Tolerance niche expansion and potential distribution prediction during Asian openbill dispersal

Yu Lei[1] and Qiang Liu[2]

[1]Southwest Forestry University
[2]National Plateau Wetlands Research Center

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Abstract

Aim: Understanding the tolerance niches of species plays an important role in studying the mechanisms of species dispersal and invasion. Taking the rapid dispersal bird, Asian openbill (Anastomus oscitans), as a model species, we identified ecological niche changes in the process of its dispersal, explored the potential distribution, and evaluated population evolution trends. Location: East Asia, South Asia, Australia. Methods: We used the ecological niche models Niche A and ecospat to compare the spatiotemporal change in the observed niche of Asian openbill, divided into original native, China, Malay Peninsula, and present distributions. Moreover, several models were generated using a biomod2 ensemble modeling framework to predict the trends and potential distribution of species. Results: The observed niche of Asian openbill was stable between the original native and present distributions. The Malay Peninsula population represented significant niche conservatism and propagable climate conditions. The rate of niche expansion reached 77.61% among the population in China, which was able to tolerate colder temperatures than the native population. Models indicated that Asian openbill dispersal was more suitable at low latitudes. According to the best performing model, Random Forest, the distribution probabilities of the China and Malay Peninsula populations were much higher than random expectations. Main conclusions: We concluded that the novel tolerance niche during northward dispersal exceeded the native observed niche, which should not be neglected because of the cold temperature tolerance for the evolution of the species in the future. In addition, northward and southward dispersal corridors have opened and the possibility of reproduction in the southward population was higher than the northward population. Asian openbill dispersal behavior will continue both north and south, but multiple factors affect dispersal rate and durability, and the model results require more fundamental data on the source and new southern populations.

1 Introduction

Species dispersal has a profound impact on species populations from ecological and evolutionary perspectives (Johnson & Gaines, 1990; Paradis et al., 1998), and represents the first stage of the invasion process (Davis, 2009). The causes of species dispersal are complex: it may be influenced by life-history, kin selection, avoiding of inbreeding depression, habitat loss, climate change, and species introductions (Clobert, 2012; Kokko, 2006; Travis & Dytham, 2002). Researching on species dispersal and distribution from the ecological niche perspective can help better understand biological responses to environmental changes (Ingenloff et al., 2017; McCauley et al., 2014). Otherwise, dispersal behavior into novel areas may pose challenges to the integrity of local ecosystems and biodiversity conservation (Tingley et al., 2014; Vilà et al., 2010). Therefore, it is necessary to study changing ecological niches and distribution trends during species dispersal.

Over the past two decades, Ecological niche models (ENM) have been widely implemented in biological invasion research. Extensive research has revealed ecological niche dynamics, potential geographical distributions, driving factors behind invasion, and assessments of invasion risk using various modeling approaches, such as

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measuring niche characteristics and comparing differences between native and novel niches, analyzing habitat suitability, and predicting future spatial distribution trends (Beukema et al., 2018; Olivier Broennimann & Guisan, 2008; Mandle et al., 2010; Ørsted & Ørsted, 2019; Parravicini et al., 2015; Tingley et al., 2014; Villaverde et al., 2017). Studies of niche dynamics under climate change, which have received more attention, show the biological invasion often accompany with niche shift (O. Broennimann et al., 2007; Gallagher et al., 2010; Stiels et al., 2014). However, such conclusions can be suspicious because of insufficient evidence or inappropriate modeling frameworks, such as lack of analyses in environmental space, and excluding factors like partial niche filling, sampling bias, or the unequal availability of environmental conditions (Guisan et al., 2014; Peterson et al., 2011; Petitpierre et al., 2012; Qiao et al., 2017). Hence, an appropriate modeling method should be chosen rather than blind trust (Joppa et al., 2013; Qiao et al., 2015).

On the other hand, the recent use of niche models for biological invasion-related studies on plants or animals have mainly focused on colonized species. For example, ring-necked parakeet (*Psittacula krameri*) (Strubbe et al., 2015), brown marmorated stink bug (*Halyomorpha halys*) (Zhu et al., 2017), and eastern gray squirrel (*Sciurus carolinensis*) (Creley et al., 2019) are such studies. They emphasize the fundamental niche of the species. With the development of niche theory, the relevant niche concepts have been constantly improved (Guisan et al., 2014; Jackson & Overpeck, 2000; Peterson et al., 2011; Sax et al., 2013). In particular, Sax (2013) proposed the existence of a marginal zone outside of the fundamental niche, a "tolerance niche" area in which individuals of a species can survive even if they do not currently have self-sustaining populations. Tolerance niches are prevalent among many species, especially those with dispersal and migration behaviors, such as the Amur falcon that breeds in east Asia and winters in Africa, so the winter niche is the tolerance niche. Combined with the stages of biological invasion (Davis, 2009), individual dispersal behavior before the establishment of a population in a new distribution area should also be included in the tolerance niche discussion. However, in contrast to colonized species, there is much less information about the niche dynamics mechanisms for species that have not yet successfully established in an invaded area (Bush et al., 2018; Feng & Papeş, 2017; Rosenblad et al., 2019). Here, we select a representative species with natural dispersal to investigate its niche dynamics and the potential effects of dispersal on the population.

The Asian openbill (*Anastomus oscitans*) is a large wading bird that specializes in forage mollusks. It belongs to the stork family Ciconiidae and is mainly distributed in South Asia and Southeast Asia, including India, Sri Lanka, Bangladesh, Myanmar, Thailand, Vietnam, and other countries (Elliott et al., 2020). Observed data in recent years describe a large-scale phenomenon of Asian openbill dispersal: the first was documented in Dali, China in 2006 (Wang, 2007), it was recorded by Perlis State in Chuping, Malay peninsula in 2008 (Lim et al., 2008), and it was first discovered in Singapore in 2013 (Low et al., 2013). The dispersal behavior can be divided into two directions: south to southern Thailand, Malaysia, Singapore and north to northern Vietnam and China, and the number of dispersed individuals has increased from a few to thousands each year (Han et al., 2016; Jiang, 2010; Liu et al., 2015; Low et al., 2013). Data showed that no breeding behavior was found in any population of Asian openbill in the new distribution areas (Han et al., 2016; Low et al., 2013; Zainul-Abidin et al., 2017), and presented that majority population are subadult birds and the population is more in summer and less in winter in China (Han et al., 2016; Lei et al., 2017). In comparison to temperate species, tropical species are generally adapted to a narrow and constant range of abiotic conditions (Gaston & Chown, 1999; Janzen, 1967), It is interesting when tropical birds naturally spread to both low and high latitudes, hence the following questions about abiotic conditions during Asia openbill dispersal: 1) Did the niche change during the dispersal process? 2) Is it possible to establish populations successfully in new areas? 3) Based on the present niche characteristics, how might the Asian openbill spread in the future?

2 Method

2.1 Occurrence data

The occurrence data on the Asian openbill consists of internet sources and field surveys. Data were downloaded from the Global Biodiversity Information Facility (GBIF, *www.gbif.org*), which contained 26905 original distribution records from 1970 to 2018. Field data consisted of 43 records obtained from our surveys in southwest China in 2016 and 2017. Firstly, 26948 records were obtained by combining the above two datasets to make up the present data on Asian openbill. Then, based on the initial dispersal event time, we extracted data before 2006 as the original native data. Finally, according to the current distribution pattern, the Chinese data were extracted from the present data as the new northern population, and data from Malaysia and Singapore represented the new southern population of the Malay Peninsula.

Without sampling bias is a critical assumptions for ENM (Peterson et al., 2011), but the occurrence data tend to be affected by spatial sampling bias (Bystriakova et al., 2012). Hence, we removed obvious erroneous data, such as duplicates, poor precision records, and conspicuously inaccurate data. Considering the relative independence of the data and the activity range of the species at a small scale, only one data point was kept for each 10km. The above steps were implemented using the Wallace package in R v3.5.1 (Kass et al., 2018), and the present dataset was finally reduced to 2,181 records.

We calculated Asian openbill distribution density in 12 recorded countries. If the distribution data were concentrated in a limited range, such as China, we excluded the other absence areas. Then we selected Bangladesh as the reference density (3.654 records 10^{-8} km $^{-2}$) in combination with the actual situations. The density values for countries higher than the reference value were randomly deleted to reduce density; otherwise all country data was retained. All processes were carried out using QGIS, version 2.18.20. Finally, we obtained balanced data as the present data, including 264 original native records, 41 new northern records, and 10 new southern records (8 records in Malaysia and 2 records in Singapore) (Fig.1).

2.2 Environmental variables and study area

We used 19 bioclimatic variables with a resolution of 2.5 minutes obtained from WORLDCLIM as predictors (*www.worldclim.org*). Although there was low spatial autocorrelation and dependence of points in environmental space (Olivier Broennimann et al., 2012; Guisan & Zimmermann, 2000), to compare the relationship between environmental factors and species, we used consistent variables used in two different space. Pearson correlation analysis was used to remove the data of 19 environmental layers by correlation value $|\ r\ | > 0.7$, considering Asian openbill habits, 10 environmental variables were retained bio1, bio3, bio8, bio9, bio10, bio12, bio15, bio17, bio18, and bio19. These nonlinear data were then converted into niche quantification analysis through principal component analysis. We used the first three principal components, which summarized 84.8% of the overall variation in the environmental data, to represent environmental variability across the landscape for model analysis. PC1 was mainly composed of precipitation factors related to annual average temperatures and low temperatures, PC2 mainly represented changes in low temperatures and temperature differences, and PC3 was related to annual precipitation and temperature in the rainy season (see Table S1).

The extent of the model calibration area had key impacts on the ENM results (Barve et al., 2011). Considering the distribution status, dispersal trends, dispersal ability, and ecological habits of the Asian openbill, we decided to use four different study areas. 1) The native range consisted of 9 administrative borders of India, Nepal, Sri Lanka, Bangladesh, Myanmar, Vietnam, Laos, Thailand, and Cambodia. 2) For the new distribution areas, we delimited the administrative boundaries of Yunnan, Guangxi and Guizhou provinces of China as the new northern range, while we chose the geographical division of the Malay Peninsula as the new southern range. 3) The calibration range, based on the native range, added accessible areas of the

species including southwest China, the Malay Peninsula, Sumatra Island, and Pakistan. 4) The modeling prediction extent was comprised of the boundaries of east Asia, southeast Asia, South Asia, and Australia (Fig.1). The native range and new distribution range were used for comparative ecological niche analysis in environmental space, while the calibration range and project range were used for modeling and prediction in geographical space.

2.3 Ecology niche analysis

Using observations to compare the differences in environmental attributes of recorded sites between the native and exotic ranges in environmental space is a main approach for quantifying niche changes (Guisan et al., 2014). Environmental context similarity is a premise of ENM niche analysis, and a valid conclusion can only be drawn under the same or similar environmental conditions (Escobar et al., 2016; Petitpierre et al., 2012). To determine the analogy environments between the native and new distribution ranges, we adopted three metrics to test as Qiao et al, (2017). We used Mobility-Oriented Parity (MOP) (Owens et al., 2013) and multivariate environmental similarity surface (MESS) to measures environmental similarity (Elith et al., 2010). Both methods are implemented in the NicheToolbox (Osorio-Olvera et al., 2016). Then we employed ExDet to identify similar or novel environments between native and new distribution areas (Mesgaran et al., 2014). ExDet identifies areas with novel univariate (novelty Type 1) or combinations (novelty Type 2) of environmental parameters, and can identify the most influential environmental variables leading to non-analogous environments between the compared areas (Mesgaran et al., 2014).

To identify niche overlap and population utilization, Niche A and Ecospat were used. We used the first three components in Niche A software (Qiao et al., 2016) to display minimum volume ellipsoid (MVE) generated from observations of three study areas, analyze the overlap of three ellipsoids, and determine analogous and non-analogous environments, then projected these environments in geographical space to identify population utilization under analogous conditions according to a species distribution map (Elliott et al., 2020).

After determining the occupation of niche and similar environments, the first two PCA axes were selected at a resolution of 100×100 to compare species density differences between the native and new distribution areas. Meanwhile, we used the Schoener's D metric to calculate the degree of overlap in the ecospat package (Di Cola et al., 2017) in R (R Core Team, 2013), including four indices overlap (D), unfilling, stability, and expansion (Guisan et al., 2014; Petitpierre et al., 2012). Overlap (D) measures niche overall match between two entities, from 0 (no Overlap) to 1 (complete Overlap) (Broennimann et al., 2012). When we overlapped the native and exotic niches, the proportion of exotic niche that did not overlap with the native niche was termed expansion, the exotic niche overlapping with the native niche was termed stability, and the native niche that did not overlap with the exotic niche was termed unfilling (Guisan et al., 2014). In addition, in order to test whether or not the niche is equivalent and similar, we used equivalency and similarity tests in ecospat (Broennimann et al., 2012; Warren et al., 2008). Niche equivalency tests were performed to determine whether the native and invaded niche generated by occurrences were identical, and sample data were randomly run 1000 times to calculate the overlap scores and actual overlap. When the actual overlap value was within 95% of the simulated value, the niche equivalency hypothesis could not be rejected. Niche similarity assesses whether the niches of two regions are higher or lower than the random expectation generated when the niche of one study area overlaps with the background of another study area after 1000 randomizations. If the actual overlap value was greater than 95% of the simulated value, the actual overlap was significantly greater than expected. According to the results of Niche A, we decided to compare the new southern and present niches to the original native population as niche conservatism (the alternative = "greater"), and to test the new northern and original native population niches as niche divergence (the alternative = "lower"). Finally, the ecospat package was used to identify response range differences of the 10 environmental variables between the new northern and original native populations.

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2.4 Potential geographic distribution

ENM or species distribution models (SDM) can predict potential spatial distributions of species. Generalized additive models (GAM), random forests (RF), boosted regression trees (BRT, or named GBM), maximum entropy (Maxent) are widely used models (Guisan et al., 2014). Although there are many model options, no single optimal metric is widely applicable in this field (Qiao et al., 2015). The consensus algorithm can balance the performance of multiple models (Marmion et al., 2009), but results are ambiguous compared to a single model (Breiner et al., 2015; Zhu & Peterson, 2017). In order to obtain an optimal result predicting potential distribution, three individual models (RF, GBM, Maxent) and an ensemble model were implemented in the biomod2 package (Thuiller et al., 2009). Seventy percent of occurrence data was used for model training and 30% for model testing. We selected the partial receiver operating characteristic (PROC) as the model evaluation criteria; in contrast with the AUC method, PROC eliminates the misleading effects of absent data on the results and emphasizes the crucial role of the omission rate to prediction performance (Peterson, 2006). An AUC ratio of 1 implies that the niche model is no better than a random prediction, and a larger AUC ratio indicates better discrimination in the partial ROC approach (Peterson et al., 2008). In addition, given criticism of the complexity and transferability of Maxent default settings, we adjusted regularization multiplier (RM) values and feature combination (FC) settings in the ENM eval package to optimize parameters and determined the delta AICc minimum and average AUCtest maximum values to generate Maxent (see Figure S3) (Muscarella et al., 2014).

A more complete niche assessment can be obtained using all species distribution data (Broennimann & Guisan, 2008), so we used total occurrence data to model and analyze the Asian openbill potential distribution. First, we generated a calibration model using the present data within calibration range, then the potential distribution was predicted to a new projected range. Due to the potential extrapolation uncertainty of the model in the transfer, we still used ExDet to determine the novel environmental parameter (Type 1 novelty)(see Figure S2.3) (Mesgaran et al., 2014).

To determine whether the probability of two new distribution areas was higher than other areas where the Asian openbill did not yet occur, we randomly created occurrence sites outside of the existing distribution area within the projected extent. A probability value of 0-1 was generated in the optimal model with the highest PROC value to compare the occurrence probability of species in the native area, new distribution areas, and absence area.

3 Results

3.1 Ecology niche analysis in environmental space

There were no novel components in the environment context comparison between study sites as shown by MOP, MESS and ExDet (see Figure S2.1-S2.2) indicated that the results of our subsequent niche analysis were reasonably comparable under similar conditions.

It can be seen in Niche A that the observed niche of two new distribution populations both overlapped with the native area, but some of the new northern area exceeded the native edge (Fig.1a). Analyzing the spatial relationships between niches (Fig.2a), we found only a small minority of low latitudes in China were analogous with Myanmar's sedentary populations and India's wintering populations in niche occupation (Fig.2b), and most of the population had no reference data because it was beyond the native niche (Fig.2d). In contrast, the niche occupation of the Malay Peninsula's populations completely overlapped with Sri Lanka's sedentary populations (Fig.2c).

The observed Malay Peninsula population niche was nearly totally within the original native range (Stability=99.42%), while the new northern population only partially overlapped with the native niche (Stability=22.39%). The results of Schoener's D quantification showed that compared with the original native area,

niche divergence of the new northern population was significantly higher than expected (P < 0.05), representing significant niche expansion. The niche equivalence and conservatism of the new southern population were significant (P < 0.05). In addition, the present population niches were still similar to the native area, and the expansion of the new northern population only accounted for 2.32% of the whole population (Fig.3) (Table 1). Nevertheless, when the three observed niches were compared with the original native niche, there was an incomplete niche match in overlap D value (the maximum value was 0.59) (Table 1), indicating that in recent dispersal years, the Asian openbill niche changed or resulted in an unbalanced regional distribution, especially for individuals in China.

A comparison of response range to occurrence within each environment variable between native and new northern populations revealed that five precipitation-related factors did not change, three of five temperature factors showed that the new northern population had a lower temperature tolerance than the native population, and the other two factors (Mean Temperature of Wettest Quarter and Mean Temperature of Warmest Quarter) were included in the native range. These results suggest that the climate conditions of the population in southwest China were similar to the native population during the high precipitation and temperature season, while temperatures in China sites were colder than native range's in the dry winter season (Fig.4).

3.2 Potential spatial distribution

The suitability prediction map representing the three individual models and the ensemble model (Fig.5) showed that, out of the native area, northern Australia and New Guinea were more suitable for the Asian openbill. Some islands in the Philippines and Malaysia also had high suitability values, but some high latitudes in the east Asia regions, such as China, Mongolia, Japan, and the Korean Peninsula, were less suitable.

All four maps showed that the lower latitudes were more suitable. However, we still found some records in new distribution areas with less suitable values, indicating that the Asian openbill can exist in low-suitability areas. Furthermore, three individual model results showed that there may have been more potential area in the east, northeast, and north of China. Based on the PROC evaluation, we found that the AUC ratio value of the RF model was significantly higher than other models, so it was chosen for probability analysis (Fig.6).

The occurrence probabilities for the two new distribution populations, original native populations, and random populations were extracted from the RF model for comparison. Although values of the two new distribution populations (China, Mean ± SD = 0.39 ± 0.07, Malay Peninsula, Mean ± SD = 0.4 ± 0.17) were lower than for native populations (Native, Mean ± SD = 0.49 ± 0.20), they were much higher than the expected probability (Random, Mean ± SD = 0.09 ± 0.12)(Fig.7). Based on the above suitability results, there is still a great potential for the stork to spread in both directions in China and the Malay Peninsula.

4. Discussion

4.1 Tolerance niche expansion during dispersal

The occurrence data used in this study were composed of breeding and non-breeding populations, so the niches of several populations were collectively referred to as the observed niche in our analysis. Compared with the original native observed niche, the two new distribution sites had different ecological niche characteristics. The Malay Peninsula had niche conservatism, but southwest China had niche expansion. As opposed to common niche expansion, however, the Asian openbill distributed in China and the Malay Peninsula did not exhibit documented breeding behavior and it lacked self-sustaining capacity (Han et al., 2016; Zainul-Abidin et al., 2017). Therefore, the measured results should be defined as the expansion of the tolerance niche.

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Niche breadth has a close relationship with range size (Kambach et al., 2019), so understanding niche breadth and physiological tolerances can result in better estimates of range size (Austin et al., 2009; Bush et al., 2018). The results of our measurements indicated that Asian openbill in China had a stronger tolerance to low temperatures. Indeed, Field surveys have found that some individuals in China can stand the temperature below zero (Han et al., 2016; Lei et al., 2017). Furthermore, native species ranges underestimate climate tolerance (Bocsi et al., 2016), especially that endotherms able to endure a wide range of environmental conditions (Strubbe et al., 2015). Hence abiotic factors were not the direct cause of the dispersal of Asian openbill.

Despite the obvious niche expansion, the observed niche of the whole population was still over a relatively short period, and niche conservatism cannot be rejected. However, this does not mean that the distribution of Asian openbill was in an equilibrium situation. At least in the tolerance niche, it is not known whether the bird has completely occupied the non-breeding space and presumably will continue to expand.

4.2 The role of new distribution areas in species evolution

A more reasonable explanation for the assumption of niche conservatism is that over a short-to-moderate time span and at lower taxonomic ranks (genus and species), niche conservatism dominates, but stability will decline over a longer time span and at higher taxonomic ranks (Peterson et al., 2011). According to the present niche occupation characteristics of various populations, it is important to discuss the future evolutionary trend of the Asian openbill.

Niche occupancy in the small area in southern China was similar to northern India, northeastern Myanmar, and northern Laos. The Malay Peninsula population niche was similar to that in southern Thailand and Sri Lanka. Although there were few recorded sites that we could reference in these similar native regions (Fig.2), many records of Asian openbill distributed around these locations. Given the potential sampling intensity bias and species dispersal capabilities (Peterson & Raghavan, 2017), in fact, there probably have more occurrences in these native regions. Although the Asian openbill distribution map may have been inaccurate due to rapid spread and data incompleteness, as a reference we could properly infer the residential types of the species (Elliott et al., 2020). The analysis found that similar areas in India and Laos were non-breeding areas of Asian openbill, and Myanmar and Sri Lanka were breeding areas. This meant that under different combinations of temperature and precipitation, the partial niche of China, which overlapped with the native niche, included some breeding and non-breeding sites with the possibility of breeding sites in southwest China Xishuangbanna and western Guangxi. The Malay Peninsula niche was similar to Sri Lanka according to breeding conditions. The expanded tolerance niche had no reference population residential information (Fig. 2).

The Asian openbill exhibited different niche changes in different directions, but they may play similar roles in the evolution of the entire population. The populations in the new distribution regions had peaks and troughs throughout the year but no breeding behavior was found. We believe that this phenomenon conformed to the source-sink theory (Dias, 1996; Pulliam, 1988), where new distribution regions serve as a sink habitat. Although the suitability or occurrence probability of these sink habitats was low, it was still higher than the expected value based on a random distribution. Therefore, the source of the new population should to be determined by further studies on bird migration. Fortunately, the population in China has a ring record that indicates that at least part of it is from central Thailand (Yang et al., 2019). The breeding time of the population in Thailand is generally around January in the local dry season (Elliott et al., 2020), and the non-breeding period is migration or dispersal, which is consistent with the characteristics of the population in China with more in summer and less in winter. Therefore, it is speculated that the spread of the population into a new area over a short time may be more dependent on the dynamic changes of the source population.

According to the continuous records of the past decade and the comparative analysis of the several population probabilities and random expectations, we believe that dispersal in two directions has begun, but the

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establishment success of the species in a new distribution area depends on propagule pressure (Lockwood et al., 2005), conspecific density (Taylor & Hastings, 2005) and species life-history traits (Blackburn et al., 2009). Historically, there have been many birds that have spread to low and high latitudes at the same time and successfully established colonies, such as the cattle egret (Lovette & Fitzpatrick, 2016), the ring-necked parakeet (Strubbe et al., 2015), the Egyptian goose and the Common waxbill (Blackburn et al., 2009). Even if the Asian openbill have not yet colonized in new distribution areas, combined with the low temperature tolerance, similar environmental requirements, and established migration corridors and niche expansion potential, a new breeding population with low temperature tolerance may appear in China. However, the southern dispersal populations have a higher reproductive potential and could form the Malay Peninsula or even Australian population.

4.3 The potential distribution and dispersal trend of Asian openbill

The model predicted that the potential distribution of the Asian openbill has not increased significantly in the new distribution area. The newly added suitable areas in China included the south of Sichuan province in the southwest, and the coastal areas of Taiwan island, Hainan island and Leizhou Peninsula in the south. It is worth mentioning that the occurrence points, which were filtered during the previous data processing, such as records from southern Sichuan and Leizhou Peninsula, were also included in the prediction results. Outside the present distribution area, the suitable area increased significantly in the low-latitude islands, such as Kalimantan, New Guinea, and northern Australia. In fact, in recent years, the number of Asian openbills that that spread outwards were quite erratic, especially the Malay Peninsula population, which declined (Zainul-Abidin et al., 2017). Even if the model predicted that there were potential suitable climatic conditions, it was still difficult to determine whether the storks would continue to spread. Analyzing the reasons for native population dispersal can help us better understand species dispersal trends.

Generally, the factors that promote species invasion are density of the native population and reproduction pressure (Lockwood et al., 2005), the shortage of food resources (Davis et al., 2000), the lack of natural enemies in the invaded area (Keane & Crawley, 2002), or a species with high environmental adaptability and physiological tolerance (Blackburn et al., 2009; Marchetti et al., 2004). Previous research has suggested that Asian openbill residential situation were most influenced by precipitation factors. Low et al. (2013) speculated that the spread of Asian openbill into the Malay Peninsula was probably caused by a large drought in Thailand. In addition, in Thailand and the Raiganj Reserve of India, water levels also affect food abundance and are directly proportional to the number of Asian openbill observed (Jinnath et al., 2016; Sawangproh et al., 2012; Sharma, 2007). In terms of food, the large-scale invasion of the golden apple snail (*Pomacea canaliculata*) in southeast Asia led to the rapid growth of the Asian openbill population (Zainul-Abidin et al., 2017). As one of the major invasive species in China (Lv et al., 2009), the golden apple snail is also one of attracting factors for the Asian openbill (Han et al., 2016). In terms of population density, Asian openbill demographics in India, Cambodia, Thailand have shown that native colonies have increased rapidly in the past decade (Han et al., 2016; Roy & Sah, 2013; Willcox et al., 2016). The above reasons provide an external driving force for Asian openbill dispersal.

On the other hand, the Asian openbill is able to migrate long distances for forage and environment adaptation (Blanford, 1898). It has been documented that the Thailand population migrates north to central and northern Thailand, northeast India, and Bangladesh during the non-breeding season (McClure, 1998); In other words, one source population in Thailand has had a life history trait of migrating northward. Considering that the Chinese population increased from one to thousands in recent years, the intra-species composition is predominantly subadult and juvenile with irregular population dynamics (Han et al., 2016; Liu et al., 2015), so the Asian openbill is considered to be a vagrant bird in China (Zheng, 2017). In general, the migration of juvenile and subadult birds is variable and unstable, and their fidelity to wintering and breeding grounds is lower than the adult birds (Bentzen & Powell, 2015). Perhaps "over-migration" occurred in Thailand when they initially migrated north, bringing a few migrants to locations out of their normal migratory range as

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vagrants (Ralph & Wolfe, 2018), and arriving in southwest China. Being far from the fundamental niche centroid accelerated the dispersal rate (Ingenloff et al., 2017), resulting in a wide distribution range that was extremely unstable in the early stage of species dispersal, such as occasional records in Shangri-La, Leizhou Peninsula, and Poyang lake in China. Then a relatively stable distribution pattern was formed after several years of dispersal.

In the Malay Peninsula, studies have suggested that food and paddy flood level may contributed to Asian openbill southward dispersal (Zainul-Abidin et al., 2017). At present, there is still a lack of information on the migration ecology and continuous population dynamic monitoring of Asian openbill in the Malay Peninsula. In summary, an understanding of the model results needs to be considered with actual information. We believe that the behavior of Asian openbill dispersal to China during the non-breeding season become stable and the range size is likely to continue expand to the north or coastal areas. More fundamental data are needed to support whether the more suitable low-latitude islands predicted by the model have sufficient natural dispersal potential.

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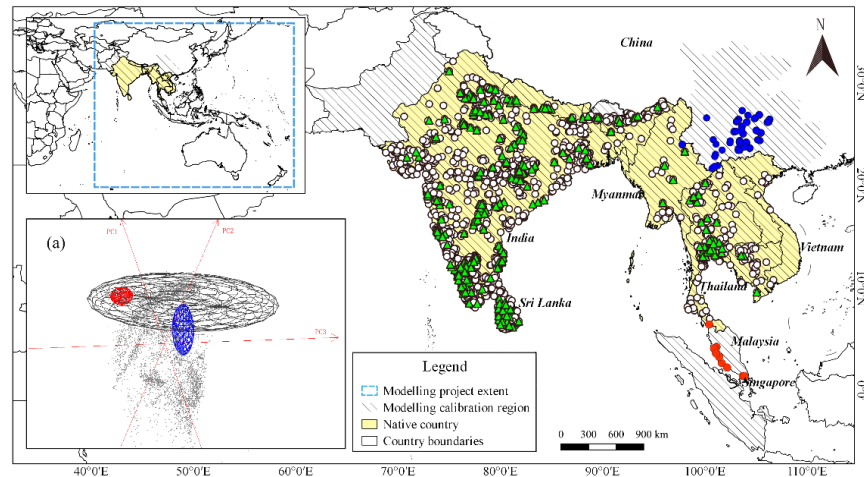
Figure 1 Asian openbill spatial occurrence and the observed niches of three populations in Niche A (a). We used all occurrence information as present data, the green triangle represents the original native population, the blue circle indicates the new northern population in China, and the red indicates the new southern population in the Malay Peninsula. The observed niche overlap (a) indicates that the new southern population niche (red ellipsoid) is a subset of the original native population (black ellipsoid), but the new northern population niche (blue ellipsoid) partially overlaps with the native niche and exceeds the native envelope.
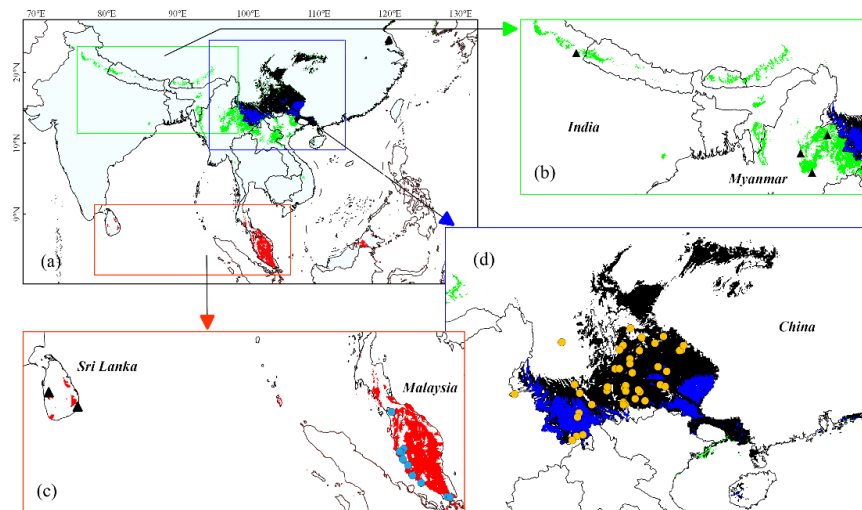
Figure 2 The observed niche based on occurrence in China and the Malay Peninsula within analogous and non-analogous environments between native and invaded range (a). The black triangle represents occurrence in the native range. Four occurrences in analogous environments between native (green region) and China (blue region) (b), yellow dots represent occurrence in China within analogous and non-analogous environments (black region) (d). Occurrences in Malay Peninsula symbolized by blue dot in analogous environments (red region) between the native population and the Malay Peninsula (c).
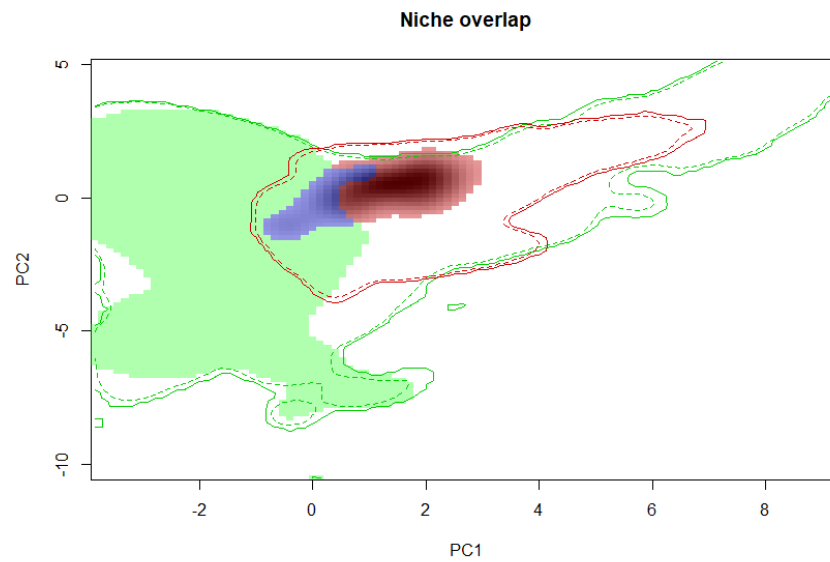
15

Niche overlap

Figure 3 Comparison of Asia openbill climatic niches from China (left), the Malay Peninsula (middle), and the present (right) with original native. Colors indicate niche expansion (red), stability (blue), and unfilling (green). Dashed contour lines represent the 90th percentile of the background environment for both ranges.
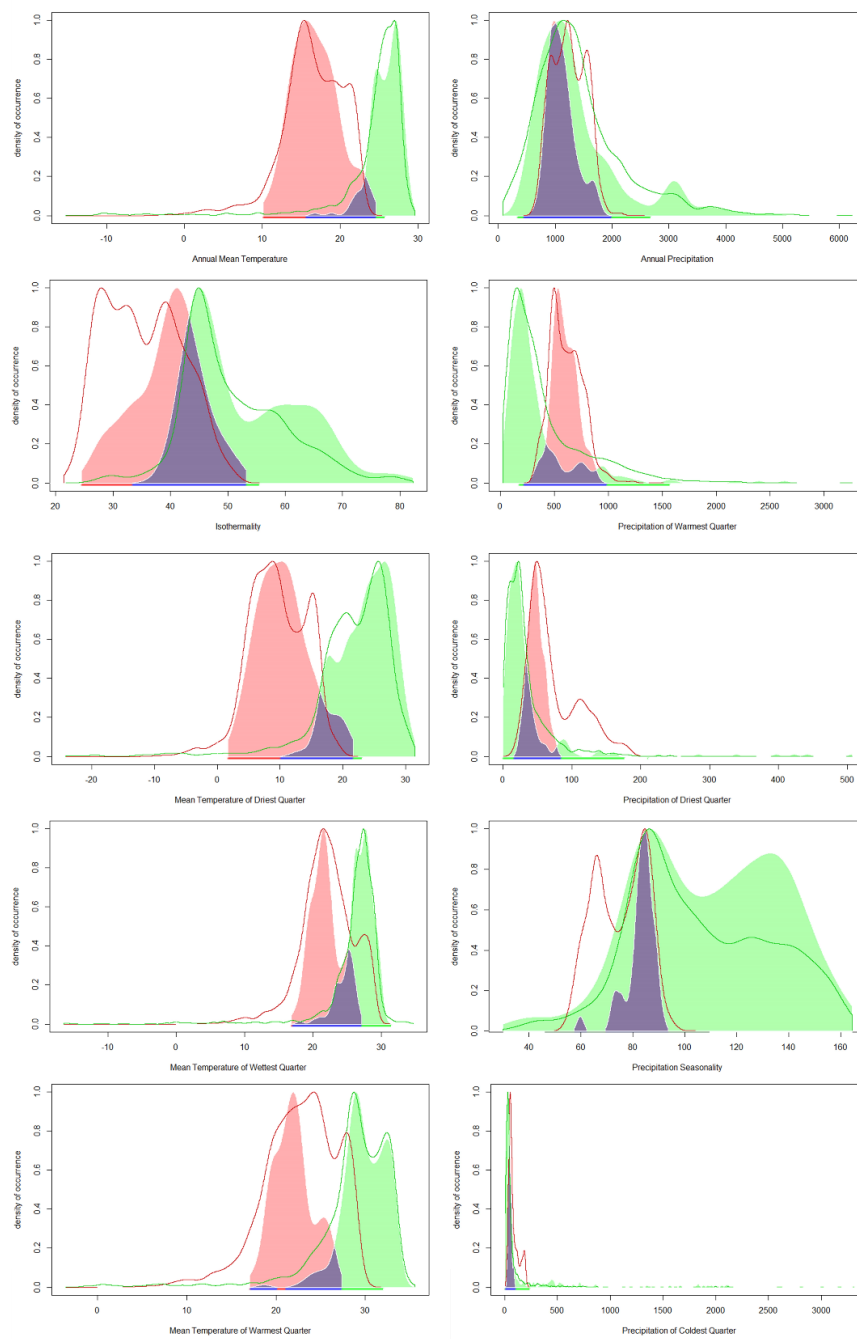
Figure 4 The left column are factors related temperature; the right column are precipitation-related factors. Notice the range of environmental response on the horizontal axis, green is the response range of native population, red is the response range of Chinese population, and purple is the area where two populations' response range overlap. We can find that the values of Chinese population lower than the native population's on Annual mean temperature, Isothermality and Mean temperature of driest quarter.
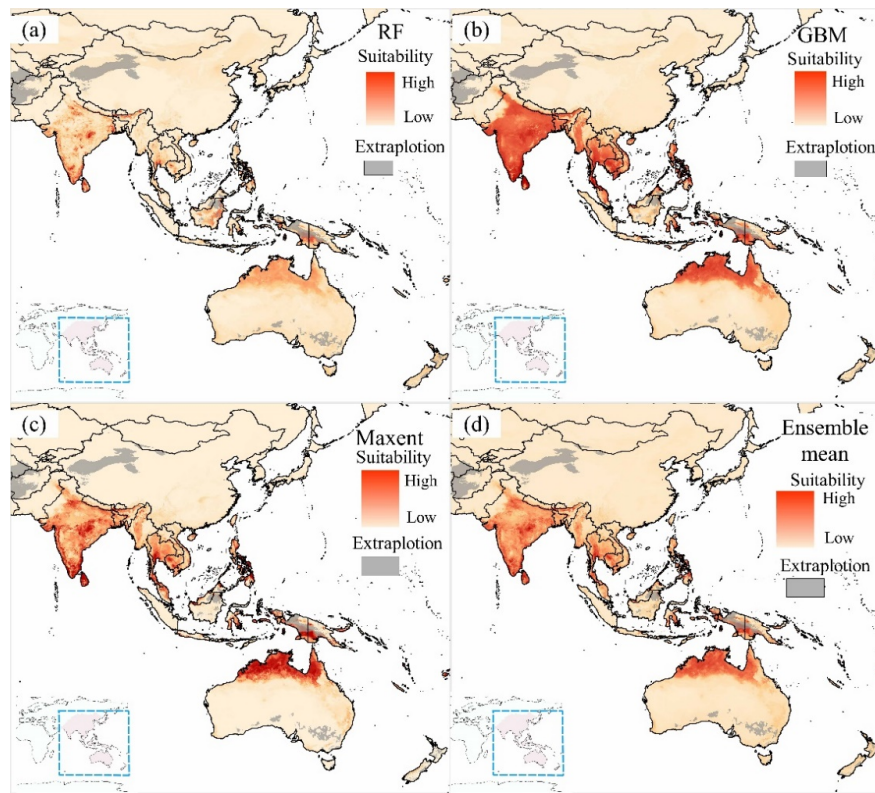
17

Figure 5 Habitat suitability for the Asia openbill, using three individual models and an ensemble algorithm from the calibration area to the projected area, including RF(a), GBM(b), Maxent(c) and ensemble model(d). Grey areas indicate regions with novel climate conditions (extrapolation) with respect to those characterizing the projected range.
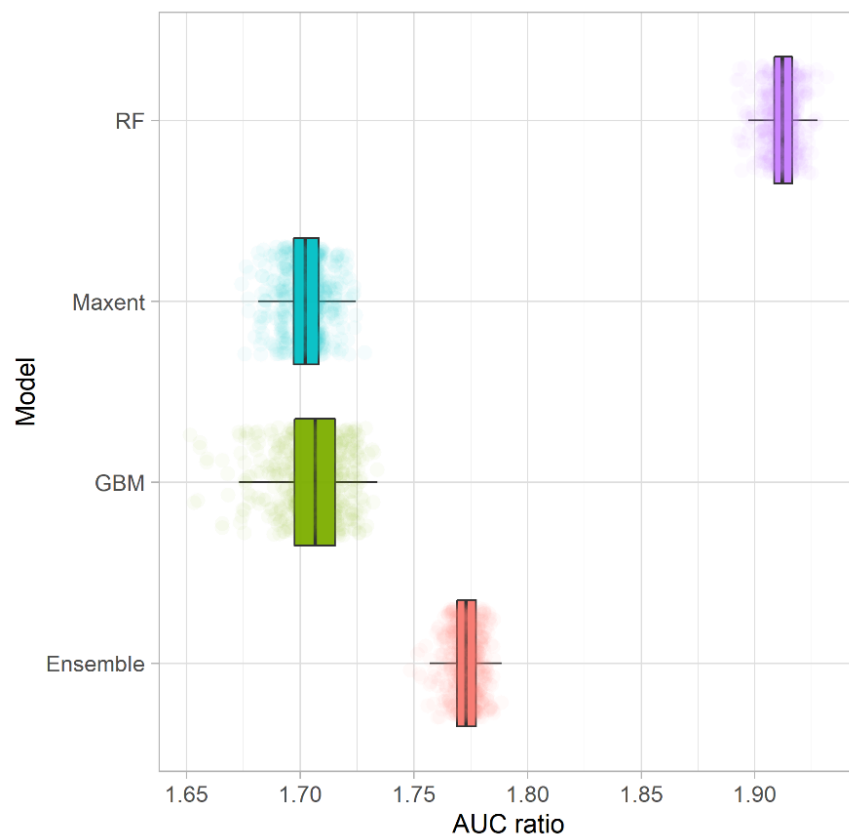
18

Figure 6 Evaluation of four models using partial ROC ratios. Boxplots denote AUC ratios for 500 replicates using 50% of evaluation occurrences in each replicate and a 5% omission error.
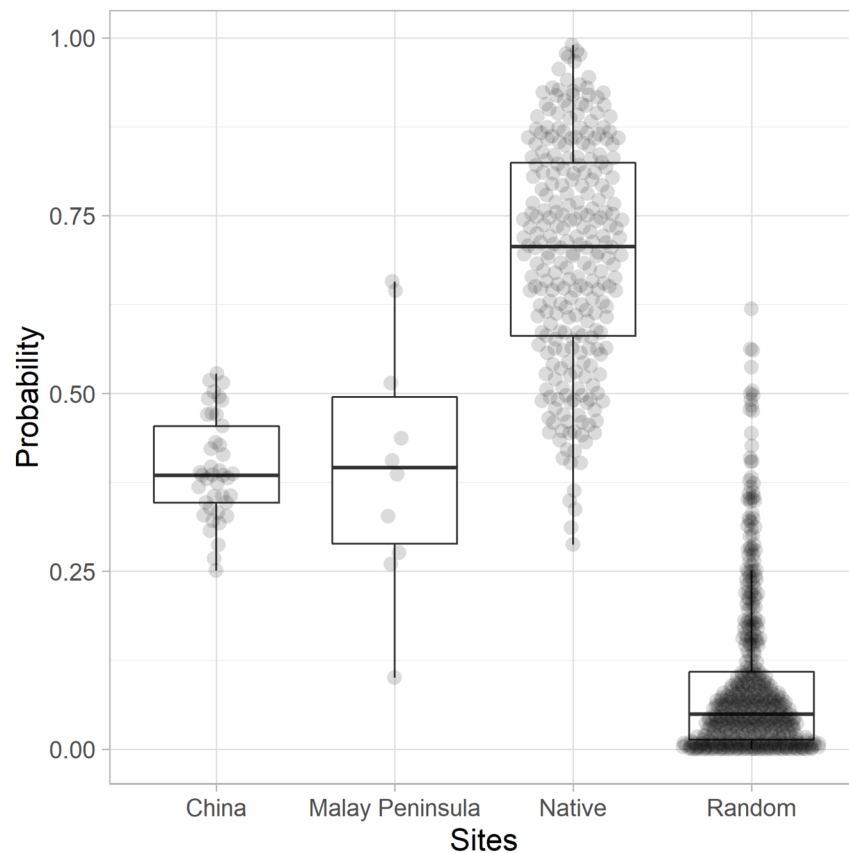
Figure 7 Probability of occurrence at four population sites

TABLE 1 Niche overlap results comparing three study areas with the original native range. The niche equivalency and similarity tests between southwest China and the native range select the lower option to emphasize niche divergence. In the other two comparison groups are test the niche conservatism in alternative by greater. p < 0.05 indicate that niches are more conserved or similar than would be expected by chance and are denoted by asterisks.

Study area	Expansion(%)	Stability(%)	Unfilling(%)	Niche overlap (D)	Niche Equivalency (p)	Niche simila
Southwest China	77.61	22.39	66.06	0.01	0.01*	0.55
Malay Peninsula	0.58	99.42	37.41	0.14	0.03*	0.04*
Present	2.32	97.68	0	0.59	0.08	0.02*