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Predicting the Potential Distribution of the Alien Invasive Alligator Gar *Atractosteus spatula* in China

Dawei Liu [1], Chunping Xie [2,*], Chi Yung Jim [3], Yanjun Liu [1] and Senlin Hou [1,4,*]

1 Faculty of Criminal Science & Technology, Nanjing Forest Police College, Nanjing 210023, China
2 College of Science, Qiongtai Normal University, Haikou 571127, China
3 Department of Social Sciences, Education University of Hong Kong, Tai Po, Hong Kong 999077, China
4 Key Laboratory of State Forest and Grassland Administration Wildlife Evidence Technology, Nanjing 210023, China
* Correspondence: xcp@mail.qtnu.edu.cn (C.X.); slhou@nfpc.edu.cn (S.H.)

Abstract: Alligator gar *Atractosteus spatula* originates from North America but has been introduced into China recently. Considered an invasive fish, it may cause losses in the diversity and number of local species and in fish catch due to its predation on numerous aquatic animals in non-native habitats. A comprehensive study of this alien invasive species' existing spatial patterns in relation to climatic variables is critical to understanding the conditions amenable to its distribution and controlling its further spread into potential range areas. We used MaxEnt and QGIS species distribution modeling to estimate the likely biogeographical range of *A. spatula* in China based on 36 validated distribution records and seven selected environmental variables. The highly suitable area was found primarily in a series of provinces extending from inland to coastal regions, covering southwest to south, central and east China. The model identified the minimum temperature of the coldest month (Bio6) and mean temperature of the warmest quarter (Bio10) as the strongest predictors of *A. spatula* distribution. The findings could offer scientific guidance for managing and preventing the spread of this invasive fish and hint at controlling invasive aquatic fauna.

Keywords: *Atractosteus spatula*; invasive species; distribution modeling; environmental factor; potential distribution area

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1. Introduction

Non-native species could be distributed into novel lands and habitats through various intentional or unintentional ways (paths). In the modern era, globalization of the world economy and trade have generated ample chances for species introduction and invasion. The transfers and influxes of alien species into foreign places and ecosystems have become spatially pervasive and rapid. They have affected many species and involved multiple sources and destinations [1,2].

Most nonindigenous species do not survive in their new locations because they are unable to adapt to the new environment or because their founder populations are usually too small for viable or sustainable population growth [3]. However, a small portion of alien species could multiply successfully and disperse widely beyond their native habitats to become established or even naturalized. Such highly adaptable and aggressive species could outcompete and harm the native flora and fauna, ecology, environment, human livelihood, and the economy [4,5]. These species are referred to as "invasive" aliens [6].

Once entrenched, some invasive species could create undue economic losses in various sectors, such as the primary production of forestry, agriculture and fisheries, and the secondary production of international trade, power production, property values, etc. [7–10]. For instance, the negative impact of invasive organisms on the economy in Europe in 2008 is estimated to be at least €12.5 billion (US $13.3 billion) per year and may exceed €20 billion (US $21.3 billion) [11]. In China, the estimated economic losses caused by invasive alien organisms were more than RMB 119,661.69 million (US $14.45 billion) in 2000 [12]. It is often impossible to eradicate the nonindigenous species once they are established, and when possible, management and reduction are costly and difficult [13]. Therefore, conducting risk assessments, predicting potential habitats, and developing early warning systems for invasive alien species are particularly crucial.

The alligator gar, *Atractosteus spatula* (Lacepède, 1803), is a species of garfish belonging to the Lepisosteidae family (Actinopterygii, Lepisosteiformes). Its native range includes the Mississippi River basin and other rivers in the United States, extending along the Gulf of Mexico coast from Florida to northern Mexico [14]. As an ornamental fish, the species has been introduced to many countries outside the US [14]. This large freshwater fish can reach a maximum adult weight of up to 179 kg and a length of 3 m [15]. Its long, cylindrical, torpedo-like body is covered in ganoid scales connecting to form a strong, flexible armor [16]. The scales can offer effective defense against predators. The gar's snout resembles the alligator's, having multiple large, conical, fanglike teeth on its jaws. With such defensive and offensive traits, the adult gar has few natural predators.

As a predator in its native habitat, the alligator gar primarily consumes fish, turtles, and crabs and also preys on birds and small mammals [14]. *A. spatula* is one of the largest freshwater fish in North America. As an introduced species in China, it has no natural predators and occupies an apex predator role in the ecosystem [17]. The gar could suppress native aquatic species through competition and predation, leading to a decline in indigenous populations; it could also alter the structure and function of the original ecosystem through its impact on the food chain [18,19]. Occasionally, it may attack humans, such as a case in Jiangsu Province, China, where one bit a child playing in the water [20]. Consequently, *A. spatula* has been included in many countries' lists of potentially risky alien fish species [21–23]. China has formulated a prevention and control plan to contain its impacts on ecology, biodiversity, and sustainable agriculture and fisheries development [24].

As an exotic species, *A. spatula* thus far has not been able to achieve abundance in China's artificial ponds, canals, and natural water bodies and has not yet caused serious damage. There are some reasons which could explain its limited spread and population growth. Firstly, as an ornamental fish, the species has been introduced into China for a relatively short period and has not yet established a stable population. Secondly, *A. spatula* is a later-maturing fish. It is estimated that female fish reach reproductive maturity at the age of 10, with the population reaching reproductive maturity at 14 [25]. Nevertheless, the species' fecundity is high, with an average of 4.1 eggs per gram of body weight and 157,000 eggs per female [25]. The adult alligator gar's annual survival rate approaches 90% [25]. Thus, once a stable population has been established, the *A. spatula* population could increase rapidly. This invasive species could prey on native species in large numbers, reducing or even extinguishing their populations and altering the food chain of the original ecosystem.

The presence of this gar in China is a relatively recent phenomenon. Little is known about the potential distribution range that it may achieve. Identifying its environmental adaptation and actual and potential distribution patterns in China is essential and urgent. Studying and resolving these problems is important for developing prevention and control strategies. Based on the occurrence records reported in mainstream public media from 2019 to 2022, we modeled the potential distribution areas of *A. spatula* under current climatic conditions in China. We then analyzed the main environmental variables affecting the potential distribution of the gar.

2. Materials and Methods

2.1. Distribution Data of A. Spatula

Public online news reports from January 2019 to September 2022 were collected using the Chinese name of the gar as the keyword. Five mainstream media in China were encompassed in the search, including The Paper (https://www.thepaper.cn, accessed on 29 September 2022), Sohu (https://www.sohu.com, accessed on 29 September 2022), NetEase (https://www.163.com, accessed on 17 October 2022), CCTV (https://www.cctv.com, accessed on 17 October 2022), and People's Daily Online (http://www.people.com.cn, accessed on 17 October 2022). The reports were assessed separately for consistency and veracity of the factual information. If a spotting incident attracted multiple records, the one with the most information was chosen. 49 records were thereby obtained. After removing the duplicate locations, 36 valid occurrence records of *A. spatula* were finally selected in the study. The data, containing province, city/district, longtitude, and latitude, were kept in an Excel worksheet and saved in a CSV file (available online: 4TU Research Data. https://doi.org/10.4121/bc06c021-ba04-49cb-bf97-da3ee96bf132.v1, published on 23 March 2023). The sample spots' coordinates in longitude and latitude were acquired using the WGS84 coordinate system.

2.2. Selecting Environmental Variables

Nineteen environmental variables (Bio1–Bio19), averaged from 1950 to 2000 data, were initially extracted as predictors to model the likely habitats of *A. spatula*. Those variables were downloaded from the WorldClim database (http://www.worldclim.org, accessed on 22 September 2022) at a spatial resolution of 2.5′ (ca. 4.5 km^2).

The multicollinearity between environmental variables can lead to the model's overfitting and reduced prediction accuracy. For a pair of strongly correlated variables, one should be eliminated [26]. Firstly, the dataset was stripped of the raw annual temperature and precipitation variables because they were deemed overly generic [27]. Then the unfavorable effects of collinearity on the modeling process and interpretation were identified using Pearson correlation analysis of the remaining 17 factors. Highly correlated variables with correlation coefficients ($|r| > 0.8$) were removed. The variables with the highest factor loading were chosen objectively using principal component analysis (PCA). Ultimately, 7 of the 19 variables were retained as evaluator variables.

2.3. Modeling Species Distribution

MaxEnt (maximum entropy) is a commonly used ecological niche model. This model uses data on the actual distribution sites of species to find the possible distribution of maximum entropy under the conditions of various environmental variables (e.g., climate). It analyzes the constraints of the species' distribution sites and predicts the suitability and spatial distribution of its habitat. We utilized the ecological niche modeling tool MaxEnt 3.4.1 [28] to predict the potential distribution area of *A. spatula*. The species occurrence data and the seven selected environmental variables, which were the minimum temperature of the coldest month (Bio2), the mean temperature of the warmest quarter (Bio3), the mean diurnal temperature range (Bio6), the precipitation of the coldest quarter (Bio10), the precipitation of the driest month (Bio14), the isothermality (Bio2/Bio7) (*100) (Bio18), the precipitation of the warmest quarter (Bio19), were loaded into the model. We trained the model with 80% of the distribution data and used the remaining 20% to evaluate the model's accuracy. The software was programmed to run until a convergence criterion of 0.00001 was met or upon reaching 500 iterations. Other parameters were set at default values throughout the calculation process. The MaxEnt model output lies between 0 and 1, and a value closer to 1 denotes a higher likelihood of a species' existence.

The spatial analysis technology in QGIS 3.12 [29] was used to analyze the MaxEnt outcomes (ASCII raster grids format). Four classes of potential habitat suitability for *A. spatula* were defined: poor (<0.2), fair (0.2–0.4), good (0.4–0.6), and excellent (>0.6) [30]. The model accuracy was evaluated by the receiver operating characteristic curve (ROC) analysis, and the area under the curve (AUC) was determined. The AUC is an index to evaluate the model's prediction accuracy. It is independent of assessment thresholds and can compare different models [31]. The AUC value ranges from 0.5 to 1.0. This study divided it into five categories: fail (0.5–0.6), poor (0.6–0.7), fair (0.7–0.8), good (0.8–0.9), and excellent (0.9–1.0) [32].

3. Results

3.1. Validating Modeling Results

Figure 1a demonstrates the model's accurate prediction of the training data. The data from the training and test sets were independent. The model's accuracy can be evaluated by the ROC curve method. The AUC value is the area under the ROC curve. As a model evaluation indicator, the AUC value has high reliability because it is not affected by the threshold index. The AUC method has been recognized to achieve the best accuracy. Figure 1b depicts the ROC of the reconstructed MaxEnt model, where the AUC value was 0.904. It rated the model's prediction accuracy as excellent.

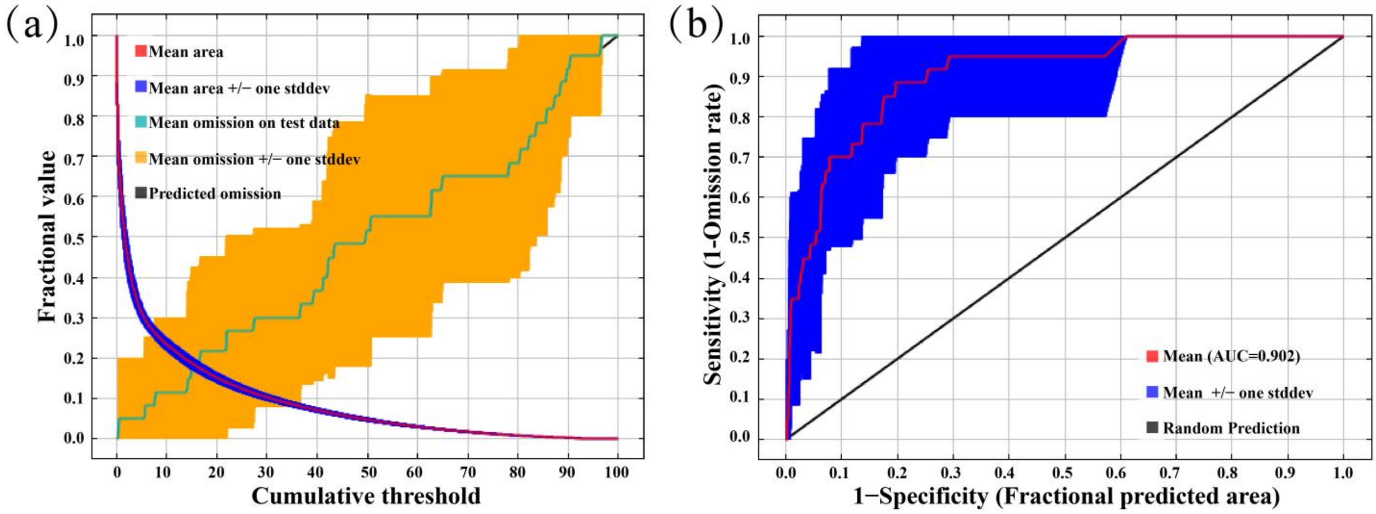

Figure 1. The validation of the model predicting *A. spatula* distribution: (**a**) Omission rate; and (**b**) ROC curve. In Figure 1a, the red curve represents the prediction mean. The black and green lines represent the model's predicted omission rate and the omission rates of test samples, respectively. The actual omission rate and the predicted omission rate converged.

3.2. Assessing Contributions of Environmental Factors

According to the contributions to the modeling process of *A. spatula* distribution, the important environmental factors were identified (Table 1). The contributions were dominated by two factors: minimum temperature of the coldest month (Bio6) and mean temperature of the warmest quarter (Bio10) at 48.9% and 33.5%, respectively, with a joint contribution exceeding 80%. These two factors also had the highest permutation importance values. The results indicated that Bio6 and Bio10 were the leading environmental factors influencing the geographical range of *A. spatula*.

Table 1. Percentage contribution and permutation importance for the seven environmental variables selected as most appropriate for inclusion in the MaxEnt models based on PCA results.

Bioclimatic Variable	Description	Percent Contribution	Permutation Importance
Bio6	Minimum temperature of the coldest month	48.9	34.4
Bio10	Mean temperature of the warmest quarter	33.5	47.6
Bio2	Mean diurnal temperature range	8.7	2.4
Bio19	Precipitation of the coldest quarter	5.8	8.7
Bio14	Precipitation of the driest month	1.3	1
Bio3	Isothermality (Bio2/Bio7) (×100)	1.1	0.5
Bio18	Precipitation of the warmest quarter	0.6	5.4

The graphs constructed by MaxEnt for the two main environmental factors are shown in Figure 2. Bio6 displayed a unimodal curve. Bio10 assumed a sigmoid curve. The optimum values of Bio6 and Bio10 were 0 °C and >32.5 °C, respectively. These response curves between environmental variables and the probability of species presence indicated the influence of environmental stresses on target-species occurrence.

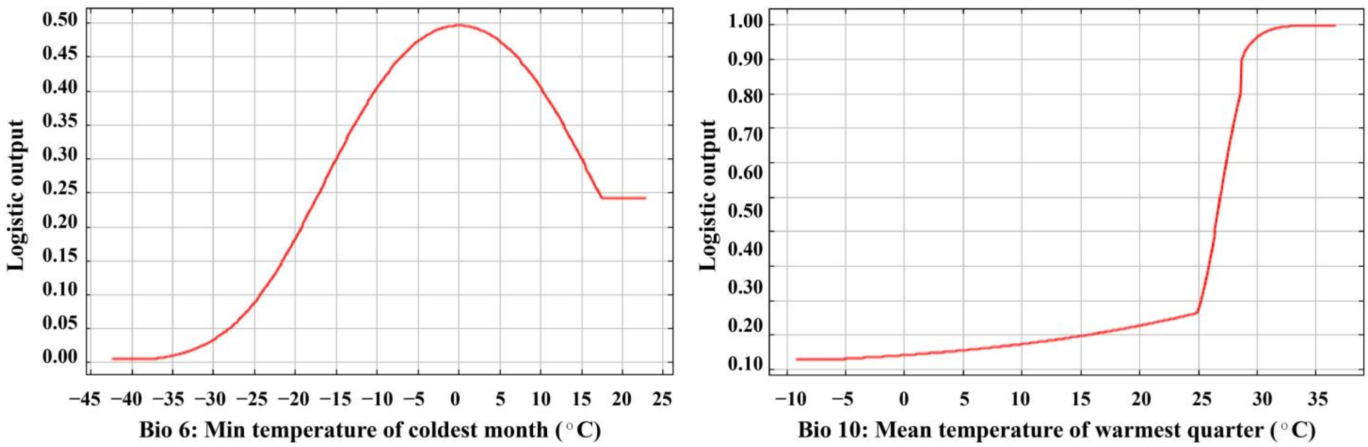

Figure 2. Response curves of *A. spatula* distribution in relation to the two leading environmental variables (Bio6 and Bio10) as determined with MaxEnt.

3.3. Predicting Distribution Pattern

The predicted suitable distribution of *A. spatula* is displayed in Figure 3. The climatic suitability of this gar followed a distribution pattern matching the predicted habitat suitability areas. It covered a relatively large and contiguous potential range stretching from southwest to central, south, and east China. The provinces included eastern Sichuan, western Chongqing, southeastern Hubei, northern Hunan, southwestern Anhui, northern Jiangxi, southern Jiangsu, Shanghai, southern Guangxi, and Guangdong, coastal parts of Zhejiang and Fujian, most of Hainan Island, and northwestern Taiwan. In addition, a small outlier was predicted in Xinjiang province.

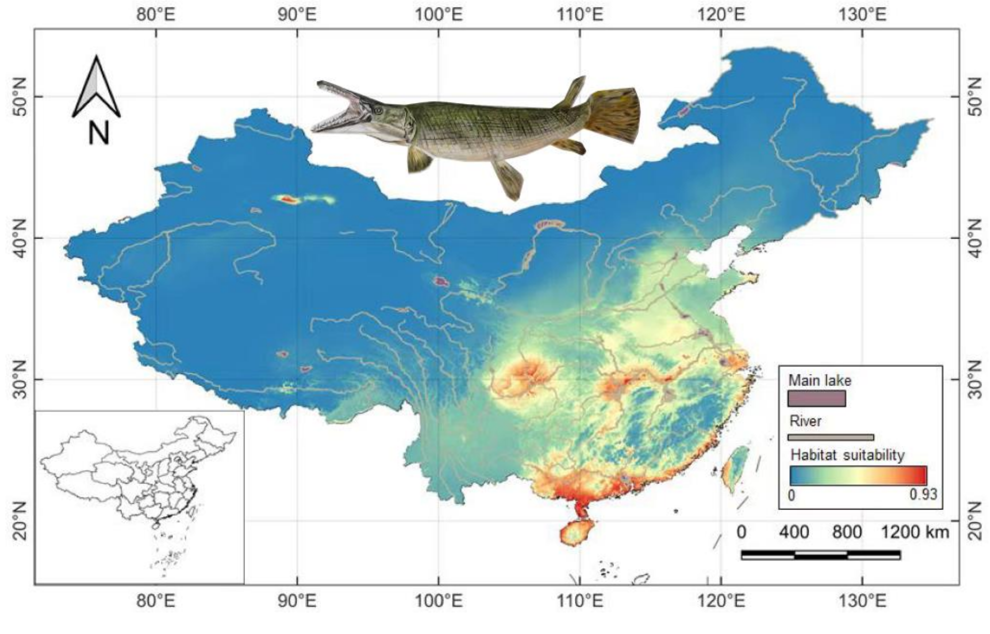

Figure 3. The predicted *A. spatula* distribution range obtained by MaxEnt modeling, on the basis of seven environmental parameters.

4. Discussion

This study provided a clear and intuitive understanding of the potentially suitable distribution areas of *A. spatula* in China. The results have important implications for managing biotic invasion and conserving native habitats and species. They could serve as an early warning signal and inform the emergency response to the continual invasion and damage. Local authorities should take timely and appropriate precautionary measures to prevent this animal's invasion in areas where it may occur.

In recent years, the MaxEnt model has been widely used in predicting species conservation priorities, species suitability for a given climate, suitable habitats for endangered wildlife, and the potential distribution of alien invasive species [33–36]. This model has multiple advantages: it is independent of species biological parameters, does not require species missing points, it avoids extensive fieldwork, it is less affected by sample size bias, and it achieves good prediction accuracy even with a small number of species distribution points (10–30) [37]. Only 36 sites were available in our study, which seems like a small number for China. We chose this model for prediction because of Maxent's last advantage. With an AUC value of 0.904, the model's accuracy was rated as excellent, indicating high confidence in predicting and assessing the gar distribution.

It should be noted that the range of the mean omission was large (Figure 1b), implying that the data are discrete. This result may be related to the small number of distribution points. As the main objective of this study focuses on the prevention of further invasion and management of *A. spatula*, the results can offer a high reference value.

Climatic factors are the primary determinants of biological distribution, playing a decisive role at a large scale [38]. Based on PCA, this study focused on seven of the 19 major climatic factors in predicting the potential distribution area of *A. spatula* in China on a large scale. If it is necessary to predict the suitability of this gar in a specific area, other small-scale environmental factors shaping its distribution, such as hydrological data on flow rate, water temperature and salinity, should be included in the evaluation. This study did not consider inter-species effects, which may influence prediction accuracy.

Our results showed that the minimum temperature of the coldest month (Bio6) and the mean temperature of the warmest quarter (Bio10), among the climatic variables, had higher percent contributions and permutation importance. They indicated that these two variables embody information and significance that other variables cannot replace. Therefore, the two leading factors play a dominant role in predicting the geographical distribution of *A. spatula* in China. Water temperature affects fish in many ways, such as growth, reproduction, metabolism, overall health, and mortality [39,40]. The temperature has been described as the "abiotic master factor" for fish [41]. Air temperature and water temperature are closely related [42]. Within a certain range, the two temperatures have a positive correlation [43]. In ecological studies, air temperature is sometimes used as a surrogate for water temperature [44].

The minimum temperature of the coldest month (Bio6) denotes the lowest temperature of the year. In nature, exposure to low temperatures is the main cause of fish deaths [45]. Compared to high temperatures, fish have a lower tolerance to low temperatures, which may induce lethargy and inhibit ability to escape [45]. Additionally, if the lowest temperature of the coldest month is too high, the distribution probability may also decrease. This response could be associated with reduced resistance to disease in the winter, and high temperatures, leading to microorganism proliferation that could induce illness and even death [46].

The effect of Bio10 on *A. spatula* may be reflected in spawning and juvenile development. Typically, alligator gar spawning occurs from April to June when the water temperatures are 20–30 °C. At water temperatures of 27–31 °C, gar eggs need 48–72 h to hatch. At the lowest temperature of 15.5 °C, the species has 0% hatching success [47]. This gar is vulnerable to low temperatures in its early life stage, with critical thermal minima of circa 13 °C [48]. A lower mean temperature of the warmest quarter could jeopardize juvenile fish development and survival, causing recruitment decline or failure.

The excellent suitability areas for *A. spatula* in China were predicted to be roughly the same latitude as the gar's native range. The climate in these areas is characterized by hot and rainy summers and mild winters with little rain [49]. Notably, most of these areas are densely populated with thriving economic activities and well-connected by dense water networks [50,51], both of which can facilitate the further invasion and spread of alligator gar. At present, the species' potential habitat is mainly located in central and southern China. In the context of global warming, the continued northward expansion of the suitable range of this temperate gar cannot be ruled out.

The MaxEnt model predictions generated in this study are based on the basal ecological requirements of the known distribution area of *A. spatula*. The projected distribution range signifies the maximum extent of its spread in China. The prediction map (Figure 3) demarcated an isolated area of suitable distribution, situated well away from the main contiguous range, with no occurrence recorded. This outlier is located at the base of the Turpan Basin on the southern slope of the eastern Tian Shan Mountains in Xinjiang Province, China. In northwest China, Xinjiang has a temperate continental climate characterized by cold and dry winters. However, the milder climate at the Turpan Basin's base may account for the suitability predictions. As this detached potential habitat enclave is located far from its current range, it is difficult for the gar to reach it by natural means. It is important to prevent the unintentional or intentional anthropogenic introduction of *A. spatula*.

Some management interventions are necessary to prevent the degradation of aquatic ecosystems from *A. spatula*. Firstly, the government can enact and enforce laws to prohibit the species' new introduction into China. Secondly, aquariums and fish breeders should be educated not to release or discard this exotic species in any water bodies. Individuals who release this gar recklessly should be punished and ordered to catch their releases by a deadline. Thirdly, based on our results, the research department could use environmental DNA techniques for early screening in suitable areas to foster dynamic monitoring and risk assessment of *A. spatula*. Fourthly, the public should be actively informed of the dangers of this species and how it can be identified and encouraged to report any sightings immediately to the aquatic animal management authorities. Fifthly, animal management authorities can develop an effective scientific early warning and response mechanism to deal with this exotic fish as soon as it is discovered.

5. Conclusions

The suitable areas for *A. spatula* in China were predicted by MaxEnt and QGIS, obtaining excellent outcomes with high accuracy. The highly suitable habitats for this gar were determined primarily in eastern Sichuan, western Chongqing, southeastern Hubei, northern Hunan, southwestern Anhui, northern Jiangxi, southern Jiangsu, Shanghai, southern Guangxi and Guangdong, parts of the coasts of Zhejiang and Fujian, most of Hainan Island, and northwestern Taiwan in China. The key environmental variables regulating its distribution are the minimum temperature of the coldest month (Bio6) and mean temperature of the warmest quarter (Bio10), with the optimal conditions at 0 °C and >32.5 °C, respectively. The findings should be useful for exotic species management and strategies.

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