

## Prediction of the Breeding and Wintering Ranges of *Pomacea canaliculata* in China Using Ensemble Models

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**ABSTRACT.** *Pomacea canaliculata* is a pest species of freshwater neotropical gastropod that has colonized the coastal regions of southern China since the 1980s and has expanded its range into temperate regions of the Yangtze River Basin. The breeding and overwintering populations of *P. canaliculata* have increased during its gradual northward expansion over the past 40 years. There is a high likelihood that *P. canaliculata* can overwinter in areas conducive to breeding due to the impacts of a changing climate. Yet, the potential future changes in the range of *P. canaliculata* and associated climatic determinants remain unclear. This study examined the relationship between the limits of geographic distribution and key climate variables determining suitability for *P. canaliculata* breeding and wintering periods using the ensemble species distribution models from the R package BIOMOD2. Future climate suitability and changes were assessed under two representative concentration pathways (RCP 4.5 and RCP 8.5). The predictions indicated that *P. canaliculata* is most sensitive to monthly minimum temperature and that this species will extend its breeding range towards northern latitudes and will establish increased wintering locations in China. The predictions for both breeding and overwintering populations suggest a northward shift in the most suitable habitat, a reduction of highly suitable areas in the south, and an increase in suitable areas along the center and east of the Yangtze River Basin extending further northwards. Within the context of an overall expansion in *P. canaliculata* and climate warming, there should be a focus on the center of the Yangtze River Basin in which this species can overwinter for breeding only. Early monitoring and proactive measures to effectively prevent further spread of this species should be prioritized in this region characterized by abundant rice cultivation and fish breeding.

**Keywords:** *Pomacea canaliculata*, distribution, breeding, overwintering, climate

### 1. Introduction

Climate is among the most dominant factors affecting the physiology, distribution, and phenology of many species (Zhao et al., 2020; Jaskuła et al., 2021). Changes in climate can lead to shifts in climatic limits constraining the range of invasive species (Kriticos et al., 2006). Therefore, a changing climate may facilitate the survival and spread of invasive species. Increasing evidence indicates that climate change may alter the ranges, establishment opportunities, and consequent impacts of invasive species, with regional changes in precipitation and temperature being particularly potent drivers (Beaury et al., 2020; Shabani et al., 2020; Bell et al., 2021). Aquatic invasive organisms are likely vulnerable to climate change (i.e., global warming) since changes in temperature directly affect their physiology and behavior (Rahel, 2002), which can possibly lead to shifts in their geo-

graphical ranges (Kernan, 2015). Therefore, studies of aquatic invasive species can facilitate the development of models predicting their current and future geographic ranges, which can guide possible control measures.

Species distribution models (SDMs) are flexible tools which can be used to access the potential spread of invasive aquatic species under current and future climates. This method generally uses species occurrences in conjunction with a set of environmental variables to develop a correlative model of the environmental conditions meeting the ecological requirements of a species (Thuiller et al., 2021). Of the varieties of SDMs developed, an ensemble-modelling approach implemented in BIOMOD2 has been successfully used for forecasting species distributions (Gillard et al., 2020; Jourdan et al., 2021; Robinson et al., 2021). The BIOMOD2 ensemble SDMs can incorporate species presence-absence data, allow multiple models to be run on the same training and testing datasets, and provide robust species occurrence-environment relationships (Hao et al., 2019; Wen et al., 2022). BIOMOD2 is more powerful than single SDMs because it can minimize potential errors originating from predictions of individual models (Brown and Yoder, 2015) and can reduce the multiple sources of uncertainty associated with different projec-

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tions according to the SDM algorithms, global circulation models (GCMs), and CO<sub>2</sub> emission scenarios, as well as uncertainty due to a lack of ecological knowledge and imperfect data (Wenger et al., 2013; Koo et al., 2017).

*Pomacea canaliculata* (Lamarck, 1822) is a freshwater snail indigenous to the lower Del Plata Basin in South America and has been widely introduced into North America, Europe, east and southeast Asia, and the Pacific Islands after around 1980 (Hayes et al., 2008; EFSA, 2013). This species is characterized by a wide host range and voracious appetite (Lach et al., 2000), large fecundity (Naylor, 1996), and high adaptability to various harsh environmental conditions (Oya, 1987; Halwart, 1994). *Pomacea canaliculata* has spread throughout tropical and subtropical regions in which it has adapted to and colonized a range of agricultural and wetland habitats. *Pomacea canaliculata* was first introduced from Taiwan to Zhongshan city, Guangdong Province, mainland China, in 1981 for aquaculture. Since then, there have been multiple introductions of *Pomacea canaliculata*, which has allowed it to establish natural populations in habitats in 17 southern provinces with a broad range of climate conditions (Yang et al., 2013). *Pomacea canaliculata* has recently spread to latitudes as far north as 30° N and up to 1,960 m above sea level in Yunnan Province, southwest China, as well as in south China, primarily Sanya City, with a latitudinal range of 18°9' N to 18°37' N (Lv et al., 2009). Previous studies have shown that this pest species has spread from the hotter coastal areas in the south to more temperate areas in the Yangtze River Basin (Yang et al., 2018). There is also evidence suggesting that *Pomacea canaliculata* is tolerant of cold winter conditions and that this species has developed a range of physiological and behavioral strategies that promote overwinter survival and establishment in temperate China (Yusa et al., 2006; Matsukura et al., 2009; Bae and Park, 2015). For example, Ji et al. (2020) found that this species can survive the winter cold by finding refuge in overwintering sites in this region that provide a buffer to environmental conditions (Ji et al., 2020). The impacts of climate warming are likely to allow *Pomacea canaliculata* to overwinter in areas allowing breeding only. Advanced knowledge of the locations in which *Pomacea canaliculata* can survive and establish after the winter months can greatly assist in the development and establishment of appropriate strategies to prevent the possible emergence of populations during the spring. Although various modeling approaches (e.g., SDMs) have been developed in recent years for predicting the habitat ranges of species, relatively few have been employed to predict the distribution of *Pomacea canaliculata* (Wang et al., 2018; Zhou, 2019). Among studies that have used SDMs to determine habitat suitability for *Pomacea canaliculata*, many have made sub-optimal use of model data (e.g., occurrence records, climatic predictor variables, and modeling algorithms). Therefore, there remains a great need to improve the data foundation for the application of SDMs to *Pomacea canaliculata*.

*Pomacea canaliculata* breeds only during the summer in its native habitat in Argentina (Scott, 1957), whereas invasive populations in China have adapted to breed in various habitats and can produce up to three generations in a single breeding season in tropical areas. *P. canaliculata* typically generates one generation per breeding season in the Yangtze River Basin

(Zhou et al., 2003). The successful establishment of *P. canaliculata* across large spatial scales in China provides an ideal opportunity to explore whether *P. canaliculata* is responding to global warming by shifting its distribution northward, particularly during winter. Although there have been multiple studies on how climatic tolerances or requirements limit the distribution of *P. canaliculata* (Park et al., 2012; Seuffert and Martín, 2017), few of these studies focused on distributions during certain biological stages (i.e., breeding and over-wintering).

The present study aimed to identify potential changes to the distribution of *P. canaliculata* in China. A sequential procedure was developed, incorporating the collection of occurrence data, selection of critical environmental variables, and the generation of ensemble SDMs. Key climate variables determining climate suitability in both breeding and wintering periods were identified, and the potential changes to the range of *P. canaliculata* breeding and overwintering populations as responses to future climate change were investigated. The exploration of the potential future changes to the spatial ranges of *P. canaliculata* breeding and overwintering populations can allow an improved understanding of risks of invasion of this species of new ecosystems and agricultural areas. The results of the present study can also act as a reference for the design of early monitoring activities and efficient methods to prevent further spread of *P. canaliculata*, given its frequent introductions into the country.

## 2. Material and Methods

### 2.1. Species Data

A breeding colony was defined in the present study as any site (under a natural environment) in which egg clutches of *P. canaliculata* were observed during the breeding season over at least two years. Data on known locations of *P. canaliculata* breeding populations in mainland China were sourced from two primary sources: (1) the National Natural Science Joint Funding Project (NSFC) and; (2) the Alien Invasive *Pomacea canaliculata* Survey Database (created by a workgroup of the Institute of Tropical and Subtropical Ecology, South China Agricultural University). Agricultural and wetland sites covering 15 provinces in the co-terminous southern China were sampled during the survey by NSFC participants and staff scientists during the spring months of 2007 to 2021 using identical methods, with most sampling occurring in 2012 and 2015. Breeding records for Hongkong and Taiwan were retrieved from published literature (Ip and Qiu, 2017) and the Taiwan Invasive Species Database. Overwintering records were restricted to observations from early December to later February of the following year. Part of the records were compiled from observation data collected using field-based methods, such as assessing snail presence in humid environments associated with canals and river margins or beneath aquatic plants by consulting with local technicians and farmers. These records originated from seven provinces (Hunan, Anhui, Jiangsu, Hubei, Jiangxi, Zhejiang, and Shanghai) in the Yangtze River Basin and were obtained during 2014 to 2019. In addition, recent observations with complete and precise locations retrieved from reports or publications were added to the *P. canaliculata* dataset (Ji et al., 2020; Liu et al., 2020a, b).

All collected records were assessed for obvious errors re-

**Table 1.** The Two Sets of Climatic Predictors Used to Develop Models and Their Importance for Each Modeling Algorithm

Biological Stages	Label	Variable	VIFs of the Remained Variable	Mean Variable Importance	CTA	RF	GBM
Breeding	bio14	Precipitation of driest month (mm)	3.275	0.032	0.043	0.059	0.026
	prec45	Cumulative precipitation in April and May (mm)	2.477	0.022	0.029	0.097	0.017
	tmin4	Average minimum temperature in April (°C)	1.586	0.789	0.947	0.579	0.841
Overwintering	alt	Elevation (m)	1.551	0.019	0.026	0.039	0.018
	bio14	Precipitation of driest month (mm)	1.807	0.005	0.000	0.031	0.002
	prec10	Precipitation in October (mm)	1.506	0.004	0.010	0.014	0.003
	tmin10	Average minimum temperature in October (°C)	9.051	0.772	0.928	0.563	0.773
	bio4	Temperature seasonality (standard deviation × 100)	9.427	0.019	0.012	0.065	0.025
	alt	Elevation (m)	7.797	0.030	0.047	0.055	0.037

Note: (1) The two sets of selected climatic predictors with the lowest correlation were identified [values of variance inflation factor (VIF) < 10] and used to construct prediction models for *Pomacea canaliculata* breeding and overwintering populations, respectively; (2) The three modeling algorithms used were: (a) CTA, classification tree analysis; (b) RF, random forests; (3) GBM, generalized boosted regression model.

**Table 2.** Evaluation Statistics (Means ± SE, N = 10) for Each Modeling Algorithm and the Ensemble Model. KAPPA: Cohen's Kappa; TSS: True Kill Statistic; ROC: Relative Operating Characteristic

Biological Stages	Model	KAPPA	TSS	ROC
Breeding	Classification Tree Analysis (CTA)	0.857 ± 0.0114	0.864 ± 0.0124	0.943 ± 0.0060
	Random Forests (RF)	0.863 ± 0.0126	0.858 ± 0.0111	0.973 ± 0.0035
	Generalized Boosting Models (GBM)	0.870 ± 0.0117	0.872 ± 0.0117	0.975 ± 0.0034
	Ensemble Model	0.897	0.896	0.994
Overwintering	Classification Tree Analysis (CTA)	0.951 ± 0.0112	0.965 ± 0.0071	0.979 ± 0.0044
	Random Forests (RF)	0.964 ± 0.0076	0.952 ± 0.0110	0.994 ± 0.0027
	Generalized Boosting Models (GBM)	0.963 ± 0.0067	0.963 ± 0.0064	0.993 ± 0.0022
	Ensemble Model	0.977	0.975	0.998

Note: KAPPA: Cohen's Kappa; TSS: true kill statistic; ROC: relative operating characteristic.

sulting from inaccurate geo-referencing in ArcGIS 10.3 (ESRI; Redlands, CA, USA). The process of assessing the occurrence of *P. canaliculata* excluded records for niche areas in which taxonomic identification of *Pomacea maculata* has been confirmed. *P. maculata* is another invasive species in China of the genus *Pomacea* which exhibits a high morphological similarity to *P. canaliculata* (Yang et al., 2018). Researchers have only substantially genetically differentiated the two species since 2010.

One record was randomly selected within each grid cell (c. 0.93 km × 0.93 km) to reduce the spatial bias of occurrence data and improve the reliability of predictions. After removing duplicates, the resulting unique 995 and 635 records of presence of the breeding and overwintering populations of *P. canaliculata*, respectively were used to develop potential distribution maps. Consequently, the modeled distribution of *P. canaliculata* was delimited by a 120-km buffering zone surrounding all records available.

## 2.2. Climatic Predictors

Distribution modelling was performed by retrieving core

sets of bioclimatic and monthly variables from the WorldClim 2.1 database (1950 ~ 2000) (Fick and Hijmans, 2017) at a resolution of 30 arc seconds (c. 0.93 km × 0.93 km) for the extent of China considered in the present study. These variables were considered as current bioclimatic variables. The same sets of bioclimatic and monthly variables as well as altitude data for the year 2050 (average for 2041 ~ 2060) with a spatial resolution of 30 seconds were also obtained. These data represent the climate projections of the Intergovernmental Panel on Climate Change (IPCC) 5<sup>th</sup> assessment report derived from Global Circulation Models (GCMs) for specific Representative Concentration Pathways (RCPs).

Two initial sets of climatic variables consisting of six and eight predictors were used to develop models for *P. canaliculata* breeding and overwintering populations, respectively (Table S1). These variables were selected based on knowledge of specialists, including ecologists, biologists, or agricultural technicians from different parts of China. Variables known beforehand to be important for the ecology and physiology of *P. canaliculata* were also incorporated. Temperature can affect a variety of physiological processes of *P. canaliculata*, including survival, growth,

and reproduction (Seuffert and Martín, 2017). The present study selected the minimum temperature of April (tmin4) among the temperature related variables since this temperature has a critical effect on the hatching rates of *P. canaliculata* after winter. This hatching rate in turn affects the capacity of individuals to build up a population during the next breeding season (Liu et al., 2011). Rainfall influences the formation and expansion of snail breeding sites (Barbosa and Barbosa, 1994). *P. canaliculata* generally begins breeding between late February and early March in the southernmost regions of its habitat, whereas egg-laying starts in mid-April or until May in middle-latitude subtropical regions (e.g., the Yangtze River Basin). Therefore, the present study summed precipitation for April and May as a variable representing cumulated precipitation during breeding.

Wintering *P. canaliculata* populations in China have been concentrated in coastal zones with mild temperatures (Zhang and Fan, 2008). Minimum winter temperatures often act as bottlenecks for overwinter survival of *P. canaliculata* and are thought to constrain its expansion in range. Therefore, the minimum temperature of the coldest month (bio6) was initially included in the set of considered predictors. The minimum temperature in October and November together with corresponding monthly precipitation may contribute to the survival of this species over the winter cold period because these variables are associated with food availability. The availability of food sources is crucial for *P. canaliculata* to meet its physiological requirements for overwintering. Temperature seasonality (bio4) and precipitation of the driest month (bio14) are also predictors and were included because they may reflect thermal or water tolerances of *P. canaliculata*.

The two sets of raw environmental variables were assessed based on Spearman correlations for continuous variables (rcorr in R package “Hmisc”; Harrell and Dupont, 2018) and variance inflation factor statistics (VIF; vif in R package “usdm”; Naimi, 2015). A VIF for a single explanatory variable was obtained using the *R*-squared value of the regression of that variable against all other explanatory variables (Lin et al., 2011). VIF > 10 is generally considered as a sign of strong multi-collinearity (Hocking, 2013). Therefore, variables not highly correlated (Spearman rank correlation  $|r| < 0.7$  and VIF < 10 (Yang and Matthews, 2012; Dormann et al., 2013)) within each environmental dataset were selected. The resulting subset of predictors for developing the snail-breeding model included the cumulative quantity of precipitation during incubation (prec45) and the minimum temperature of April (tmin4), whereas predictors for the snail-wintering model included the minimum temperature of October (tmin10), average precipitation in October (prec10), and temperature seasonality (bio4). Two additional predictors, precipitation of driest month (bio14) and elevation were considered in both sets of predictors used in the final models (Table 1). Variable importance was determined by calculating the correlation between model predictions, including all remaining variables (a “full model”) and predictions excluding the tested variable (a “reduced model”). The return score was the result of the subtraction between the calculated correlation values and 1 (Duque-Lazo et al., 2016). The variable importance scores were averaged

across all pseudo-absence sets, train rounds, and algorithms. The score was proportional to the influence of a variable in model predictions (Thuiller et al., 2009).

### 2.3. Future Climate Projections

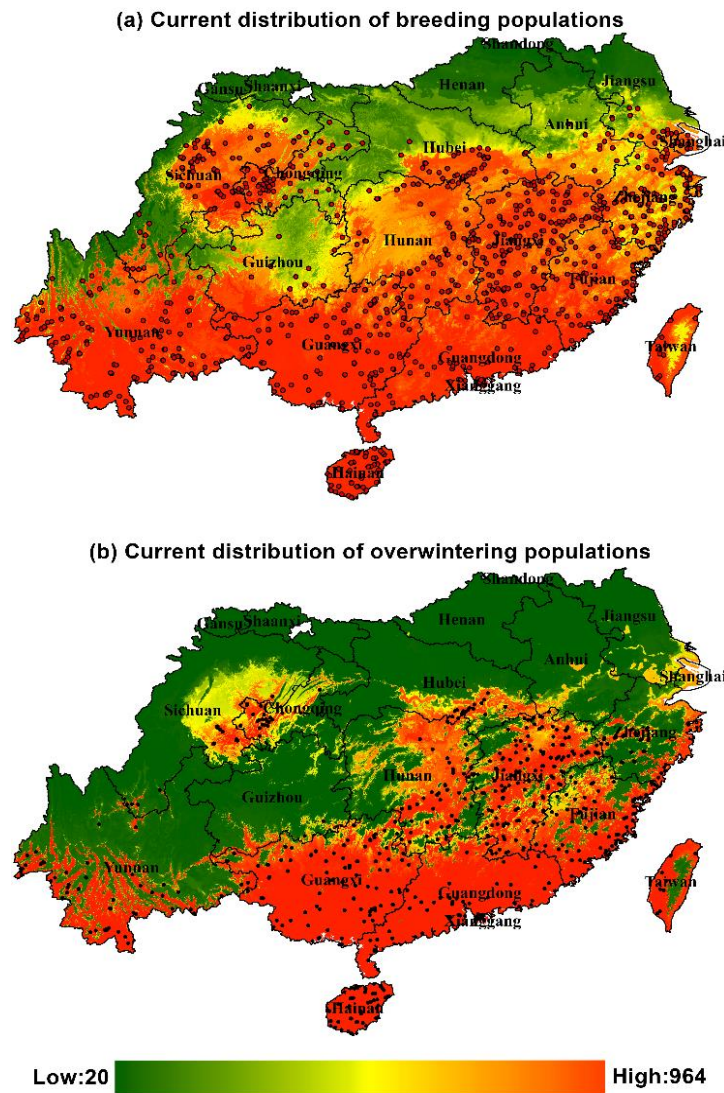
Future climate projections for *P. canaliculata* breeding and overwintering populations were explored respectively. Four Global Circulation Models (GCMs) taken from the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP) were employed as an ensemble approach: (1) BCC\_CSM1.1; (2) CNRM-CM5; (3) HadGEMs-ES and; (4) MIROC5. These models cover a range of climate sensitivity and are among the optimal models for global or regional monsoon assessment (Xin et al., 2013; Lee et al., 2014). Notably, the four GCMs have been successfully used to predict the potential geographic distributions of invasive weeds and to generate projections of future changes (Qin et al., 2016, 2022). Projections of climate parameters derived from two representative CO<sub>2</sub> emissions scenarios (RCP 4.5 and RCP 8.5) were used for each GCM, in which RCP 4.5 corresponds to a midrange (+ 1.1 ~ 2.6 °C by year 2100), whereas RCP 8.5 corresponds to a more pessimistic scenario (+ 2.6 ~ 4.8 °C by 2100) (Buczowski and Bertelsmeier, 2017). Therefore, the resulting future predictions from the four models were averaged for each RCP scenario to produce a *P. canaliculata* probability distribution map. Future and current SDMs were subtracted as a measure of the predicted changes in distribution for *P. canaliculata*, and areas of contraction, expansion, and stability were calculated.

### 2.4. Model Algorithms and Evaluation

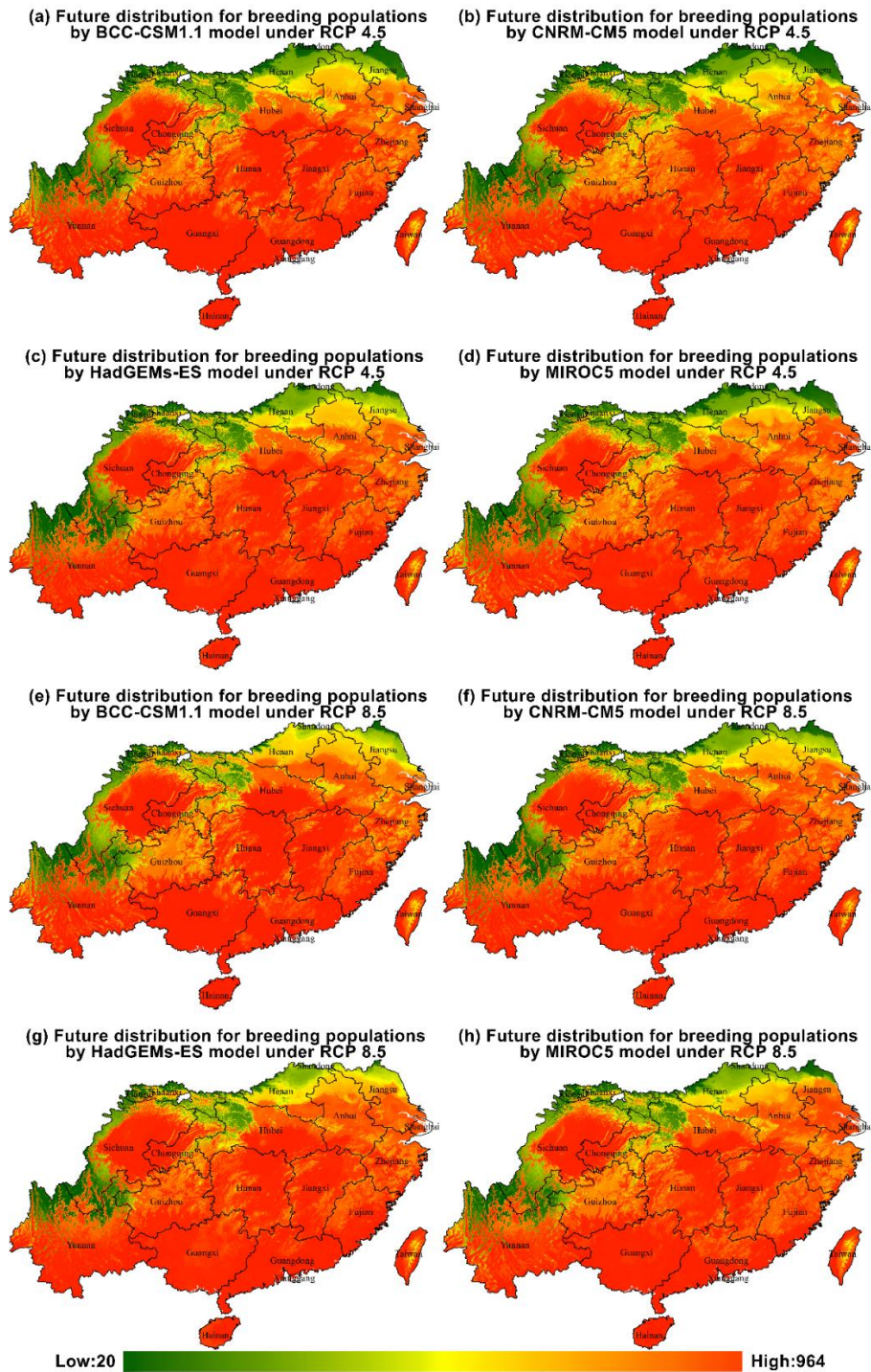
The present study conducted SDM analysis for *P. canaliculata* breeding and overwintering populations, respectively, using the BIOMOD2 modelling framework implemented in R 4.0 (R Development Core Team 2012). For each analysis, each of the three algorithms used required the same number of pseudo-absences: (1) generalized boosting models (GBM; also referred to as boosted regression trees); (2) random forests (RF), and; (3) classification tree analysis (CTA). The mean of probabilities of the three selected algorithms has been proved to supply more robust predictions compared with other ensemble building techniques (Marmion et al., 2009). The present study generated a random absence dataset with climatic and spatial constraints using ArcGIS to meet the requirement for the input of pseudo-absences. Here, random pseudo-absences were generated in locations suitable for the survival of *P. canaliculata*. In contrast, true absences were randomly sampled outside the restriction zone, defined as invulnerable to *P. canaliculata* in the previous step, and outside of high northern latitudes (> 32° N) with climate conditions not suitable for the survival and establishment of *P. canaliculata*. The absence dataset was randomly selected outside a rectilinear surface envelope generated from the presence locations to reduce the effect of sampling bias. This approach has been demonstrated to be suitable for SDMs, including CTA and RF (Barbet-Massin et al., 2012). The present study employed the equal number of pseudo-absences represented by the presences of *P. canaliculata* since this approach has been shown to be optimal when using classification and machine-learning techniques (Barbet-Massin et al., 2012).

Apart from using 3,000 and 500 trees as the bases for fitting GBMs and RF, respectively, as recommended by Reiss et al. (2011), the present study applied default settings within the application of the three modeling techniques. Ten replicate runs were performed for each modeling technique to account for model variability (Teixeira et al., 2016). A randomly sub-sampled 70% subset of the presences records was used for model calibration (i.e., training data), with the remainder used to evaluate the models (i.e., test data) (Guisan and Zimmermann, 2000). Consensus prediction models were obtained to constrain model uncertainty using a TSS weighted average method to account for the predictive power of each algorithm. After fitting, the models were evaluated based on the Kappa, True Skill Statistic (TSS), and Area Under (the receiver operating characteristic) Curve (AUC) metrics. These three measures attribute different

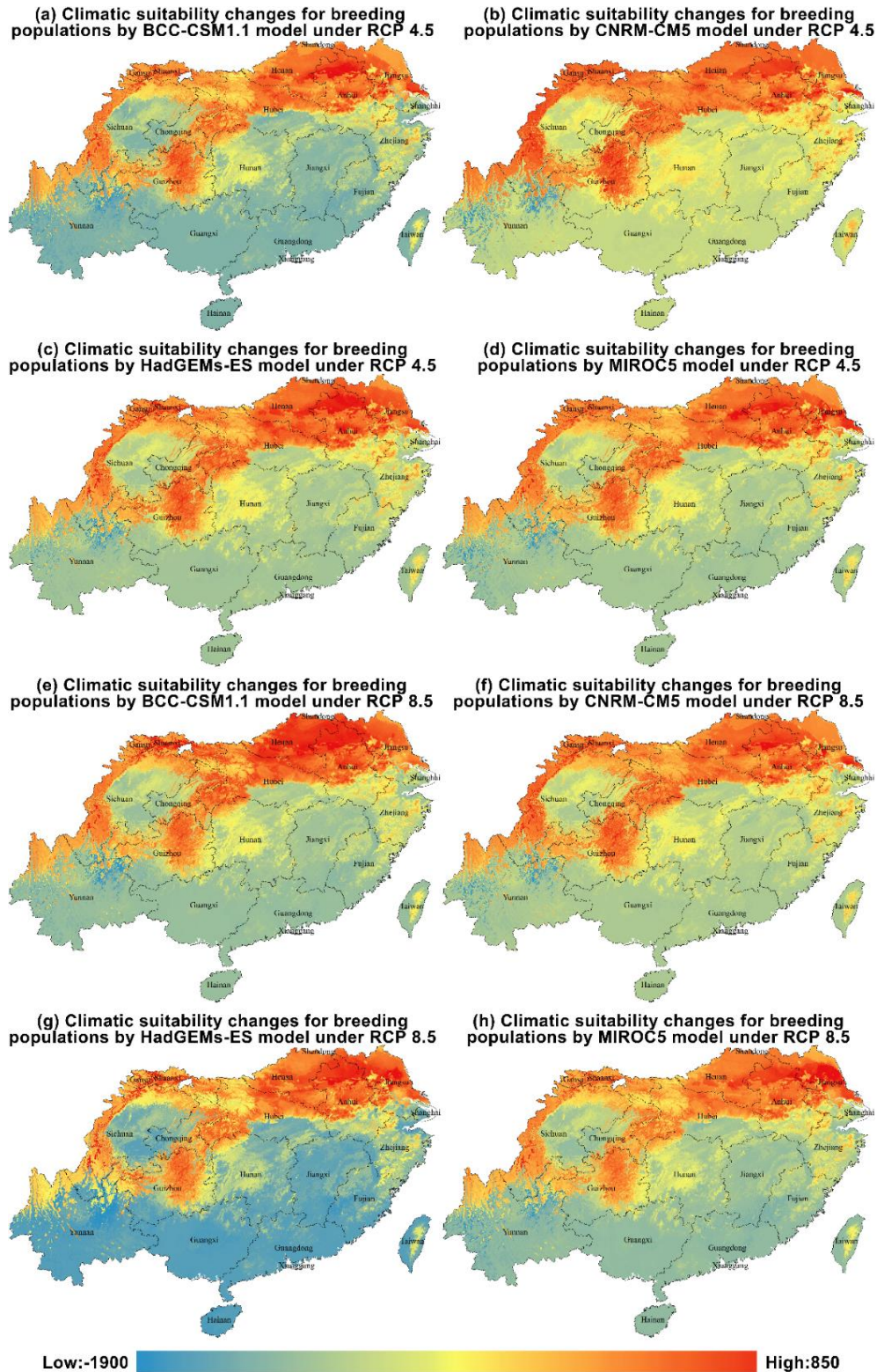
weights to the various types of prediction errors (e.g., omission, commission, or confusion). TSS, which considers omission and commission errors and ranges from -1 to 1, has the additional advantage of full independence from species prevalence and the size of the validation dataset (Allouche et al., 2006). The AUC is an effective, threshold-independent model evaluation indicator and is also independent of prevalence (i.e., frequency of occurrence) of target species (Fielding and Bell, 1997). Because AUC for models was never below the acceptable threshold (0.7) (Hosmer Jr et al., 2013) and TSS values were above the minimum threshold of 0.4 generally (Jarnevich et al., 2018), only the best fitted model runs above critical TSS values (> 0.4) and AUC (> 0.7) was implemented in the final ensemble model run to create the most accurate model predictions (Kärcher et al., 2019).



**Figure 1.** Model simulated current distribution of *Pomacea canaliculata* (a) breeding and (b) overwintering populations, with known records shown as dark filled circles. Higher values in the two small maps suggest a higher climatic suitability for *P. canaliculata* populations.



**Figure 2.** Projected future distributions of *Pomacea canaliculata* breeding populations under the two representative concentration pathways, RCP 4.5 and RCP 8.5 [corresponding to a–d and to e–h, respectively]. Under the two RCP scenarios, the maps show the projected spatial distributions of *P. canaliculata* breeding populations in 2050 as predicted by four global circulation models (BCC-CSM1.1, CNRM-CM5, HadGEMs-ES, and MIROC5). The values shown in the maps indicate suitability of climate for *P. canaliculata* breeding populations.



**Figure 3.** Changes in suitable climate for *Pomacea canaliculata* breeding populations under two representative concentration pathways, RCP 4.5 and RCP 8.5 [corresponding to a–d and to e–h, respectively]. Under the two RCP scenarios, the maps show the changes in climate suitability for *P. canaliculata* breeding populations in 2050 as predicted by four global circulation models (BCC-CSM1.1, CNRM-CM5, HadGEMs-ES, and MIROC5). The values shown in the maps indicate changes in climate suitability for *P. canaliculata* breeding populations.

**Table 3.** Changes in Climatic Suitability for *Pomacea canaliculata* Breeding (a) and Overwintering (b) Populations by 2050 Based on Ensemble Models under the Two Representative Emissions Scenarios (RCP 4.5 And RCP 8.5)

Representative CO <sub>2</sub> Emissions Scenarios	Range Change	GCMs Used				Scenario Average
		BCC_CSM1.1	CNRM-CM5	HadGEMs-ES	MIROC5	
<sup>a</sup> RCP 4.5	CurrentRangeSize	28585	19830	28124	26892	9.07%
	PercLoss (%)	49.75	52.82	55.15	51.53	
	PercGain (%)	64.40	52.54	52.56	65.91	
	SpeciesRangeChange (%)	14.66	-0.28	-2.59	14.38	
<sup>a</sup> RCP 8.5	FutureRangeSize.FullDisp	32775	19774	27397	30760	15.38%
	CurrentRangeSize	26203	19381	29306	24675	
	PercLoss (%)	46.97	51.83	59.87	48.42	
	PercGain (%)	71.12	66.51	40.06	90.62	
<sup>b</sup> RCP 4.5	SpeciesRangeChange (%)	24.15	14.67	-19.81	42.20	36.71%
	FutureRangeSize.FullDisp	32532	22225	23500	35088	
	CurrentRangeSize	26095	67988	38155	65237	
	PercLoss (%)	46.26	38.01	50.46	42.18	
<sup>b</sup> RCP 8.5	PercGain (%)	46.40	28.16	41.33	28.13	36.55%
	SpeciesRangeChange (%)	0.14	-9.85	-9.12	-14.04	
	FutureRangeSize.FullDisp	26132	61289	34674	56075	
	CurrentRangeSize	27993	35794	39514	33393	
	PercLoss (%)	47.79	43.91	51.36	51.45	
	PercGain (%)	59.10	58.12	63.42	76.36	
	SpeciesRangeChange (%)	11.31	14.22	12.06	24.92	
	FutureRangeSize.FullDisp	31159	40882	44279	41713	

Notes: (1) Lowercase “a” and “b” represent results for *P. canaliculata* breeding and overwintering populations, respectively. (2) Range changes in suitability were calculated by the “BIOMOD\_RangeSize” function of BIOMOD2 framework (Thuiller et al., 2009). CurrentRangeSize: represents the modelled current range size (number of pixels occupied) of the given species. PercLoss: corresponds to the percentage of currently occupied sites to be lost. PercGain: corresponds to the percentage of new sites considering the species' current distribution size. SpeciesRangeChange: represents the overall projection outcome, which strictly compares the range sizes between current and future states.

### 3. Results

#### 3.1. Variable Contributions and Model Performance

Both the ensemble model and all three individual models yielded satisfactory predictions of breeding and overwintering distributions according to the threshold dependent (Kappa, TSS) and independent (AUC) evaluation metrics (Table 2). However, the ensemble model provided more robust predictions compared with those of each individual model, with maximum TSS values of 0.896 and 0.975 for the breeding and overwintering distributions, respectively. All three algorithms of the overwintering model had TSS values exceeding 0.95, indicating a higher performance compared with the breeding model (Table 2). The performances of all models representing both breeding and overwintering distributions suggested good model predictions and that they can be used for estimation of future distributions in China.

The best predictors of current distributions of the breeding and overwintering populations of *P. canaliculata* showed considerable variability. Models of the breeding distribution of *P. canaliculata* under current climatic conditions showed that the minimum temperature of April (tmin4) contributed most to occurrence of the snail (average contribution of 78.9%), followed by precipitation of the driest month (bio14) (Table 2). Like-

wise, models of the current overwintering distribution determined the minimum temperature of October (tmin10) to be the most influential factor for predicting the wintering presence of the snail (average contribution of 77.2%). Elevation showed only a minor influence on breeding and overwintering of the snail, with a mean contribution of  $\leq 5\%$ .

#### 3.2. Current and Future Distributions

The model simulations of current snail breeding and overwintering distributions were highly consistent with recorded occurrences for the main regions identified as suitable. The most favorable climatic conditions for both breeding and overwintering populations were identified in large parts of Taiwan, locations scattered from the east coast to central mainland, coastal areas of South China, and southern Yuannan. The lowlands of Sichuan Basin were also identified as suitable for breeding and overwintering (Figure 1). Although the results showed that *P. canaliculata* could overwinter in many favorable environments for breeding, their overwintering ranges contracted greatly in comparison to those for breeding, with northward suitable habitats restricted in the subtropical zone in which winter temperatures remained above temperatures required to lead to inactivity of the snails.

Future model projections indicated possible changes in ar-

areas of suitability for snail breeding and overwintering, with substantial variations between predictions of areas gained and lost. The ensemble model detected an overall expansion of suitable habitats for both breeding (Figure 2) and overwintering (Figure S1) populations under intermediate and intense climate change scenarios. The four GCMs projected a net increase in range (i.e., SpeciesRangeChange calculated as  $[\text{PercGain} - \text{PercLoss}]$ , shown in Table 3) of between 11.31 ~ 24.92% for overwintering populations under RCP 8.5. Future range sizes were predicted to decline by 9.85 ~ 14.04% under RCP 4.5, except one GCM (BCC\_CSM1.1 model) under which there was projected net expansion in its range of 0.14%. Areas with climate suitable for breeding increased by ~ 14% according to two GCMs (BCC\_CSM1.1 and MIROC5 models) under the RCP 4.5 scenario, although minor decreases in breeding area (less than 3.0%) were predicted by another two GCMs. Model simulations showed a large increase in area suitable for breeding populations (14.67 ~ 42.20%) for all GCMs under RCP 8.5, except for the HadGEMs-ES model which projected a decline in suitable area of 19.81% (Table 3). The overlapping areas of GCM predictions indicated agreement between the models. Based on this overlap, the range of the breeding population was projected to increase in 2050 by 9.07% and 15.38% under RCP 4.5 and RCP 8.5, respectively (Figure S2). The range of over-wintering distributions was projected to expand by about 36% under both RCPs (Figure S3).

### 3.3. Range Changes and Related Predictors

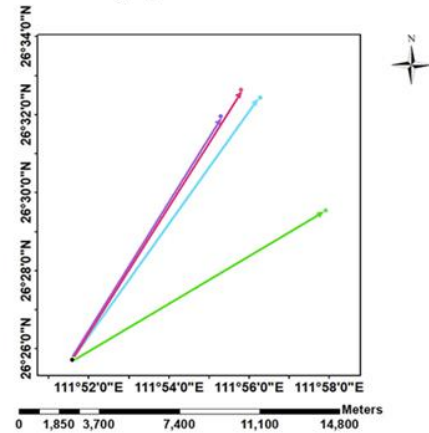
In addition to overall expansive distribution probabilities for both breeding (Figure 3) and overwintering (Figure S4) populations, future model projections showed a northward shift in the most suitable habitats, a reduction in highly suitable areas in the south, and an increase in highly suitable areas along the center and east of the Yangtze River Basin. In comparison to future areas suitable for overwintering, those suitable for breeding were shown to extend further northwards, reaching the marginal western Sichuan Basin and parts of Henan (Figure 3). The predicted areas of suitable habitat under all future scenarios encompassed currently known breeding and overwintering sites, despite the shifts and changes in distribution probabilities.

The projections showed a northward shift in the centroid of snail breeding range by 2050 (Figure 4). In comparison with the results of the model based on current datasets, the latitudes of the centroids of the breeding ranges under the RCP 4.5 and RCP 8.5 scenarios were predicted to move northward by between 12.7 ~ 14.7 km and 8.9 ~ 15.6 km respectively. The shift in direction (with north representing 0°) was between 27.9° ~ 55.8° and 15.4° ~ 25.0° under RCP 4.5 and RCP 8.5, respectively. The centroids of the overwintering ranges were predicted to move northward by between 0.74 ~ 4.75 km (shift direction: 11.1° ~ 223.4°) and 1.04 ~ 4.83 km (shift direction: 15.9° ~ 315.2°) under RCP 4.5 and RCP 8.5, respectively (Figure S5).

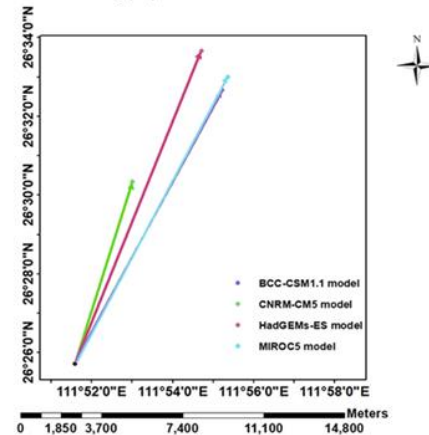
Changes in critical climatic predictors between current conditions and future scenarios were the drivers of shifts in suitable snail habitats. The results indicated future northward shifts in breeding populations in the form of patches. Patches of breeding populations at lower altitudes are expected to experience

wetter winters characterized by increased precipitation of the driest month (bio14) and a warming April (Figure S6 ~ S7). The overwintering populations were projected to shift toward habitats with milder winters, characterized by a higher average minimum temperature in October (tmin10) and lower temperature seasonality (bio4) in the center and east of the Yangtze River Basin (Figure S8 ~ S9).

(a) Centroid shift of future climate suitability for breeding populations under RCP 4.5



(b) Centroid shift of future climate suitability for breeding populations under RCP 8.5



**Figure 4.** Shifts in the centroids of areas of future climate suitability for *Pomacea canaliculata* breeding populations with respect to current distribution under the two representative concentration pathways, RCP 4.5 and RCP 8.5 [corresponding to (a) and (b), respectively]. Vector colors represent the results of the four global circulation models (GCMs).

## 4. Discussion

### 4.1. Model Projections of the Distribution of *P. canaliculata*

The present study estimated the current overwintering range of *P. canaliculata* based primarily on matching the minimum temperature of October (tmin10) isoline with the southern-most collection sites. The tmin10 of 13.7 °C was within the temperature range suggested by Li (1995) who found that snail growth

and spawning were initiated at 12 °C and 14 °C, respectively. Their study also showed a decline in the activity and feeding of *P. canaliculata* below 15 °C, with the species gradually entering a dormant state with a continuous drop in temperature. The results of the present study suggested that the overwintering range may include the central area south of Sichuan Basin and parts of the middle-lower Yangtze River Basin.

The model forecasts of the present study indicated that the Yangtze River Basin will become a major wintering area for *P. canaliculata* over the next few decades. Cases of wintering *P. canaliculata* populations have recently been observed in Yuan'an County at the margins of the northern range (31°3' N, 111°4' E) in Hubei Province in central Yangtze River Basin. Continuous field surveys in Hubei from 2008 to 2019 conducted by Liu (2020) and Li et al. (2020) identified three types of habitats most vulnerable to wintering of *P. canaliculata*: (1) habitats at a water depth of  $\leq 10$  cm; (2) habitats at a sludge depth  $> 10$  cm; (3) habitats with a high coverage of aquatic vegetation. The results of the present study indicate a likelihood of dispersal of *P. canaliculata* populations further north and their residence of the entire Hubei region due to this region containing habitats suitable for overwintering survival of this species (Liu et al., 2020). Extensive field surveys by Zhou et al. (2015) also confirmed the presence of *P. canaliculata* in other areas of the Yangtze River Basin. These areas have been reported as containing overwintering habitats in which *P. canaliculata* can survive the cold by embedding themselves in wet mud, burrowing under rice straw, or finding other protective niches within the aquatic environment (Halwart, 1994). There is a need for further studies on the habitats, geographical distribution, and behavior of *P. canaliculata* under climate change for early detection and effective management strategies in this region.

#### 4.2. Trends of Future Range Expansion

The ensemble model predictions of the present study indicate increases in the extents of suitable habitats for *P. canaliculata* breeding and overwintering populations in China over the next 20 to 30 years, particularly under the most extreme climate scenario (RCP8.5: high emissions scenario). More specifically, the results indicate a reduction in current suitable habitats in the south, whereas habitats in the eastern and central parts of China will become more favorable for *P. canaliculata* due to the presence of large freshwater bodies, cultivated areas, and wetlands. These ranges of future suitable habitat for *P. canaliculata* identified in the present study are consistent with those identified as vulnerable to *P. canaliculata* by the GARP model (Wang et al., 2018). There will be considerable variation in the responses of breeding and overwintering populations of *P. canaliculata* to moderate climate change. There will be a significant reduction in suitable areas for breeding populations under moderate climate change scenarios (Figure 4). In contrast, the northward ranges of breeding populations will expand substantially under these climate change scenarios, with *P. canaliculata* breeding populations predicted to occur in much of the Yangtze River Basin.

Many terrestrial organisms are expected to exhibit an adjustment of their geographical distribution in response to a chang-

ing climate (Huntley et al., 2010). Other species with a southerly distribution have already shown a northward shift in their northern boundaries of their distributions (Pateman and Hodgson, 2015). The northward expansion of *P. canaliculata* populations predicted in the present study is consistent with findings of studies on other agricultural pests, such as the Colorado potato beetle (*Leptinotarsa decemlineata*) (Baker et al., 2000), *Thrips palmi* Karny (Park et al., 2014), and *Spodoptera frugiperda* (Ramirez-Cabral et al., 2017). Similar northward range expansions of *P. canaliculata* in China have been reported by several studies using Maxent (Zhou, 2019), GARP (Wang et al., 2018), or other methods (Yang et al., 2018). Despite the predicted potential northward shift of *P. canaliculata*, there has been relatively little focus on the possible reduction of the range of suitable habitat due to a warmer and drier climate in south China. For example, the future projections of *P. canaliculata* breeding populations in the present study showed large areas of south China to have less suitable habitat for this species, although most of areas remained vulnerable to *P. canaliculata* breeding populations (Figure 4). A reduction in the *P. canaliculata* habitat suitability of these areas could be attributed to the negative impact of elevated temperatures beyond the thermal tolerance of *P. canaliculata* in combination with declining precipitation (Figures 10 and 11).

#### 4.3. Limitations and Uncertainties

The present study evaluated the current distribution and shifts in areas of suitability for *P. canaliculata* by 2050, with an assumption of no constraints by living space and nutrients across contiguous China. This assumption allowed the present study to focus on climate-related factors as the primary drivers of the survival and expansion in range of *P. canaliculata*. However, other physical and biological factors, including various aquatic parameters (e.g., water depth, flow velocity), trophic resources (e.g., food availability, palatability), field management practices (e.g., sowing methods, irrigation, cropping pattern) were not addressed in the present study. These omissions can contribute to large uncertainties and difficulties in the interpretation of model projections. For example, the application of molluscicides or repellents in paddy fields and the removal of rice straw and drainage after harvesting may reduce the density of *P. canaliculata*, thereby affecting the density of this species in both the current and subsequent seasons (Yusa and Wada, 1999). Since *P. canaliculata* is a generalist due to its physiological and behavioral adaptations developed in association with starvation, food availability is not a crucial factor impacting on its survival (Estoy et al., 2002; Qiu et al., 2011). However, reductions in food availability will result in a decrease in the population growth rate due to a decline in fecundity and an increase in generation time (Tamburi and Martín, 2011). This in turn would impact on the potential of *P. canaliculata* to establish populations and spread to uncolonized areas. Given the reports that physical and biological factors could influence the projected suitability of *P. canaliculata* (e.g., Hayes et al., 2015), investigation on complex interactions among *P. canaliculata* and these factors under different climatic conditions is very necessary in determining the suitable ranges, since climatic factors alone fail

to provide a clear explanation for its spread at regional scale.

The present study fitted models relating *P. canaliculata* occurrences to key environmental variables using the BIOMOD2 framework. However, we did not consider the impact of a changing climate on food plants (e.g., rice, aquatic vegetable), and in turn on the distribution of this species, and assumed that the areas of agricultural and non-agricultural wetlands hosting this species would remain constant over time. Numerous studies demonstrated that climate change can alter ecological community structure because plant and insect species may show species-specific responses in phenology, distribution, and abundance (Forrest, 2016; Ekholm et al., 2021). *P. canaliculata* has currently invaded a wide range of habitats in tropical and subtropical regions in China after several introductions, whereas rice (*Oryza sativa* L.; including single- and double-crop rice) is grown from south to north across five climate zones (i.e., the tropics, subtropics, warm temperate, medium temperate, and cool temperate zones) (Chen et al., 2020). Therefore, there is a local-scale spatial mismatch between areas of current *P. canaliculata* habitat and rice cultivation due to their difference in sensitivity to low winter temperature. However, future greater warming in northern China and a faster warming trend under RCP8.5 can result in a shift in areas suitable for the cultivation of rice northward and their expansion from northwestern China to northern China, with a gradual disappearance of suitable areas in some parts of southern China (Zhang et al., 2017). The results of the present study indicated that a future elevated temperature will allow *P. canaliculata* to overwinter and survive in the upcoming decades. This result suggests that the current mismatch between areas of rice cultivation and *P. canaliculata* may decline as this pest species is able to disperse and establish populations in habitats in which it currently cannot overwinter. This potential geographical shift may result in adult spawn and outbreak of *P. canaliculata* coinciding more closely with the most vulnerable stages of wet-direct seeded rice or transplanted rice seedlings (< 20 days old) (Horgan et al., 2018) at higher latitudes. However, there remain no assessments of how climate warming impacts spatial interactions between *P. canaliculata* and its food plants. With the growing interests in effective control of invasive *P. canaliculata*, acknowledging the importance of rice plant-snail distribution and phenological matching would be very necessary to track climate change and further assessing the extent and discrepancy of their response.

The ensemble model presented in this study provides an approximation of the responses of *P. canaliculata* to a changing climate given simple correlative relationships between snail occurrence records and relevant climatic variables. Caution is needed when interpreting the capacity or extent of *P. canaliculata* populations to shift their ranges in response to climate change, considering the limits of physiological tolerance of this species to temperature and precipitation (Joshi et al., 2017; Seuffert and Martín, 2017). The ever-increasing impact of anthropogenic activities, rapid land use changes, complexities of climate variability, and extreme weather events in China emphasize the likelihood of a patchy distribution of *P. canaliculata* in the coming decades in tropical and subtropical regions, reflecting the availability of favorable microhabitats. Because we

employed statistical correlative SDMs for predicting and interpreting regional-scale locations at which climatic factors are the primary drivers of the distributions of *P. canaliculata* populations, the influences of other factors (e.g., species interactions, dispersal constraints, and adaptation capacity) were not considered. Therefore, the present study can act as a baseline for further studies that do consider these factors when investigating the distributional ecology of this species. For making sensible control strategies in preventing the spread of *P. canaliculata*, development of detailed mechanistic models is very necessary to enhance understanding of constraints on *P. canaliculata* range expansion and allow us to explore the interplay among multiple factors (e.g. climatic extremes, behavioral strategies and trophic complexity) and that significantly impact disperse and colonization of *P. canaliculata* in norther locales of China.

## 5. Conclusions

The present study documented the available occurrence of *P. canaliculata* breeding and overwintering populations in China and predicted their distributions and potential changes to habitat ranges in response to a changing climate. The results indicated that the northern range boundaries of *P. canaliculata* populations in the Yangtze River Basin due to sensitivity to cold are expanding northward, whereas their sensitivities to warmer temperatures are resulting in a movement of the southern boundaries northwards. Future climate warming will allow *P. canaliculata* to overwinter in areas that allow for breeding only. Specifically, the results of the present study suggest that early detection, monitoring, and proactive measures are required to prevent further invasion of potential breeding sites in eastern and central China and the expansion of recently established populations in the center and east of the Yangtze River Basin, which likely represent the frontier of future northward expansion of the species in China. The present study constructed ensemble-SDMs based on the available bioclimatic and monthly variables due to a lack of data for future conditions of additional predictors. Future studies should focus on combining biotic (e.g., eco-physiological tolerances, behavior flexibility, adaptive genetic variation, competition) and abiotic factors (e.g., land cover, habitat type) in the distribution models for more precise predictions of the spread of *P. canaliculata*.

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