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Impacts of Climate Change on the Potential Habitat Suitability of *Pomacea canaliculata* and *Pomacea maculata* in East Asia

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Climate change and biological invasions have had significant impacts on ecosystems and biodiversity. To assess how environmental changes affect two key invasive snails- *Pomacea canaliculata* and *Pomacea maculata*- in East Asia, we built species distribution models (SDMs) and ecological niche models. These apple snails (Gastropoda: Ampullariidae) have negatively impacted ecosystems and human health. Understanding their distribution is crucial for containing invasions under current and future climates. Our findings indicate that these two species occur primarily in China and Japan but occupy different suitable habitats, and the highly overlapping niches suggest interspecific competition. *P. canaliculata* is more adaptable extreme environments. The projections show that the sustainable development pathway (SSP126) best limits these invaders by suppressing reproduction and dispersal. This study provides predictive information that can be utilized to reduce the invasiveness and spread of these two *Pomacea* species. To prevent further increases in suitable habitat, control measures should be taken as early as possible.

Keywords: *Pomacea canaliculata*; *Pomacea maculata*; invasive snails; MaxEnt; climate change; habitat suitability

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BACKGROUND

Climate change and biological invasions significantly impact biodiversity (Secretariat of the Convention on Biological Diversity 2014; Theobald et al. 2015). Numerous studies have demonstrated that climate change will have profound effects on the spatial distribution of alien invasive organisms (Hellmann et al. 2008; Godoy et al. 2011; Zettlemoyer et al. 2019). For example, when future climate conditions are considered, invasive ants (*Linepithema humile*) will likely adapt to higher latitudes (Li et al. 2022). Climate change may also exacerbate the threat posed by the sultana borer (*Cadra figulilella*) to fresh and dried fruits (Wang et al. 2023). Additionally, climate change is causing an expansion in the geographical range of the *Corbicula fluminea* (McDowell et al. 2014). Invasive species have become a global issue due to intercontinental trade (Seebens et al. 2021; Diagne et al. 2021); therefore, understanding the effects of climate change on the dissemination of invasive organisms is needed to stabilize ecosystems, control pests, conserve biodiversity and promote the health of all organisms, including humans (Sun et al. 2024).

The *Pomacea* species complex (Gastropoda: Ampullariidae) is harmful to rice production but also impacts the ecological landscape. *Pomacea* spp. harbor the nematode *Angiostrongylus cantonensis* and neurotoxins in the yolk glands of female apple snails pose a threat to human health (Cowie 1998; Frassa 2010). *Pomacea* species are especially damaging in tropical and subtropical geographic regions where the environment fosters their population growth (Cowie 2002). The apple snails, *Pomacea canaliculata* and *Pomacea maculata*, are two main invasive cryptic species (Hayes et al. 2012), which are morphologically indistinguishable but reproductively isolated. Furthermore, *P. canaliculata* is regarded as one of the top 100 invasive species worldwide (Luque et al. 2014). Both species have rapidly spread throughout agricultural production regions, causing significant

damage (Hayes et al. 2010; Liu et al. 2019). Furthermore, Yang and Yu (2019) identified a new species of *P. occulta* in China, which is distributed in the Zhejiang and Fujian Provinces.

The species distribution model (SDM) is a crucial tool for predicting the potential habitat suitability zones of organisms exposed to current or future climates and has been utilized to assess the risk of alien invasive species (Guisan and Zimmermann 2000; Lamsal et al. 2018). SDM uses existing distribution data and the environmental factors associated with spread to analyze the potential distribution of a species in a target area and the significance of the environmental variables using a jackknife method. The use of existing data and species distributions modelling to guide fieldwork can reduce the cost of field surveys, reduce the time and cost of large-scale biodiversity studies of large numbers of species (Kamino et al. 2012; Fois et al. 2018), and combining the two provides an avenue for policy development at the cutting edge of biodiversity conservation (Mccain and Colwell 2011). Maximum Entropy (MaxEnt) is widely recognized as the most accurate modeling method (Elith et al. 2006; Wisz et al. 2008), which is characterized by rapid operation, high prediction accuracy, and automatic assessment of important environmental factors (Phillips and Dudik 2008; Phillips et al. 2017). Recently, the impacts of carbon emissions, social developments and other factors were published by the Coupled Model-based Intercomparison Project Phase 6 (CMIP6), which considers the biological impacts of socioeconomic pathways (Zhai et al. 2020).

Previous studies have shown that in *Pomacea* populations co-existing with *P. maculata*, *P. canaliculata* is generally the dominant species and has a wider dispersal range and exhibits higher temperature and environmental tolerance (Gao et al. 2022). In China, the two species were often misidentified due to their extreme morphological similarity. As cryptic species, they exhibit differences in habits and other traits, yet their accurate differentiation remains challenging, which has hindered targeted prevention and control efforts. Considering these differences, it is important to understand differences among the members of the *Pomacea* species complex in order to accurately predict and compare suitable habitats (Kwong et al. 2009; Kyle et al. 2013; Bernatis et al. 2016). In consideration of the limited number of distribution loci for *P. occulta*, they were not included in the model construction for this study. In previous studies, Zhou et al. (2018) estimated the distribution of the *Pomacea* spp. complex as a single species, rather than the distribution of different cryptic species; Yin et al. (2022) used MaxEnt to predict only the distribution of *P. canaliculata* and ignored the distribution data for China, while Zhong et al. (2023) only analyzed

the distribution of the historical climate data. Similarly, Wang et al. (2024) only predicted the potential distribution of *P. canaliculata*. Comparative studies on the two main species of the *Pomacea* complex are lacking.

We hypothesize that interspecific differences drive asymmetric range expansion. Therefore, we investigated the responses of the two species to global climate change, modelled the distribution of *P. canaliculata* and *P. maculata* in East Asia, identified key climatic factors affecting dispersal of these two species and assessed the impact of climate change on their potential distribution, and the differences between the two cryptic species in response to climate change and suitable habitats. This will provide more insights into the dispersal mechanisms of invasive organisms under global warming and elucidate the impacts of climate change on the ecosystems of these invasive organisms.

MATERIALS AND METHODS

Study area and data collection

The occurrence of *P. canaliculata* and *P. maculata* in East Asia was surveyed using two sources. First, we collected *Pomacea* spp. from rivers, ponds, and farmland at various sites throughout China from 2019-2023 and recorded locations by latitude and longitude. The collected *Pomacea* spp. were identified using the method of Wei et al. (2024) to distinguish the two species, and the results of the identifications are shown in table S1. *P. maculata* were found in Lianyungang, Jiangsu Province, Yiyang, Hunan Province, and Xiamen, Fujian Province. Notably, the number of loci was significantly fewer than that of *P. canaliculata*. Secondly, occurrence data was obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org) and used to provide detailed information on coordinates in East Asia, which are used after checking with existing reports (Yin et al. 2022; Xue et al. 2022). A total of 2396 and 57 loci were searched for the occurrence of *P. canaliculata* and *P. maculata*, respectively. To minimize deviations among samples, a single occurrence was placed in individual cells of the grid to match the spatial autocorrelation and sampling bias of the environmental variable data. After filtering, 306 and 10 occurrence records of *P. canaliculata* and *P. maculata*, respectively, remained for modeling (Fig. 1;

Table S1), which are mainly distributed in southern China and south-western Japan.

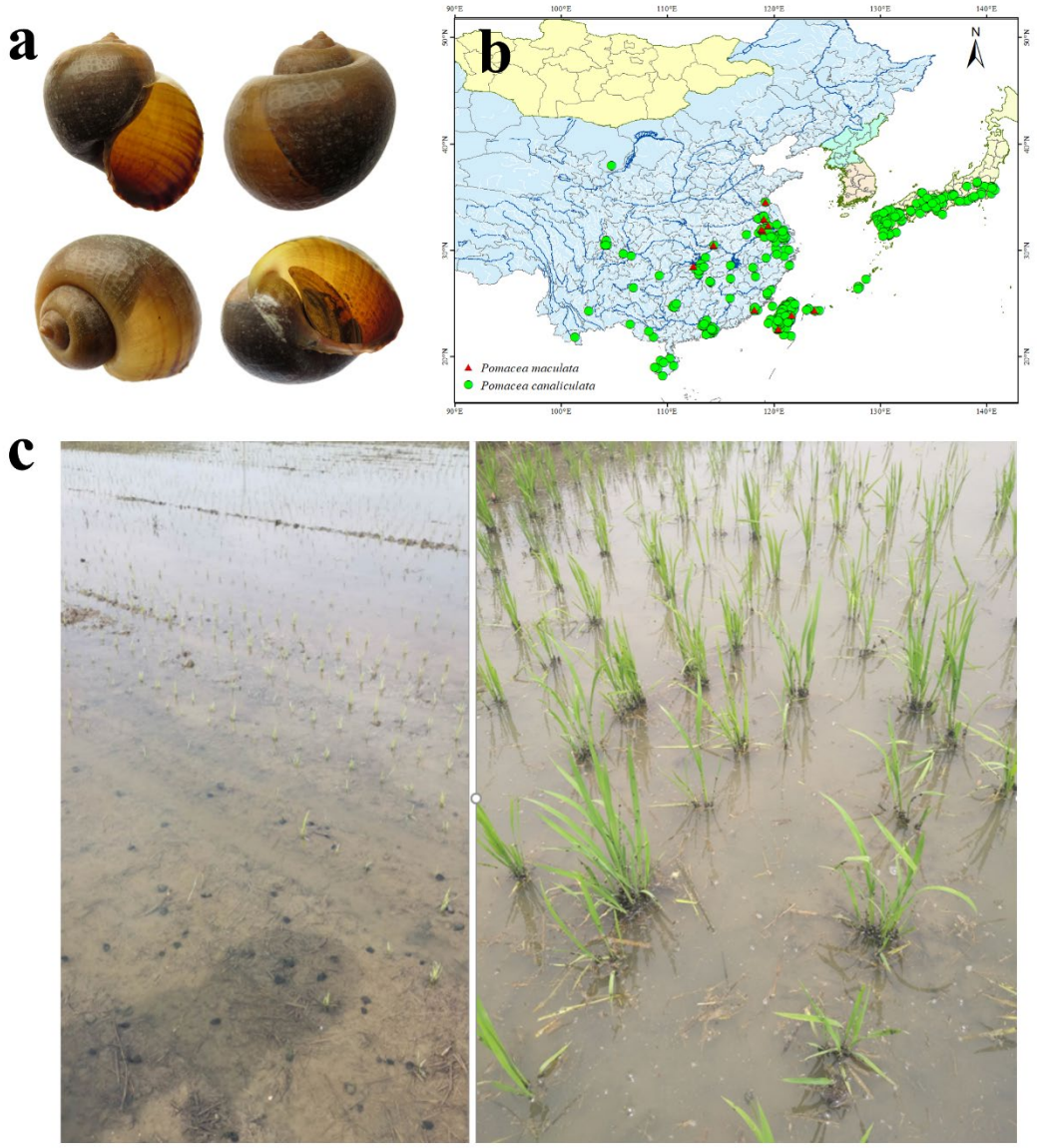

Fig. 1. The infestation of *Pomacea* spp. and their natural habitat. (a)adult of *P.canaliculata*; (b) distribution of occurrence records used in the MaxEnt models of *P. canaliculata* and *P. maculata* in East Asia, the red triangle represents the *P. maculata*, the green circle represents the *P. canaliculata*; (c)natural habitat and host plants of *Pomacea* spp. in Jiangsu, China.

Environmental variables

Prevailing climate data (1970–2000) were acquired from the World Climate database (https://worldclim.org/) (Fick and Hijmans 2017) with a spatial resolution of 2.5 km, and the data contain 19 bioclimatic variables (BIO1-BIO19) (Table S2). Future climate data (20212040, 2041-2060, 2061-2080, 2080-2100) for East Asia were simulated with the Beijing Climate Center Climate System Middle Resolution Model (BCC-CSM2-MR) (Yang et al. 2016; Wu et al. 2019; Shi

et al. 2020). These data originate from the latest Coupled Model Intercomparison Project Phase 6 (CMIP6) datasets, integrating Shared Socio-economic Pathways (SSPs) with representative concentration pathways. Four SSPs were selected including the sustainability path (SSP126), the moderate path (SSP245), the regional rivalry path (SSP370), and the fossil fuel-driven development path (SSP585). These pathways were selected as the first choice for future climate information with high ability to simulate East Asia's temperature (Yang et al. 2016; Wu et al. 2019; Shi et al. 2020).

Bioclimatic variables were transformed using the American Standard Code for Information Interchange (ASCII), and ArcGIS v. 10.6 (Esri, Redlands, CA, USA) was used to extract data from the base map of East Asia. Correlation coefficients (R) for these variables were calculated using ENMtools (http://purl.oclc.org/ENMtools) (Warren et al. 2010). To eliminate possible multicollinearity between environmental variables, which might affect the accuracy of prediction and reduce model performance (Thuiller et al. 2008). If two variables were highly correlated ($|R| \geq 0.85$), only one was used in the final model (Olson et al. 2014; Lei et al. 2017). A jackknife test was utilized to assess the importance of variables, and those with contributions lower than 1% were discarded. GraphPad Prism v. 8 (San Diego, CA, USA) was used for the analysis. The normalized training gains and the response of each environmental variable in the model were analyzed using the Microsoft Excel software.

Moreover, incorporating biological traits and historical distribution data of *Pomacea* snails, key environmental drivers for their expansion were considered. Laboratory data show 2.1–25.0% overwinter survival in northern Jiangsu, and field records confirm established populations in Jining, Shandong (extreme lows: -8°C to -13°C) (Wang et al. 2022). Previous studies identify temperature and drought as primary factors affecting spread and growth (Matsukura et al. 2009; Gilioli et al. 2017). Therefore, for niche differentiation between two *Pomacea* species, distinct environmental factors were selected.

Model building and evaluation

MaxEnt v. 3.4.3 was utilized to predict the distribution of *P. maculata* and *P. canaliculata* under historical and future climates, respectively, due to this software's ability to ensure model accuracy even with limited sample sizes (Phillips et al. 2006). Importing species distribution data

and environmental variable data by calling the MaxEnt software running via Java. The relevant equations are as follows: Fundamental model equation (1), Where f(x) is the probability density of species occurrence at environmental variables x; (2) is the normalization constant; βi are coefficients for the *i*-th feature, estimated via maximum likelihood; $fi(x)$ are the *i*-th environmental feature functions, typically including linear, quadratic, and product terms. Model parameters are solved by maximizing the log-likelihood function (3), Where *N* is the number of presence points, and *xj* denotes environmental values for the *j*-th presence point. Final suitability probabilities are transformed via the logistic function (4).

$$f(x) = \frac{1}{Z(\beta)} + \exp\left(\sum_{i=1}^{M} \beta_i f_i(x)\right) \quad (1)$$

$$Z(\beta) = \int \exp\left(\sum_{i=1}^{M} \beta_i f_i(x)\right) dx \quad (2)$$

$$\ln L(\beta) = \sum_{j=1}^{N} \ln f\left(x_j\right) - \int f(x) \ln f(x)\, dx \quad (3)$$

$$p(x) = \frac{1}{1+\exp(-\ln f(x))} \quad (4)$$

Bootstrapping with 10 repetitions was conducted to determine the reliability of models; 75% of the records were used to calibrate the models, and the other 25% were used for the final evaluation. Feature classes used the LQHPT custom combinations. Models were analyzed using AUC (area under the curve), TSS (true skills statistics), and ROC (receiver operating characteristic curve) to evaluate the data for both predicted and current climate scenarios (Allouche et al. 2006; Peterson et al. 2008; Jimenez-Valverde 2012). Given that higher AUC scores indicate stronger reliability, only models with AUC values greater than 0.8 were included (D'Amen et al. 2011).

Visual and statistical analysis of suitable habitat patterns

The results generated from MaxEnt were imported into ArcGIS 10.6 to evaluate both visual interpretation and suitability. Values within cells of the grid varied from 0 to 1. We used the Jenks natural breaks classification method to identify suitable and unsuitable habitats, defining five levels of habitat suitability accordingly: unsuitable (0-0.25), low suitability (0.25-0.50), general suitability (0.50-0.75), moderate suitability (0.75-0.90), and high suitability (0.90-1.00), and comparing habitat suitability for four future climate scenarios with the current suitability area using the spatial analysis

tool SDM Toolbox (http://www.sdmtoolbox.org/) (De Souza et al. 2018; Park et al. 2022). GraphPad Prism v. 8 (San Diego, CA, USA) was used for the graphing. Furthermore, the direction and distance of the spatial movement of the centroid migration for the four future climate scenarios for different periods were measured using the spatial analysis tool, the spatial statistics tool and the data management tool of the SDM Toolbox in order to predict the overall trend of the distribution of the two cryptic species (Brown 2014).

RESULTS

Model performance and the value of environmental variables

Using Pearson's correlation matrix of environmental variables (Fig. 2), the following seven environmental variables were selected for *P. canaliculata* and used for modeling: bio2, average diurnal temperature; bio3, isothermality; bio6, lowest temperature in the coldest month; bio8, average temperature in the wettest quarter; bio12, annual precipitation; bio15, seasonality of precipitation; and bio19, precipitation during the coldest quarter. The seven environmental variables used to model *P. maculata* were bio2, bio3, bio7, bio10, bio15, bio17 (precipitation during the driest quarter), and bio18 (precipitation in the warmest quarter).

The MaxEnt models exhibited a high degree of predictive ability and were considered to be reliable (Fig. S1; Table S3). The jackknife method was used to normalize the training gain of environmental variables for the two cryptic species (Fig. 3), and the primary factors impacting suitable habitats for *P. canaliculata* were the minimum temperature of the coldest month and precipitation in the coldest quarter (Fig. 4a). In contrast, the principal factors impacting suitable habitats for *P. maculata* were the mean diurnal range and temperature of the warmest quarter (Fig. 4b).

The response data from environmental factors were combined to generate response curves for individual factors in an integrated model. For *P. canaliculata*, the probability of species presence was greater than 0.5 when precipitation in the coldest quarter exceeded 200 mm; as precipitation increased, the probability approached 1 and remained stable (Fig. 4a). The probability of presence gradually increased as the minimum temperature of the coldest month approached 10°C and

stabilized when temperatures exceeded 20°C (Fig. 4a). With respect to *P. maculata*, the mean temperature of the warmest quarter ranged from 27-37°C (Fig. 4b). Furthermore, the probability of presence gradually decreased as the mean diurnal range reached 6°C; this value became 0 when the range exceeded 15°C (Fig. 4b).

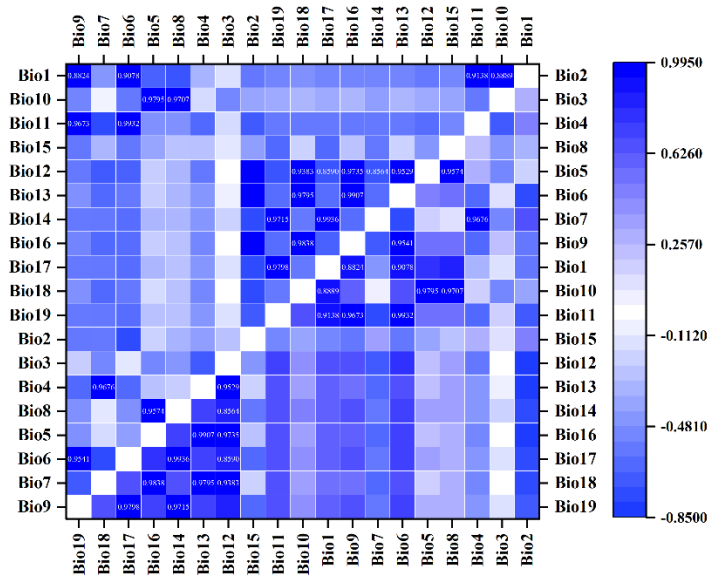

Fig. 2. Heatmap showing Pearson's correlation matrix of environmental variables. Upper left panel represents *P. canaliculata*, lower right panel represents *P. maculate*.

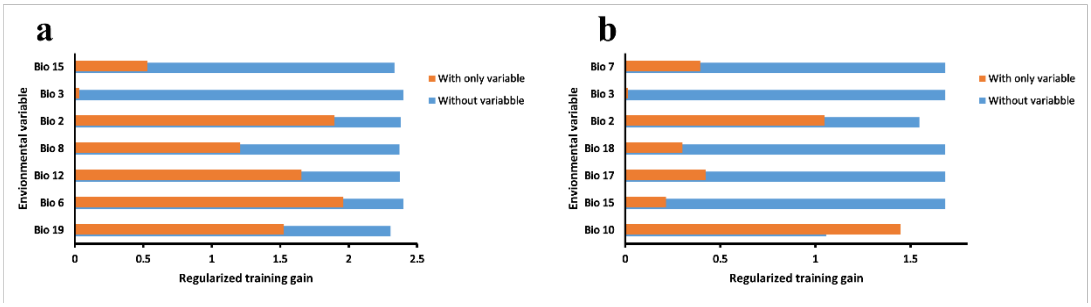

Fig. 3. Normalized training gains for environmental variables using MaxEnt (a) *P. canaliculata*, (b) *P. maculata*.

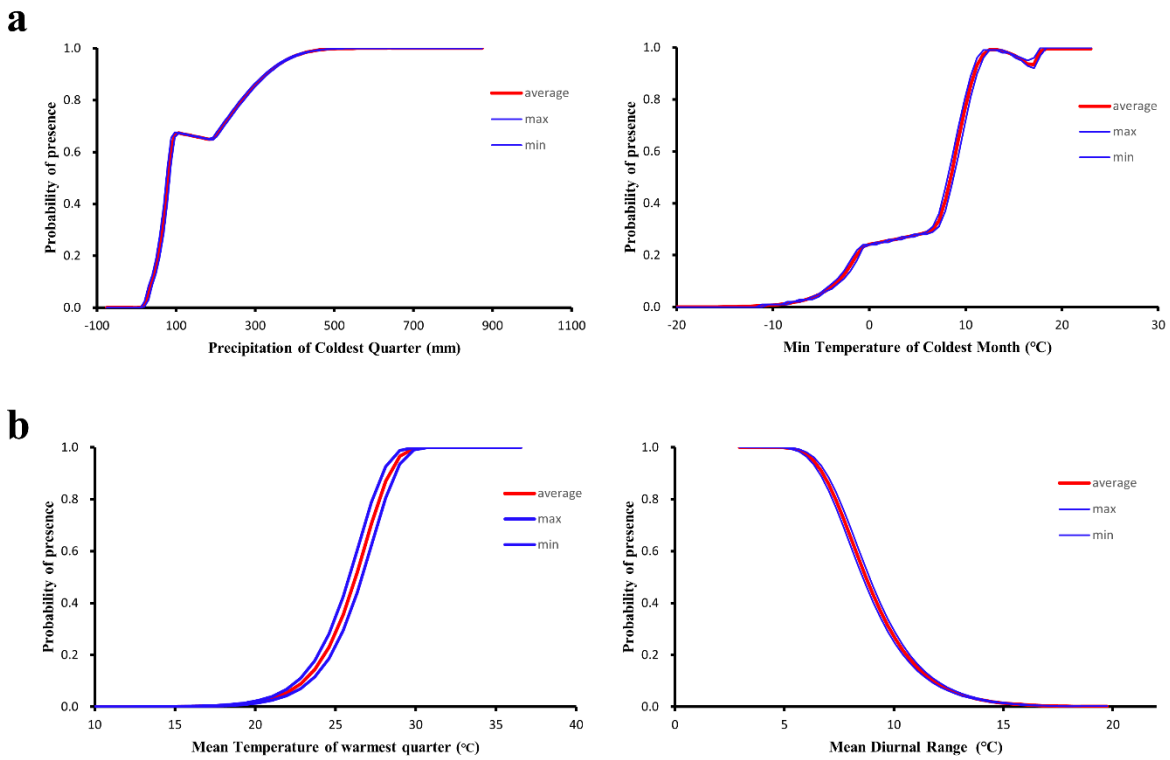

Fig. 4. Response curves of the probability of presence for (a) *P. canaliculata*: Precipitation of coldest quarter and Min temperature of coldest month, (b) *P. maculata*: Mean temperature of warmest quarter and Mean diurnal range.

Current geographic distributions

The records on the distribution of *P. canaliculata* and *P. maculata* were diverse, indicating that suitable habitats and ecological niches are also likely different. Consequently, suitable habitats for the two species were predicted using current climatic conditions in East Asia (Fig. 5). The distribution of both *P. canaliculata* and *P. maculata* are primarily concentrated in the southern and southeastern regions of China, southern South Korea, and southern and southeastern Japan. The suitable habitats for *P. canaliculata* and *P. maculata* in East Asia were determined to be 204.08 × 10^5 km^2 and 212.72 × 10^5 km^2, respectively. The highly suitable habitats for *P. canaliculata* were located in Taiwan, Shanghai, and Shizuoka and covered an area of 16.57 × 10^5 km^2. Moderately suitable habitats were 43.17 × 10^5 km^2; these habitats were primarily located in Guangdong, Guangxi, Kyushu and Nagoya. The most suitable habitats for *P. maculata* encompassed 37.55 × 10^5 km^2; these habitats were located in Hainan, Guangxi and Guangdong. Moderately suitable habitats covered 39.98×10^5 km^2; these habitats were located in Chongqing and Anhui. Unsuitable habitats for *P. canaliculata* and *P. maculata* were 1003.24 × 10^5 km^2 and 994.60 × 10^5 km^2, respectively, and

were located in northeastern, North and northwestern China, South Korea, North Korea and Mongolia (Fig. 5).

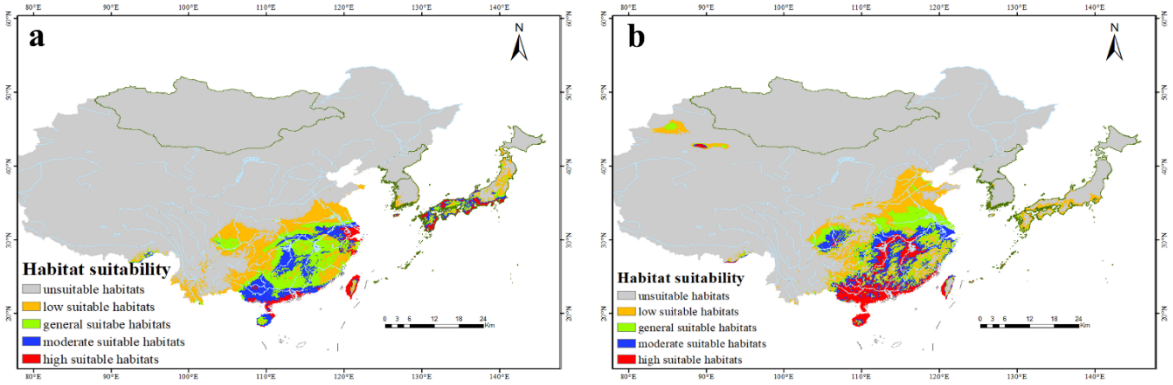

Fig. 5. Current data showing suitable habitats for (a) *P. canaliculata* and (b) *P. maculata*, red represents high suitable habitat, blue represents moderate suitable habitat, green represents general suitable habitat, orange represents low suitable habitat and grey represents unsuitable habitat.

Potential geographic distributions under future climate conditions

The potential dissemination of *P. canaliculata* and *P. maculata* were projected using future climate scenarios and a global climate model that is appropriate for East Asia (Figs. 6–8). Using SSP, the two cryptic species exhibited distinct dispersal characteristics. The climate scenarios impacted suitable habitats at different times, and many areas were predicted to become moderately or highly suitable as dissemination occurred over time. With the SSP370 path, both *P. canaliculata* and *P. maculata* will reach their maximum suitable area in the 2090s. The most stable, suitable habitats for *P. canaliculata* were predicted for SSP126 and SSP370 (Fig. 6). *P. maculata* is expected to expand into suitable areas located in Guangxi, Hunan, and Jiangxi, as well as regions in northern Xinjiang in China and Japan. SSP245 and SSP370 are more suitable for stable population growth of *P. maculata*, whereas SSP126 will become less suitable over time (Fig. 7).

P. maculata had a greater habitat suitability than *P. canaliculata*, particularly in Shandong, parts of Hebei, and a small part of Xinjiang; the other potential habitat suitability zones largely overlapped. Under different SSP, Highly and moderately suitable areas for *P. canaliculata* were 13.82×10^5 km^2 – 22.67×10^5 km^2 and 25.64×10^5 km^2 – 57.61×10^5 km^2, respectively. For *P. maculata,* highly and moderately suitable habitats were 28.78×10^5 km^2–36.13×10^5 km^2 and 29.86×10^5 km^2 – 39.70×10^5 km^2, respectively. The number of highly and moderately suitable areas for

P. maculata is 2.08–1.59- and 1.16–0.69-fold larger than *P. canaliculata*, respectively (Fig. 8).

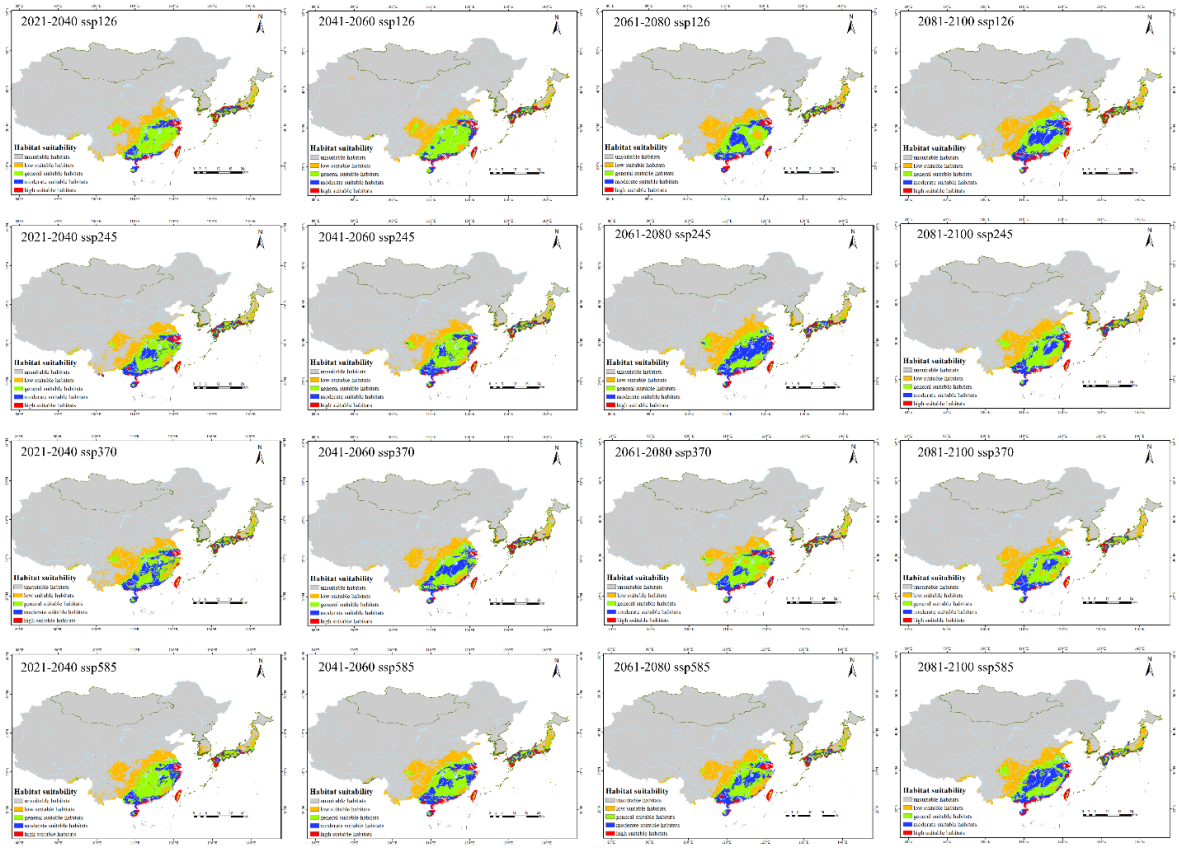

Fig. 6. Changes in the potential distribution of *P. canaliculata* in East Asia from 2021 to 2100 under four shared socioeconomic pathways (SSPs), red represents high suitable habitat, blue represents moderate suitable habitat, green represents general suitable habitat, orange represents low suitable habitat and grey represents unsuitable habitat.

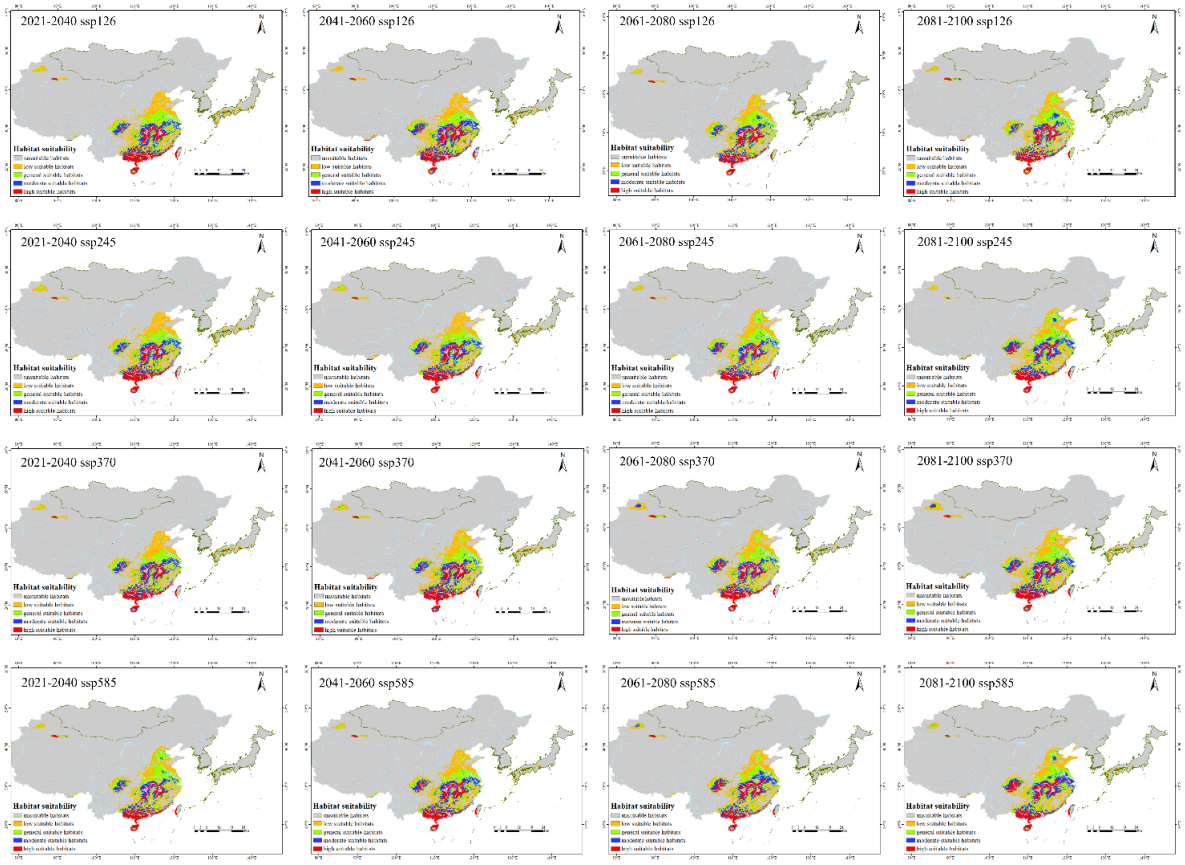

Fig. 7. Changes in the potential distribution of *P. maculata* in East Asia from 2021 to 2100 under four shared socioeconomic pathways (SSPs), red represents high suitable habitat, blue represents moderate suitable habitat, green represents general suitable habitat, orange represents low suitable habitat and grey represents unsuitable habitat.

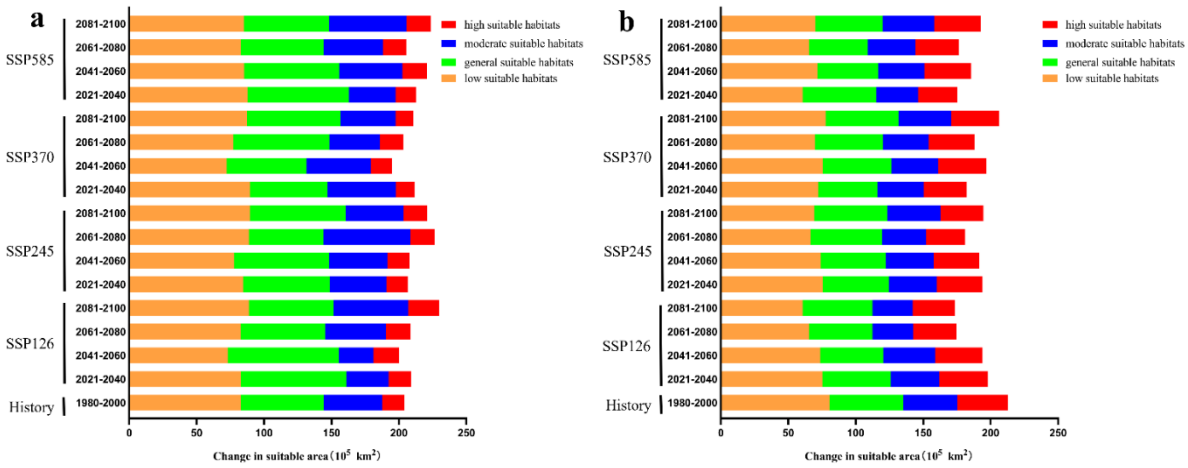

Fig. 8. The proportion of suitable habitats in response to historical and future climate change scenarios in East Asia. Panels: (a) *P. canaliculata*; (b) *P. maculata*, red represents high suitable habitat, blue represents moderate suitable habitat, green represents general suitable habitat and orange represents low suitable habitat.

Centroid migration patterns

The centroids of potential suitable areas for *P. canaliculata* and *P. maculata* in East Asia were examined using current and future climate scenarios, and the results indicate potential shifts in distribution of the two species with respect to time and climate change (Fig. 8). Under current climate conditions in East Asia, the centroid of suitable areas for *P. canaliculata* was located in Hangzhou City, Zhejiang Province (114.04°E, 27.56°N) (Fig. 9a), whereas the centroid for *P. maculata* was located in Pingxiang City, Jiangxi Province (119.81°E, 29.78°N) (Fig. 9b). When future climate scenarios are considered, the suitable areas for *P. maculata* move northward and to higher latitudes, and centroid migration occurs around 2021–2040 under the SSP245, SSP370, and SSP585 scenarios. For *P. canaliculata*, migration was predicted to occur in different directions and distances for each period, with the farthest distance under SSP370.

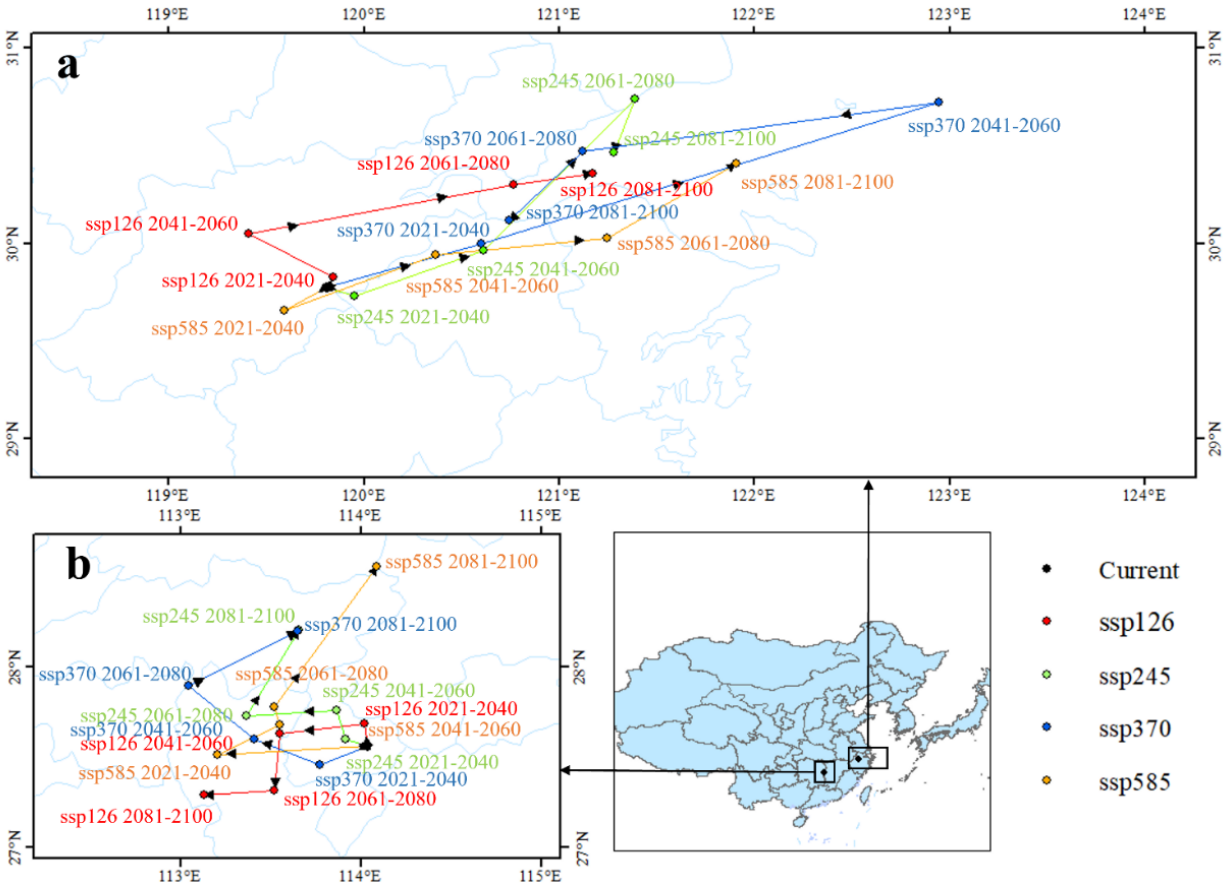

Fig. 9. Changes in centroid migration in East Asia from 2021 to 2100 under four shared socioeconomic pathways (SSPs). Panels: (a) *P. canaliculata* and (b) *P. maculata*, black represents the centroid of current climate data, red represents SSP126, green represents SSP245, blue represents SSP370 and orange represents SSP585.

DISCUSSION

This study leverages the robust predictive performance of the MaxEnt model to explore and compare the distribution dynamics of *P. canaliculata* and *P. maculata* in East Asia, yielding findings with important implications for understanding their invasive potential. MaxEnt was selected for its proven reliability in species distribution modeling, particularly its ability to generate biologically meaningful predictions even with limited occurrence data—a strength validated by Pearson et al. (2007) and Elith et al. (2006), who demonstrated its powerful predictive capacity even for sample size as small as five. We modeled each species separately to account for their unique climatic niches, a critical step given the distinct distribution ranges often exhibited by closely related invasive taxa (De kort et al. 2021). While both species are already established invaders in China and Japan, our results highlight key uncertainties in *P. maculata*'s future potential distribution under climate change--uncertainties that the MaxEnt framework helps clarify despite data limitations. Consistent with expectations, *P. canaliculata*'s predicted distribution aligns well with current survey records, reinforcing model validity. For *P. maculata*, the model identified a broader range of suitable habitats than observed to date, a pattern consistent with ecological niche theory (Hirzel et al. 2002; Soberon and Peterson 2005), where models often reflect fundamental niches rather than realized distributions constrained by dispersal or biotic interactions. Most importantly, our analysis reveals that while *P. canaliculate* and *P. maculata* share extensively overlapping suitable habitats in East Asia, they exhibit striking differences in habitat suitability gradient—particularly in the spatial configuration of low, moderate, and highly suitable areas (Fig. 6 and Fig. 7). These differences likely stem from divergent adaptive traits, underscoring the need for species-specific management strategies (Cheng and Sha 2017).

Although *P. canaliculata* adult snails overwinter in the mud and become active when temperatures are favorable (Gilioli et al. 2017). Model-based projections further identify temperature and precipitation as dominant drivers of their geographic distribution (Zhong et al. 2023; Wang et al. 2024). Our study shows that the minimum temperature during the coldest month is a significant climatic factor that affects the distribution of *P. canaliculata* (Fig. 4a), which is consistent with previous research and helps explain why these species cannot survive annually in northern regions like Beijing and Shandong (Lv et al. 2011; Lei et al. 2017; Zhong et al. 2023). However, it remains possible that *P. canaliculata* possesses improved its cold tolerance and

supercooling ability through constant domestication in response to low temperature, which may have fostered its continuous, northward spread. Additionally, global warming may also play a role in northward movement due to increases in winter temperatures and a shift from wet to dry conditions in some areas (Pasiecznik et al. 2003). From our observations that *P. canaliculata* can be active in arid regions but cannot survive in dry environments for extended periods since precipitation is a crucial climatic factor that affects its distribution (Glasheen et al. 2017). Generally, *P. canaliculata* is more likely to survive in warm, wet areas; however, the centroid migration pathways of suitability zones for *P. canaliculata* are very complex and variable when considering future climate scenarios (Dumidae et al. 2021; Wang et al. 2024).

Seven climatic factors were screened to construct the distribution model of *P. maculata*, and the contribution and importance of the average temperature during the warmest quarter and mean diurnal range was 100%, while the contribution and importance of other climatic factors was 0% (Fig. 2 and Fig. 3). Therefore, the main factor affecting the distribution of suitable habitats for *P. maculata* is temperature. We also observed that survival rates for *P. maculata* decreased as temperature differences increased, and the survival rate was zero when temperature differences exceeded 15 ℃ (Fig. 4b). This is explaining why *P. maculata* finds suitable habitats in southeastern China and a small part of Xinjiang Uygur Autonomous Regin, but it can be concluded that it will not spread to Xinjiang unless artificially introduced. Its distribution is limited due to its weak adaptability, which is consistent with the dominance of *P. canaliculata* (Gao et al. 2022). While Zhong et al. (2023) identified temperature and precipitation as key factors, this discrepancy underscores the imperative for expanded datasets to validate distribution mechanisms. Until the end of the 21st century, the centroid migration paths for *P. maculata* will continue to spread northward under the SSP245, SSP370, and SSP585 scenarios. This suggests that global warming will significantly impact the distribution of *P. maculata*, and the invasiveness of *P. maculata* will become more severe as greenhouse gas emissions increase (Fig. 9).

The northward migration of the two species may breach original geographical barriers, such as low-temperature thresholds (Stralberg et al. 2017). This discovery is the way for subsequent molecular research: by screening target genes that regulate low-temperature responses (Liu et al. 2018), blocking their adaptive capacity in cold regions through gene interference or gene drive technologies to achieve precise control. The colonization of *Pomacea* spp. in regions above -10℃ requires niche overlap analysis for northern aquatic ecosystems (Yoshida et al. 2014; Deaton et al.

2016). Native snails in northern waters have strong cold adaptability but weak competitiveness, and northward migration of *Pomacea* may compress native species' ecological niches (Yin et al. 2022). This ecological risk extends beyond biodiversity degradation and agricultural losses, further necessitating systemic overhauls of management strategies. These overhauls require substantial human, material, and financial investments--particularly for establishing interagency coordination mechanisms, developing advanced monitoring technologies, and redesigning policy frameworks.

We employed MaxEnt exclusively to construct this model, which primarily relies on climatic variables for predictions. This decision was based on two key considerations. First, the *Pomacea* species complex are invasive omnivores that lack effective natural enemies in East Asia, minimizing the influence of top-down biological control (e.g., predation and parasitism) on their distribution, as no native species can substantially regulate their population. Second, data on species-specific biological interactions for *Pomacea* in East Asia remain scarce and fragmented. Most existing studies focus on the ecological impacts of these snails rather than providing quantifiable interaction data, making it difficult to parameterize biological interaction variables in the MaxEnt model. *Pomacea* spp. are more capable of spreading than many native species (Godoy et al. 2011) and can displace native organisms (Ramasamy et al. 2022). Suitable habitats for *Pomacea* spp. are influenced by the water source and composition of the habitat (Ibanez et al. 2014; Cieplok and Spyra 2020). *Pomacea* spp. are well-suited for water dispersal due to the dense water network in southern China and Japan and their tolerance to harsh environments (Byers et al. 2013). Human activities also affect the spread of invasive organisms (Wan and Yang 2016); however, obtaining and using these data as a predictive tool is difficult and requires further investigation.

The study by Pearson et al. (2007) demonstrated that under-documentation of the distribution does not affect the accuracy of the model with model accuracy increasing as the sample size increases. Hernandez et al. (2006) argued that models that can be generated with a sample size of only 5-10 samples are not as accurate as those constructed with larger sample sizes but are still useful (Stockwell and Peterson 2002). Moreover, models are more accurate for species with small geographic ranges and limited environmental tolerances. However, the sample size for *P. maculata* is limited, which may affect the spatial bias, followed by incomplete feature space coverage, which affects the model generalization ability. Additionally, there is a tendency to use different procedures to develop species distribution models and compare the results of each model. Therefore, future studies should consider the effect of sample size on model accuracy and choose carefully.

CONCLUSIONs

Our results indicate that *P. canaliculata* and *P. maculata* both threaten East Asia's biosecurity. Under the sustainable development pathway (SSP126), the lowest mean annual temperature increase and highest global wetland conservation rate collectively reduce invasive dispersal capacity, thereby appears to limit spread more effectively than other scenarios, whereas fossil fuel-driven development (SSP585) result in their northward migration. Sustainable development may protect the environment and biodiversity. However, predictions and early warnings are insufficient to prevent the spread of invasive organisms. More comprehensive control and quarantine measures need to be instigated to prevent further spread of apple snails in East Asia.

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Supplementary Materials

Table S1. Detailed information for the occurrence records of *Pomacea canaliculata* and *Pomacea maculata* in East Asia. (download)

Table S2. Abbreviations and descriptions of bioclimatic variables used. (download)

Table S3. Accuracy test AUC and TSS for different models. (download)

Fig. S1. Mean AUC values of the MaxEnt model. (a) *Pomacea canaliculata*, (b) *Pomacea maculata*. (download)