 2013), while salt-tolerant microalgae predominated in response to increasing salinity and impacted the seagrass ecosystems negatively (Huang et al., 2006). Nutrients promote seagrass growth in oligotrophic environments, whereas excess nutrients cause seagrass to decline by creating imbalances in the internal nutrient supply ratios (Liu et al., 2017). Besides, nutrient pollution is one of the most serious anthropogenic sources that affect the seagrass meadow decline, as it leads to undesired epiphytic algal coverage. Epiphytic algal growth not only increases the risk of leaf breakage, but also prevents light from reaching the seagrasses (Foster et al., 2017).

Moreover, nutrients and salinity synergistically influence seagrass carbon fixation and nitrate absorption (Zhang et al., 2018). Temperature is another driving factor of global seagrass distribution. The optimal temperature ranges for tropical/subtropical seagrass growth and photosynthesis are 23–32 °C and 24.5–32.5 °C, respectively (Lee et al., 2007).

Compared with previous modeling studies, here we found that the relative importance of each environmental driver varied with study scale. In the global model, SST and distance from land contributed the most in predicting seagrass distribution (Jayathilake and Costello, 2018). At regional scales (such as the Mediterranean), the most important variables determining the seagrass presence-absence were chlorophyll-α levels and distance-to-coast (Effrosynidis et al., 2018). On the local scale (1,000 s of km^2), surface nitrate concentration, benthic light

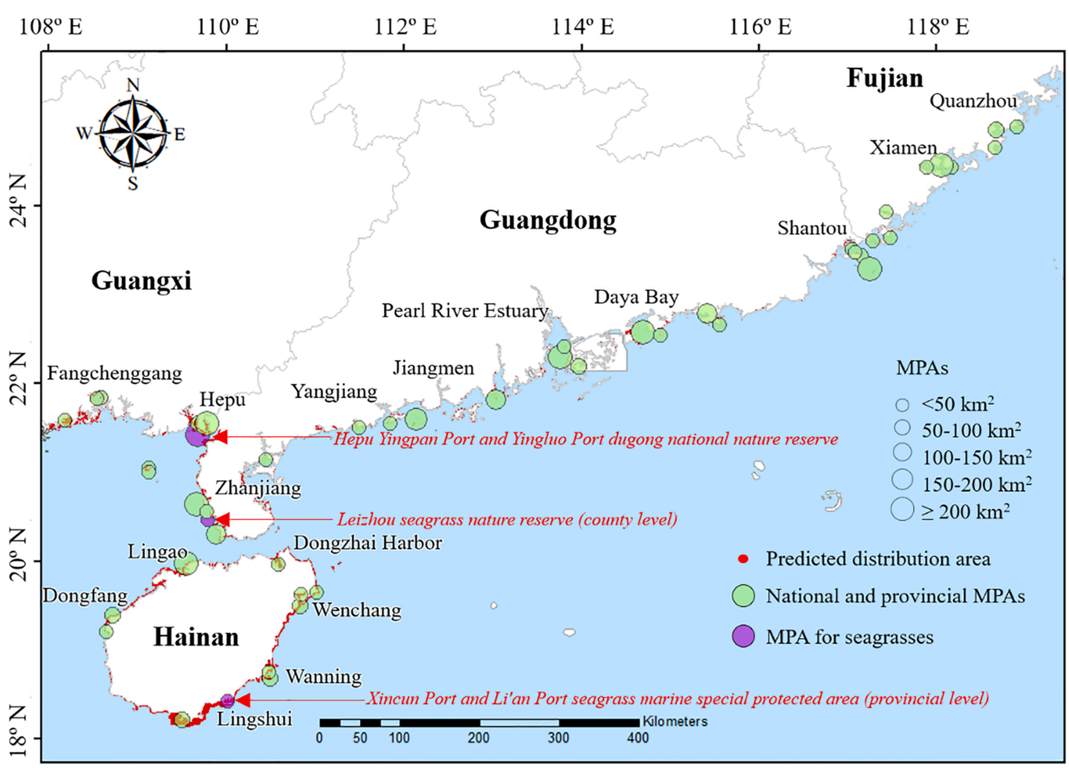

Fig. 7. Distribution of MPAs and current status of seagrass conservation.

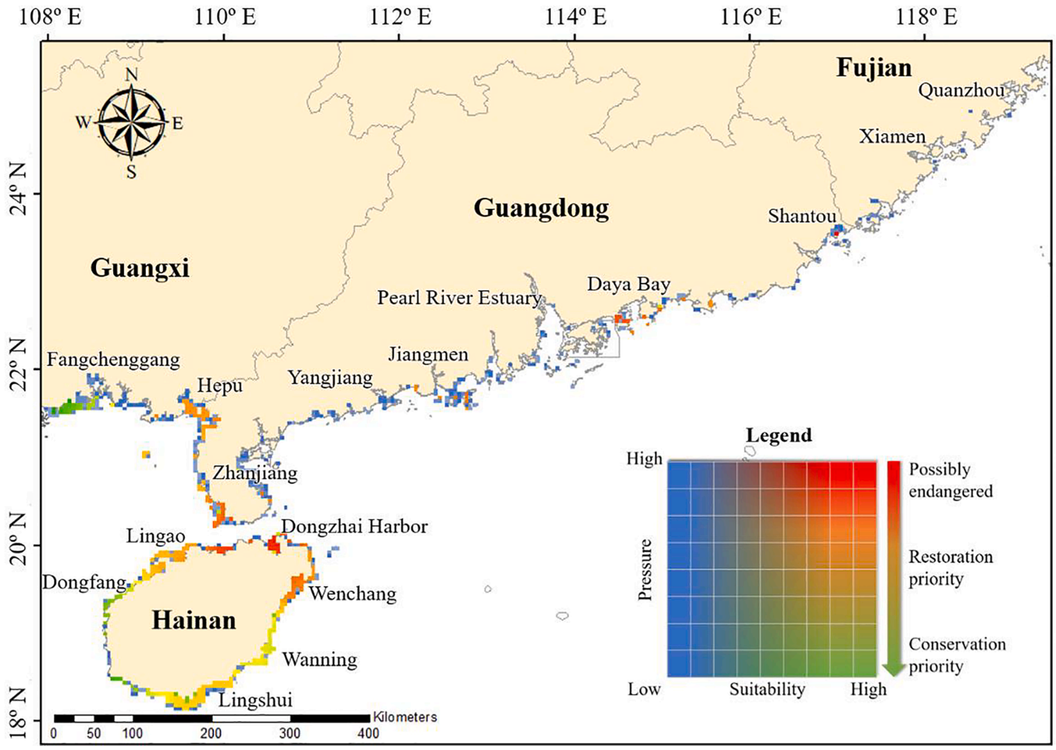

Fig. 8. Spatial pattern of conservation and restoration priorities.

availability, wave exposure, and distance to sandy shore determined suitable seagrass habitat distribution (Bittner et al., 2020; Downie et a., 2013). On even smaller scales, models have identified sedimentation rate and light intensity as the most important factors, followed by porewater nitrate content (Stankovic et a., 2019). In the present study, we identified driving factors that were similar to those of previous studies on regional and local scales, e.g., distance to the shore and nitrate concentration. Therefore, in future seagrass distribution research, environmental variable selection should be adjusted according to the study scale.

4.2. Model adaptation and the application of habitat suitability map

SDMs provide valuable and cost-effective tools for conservation planning, especially in poorly surveyed regions under accelerating pressure of habitat loss and degradation (Marmion et al., 2009). Our results demonstrated that seagrass distribution in the South China region can be successfully modeled using different algorithms. Though RF requires presence-absence data while MaxEnt is based on presence-only data, each model generates satisfactory results when it is used independently. The results of our study indicated that, although the RF and ensemble models performed well in certain earlier studies (Effrosynidis et al., 2018; Stankovic et al., 2019), MaxEnt can still be used as an alternative tool for effective modeling when reliable absence data is deficient or lacking, without leading to significant performance degradation.

The extent of suitable regions predicted by MaxEnt was slightly smaller than that predicted by RF. This finding is consistent with previous comparison studies reporting that MaxEnt generally predicted the lowest seagrass habitat suitability scores while RF frequently predicted larger areas of intermediate seagrass habitat suitability (Georgian et al., 2019). MaxEnt is relatively more prone to overfitting than the classification and regression tree algorithms (Anderson et al., 2016a, 2016b; Downie et al., 2013). In general, both models predicted similar spatial patterns in seagrass distribution, whose area differed by only $< 10\%$. In contrast, the ensemble model predicted the smallest suitable area. Downie et al. (2013) stated that the ensemble shifted the model towards a more conservative prediction, thereby increasing specificity at the expense of sensitivity. We believe this is because the ensemble model has excluded the differences between MaxEnt and RF while retaining their most reliable aspects. As the ensemble models typically make robust predictions, they are preferred for spatial management applications (Anderson et al., 2016a, 2016b; Araújo and New, 2007).

This study predicted more distribution sites, such as south Fujian, Hong Kong, and the west coast of Hainan Island, than the presence dataset. According to historical records, seagrasses were once found in Quanzhou, Xiamen, Dongshan in Fujian, and Hong Kong (Zheng et al., 2013). Newly discovered seagrass meadows were also reported along the western coasts of Hainan Island (Huang, 2019; Jiang et al., 2017). Therefore, the present study provides a reliable basis map for future seagrass surveys. Many unrecorded seagrass meadows might exist in areas that are highly suitable as habitats. These uncharted seagrass beds must be discovered and plotted before they “silently disappear” under rapid economic development (Jiang et al., 2017). The Chinese government plans to launch national seagrass survey and monitoring within the next few years. To obtain a comprehensive baseline of seagrass habitat, we suggest that the survey should focus on unexplored areas with potentially high seagrass habitat suitability, e.g., the northwest coast of Hainan Island, the west margin of Guangxi, and south Fujian . Meanwhile, attention should be paid to the subtidal zone, as previous surveys mainly focused on the intertidal section (Yang, 2017).

4.3. Suggestions for seagrass conservation and restoration management

Ecological niche modeling visualizes suitable biomes and species habitats and identifies priority protection and restoration areas to guide decision-makers (Silva et al., 2018). Coupling the modeling method and exposure assessment, the results of the present study allowed us to propose management strategies for sustainability of seagrass habitats and support the nature-based solutions within the region.

Although the global conservation percentage of recorded seagrass is as low as 26% (UNEP, 2020), the corresponding percentage for China is even lower. Moreover, the seagrass meadows in the nature reserves are facing large-scale degradation. In all three seagrass MPAs, there is negligible control of anthropogenic activity as there is insufficient human intervention or financial support. In Lingshui and Hepu, aquaculture, sand pumping, and artisanal fishing have negatively impacted the seagrass meadow status (Huang, 2019; Lin et al., 2020). During our investigation, we found that the surrounding shrimp pond and cage culture accelerated the degradation of seagrass meadows in Lingshui and Wenchang. *Sipunculus nudus* excavation and clam harrowing damaged seagrass roots and benthic habitats in Hepu. Thus, we believe that it is imperative to strengthen the protection of seagrass meadows.

Despite the huge conservation gaps observed, we found that certain existing MPAs actually have seagrass distribution. Nevertheless, seagrass meadows are not considered as protected objects in areas such as the Wenchang Eucheuma provincial nature reserve in Hainan and Hailing Island national marine park in Guangdong. Therefore, we propose that seagrass meadows should be categorized as protected objects of the aforementioned MPAs, with implementation of multi-target protection. Continuous seagrass monitoring in these areas should be conducted to determine seagrass status and apply timely protective countermeasures. In addition, new MPAs or restoration projects could be implemented after further investigation and research in the predicated priority areas. For example, Lingshui, Lingao, and Hepu were identified as candidates for restoration, where the known seagrass area exceeds 1000 ha, but face serious degradation (Chen et al., 2015; Zheng et al., 2013).

Indeed, it has been confirmed that the removal of threats is important prior to replanting. For example, reduced water quality (mainly eutrophication) and construction activities impede restoration success more than local direct impact and natural causes (van Katwijk et al., 2016). In the current study, we sought to explore the anthropogenic pressure gradient within the seagrass distribution areas of South China. Importantly, the pressure in the north is greater than that in the south due to the concentration of fishery and aquaculture activities within the northern area. For instance, the population of Guangdong Province alone is approximately twice that of Guangxi and Hainan provinces. Moreover, the fishery production value of the former is approximately 13 times greater than that of the latter, with the marine aquaculture area nearly three times that in the Guangxi and Hainan provinces (MARA of PRC, 2016). The results from the current study indicate that among the four pressure indices, aquaculture made the strongest contribution. In fact, China is the main producer of aquaculture fish raised for food, accounting for approximately 60% of the global production (FAO, 2020; Thomsen et al., 2020). Seagrass often disappears under floating fish cages, while the surrounding areas display signs of degradation, such as increasing seagrass shoot mortality and low seagrass abundance, shoot density, biomass, and vertical rhizome growth (Herbeck et al., 2014). Nutrient enrichment was found in seagrasses and their epiphytes near aquaculture sites (Liu et al., 2016). In Northeast Hainan, high exposure to aquaculture effluents has caused the degradation or even the loss of seagrass (Herbeck et al., 2014). Therefore, we suggest that when undertaking restoration projects in priority sites, the scale of aquaculture activities should be reduced to remove some pressures, thereby contributing to better restoration effectiveness.

5. Study uncertainty and limitations

The results of the present study were compared with the two published global seagrass distributions (Jayathilake and Costello, 2018; UNEP-WCMC and Short, 2020). Our models predicted an average area of 4,269 km^2, whereas UNEP-WCMC and Short (2020) estimated an area of 7,622 km^2 for the same region according to their polygon dataset. The UNEP-WCMC and Short (2020) dataset omitted the sites in Guangxi and Fujian and was quite rough in Guangdong and Hainan. This may be owing to the lack of reliable presence records for East Asia. The seagrass distribution area predicted by Jayathilake and Costello (2018) was 14947 km^2, which was nearly double that predicted by UNEP-WCMC and Short (2020). In addition to the unreliable presence records, this could potentially be attributed to the excessive extrapolation of the model. When we account for seagrass habitat degradation and fragmentation, the actual seagrass distribution in South China is possibly$<$4,000 km^2. The overall results of UNEP-WCMC (2020) and Jayathilake and Costello (2018) are global in scope. At the regional South China level, however, both studies may have overestimated the real seagrass distribution area.

The greatest total seagrass distribution area in the global model may occur in the 20–25 °N latitudinal band (Jayathilake and Costello, 2018). According to our study, the largest seagrass area in mainland China was localized to 18–22 °N. By contrast, the estimated extent of seagrass meadows in Southeast Asia is more than 36,762.6 km^2 (Fortes et al., 2018), occurring at a much lower latitude than South China. Large and lush seagrass meadows have been recorded in Indonesia (Du et al., 2016; 2018;; Unsworth et al., 2018) and the Gulf of Thailand (Du et al., 2020), supporting high fish species richness. Therefore, seagrass meadow distributions may regionally differ along the same latitude. For instance, the largest seagrass meadow distribution in the Indo-Pacific region occurs at far lower latitudes than those elsewhere.

The present study mapped seagrass distribution in South China according to various environmental factors. However, SDMs cannot fully consider seagrass habitat occupancy or degradation. For example, the models we established used predictors of resolution $\geq$ 1 km and, thus, may not capture small scale heterogeneity within 1 km^2. This may also cause the model to be more highly driven by factors with significant large-scale gradients, while identification of the small scale effects of environmental factors is more challenging. Moreover, when assessing anthropogenic pressure, only four indicators were selected to map the integrated exposure; however, various other anthropogenic activities may also impact seagrass. For instance, it has been found that recreational boating damages seagrass, which is also one of the reported causes responsible for seagrass restoration failure (Hotaling-Hagan et al., 2017; Van Katwijk et al., 2016). Hence, the actual seagrass distribution under various pressures may, in fact, be much lower than predicted. A comprehensive field survey is required to determine the true seagrass distribution and threats to it. Moreover, in the future, the existing presence dataset must be enhanced with records of different genera or species as each taxon might have its own unique environmental drivers and distribution ranges (Bittner et al., 2020; Jayathilake and Costello, 2018). Furthermore, conservation and restoration measures must assign top priority to rare and endangered species. These inter-specific differences were not considered in the present study. Finally, whereas pseudo-absence records were used in RF modeling here, future studies should integrate true absence data into their models (Georgian et al., 2019).

6. Conclusions

Currently, the lack of accurate information regarding seagrass distribution and the threats they face in China hinders the effective conservation and restoration of seagrass habitat. In this study, we mapped a potentially suitable seagrass habitat range of 3,536–4,852 km^2 in the southern region of mainland China, which was far smaller than the prediction made by a global model of the same region. Three different models were used and have been proved to be effective, of which RF was relatively more powerful at predicting marginal distributions. The main environmental drivers included distance from shore, annual mean SSS, and nitrate content. The results disclosed large seagrass conservation gaps. With a very low protection percentage of$<$5%, the seagrass beds in South China are facing degradation caused by anthropogenic pressures. However, there may remain numerous undiscovered seagrass meadows. By combining habitat suitability with integrated exposure, we proposed a framework for targeting seagrass conservation and restoration priorities. Spatial analysis was performed to map these locations in order to promote targeted management. Developing these maps based on SDMs and pressure assessment can contribute to a better understanding regarding the status of, and threats faced by seagrasses, as well as help prioritize locations for future surveys, especially in regions deficient in seagrass distribution data. We expect that the habitat suitability-anthropogenic pressure framework established here could be used as an efficient tool for ecosystem management contributing to the sustainability of seagrasses and the ecosystem services they provide.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was financially supported by the National Key Research and Development Program of China (grant numbers 2018YFC0507205, 2019YFE0124700 and 2018YFC1406503), the National Natural Science Foundation of China (grant numbers 41906127 and 41676096), the Provincial Natural Science Foundation of Fujian (grant number 2020J05078), and the China-ASEAN Maritime Cooperation fund "Monitoring and conservation of the coastal ecosystem in the South China Sea" and "Marine Protected Areas Network in China-ASEAN Countries".

References

Adams, M.P., Koh, E.J.Y., Vilas, M.P., Collier, C.J., Lambert, V.M., Sisson, S.A., Quiroz, M., McDonald-Madden, E., McKenzie, L.J., O'Brien, K.R., 2020. Predicting seagrass decline due to cumulative stressors. Environ. Model. Softw. 130, 104717. https://doi.org/10.1016/j.envsoft.2020.104717.

Allouche, O., Kadmon, T.R., 2006. Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS). J. Appl. Ecol. 43, 1223-1232.

Anderson, O.F., Guinotte, J.M., Rowden, A.A., Clark, M.R., Mormede, S., Davies, A.J., Bowden, D.A., 2016a. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. Ocean. Coast. Manag. 120, 110–126.

Anderson, O.F., Guinotte, J.M., Rowden, A.A., Tracey, D.M., Mackay, K.A., Clark, M.R., 2016b. Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. Deep. Sea. Res. Part. 1. Oceanogr. Res. Pap. 115, 265–292.

Araujo, M., New, M., 2007. Ensemble forecasting of species distributions. Trends. Ecol. Evol. 22 (1), 42–47.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., Tittensor, D., 2017. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Global. Ecol. Biogeogr. 27 (3), 277–284.

Beca-Carretero, P., Varela, S., Stengel, D.B., 2020. A novel method combining species distribution models, remote sensing, and field surveys for detecting and mapping subtidal seagrass meadows. Aquatic Conserv: Mar. Freshw. Ecosyst. 30 (6), 1098–1110.

Bittner, R.E., Roesler, E.L., Barnes, M.A., 2020. Using species distribution models to guide seagrass management. Estuar. Coast. Shelf. Sci. 240, 106790. https://doi.org/10.1016/j.ecss.2020.106790.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.

Chen, S.Q., Wang, D.R., Wu, Z.J., Zhang, G.X., Li, Y.C., Tu, Z.G., Yao, H.J., Cai, Z.F., 2015. Discussion of the change trend of the seagrass beds in the east coast of Hainan Island in nearly a decade. Marin. Environ. Sci. 34, 48–53 (in Chinese with English Abstract).

Collier, C.J., Waycott, M., 2014. Temperature extremes reduce seagrass growth and induce mortality. Mar. Pollut. Bull. 83 (2), 483–490.

Crimmins, S.M., Dobrowski, S.Z., Mynsberge, A.R., 2013. Evaluating ensemble forecasts of plant species distributions under climate change. Ecol. Model. 266, 126–130.

Deng, C.B., 2002. The Dugong dugon of Beibu gulf and marine biodiversity. Guangxi Science and Technology Press, Nanning (in Chinese with English Abstract).

Dennison, W.C., 2009. Seagrasses: biology, ecology and conservation. Bot. Mar. 52, 365–366.

Downie, A.-L., von Numers, M., Boström, C., 2013. Influence of model selection on the predicted distribution of the seagrass *Zostera marina*. Estuar. Coast. Shelf. Sci. 121-122, 8–19.

Du, J., Hu, W., Nagelkerken, I., Sangsawang, L., Loh, K.H., Ooi, J.-S., Liao, J., Zheng, X., Qiu, S., Chen, B., 2020. Seagrass meadows provide multiple benefits to adjacent coral reefs through various microhabitat functions. Ecosyst. Health. Sust. 6 (1), 1812433. https://doi.org/10.1080/20964129.2020.1812433.

Du, J., Wang, Y., Peristiwady, T., Liao, J., Makatipu, P.C., Huwae, R., Ju, P., Loh, K.H., Chen, B., 2018. Temporal and spatial variation of fish community and their nursery in a tropical seagrass meadow. Acta. Oceanol. Sin. 37 (12), 63–72.

Du, J., Xie, M., Wang, Y., Chen, Z., Liu, W., Liao, J., Chen, B., 2020. Connectivity of fish assemblages along the mangrove-seagrass-coral reef continuum in Wenchang, China. Acta Oceanol. Sin. 39 (8), 43–52.

Du, J., Zheng, X., Peristiwady, T., Liao, J., Ch. Makatipu, P., Yin, X., Hu, W., Koagouw, W., Chen, B., 2016. Food sources and trophic structure of fishes and benthic macroinvertebrates in a tropical seagrass meadow revealed by stable isotope analysis. Mar. Biol. Res. 12 (7), 748–757.

Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29 (2), 192–206.

Duarte, C.M., Marbà, N., Gacia, E., Fourqurean, J.W., Beggins, J., Barrón, C., Apostolaki, E.T., 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. Global. Biogeochem. Cy. 24 (4), n/a–n/a.

Effrosynidis, D., Arampatzis, A., Sylaios, G., 2018. Seagrass detection in the mediterranean: A supervised learning approach. Ecol. Inform. 48, 158–170.

Elith, J., Graham, C.H., 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography. 32 (1), 66–77.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2015. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43-57.

Evans, J.S., Murphy, M.A., Holden, Z.A., Cushman, S.A., 2011. Modeling species distribution and change using random forest. In: Ashton Drew, C., Wiersma, Y.F., Huettmann, F. (Eds.), Predictive Species and Habitat Modeling in Landscape Ecology. Springer, New York, pp. 139–159.

FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action, Rome.

Fortes, M.D., Sim, O.J.L., Tan, Y.M., Anchana, P., Sidik, B.J., Maryam, Y.S., 2018. Seagrass in Southeast Asia: a review of status and knowledge gaps, and a road map for conservation. Bot. Mar. 61, 269–288.

Foster, N.R., Fotheringham, D.G., Brock, D.J., Waycott, M., 2017. A resourceful and adaptable method to obtain data on the status of seagrass meadows. Aquat. Bot. 141, 17–21.

Fourcade, Y., Besnard, A.G., Secondi, J., 2018. Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. Global. Ecol. Biogeogr. 27 (2), 245–256.

Georgian, S.E., Anderson, O.F., Rowden, A.A., 2019. Ensemble habitat suitability modeling of vulnerable marine ecosystem indicator taxa to inform deep-sea fisheries management in the South Pacific Ocean. Fish. Res. 211, 256–274.

Gessler, P.E., Moore, I.D., McKenzie, N.J., Ryan, P.J., 1995. Soil-landscape modeling and spatial prediction of soil attributes. Int. J. Geogr. Inf. Sci. 9, 421–432.

Green, E.P., Short, F.T., Frederick, T., 2003. World Atlas Of Seagrasses. Univ of California Press.

Han, Q.Y., 2016. Decline mechanism and management of seagrass beds. Science Press, Beijing (in Chinese with English Abstract).

Hashim, M., Ito, S., Numata, S., Hosaka, T., Hossain, M.S., Misbari, S., Yahya, N.N., Ahmad, S., 2017. Using fisher knowledge, mapping population, habitat suitability and risk for the conservation of dugongs in Johor Straits of Malaysia. Mar. Policy. 78, 18–25.

He, X., Bai, Y., Pan, D., Huang, N., Dong, X.u., Chen, J., Chen, C.-T., Cui, Q., 2013. Using geostationary satellite ocean color data to map the diurnal dynamics of suspended particulate matter in coastal waters. Remote. Sens. Environ. 133, 225–239.

Hearne, E.L., Johnson, R.A., Gulick, A.G., Candelmo, A., Bolten, A.B., Bjorndal, K.A., 2019. Effects of green turtle grazing on seagrass and macroalgae diversity vary spatially among seagrass meadows. Aquat. Bot. 152, 10–15.

Heck Hay, K.L., Hays, G., Orth, R.J., 2003. A critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.

Herbeck, L.S., Sollich, M., Unger, D., Holmer, M., Jennerjahn, T.C., 2014. Impact of pond aquaculture effluents on seagrass performance in NE Hainan, tropical China. Mar. Pollut. Bull. 85 (1), 190–203.

Hotaling-Hagan, A., Swett, R., Ellis, L.R., Frazer, T.K., 2017. A spatial model to improve site selection for seagrass restoration in shallow boating environments. J. Environ. Manage. 186, 42–54.

Hu, W., Liu, J., Ma, Z., Wang, Y., Zhang, D., Yu, W., Chen, B., 2020. China's marine protected area system: Evolution, challenges, and new prospects. Mar. Policy. 115, 103780. https://doi.org/10.1016/j.marpol.2019.103780.

Huang, X.P., 2019. Studies on the ecology of tropical seagrass in China. Science Press, Beijing (in Chinese with English Abstract).

Huang, X., Huang, L., Li, Y., Xu, Z., Fong, C.W., Huang, D., Han, Q., Huang, H., Tan, Y., Liu, S., 2006. Main seagrass beds and threats to their habitats in the coastal sea of South China. Chinese. Sci. Bull. 51 (S2), 136–142.

Huang, X.P., Jiang, Z.J., Zhang, J.P., Shi, Z., Wang, F., Ye, F., Li, L., 2010. Newly discovered seagrass beds in the coastal seas of Guangdong Province. J. Oceanogr. 29, 132–135 (in Chinese with English Abstract).

Jayathilake, D.R.M., Costello, M.J., 2018. A modelled global distribution of the seagrass biome. Biol. Conserv. 226, 120–126.

Jiang, Q., He, J., Wu, J., He, M., Bartley, E., Ye, G., Christakos, G., 2019. Space-time characterization and risk assessment of nutrient pollutant concentrations in China's near seas. J. Geophys. Res. 124 (7), 4449–4463.

Jiang, Z., Huang, X., Zhang, J., 2013. Effect of nitrate enrichment and salinity reduction on the seagrass *Thalassia hemprichii* previously grown in low light. J. Exp. Mar. Bio. Ecol. 443, 114–122.

Jiang, Z., Liu, S., Zhang, J., Zhao, C., Wu, Y., Yu, S., Zhang, X., Huang, C., Huang, X., Kumar, M., 2017. Newly discovered seagrass beds and their potential for blue carbon in the coastal seas of Hainan Island, South China Sea. Mar. Pollut. Bull. 125 (1-2), 513–521.

John, E., O'Reilly, P., Jeremy, W., 2019. Chlorophyll algorithms for ocean color sensors - OC4, OC5 & OC6. Remote. Sens. Environ. 229, 32–47.

Kaky, E., Nolan, V., Alatawi, A., Gilbert, F., 2020. A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: A case study with Egyptian medicinal plants. Ecol. Inform. 60, 101150. https://doi.org/10.1016/j.ecoinf.2020.101150.

Lamb, J.B., van de Water, J.A.J.M., Bourne, D.G., Altier, C., Hein, M.Y., Fiorenza, E.A., Abu, N., Jompa, J., Harvell, C.D., 2017. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. Science. 355 (6326), 731–733.

Lee, K.-S., Park, S.R., Kim, Y.K., 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. J. Exp. Mar. Bio. Ecol. 350 (1-2), 144–175.

Lee, ZhongPing, Shang, S., Hu, C., Du, K., Weidemann, A., Hou, W., Lin, J., Lin, G., 2015. Secchi disk depth: A new theory and mechanistic model for underwater visibility. Remote Sens. Environ. 169, 139–149.

Li, S., Fan, H.Q., Qiu, G.L., Shi, Y.J., 2010. Review on research of seagrass beds restoration. Acta Ecologica Sin. 30, 2443–2453 (in Chinese with English Abstract).

Liaw, A., Wiener, M., 2002. Classification and Regression by random Forest. R News. 2, 18–22.

Lin, J.L., Liu, X.M., Lan, W.L., Huang, Z.J., 2020. Conservation effectiveness of Hepu Dugong dugon National Nature Reserve of Guangxi Zhuang Autonomous Region. Wetland Science. 18, 461–467 (in Chinese with English Abstract).

Liu, S.L., Jiang, Z.J., Zhou, C.Y., Wu, Y.C., Gan, M.L., Zhang, J.P., Huang, X.P., 2016. Temporal and spatial variation of dissolved organic matter and its controlling factors in seagrass bed ecosystem of Xincun Bay. Hainan Island. Chinese J. Ecol. 35, 2144 (in Chinese with English Abstract).

Liu, W.Y., Han, Q.Y., Tang, Y.Q., Sun, X.Y., 2017. Review of nutrient enrichment and global warming effects on seagrasses. Chinese Journal of Ecology. 36, 1–4 (in Chinese with English Abstract).

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science. 312, 1806–1809.

MARA of PRC (Ministry of Agriculture and Rural Affairs of the People's Republic of China), 2016. China Fishery Statistical Yearbook. China Agriculture Press, Beijing.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59-69.

McMahon, K., Collier, C., Lavery, P.S., 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecol. Indic. 30, 7–15.

Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecol. Model. 415, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837.

Moore, I.D., Gessler, P.E., Nielsen, G.A., Petersen, G.A., 1993. Terrain attributes: estimation methods and scale effects. In: Jakeman, A.J. (Ed.), Modeling Change in Environmental Systems. M.B. Beck and M. McAleer Wiley, London, pp. 189–214.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant. Cell. Environ. 25, 239–250.

Fedrizzi, N., Stiassny, M.L.J., Boehm, J.T., Dougherty, E.R., Amato, G., Mendez, M., Arthofer, W., 2015. Population Genetic Structure of the Dwarf Seahorse *(Hippocampus zosterae)* in Florida. Plos. One. 10 (7), e0132308.

Orth, R.J., Carruthers, T.J., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A Global Crisis for Seagrass Ecosystems. Bioscience. 56 (12), 987.

Parravicini, V., Rovere, A., Vassallo, P., Micheli, F., Montefalcone, M., Morri, C., Paoli, C., Albertelli, G., Fabiano, M., Bianchi, C.N., 2012. Understanding relationships between conflicting human uses and coastal ecosystems status: A geospatial modeling approach. Ecol. Indic. 19, 253–263.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. ORIGINAL ARTICLE: Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190 (3-4), 231–259.

R Development Core Team., 2009. An introduction to R.

Reynolds, P.L., Stachowicz, J.J., Hovel, K., Boström, C., Boyer, K., Cusson, M., Eklöf, J.S., Engel, F.G., Engelen, A.H., Eriksson, B.K., Fodrie, F.J., Griffin, J.N., Hereu, C.M., Hori, M., Hanley, T.C., Ivanov, M., Jorgensen, P., Kruschel, C., Lee, K.-S., McGlathery, K., Moksnes, P.-O., Nakaoka, M., O'Connor, M.I., O'Connor, N.E., Orth, R.J., Rossi, F., Ruesink, J., Sotka, E.E., Thormar, J., Tomas, F., Unsworth, R.K.F., Whalen, M.A., Duffy, J.E., 2018. Latitude, temperature and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. Ecology. 99 (1), 29–35.

Shilland, R., Grimsditch, G., Ahmed, M., Bandeira, S., Kennedy, H., Potouroglou, M., Huxham, M., 2021. A question of standards: Adapting carbon and other PES markets to work for community seagrass conservation. Mar. Policy. 129, 104574. https://doi.org/10.1016/j.marpol.2021.104574.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. 23 (1), 17–27.

Short, F., Carruthers, T., Dennison, W., Waycott, M., 2007. Global seagrass distribution and diversity: A bioregional model. J. Exp. Mar. Bio. Ecol. 350 (1-2), 3–20.

Short, F.T., Coles, R.G., 2001. Global Seagrass Research Methods. Elsevier. 212, 482.

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Judson Kenworthy, W., La Nafie, Y.A., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Tussenbroek, B.V., Vergara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. Biol. Conserv. 144 (7), 1961–1971.

da Silva, U.B.T., Delgado-Jaramillo, M., de Souza Aguiar, L.M., Bernard, E., 2018. Species richness, geographic distribution, pressures, and threats to bats in the Caatinga drylands of Brazil Biol. Conserv. 221, 312–322.

SOA, 2005. Technical specification for eco-monitoring of seagrass bed (HY/T083). Beijing.

Stankovic, M., Ambo-Rappe, R., Carly, F., Dangan-Galon, F., Fortes, M.D., Hossain, M.S., Kiswara, W., Van Luong, C., Minh-Thu, P., Mishra, A.K., Noiraksar, T., Nurdin, N., Panyawai, J., Rattanachot, E., Rozaimi, M., Soe Htun, U., Prathep, A., 2021. Quantification of blue carbon in seagrass ecosystems of Southeast Asia and their potential for climate change mitigation. Sci. Total Environ. 783, 146858. https://doi.org/10.1016/j.scitotenv.2021.146858.

Stankovic, M., Kaewsrikhaw, R., Rattanachot, E., Prathep, A., 2019. Modeling of suitable habitat for small-scale seagrass restoration in tropical ecosystems. Estuar. Coast. Shelf. Sci. 231, 106465. https://doi.org/10.1016/j.ecss.2019.106465.

State Oceanic Administration. Technical specification for eco-monitoring of seagrass bed. HY/T 083—2005.

Tassan, S., 1994. Local algorithm using SeaWiFS data for the retrieval of phytoplankton, pigments, suspended sediment and yellow substance in coastal waters. Appl. Optics. 33, 2369–2378.

Thomsen, E., Herbeck, L.S., Jennerjahn, T.C., 2020. The end of resilience: Surpassed nitrogen thresholds in coastal waters led to severe seagrass loss after decades of exposure to aquaculture effluents. Mar. Environ. Res. 160, 104986. https://doi.org/10.1016/j.marenvres.2020.104986.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., Clerck, O.D., 2012. Bio-ORACLE: A global environmental dataset for marine species distribution modelling. Global. Ecol. Biogeogr. 21, 272–281.

Udyawer, V., Somaweera, R., Nitschke, C., d'Anastasi, B., Sanders, K., Webber, B.L., Hourston, M., Heupel, M.R., 2020. Prioritising search effort to locate previously unknown populations of endangered marine reptiles. Glob. Ecol. Conserv. 22, e01013. https://doi.org/10.1016/j.gecco.2020.e01013.

UNEP, 2020. Out of the Blue: The value of seagrasses to the environment and to people.

UNEP-WCMC, Short, F.T., 2020. Global distribution of seagrasses (version 7.0). Seventh update to the data layer used in Green and Short (2003). Cambridge (UK): UN Environment World Conservation Monitoring Centre. URL: http://data.unep-wcmc.org/datasets/7.

Unsworth, R.K.F., Ambo-Rappe, R., Jones, B.L., La Nafie, Y.A., Irawan, A., Hernawan, U.E., Moore, A.M., Cullen-Unsworth, L.C., 2018. Indonesia's globally significant seagrass meadows are under widespread threat. Sci. Total Environ. 634, 279–286.

Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., Jones, B.L., Nordlund, L.M., 2019a. Global challenges for seagrass conservation. Ambio. 48 (8), 801–815.

Unsworth, R.K.F., Nordlund, L.M., Cullen-Unsworth, L.C., 2019b. Seagrass meadows support global fisheries production. Conserv. Lett. 12 (1), e12566. https://doi.org/10.1111/conl.2019.12.issue-110.1111/conl.12566.

Valle, M., Borja, Á., Chust, G., Galparsoro, I., Garmendia, J.M., 2011. Modelling suitable estuarine habitats for Zostera noltii, using Ecological Niche Factor Analysis and Bathymetric LiDAR. Estuar. Coast. Shelf. Sci. 94 (2), 144–154.

Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S., Meinesz, A., Nakaoka, M., O'Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A., Verduin, J.J., Österblom, H., 2016. Global analysis of seagrass restoration: the importance of large-scale planting. J. Appl. Ecol. 53 (2), 567–578.

Vincenzi, S., Zucchetta, M., Franzoi, P., Pellizzato, M., Pranovi, F., De Leo, G.A., Torricelli, P., 2011. Application of a Random Forest algorithm to predict spatial distribution of the potential yield of Ruditapes philippinarum in the Venice lagoon. Italy. Ecol. Model. 222 (8), 1471–1478.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106 (30), 12377–12381.

Xiao, X.i., Huang, Y., Holmer, M., 2020. Current trends in seagrass research in China (2010–2019). Aquat. Bot. 166, 103266. https://doi.org/10.1016/j.aquabot.2020.103266.

Xu, X.L., 2017a. Grid dataset of China's population distribution. Resour. Environ. Sci. Data Center Chin. Acad. Sci. https://doi.org/10.12078/2017121101.

Xu, X.L., 2017b. Grid dataset of China's GDP distribution. Resour. Environ. Sci. Data Center Chin. Acad. Sci. https://doi.org/10.12078/2017121102.

Xu, S., Qiao, Y., Xu, S., Yue, S., Zhang, Y.u., Liu, M., Zhang, X., Zhou, Y.i., 2021. Diversity, distribution and conservation of seagrass in coastal waters of the Liaodong Peninsula, North Yellow Sea, northern China: Implications for seagrass conservation. Mar. Pollut. Bull. 167, 112261. https://doi.org/10.1016/j.marpolbul.2021.112261.

Yang, D.T., 2017. Seagrass Distribution, Ecological System Structure And Carbon Flux in China with Satellite Remote Sensing. Science Press, Beijing.

Yin, Q.T., Zhong, C., 2018. Condition and conservation of seagrass resources in South China. Adv. Environ. Protect. 8, 208–212 (in Chinese with English Abstract).

Zhang, L.L., Han, Q.Y., Shi, Y.F., Zhao, M.Q., 2018. Synergistic effects of eutrophication and salinity on biomass and carbon and nitrogen contents of *Zostera japonica*. J. Mar. Syst. 42, 55–61.

Zheng, F.Y., Qiu, G.L., Fan, H.Q., Zhang, W., 2013. The diversity, distribution and conservation of seagrass in China. Biodiv. Sci. 21, 517–526 (in Chinese with English Abstract).