

Mapping the potential distribution of the schistosomiasis intermediate host *Biomphalaria straminea* in China

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Abstract

Biomphalaria straminea is native to Brazil but has established a population in Guangdong Province, China. Its potential of expanding and transmitting *Schistosoma mansoni* is of great concern. We seek to map *S. mansoni* transmission potential by predicting ecological dimensions and potential distributions of *B. straminea* using state-of-the-art ecological niche model approaches. Two environmental datasets were selected to fit individual and ensemble niche models, together with the evaluation of niche conservatism during *B. straminea* invasion in China. A small area is still occupied by the introduced population compared to that in Brazil. A vast space with suitable climate remains unfilled and might be available to *B. straminea*. Contrasting results of niche

conservatism evaluation were attained based on the two environmental datasets. The coastal areas in southern China, together with south-western Yunnan and southern Hainan and Taiwan were consistently supported by multiple model approaches, showing high climate suitability for *B. straminea*. Attention should be paid to the possibility of *S. mansoni* epidemic in these identified areas, as high pressure due to propagation and future climate change may further complicate conditions. Our results call for rigorous monitoring and supervising along these areas in China.

Introduction

Biological invasion represents a major threat to the sustainable development of our society (Mack *et al.*, 2000), resulting in serious damages to environment and human health, which can eventually lead to great economic loss (Liu *et al.*, 2011). Many strategies and actions are attempted to reduce the effect of invasive species, especially those that spread disease. Eradication is usually difficult once the invasive species has passed the bottleneck and established populations (Kolar and Lodge, 2001). The most effective way might be to prevent initial invasion or restrain future expansion rather than trying to curb outbreaks. It is therefore a priority to consider spatial deployment of efforts and resources for field management with regard to invasive species.

Predicting potential distribution of invasive species via ecological niche modelling (ENM) approaches could be useful by offering information on allocating efforts in this regard (*e.g.*, Roura-Pascual *et al.*, 2011; Beans *et al.*, 2012). ENM seeks to characterize ecological requirements of species using environmental variables associated with observed data and then identify how suitable environmental space are distributed. This correlative approach is now routinely used with respect to biological invasion (Peterson *et al.*, 2012), and increasingly used in disease ecology (Peterson *et al.*, 2014).

Schistosoma mansoni is the parasite species responsible for schistosomiasis in tropical and subtropical areas in Africa and Latin America, especially in Brazil. One of its intermediate snail hosts, *Biomphalaria straminea*, is native to Brazil but has established populations in many countries in Central and North America and Asia. The first detection of *B. straminea* in China was in Kowloon in Hong Kong in the 1970s, where it was collected by shellfish amateurs in irrigation trenches (Fernandez, 2002). Pan *et al.* (1983) first reported its existence in Shenzhen in mainland China. By 2013, the snail had spread to surrounding regions of Dongguan City and Huizhou City in Guangdong Province (Figure 1) where it had established populations in freshwater habitat throughout urban and rural areas. Its further expansion and potential for transmitting *S. mansoni* have been much discussed. Habib *et al.* (2016) and Yang *et al.* (2018) employed the maximum

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See online Appendix for additional Figures.

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entropy model (MaxEnt) (www.gbif.org/tool/81279/maxent) to produce risk maps for *B. straminea* in China. However, their models were either based on the population of a non-equilibrated state (*i.e.* the introduced population did not inhabit the entire habitable area), violating key assumption of ENM applications (Peterson *et al.*, 2011) or employing a single-model approach without consideration of model uncertainty (Yang *et al.*, 2018). Human impacts appeared to be an important factor for the establishment and expansion of *B. straminea*, Yang *et al.* (2018) added human factors in a niche model to predict the potential distribution but did not calculate human populations that at risk of *S. mansoni* transmission.

In this study, classical niche models based on a native equilibrium population were used to map ecological dimensions and potential distributions of *B. straminea* using multiple model approaches. In addition, climate niche conservatism during the invasion of *B. straminea* in China, which is another key assumption in ENM applications (Peterson *et al.*, 2012), was tested using two environmental datasets. The aims of this study were i) to compare climate spaces occupied by native Brazilian populations and populations introduced into China; ii) to address whether the climate niche was diverged during *B. straminea* invasion in China; and iii) to predict its potential distribution in China using a fine-tuned individual MaxEnt approach and collective model ones.

Materials and Methods

Input data

Occurrence records of *B. straminea* were assembled from online databases (Global Biodiversity Information Facility (www.gbif.org/) and the published literature (*e.g.*, Scholte *et al.*, 2012; Habib *et al.*, 2016; Zeng *et al.*, 2017). These records were overlaid on the administrative maps and compared with their original descriptions to remove errors. Records lacking geographic coordinates were georeferenced using Google Maps. Spatial aggregations of distributional records were filtered at a 10 arc grid, where only a single record per raster cell was reserved for model calibration and evaluation to minimize possible effects of spatial autocorrelation (Veloz, 2009). A total of 542 records (507 native and 35 Chinese) reflecting the present-day distribution of *B. straminea* were retained for analysis.

Bioclimatic variables representing annual trends, extreme conditions of temperature and precipitation according to Hijmans *et al.* (2005) were considered. Variables combining temperature and precipitation were excluded because they displayed artificial discontinuities among adjacent grid cells in some areas (Escobar *et al.*, 2014). Two environmental datasets were selected based on their ecological relevance and independence from other variables. Dataset A summarized the aspects of temperature, and precipitation and had a Pearson correlation value of <0.85. It included mean diurnal range (Bio2), temperature seasonality (Bio4), maximum temperature of warmest month (Bio5), mean temperature of coldest quarter (Bio11), annual precipitation (Bio12), precipitation seasonality (Bio15) and precipitation of driest quarter (Bio17).

The snail mainly lives in fresh water in tropical areas but grows fast and adapts to diverse environments well. We assume that annual mean and extreme values of temperature and precipitation might be more important than others in limiting snail distribution. Therefore, a dataset B was made to reflect primary relevance in imposing constraints upon snail distribution, including annual

mean temperature (Bio1), Bio5, minimum temperature of coldest month (Bio6), Bio12, precipitation of wettest month (Bio13), precipitation of driest month (Bio14) and Bio15. All analyses were based on the above two datasets at a spatial resolution of 2.5'.

Climate space comparison

Climate spaces occupied by native Brazilian and introduced Chinese populations were compared and mapped in reduced dimensions using principle component analysis (PCA) using NicheA, version 3.0 according to Qiao *et al.* (2015). NicheA is an open-source platform that can be used to simulate ecological niches (Qiao *et al.*, 2015) it assumes that fundamental species niches are convex in shape as suggested by available evidence (*e.g.*, Soberón and Nakamura, 2009). Niches therefore can be operated as minimum volume ellipsoids (Van Aelst and Rousseeuw, 2009). NicheA can quantify similarity among multiple niches in terms of overlap in n-dimensional environmental spaces (Qiao *et al.*, 2015). Here, we mapped ecological dimensions for *B. straminea* by comparing climate spaces occupied by native and introduced populations in three reduced dimensions based on the two datasets mentioned above.

Climate niche conservatism during the invasion of *B. straminea* was investigated. We used *ecospat* of the R package (R Core Team, 2015), a statistical software supporting spatial analyses and modelling of species niches and distributions (Cola *et al.*, 2017), to test whether the snail's climate niche was diverged in environmental spaces. This programme uses kernel density to fit species distribution points and environmental variables associated with geographical region to test niche conservatism. Climate niche overlaps between native and introduced ranges were measured by the first two axes of PCA (Broennimann *et al.*, 2012). Schoener's *D*, which varies between 0 (no overlap at all) and 1 (complete overlap) according to Petitpierre *et al.*, (2012) was used to measure the overall match between the two niches.

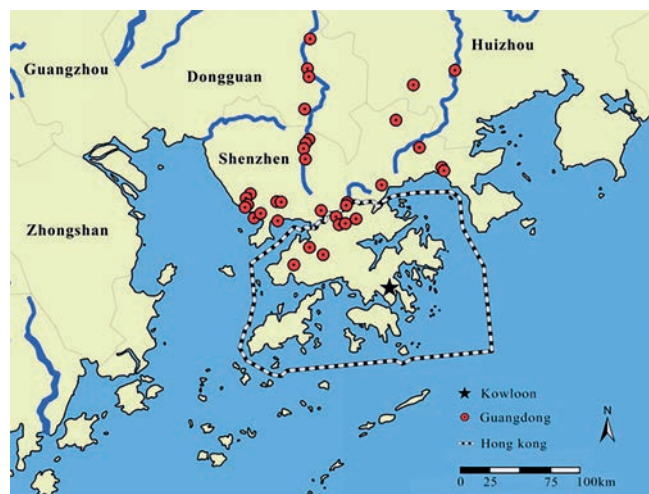


Figure 1. Map showing distribution and expansion of *Biomphalaria straminea* in southern China. The snail was first reported in Kowloon in Hong Kong and then expanded into surrounding areas.

Two alternative hypotheses of equivalency and similarity in statistical tests were used to test niche conservation. The former, which was used to compare niche similarity between geographic populations, works by comparing niche overlap values generated by actual occurrence data with those generated by empirical data randomly sampled across the two regions. The latter, which was used to test whether this similarity is due to the geographical area in which they occur, works by comparing actual niche overlap with that generated using points drawn at random from the region defined as environmental background for one of the populations (Broennimann *et al.*, 2012; Petitpierre *et al.*, 2012).

Background environments for the comparisons of climate space and niche modelling should include areas accessible to the species (Barve *et al.*, 2011). Here, we delimited this area by buffering known occurrences by 400 km, which reflects a compromise between including all accessible environments (Barve *et al.*, 2011) and covering an extent broad enough to minimize extrapolation and detect climatic differences between presence and background records (Owens *et al.*, 2013). Climatic similarities between native and introduced populations were assessed using mobility-oriented parity (MOP) metrics for the two environmental datasets. MOP is a correction and improvement of multivariate environmental similarity surfaces (Owens *et al.*, 2013).

Ecological niche modelling calibration and evaluation

Native models were fitted using the two datasets and then transferred across the globe to predict areas of potential distributions. 70% of native-range points were used to fit the model, the rest of them and introduced Chinese points were used for model interpolative and extrapolative evaluations respectively.

We sought to adopt both individual and collective model approaches to predict the potential distribution because each approach has its advantages and disadvantages (Zhu and Peterson, 2017). The ensemble model approach is widely used to reduce

model-based uncertainty but it is not better than the individual model. Therefore, five individual commonly used modelling algorithms, *i.e.*, generalized additive models, generalized boosted models (GBMs), generalized linear models, random forests, and MaxEnt models were developed using default parameters in biomod2 (Thuiller, 2003) implemented in R software (R Core Team, 2015) and then averaged to produce ensemble models. Eventually, two individual models were considered: MaxEnt and GBM. The former follows the principle of maximum entropy and is the most popular model algorithm, whereas the latter uses boosting to combine large numbers of relatively simple tree models, which is recommended by Jane Elith *et al.* (2006). Recently, Maxent based on default setting has been criticized because of its complexity and low transferability (*e.g.*, Muscarella *et al.*, 2014). In this study, the MaxEnt model was optimized using the ENMeval package (Muscarella *et al.*, 2014), which provides an automated way to execute MaxEnt models across a user-specified range of regularization multiplier (RM) values and feature combination (FC). We set the RM range to 0.5–4.0 with increments of 0.5 and used six FCs, *i.e.* linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) to cover a broad range of model settings. The fine-tuned MaxEnt models were made by seeking the minimum value of Akaike's information criterion (AIC) among candidate models (Muscarella *et al.*, 2014).

Partial receiver operating characteristic (ROC) and omission error were used to evaluate model interpolation and transferability, respectively. The traditional area under the curve (AUC) approach is misleading according to Peterson *et al.* (2008) and Jiménez-Valverde *et al.* (2012), so we adopted partial ROC approach, which considers the quality of occurrence points and weights more on omission error (Peterson *et al.*, 2008; Zhu *et al.* 2017a). An AUC ratio of 1 implies that the niche model is no better than a random prediction; the larger the AUC ratio, the better the discrimination in partial ROC approach (Peterson *et al.*, 2008). The omission

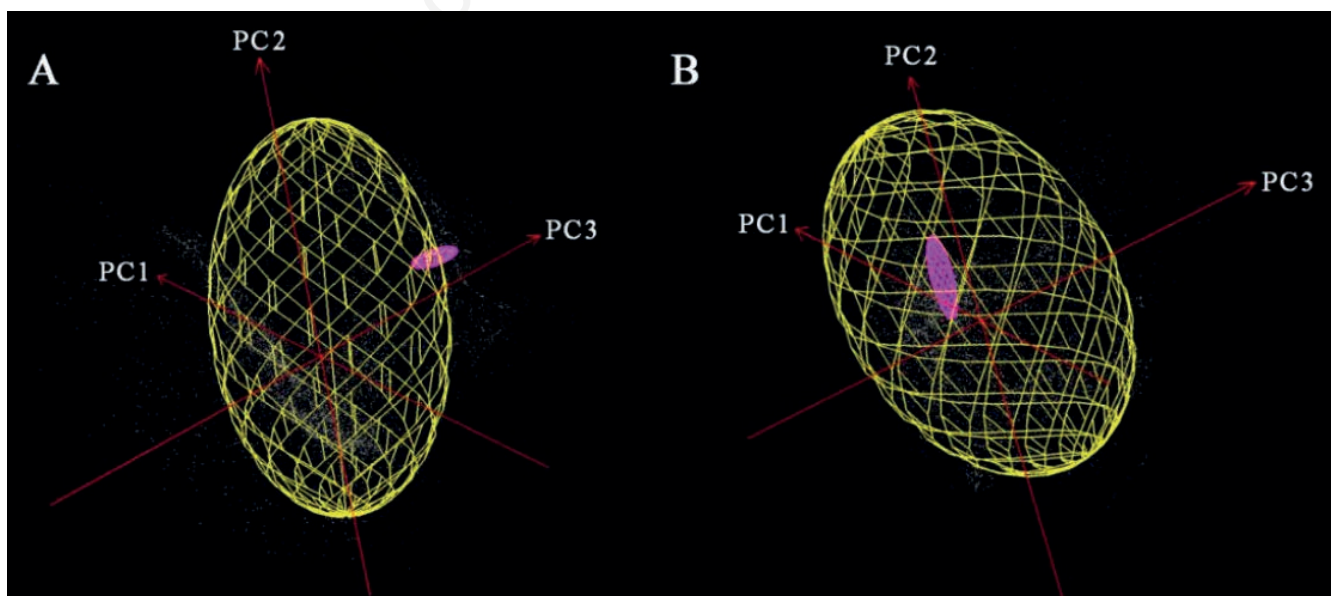


Figure 2. Climate niche spaces of *Biomphalaria straminea* based on two environmental datasets (datasets A and B). Yellow and pink ellipsoids represent niche spaces occupied by native and invading populations, respectively.

error was calculated by the proportion of testing points not predicted at a threshold. Here, occurrence data in China were used to calculate omission error across the threshold spectrum of model output. Specifically, we calculated the omission error at the increment of 10 against the total 1,000.

Human risk assessment

The human population that fell into suitable areas of *B. straminea* were estimated in four cities (*i.e.*, Hong Kong, Dongguan, Huizhou and Shenzhen) based on our predictions. To do so, the suitability maps generated by GBM model (which showed the best performance, see results) were converted into binary prediction at the 10 percent training threshold, the population that fell into the *positive* predicted areas were estimated based on a global population distribution data, which were obtained from Oak Ridge National Laboratory (www.ornl.gov/sci/landscan).

Results

Climate space

PCA of the climate variables associated with snail occurrences revealed reduced dimensions that accounted for the observed distribution. In dataset A, the first three components (PC1, PC2 and PC3) explained 88.6% of the variance; PC1 was associated with mean diurnal temperature range (Bio2) and accounted for 51.5%, PC2 was associated with precipitation seasonality (Bio15) and accounted for 23.3%, and PC3 accounted for 13.7% and was less associated with a single dimension. In dataset B, the first three components (PC1, PC2, and PC3) explained 88.6% of the vari-

ance; PC1 was associated with annual precipitation (Bio12) and accounted for 57.7%, PC2 was associated with precipitation seasonality (Bio15) and accounted for 24.8%, and PC3 accounted for 11.5% and was less associated with a single dimension.

Contrasting size of ellipsoid volumes between native and introduced populations were observed in both datasets: native population occupied a large ellipsoid, whereas the introduced Chinese population occupied a relatively small ellipsoid (Figure 2). Nonetheless, the overlaps of climate spaces occupied by native and introduced populations varied between the two datasets: the two ellipsoids were partially overlapped in dataset A, but the Chinese population ellipsoid fell well into that of the native population in dataset B (Figure 2).

Niche conservatism

Climate niche conservative evaluation showed contrasting results based on the two datasets. Non-equivalency niche spaces occupied by native and introduced populations were consistently supported (dataset A: Schoener's $D = 0$, $P < 0.5$; dataset B: Schoener's $D = 0.002$, $P < 0.5$), as actual niche overlaps, were quite different from those of random data (Figure 3), whereas the results of similarity tests varied between the two datasets. In dataset A, the non-equivalency niche results were supported in similarity tests, as actual niche overlap fell far away from random overlaps; however this was not the case for dataset B as actual niche overlap fell inside of random overlaps (Figure 3).

Model performances

Fine-tuned parameters of MaxEnt models identified by ENMeval package were quite different from those default param-

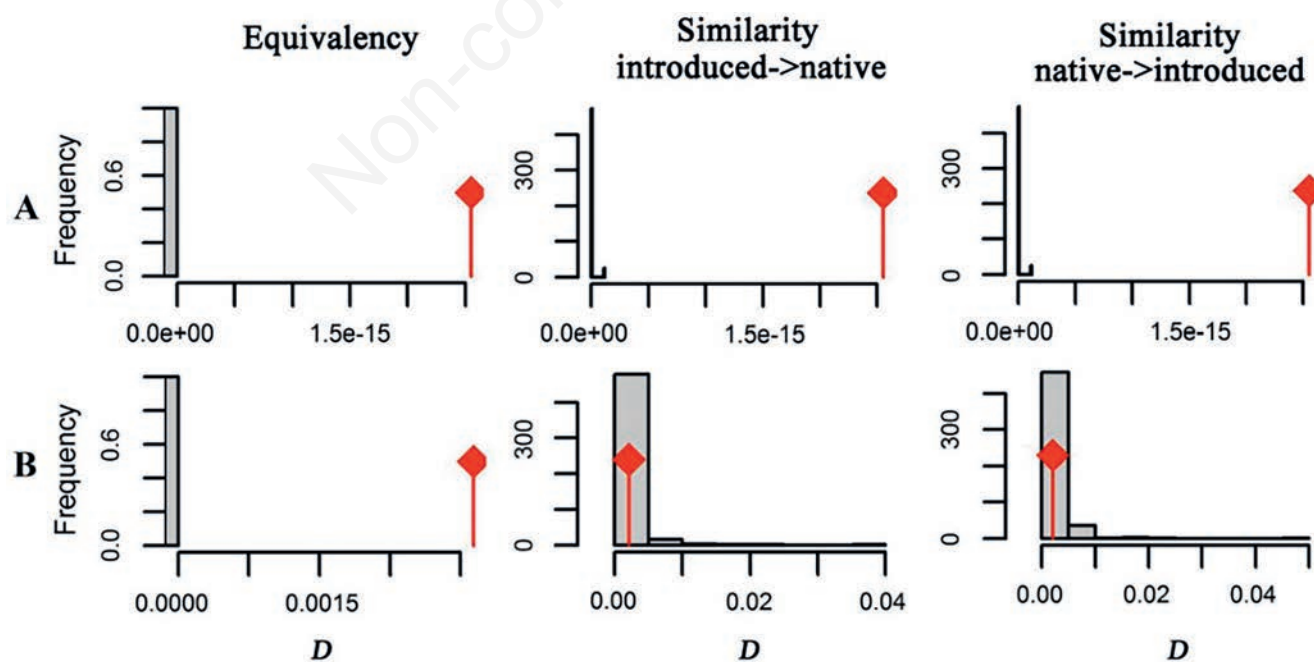


Figure 3. Histograms of niche equivalency and similarity tests between native and introduced ranges based on the two datasets. Red lines with a diamond represent the observed niche overlap, and gray bars represent simulated niche overlaps.

eters. In dataset A, the minimum AICc was attained based on the parameters of RM = 4 and Features = L, Q, H and P. In dataset B, the best parameters of RM = 2 and Features = L, Q, H, and P were attained. All individual and ensemble models performed better than random predictions based on the two datasets in interpolative evaluations (AUC ratios in dataset A: MaxEnt = 1.92, GBM = 1.91, ensemble = 1.94; AUC ratios in dataset B: MaxEnt = 1.92, GBM = 1.92, ensemble = 1.93). Ensemble models generally performed better than those individual models used to generate them in native model evaluations.

When the models were transferred into China, omission errors varied across the spectrum of thresholds (Figure 4). Similar omission errors were attained in MaxEnt models between the two datasets, whereas outputs based on dataset B generally outperformed those based on dataset A in GBM and ensemble models. In GBM outputs, models based on dataset B showed lower omission errors at thresholds of 180–400 than those based on dataset A but not at thresholds less than 180 or larger than 400. In ensemble outputs, models based on dataset B showed lower omission errors at thresholds of 100–600 but not at thresholds of less than 100 or larger than 600.

Model predictions

Projecting native-range ENMs based on the two datasets onto the globe generally involved only minor amounts of strict extrapolation in dataset A, but not dataset B (MOP analysis – Appendix Figure A3). Spatial predictions by our native models showed that the suitable areas are in Central America, Sub-Saharan Africa, and Southeast Asia (Appendix Figure A1). These predictions for *B. straminea* closely matched its present-day distribution, *i.e.* mostly tropical and subtropical areas. Predictions of collective models were generally consistent between the two datasets, but they were more conservative than those based on individual models (Appendix Figure A1).

In China, all models showed a trend of suitability descending from southern coastal areas to the North (Figure 5; Appendix Figure A2). Areas of high suitability consistently supported by present models included coastal areas in southern China, south-western Yunnan and most areas in southern Hainan and Taiwan. The south-eastern areas in Guangdong showed high suitability and were supported by both individual and ensemble models (Figure 5;

Appendix Figure A2). In MaxEnt models, predictions based on dataset B were more liberal than those based on dataset A in Guangdong Province and other areas in southern China (Figure 5; Appendix Figure A2). In GBM and ensemble models, predictions of dataset B were more conservative than those based on dataset A (Figure 5; Appendix Figure A2). Transfers of models between native and coastal areas in southern China generally involved little extrapolation (see MOP results in Appendix Figure A3).

Human risk assessment

The human populations at risk of *S. mansoni* infection were estimated for Hong Kong, Dongguan, Huizhou and Shenzhen based on GBM predictions (Figure 5). Among the four cities, Hong Kong has the largest human population at risk of *S. mansoni* infection, *i.e.* there were about 40,000 humans at risk, whereas in Dongguan, Huizhou, and Shenzhen, there were less than 10,000 at risk in each city (Figure 6).

Discussion

Contrasting volume size, together with the overlaps of climate spaces occupied by native and introduced populations (Figure 2), suggest there are vast areas with suitable climate for *B. straminea* in China compared with those of the native Brazilian population. *B. straminea* is currently restricted to coastal areas in Guangdong Province but might have a large invasion potential in China. As can be seen in Figure 5, many suitable areas were identified in the coastal areas in Fujian, Hainan, Guangxi, Yunnan and Taiwan. High temperature is beneficial to snail spawning and may therefore create more suitable conditions for the reproduction and propagation of *B. straminea* (*e.g.*, Scholte *et al.*, 2012). Nonetheless, future climate warming will have complex effects on schistosomiasis transmission (Stensgaard *et al.*, 2013; Pedersen *et al.*, 2017; Zhu *et al.*, 2017b), and it is conceivable that climate change will affect aquatic environments, and hence, alter the transmission and distribution of *S. mansoni* in this country.

Niche conservatism is much discussed with relevance to the ongoing climate change. For example, two major studies showed opposite results of niche conservatism during terrestrial plant inva-

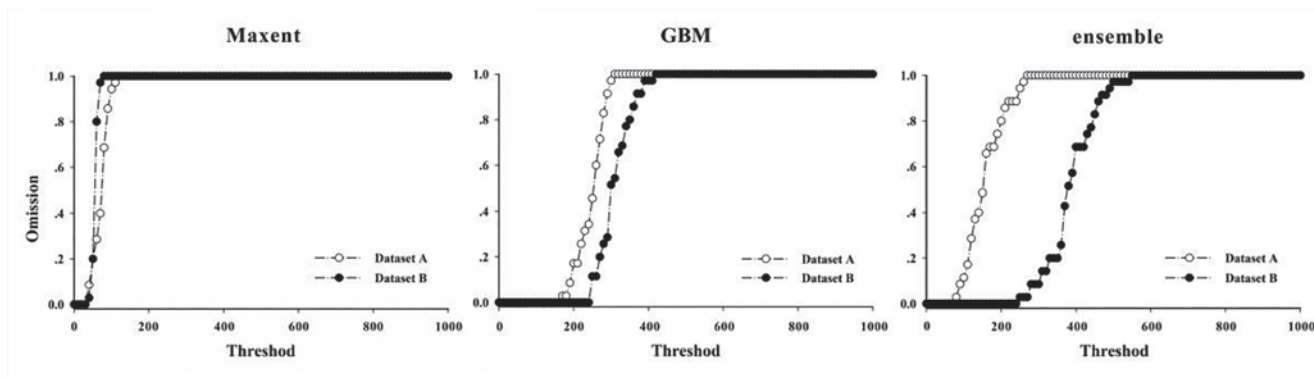


Figure 4. Omission errors of individual and consensus models based on the two datasets in anticipating introduced Chinese points. GBM, generalized boosted models.

sion (Petitpierre *et al.*, 2012; Atwater *et al.*, 2017). In this study, the contradictory results of niche conservatism were observed based on the two datasets, with niche divergence supported in dataset A but not in dataset B. Thus, the environmental variables play an

important role in niche conservatism evaluation (Zhu and Peterson, 2017). Niche conservatism represents the key assumption necessary for ENM application, especially when the models are used in an extrapolative manner (Owens *et al.*, 2013). In this study, niche model predictions based on dataset B might be more reliable for *B. straminea*, showing highly suitable areas along coastal areas in Guangdong, Hainan, Taiwan as well as areas in south-western Yunnan Province (Figure 5).

Assessment of transmission risk and establishment of surveillance–response systems are critical to prevent *B. straminea* expansion. In China, the sampling sites of *B. straminea* were mostly in areas of fishing and farming, such as reservoirs, streams, and rivers (Figure 1). The main route of *B. straminea* expansion is from port city to mainland city (Pan *et al.*, 1983). Among the four cities, many humans in Hong Kong reside within the suitable areas of *B. straminea*, where the highest probability of *S. mansoni* transmission may happen (Figure 4). Our predicted maps identified many suitable areas around its present distribution (Figure 5; Appendix Figure A2), the potential of *B. straminea* to disperse further in China is of great concern. The suitable map for *B. straminea* distribution identified in the present study will have implications in public health strategies, monitoring and guide fieldwork for earlier detection.

Contrary to former predictions, which either were based on introduced populations of a non-equilibrium state and identified suitable areas that clustered around observed points (Habib *et al.*, 2016), or used single model that inherent uncertainty (Yang *et al.*, 2018), our native models identified many suitable areas along southern coastal China and were consistent supported by multiple model approaches (Figure 5; Appendix Figure A2). These coastal cities are key areas of labour export, bearing high population mobility propagating pressure (Chen and Jiang, 2008), they deserve high attention regarding *S. mansoni* transmission or epidemics may happen, considering the synergistic effect of high climate suitability and propagation pressure (Simberloff, 2009).

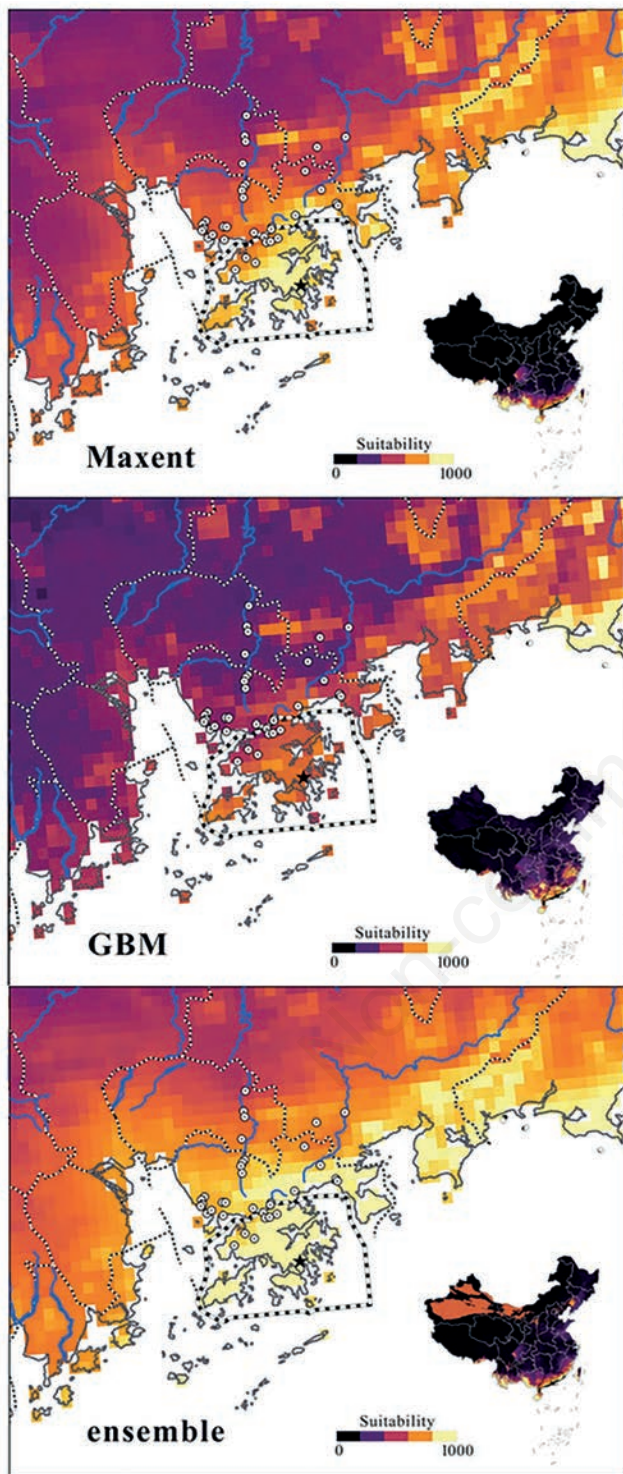


Figure 5. Potential distributions of *Biomphalaria straminea* in southern China. Native model transfers in China were based on three approaches (Maxent, generalized boosted model – GBM – and ensemble) using dataset B.

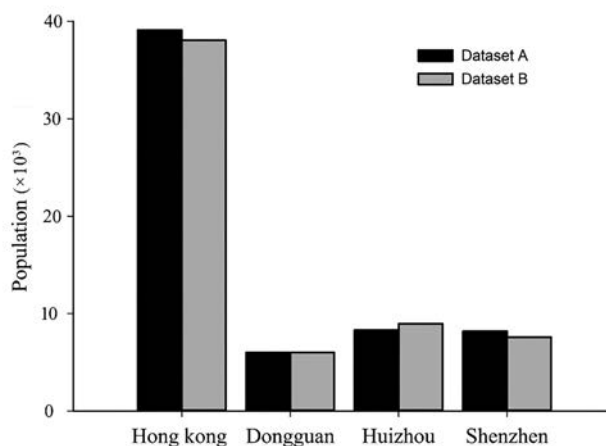


Figure 6. Human populations at risk of infection in four cities estimated by generalized boosted model.

Conclusions

In this paper, we mapped the transmission potential of *S. mansoni* by predicting ecological dimensions and potential distributions of *B. straminea* using state-of-the-art ecological niche model approaches. Much suitable spaces were found to be unfilled in China, and might be available to *B. straminea*. Attention should be paid to *S. mansoni* epidemic may happen in coastal areas in Guangdong, Hainan, Taiwan, and areas in south-western Yunnan Provinces, considering high pressure of propagation, while future climate change may create even better conditions. Our results call for rigorous monitoring and surveillance in these identified areas in China.

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