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RESEARCH

Assessing the invasive risk of *Procambarus virginalis* (marbled crayfish) in South Korea

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Background: Introducing invasive alien species can reduce biodiversity by interfering with native species or spreading disease and having socioeconomic consequences. Therefore, international society has set goals for preventing and suppressing the introduction and spread of invasive alien species. Nevertheless, humans intentionally introduce and release alien species into the wild, facilitating their invasion. *Procambarus virginalis* (marbled crayfish) is a Decapoda invertebrate sold for ornamental purposes. Ecological repercussions are anticipated because individuals have been verified to exist in the wild in South Korea. *P. virginalis*, believed to have originated in Europe and North America, is parthenogenetic. Therefore, there is concern that its population may quickly expand in the natural environment.
Results: This study examined the invasion risk of *P. virginalis* in South Korea and predicted its dispersal under future climatic circumstances. The habitat suitability for *P. virginalis* in Europe, North America, and Northeast Asia was determined using an ensemble species distribution model, and climatic niches were compared. Furthermore, the distributions of South Korea under the SSP2-4.5 and SSP5-8.5 scenarios are provided. The Northeast Asian region had habitat suitability comparable to that of Europe, and there was evidence that its climatic niche overlapped Europe (Schoener's D = 0.29). In the future climatic scenario, 38% of South Korea is at risk of moderate to low invasion. The human disturbance index was the most critical variable in the distribution.
Conclusions: We believe the hazards of its invasion of South Korea are significant. Additionally, there is a high possibility that they will be established in nature due to artificial releases. Therefore, continuous monitoring and appropriate management are needed for areas with a high risk of *P. virginalis* invasion.

Keywords: ensemble species distribution model, human influence index, invasive species, niche overlap, *Procambarus virginalis*

Introduction

The invasion of alien species occurs when humans intentionally or accidentally transport individuals or propagules beyond their natural biogeographic borders (Blackburn et al. 2011; Essl et al. 2015; Lehan et al. 2013; Turbelin et al. 2022). The spread of alien species endangers natural ecosystems, and its reduction of biodiversity is well documented (McGeoch et al. 2023). They can raise the danger of species extinction by competing with native species and affecting ecosystems' productivity, nutrients, material cycling, and hydrology (Blackburn et al. 2019; Pyšek et al. 2020; Ricciardi et al. 2013; Suarez and Tsutsui 2008). Despite these concerns, alien species continue to be introduced via human economic activities (Turbelin et al. 2022). Therefore, the UN Biodiversity Conference emphasized the global goal of slowing the entry and establishment of invasive alien species to eliminate, prevent, and minimize the damage to biodiversity (McGeoch et al. 2023).

Introducing alien ornamental species due to undesired human actions can have profound ecological implications (Pyšek et al. 2020). *Lantana camara*, a member of the genus *Lantana*, was introduced as an ornamental plant and has since become a representative invasive alien species across Africa and Asia. African giant snails have also been brought as pets to Asia and are considered agricultural and garden pests (Aravind et al. 2022; Bhagwat et al. 2012; Nentwig 2008). *Lithobates catesbeianus* was introduced into South Korea as an ornamental and edible frog but spread into the wild after being intentionally released. After establishing a wild population in the southeast, the South Korean Ministry of Environment declared *L. catesbeianus* an "ecosystem-disturbing species" (Park et al. 2022). The ecological implications of these established alien species are difficult to predict, and social costs will be involved in solving this problem.

Given the difficulties of predicting the release of alien species into the wild due to unauthorized human activity, consistent monitoring of areas with a high risk of introduction and establishment is crucial. Coordinate data collected from individual samples and eDNA can be used as a starting point to estimate the occurrence area and anticipate distribution (Chucholl et al. 2021). Species distribution models (SDM) use surveyed occurrence data to identify areas suitable as alien species habitats and forecast future spread (Mainali et al. 2015). Ensemble species distribution models (ESDM) integrate the results of each model using regression analysis and machine learning to provide results. Although Maximum Entropy Model (MaxEnt), based on the maximum entropy theory, has been widely used in research, the ensemble model may be able to forecast narrower areas with greater accuracy. Furthermore, the distribution data may only include newly introduced populations when projecting the spread of alien species. This may result in underestimating the habitat suitability for the alien species. To compensate for this, it would be helpful to compare the environmental niches of native and invaded locations. By comparing ecological niches, we can determine whether invasive alien species will likely be established in similar habitats.

Procambarus virginalis (marbled crayfish) is sold as an ornamental decapod worldwide, but it is also considered a highly invasive alien species in Europe, Madagascar, and Japan (Sheppard et al. 2024). These aggressive invasions are caused by the parthenogenetic characteristics and high reproductive ability of *P. virginalis*, which allow a new population to arise from a single individual (Liptak et al. 2016; Martin et al. 2007, 2016). *P. virginalis* is known to transmit *Aphanomyces astaci*, which causes fungal infections in crayfish. As a result, the possible impact on native species is cause for concern (Lipták et al. 2016). Therefore, the EU prohibits *P. virginalis* from being imported, bred, transported, commercialized, or released into the wild (Regulation No. 1143/2014 on the prevention and management of the introduction and spread of invasive alien species). In Madagascar, the dramatic increase in *P. virginalis* populations during the last decade is seen as a severe ecological issue (Andriantsoa et al. 2019, 2020; Vogt 2021). *P. virginalis* was also introduced and bred commercially in South Korea, and there were concerns about disruption to the natural ecosystem. Despite major ecological concerns about introducing *P. virginalis*, people are releasing it into the wild. Humans have released ornamental *P. virginalis* into natural lakes in South Korea. As individuals have been identified in the wild and young crayfish have been discovered, the risk of rapid growth of the population exists. In South Korea, efforts are being made to prevent the invasion of *P. virginalis* by designating it as an "alert alien species."

This study aimed to provide ecological information to prevent the introduction and establishment of *P. virginalis*. We divided into three geographical regions and performed a species distribution analysis: North America (NA), the presumed origin; Europe (EU), the primary habitat; and Northeast Asia (ASIA), where it was a newly introduced region. We also anticipated distribution patterns in South Korea based on climate forecasts. Here, we try to answer the following questions: 1) In which sub-region of South Korea is *P. virginalis* most likely to be introduced and established? 2) Will a region with a possible invasion risk expand in response to climatic change? 3) Do the ecological niches of *P. virginalis* in the newly introduced region overlap with those of the core habitat regions?

Materials and Methods

Study species: *Procambarus virginalis*

P. virginalis was first identified in Germany (Andriantsoa et al. 2020; Chucholl et al. 2021). However, genome assembly studies suggest that *P. virginalis* were inherited from the Everglades in Florida subpopulation of *Procambarus fallax* (Gutekunst et al. 2021), so it is may be native to NA. All individuals are female and the only decapods that reproduce parthenogenetically; therefore, all offspring are genetically identical to their parents (Martin et al. 2007). *P. virginalis* is a triploid species with 276 chromosomes, which are thought to be responsible for parthenogenetic reproduction (Martin et al. 2016). Its tolerance of low dissolved oxygen levels and wide range of habitable water temperatures make it highly invasive. *P. virginalis* occurrence data were obtained from the Global Biodiversity Information Facility (GBIF 2024) and the Marmorkrebs.org (Sánchez et al. 2024; https://sites.google.com/view/marmorkrebs/) in NA, EU, and AISA. We evaluated the habitat suitability of AISA, a newly introduced location for *P. virginalis*. Occurrence data from South Korea were also included, based on specific locations surveyed by the National Institute of Ecology (National Institute of Ecology 2022). *P. virginalis* have been identified in ponds and megacities (Seoul and Busan) parks and streams of densely populated areas (Fig. 1). The number of locations where *P. virginalis* are identified is increasing through annual surveys.

Environmental variables

We analyzed habitat suitability in three regions (EU, NA, and ASIA) and assessed the invasion risk due to climate change in South Korea. First, we selected 19 bioclimatic variables (30 seconds resolution) from the Worldclim 2.1

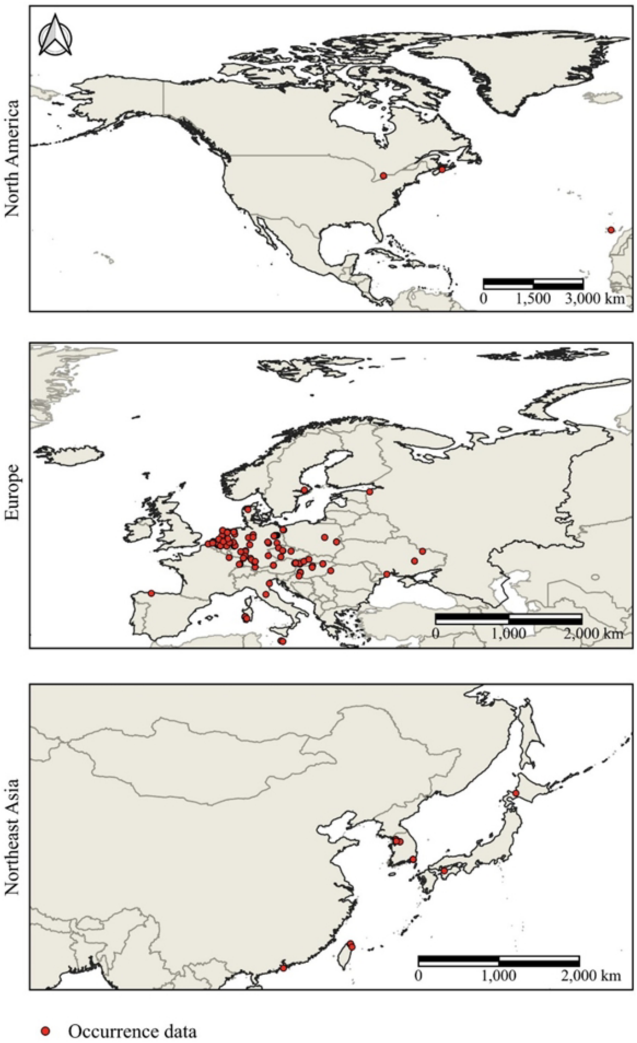

Fig. 1 *Procambarus virginalis* occurrence data for three regions. The data from the Global Biodiversity Information Facility (GBIF), Marmorkrebs.org (https://sites.google.com/view/marmorkrebs/), and the National Institute of Ecology in South Korea are presented.

database (www.worldclime.org) to evaluate the habitat suitability of the three regions. All variables were checked for multicollinearity using the variance inflation factor (VIF) procedure based on the Pearson correlation of the USDM package in R programming (Naimi et al. 2014; R Core Team 2021). In general, if the VIF is greater than 10, it is difficult to function as an independent variable (Naimi and Araújo 2016). Finally, variables with a VIF more significant than 8 were removed, and six bioclimatic variables were chosen for modeling and niche overlap tests.

Second, we added three variables to assess the invasive risk in South Korea after testing for multicollinearity with six bioclimatic variables. The human influence index (HII, https://earthdata.nasa.gov/), distance to the drainage system (Distance, http://wamis.go.kr), and water temperature during the coldest month (WTC, http://water.or.kr) were also included (Table 1). We considered that *P. virginalis* are mainly sold as ornamental species and are artificially released into urban lakes. Therefore, we believed accessible

Table 1 A multicollinearity test retained environmental variables to model the distribution of *Procambarus virginalis*

Variables	
BIO1	Annual mean temperature
BIO3	Isothermality (mean diurnal range/temperature annual range)
BIO4	Temperature seasonality (standard deviation × 100)
BIO12	Annual precipitation
BIO13	Precipitation of wetted month
BIO14	Precipitation of the driest month
HII	Human influence index
Distance	Distance to the drainage system
WTC	Water temperature of coldest month (January)

water systems and urban development with high population density were important. The HII is a global dataset that includes human population density, land use, and infrastructure. HII is based on population density, human land use, infrastructure, and accessibility (Earthdata 2005). Also, cold water temperature in winter was added as a variable that can explain the possibility of establishment. Winter water temperatures are considered important for establishment potential, as water temperatures below 15°C can limit the growth and reproduction of *P. virginalis* (Seitz et al. 2005). Water temperature data was converted into spatial data using inverse distance weighted interpolation from measurements taken at 1,061 locations in South Korea (Khouni et al. 2021). Furthermore, projected bioclimatic datasets from 2040 to 2060 and 2060 to 2080 were obtained from the new WorldClim 2.1 database, MIROC6 (https://worldclim.org). We assessed future suitability by applying climate change scenarios according to shared socioeconomic pathways (SSP). SSP considers various socioeconomic factors, such as demographics, economic development, ecosystems, resources, systems, and technological development (Riahi et al. 2017). SSP has climate scenarios for continued moderate (SSP2-4.5) or severe (SSP5-8.5) greenhouse gas emissions. All environmental data were accessed as of July 2024.

Ensemble species distribution model

We used an ESDM to assess the habitat suitability of three regions (EU, NA, and ASIA) and the possible invasion risk of *P. virginalis* in South Korea. ESDM was assembled using Biomod2 package in R programming with eight modeling methods (R Core Team 2021; Thuiller et al. 2024), namely Artificial Neural Networks (ANN), Flexible Discriminant Analysis (FDA), General Linear Models (GLM), General Additive Models (GAM), General Boosted Models (GBM), Classification Tree Analysis (CTA), Multiple Adaptive Regression, Splines (MARS), Random Forests (RF), and MaxEnt. To assess the habitat suitability for three regions, we used 310 presence points and generated 1,000 pseudo-absence points in 10 iterations (three times the number of presence suggested by Biomod2 based on Barbet-Massin et al. (2012). To predict invasion risk in South Korea, we used 39 presence points and generated 120 pseudo-absence points in 10 iterations. In the model-ensemble process, the GLM and GBM algorithms require updated arguments. The GLM function defined the given formula as quadratic, and the Akaike information criterion (AIC) served as the information criterion for the stepwise selection approach. There were 1,000 decision tree arguments in the GBM function. Each algorithm was run 10 times, for a total of 80 runs for the eight algorithms. For cross-validation, split the training and testing sets in a ratio of 80:20 and run 20 iterations. We chose the median for true skill statistics (TSS) because it is a static that has the advantages of Kappa and can compensate for the limitations of unimodal curve responses (Allouche et al. 2006). We computed an ensemble model with probabilities of models weighted by their evaluation scores using the EMwmean function in biomod2 (Ruzzier et al. 2024) and selected those with TSS > 0.8 for integration to generate an ensemble model.

In addition, the variable importance was calculated by shuffling a single data variable based on the random-forest algorithm in biomod2. The importance was calculated as the correlation between the shuffled data to exclude variable effect and the given data. The smaller the correlation between two predictions from shuffled and given data, the more important the variable is in the model (1- Pearson's correlation coefficient between shuffled and given predictions).

Ecological niche comparison

We used the method of Broennimann et al. (2012) and Guisan et al. (2014) to investigate the extent to which the three regions' climatic niches overlap. To assess the niches of the three regions, presence points were calculated using the ESDM's average cutoff value (> 0.64) of habitat suitability. Next, we ran a principal component analysis of the habitat (PCA-env) using integrated bioclimatic variables by presence point, and Schoener's D was calculated. Schoener's D measures niche overlap and ranges from zero (no overlap) to one (complete overlap). Niche conservatism was measured by comparing niche stability, expansion, and unfilling between the two regions using PCA (Guisan et al. 2014). The expansion (E) is the extent to which the invaded niche extends beyond the native niche, stability (S) is the extent to which the invaded niche overlaps the native niche, and unfilling (U) is the extent to which habitat is available, but its distribution is not yet established. The lower the expansion and unfilling, the higher the stability, and the less the species' niche changes, making it conservative. Niche equivalency and similarity tests were also conducted using a 95% confidence interval to test the null hypothesis of similar and equivalent niches by comparing it to random niche overlap between primary and invaded regions (Broennimann et al. 2012). Both tests were repeated 1,000 times. Finally, the six climatic variables were examined separately to establish the extent of overlap between the regions. Calculations were performed using the 'ecospat' package (Di Cola et al. 2017).

Results

Habitat suitability of three regions

Considering single models for a global scale with three regions, the RF model had the best performance (TSS = 0.992 and ROC = 0.988). The ANN model showed the lowest TSS and ROC values (TSS = 0.839 and ROC = 0.949, respectively), and all eight models that met the criteria were used. An ESDM was used to assess the habitat suitability of EU and NA, the primary habitat of *P. virginalis*, and ASIA (Fig. 2). Areas with high habitat suitability (0.8–1.0) were

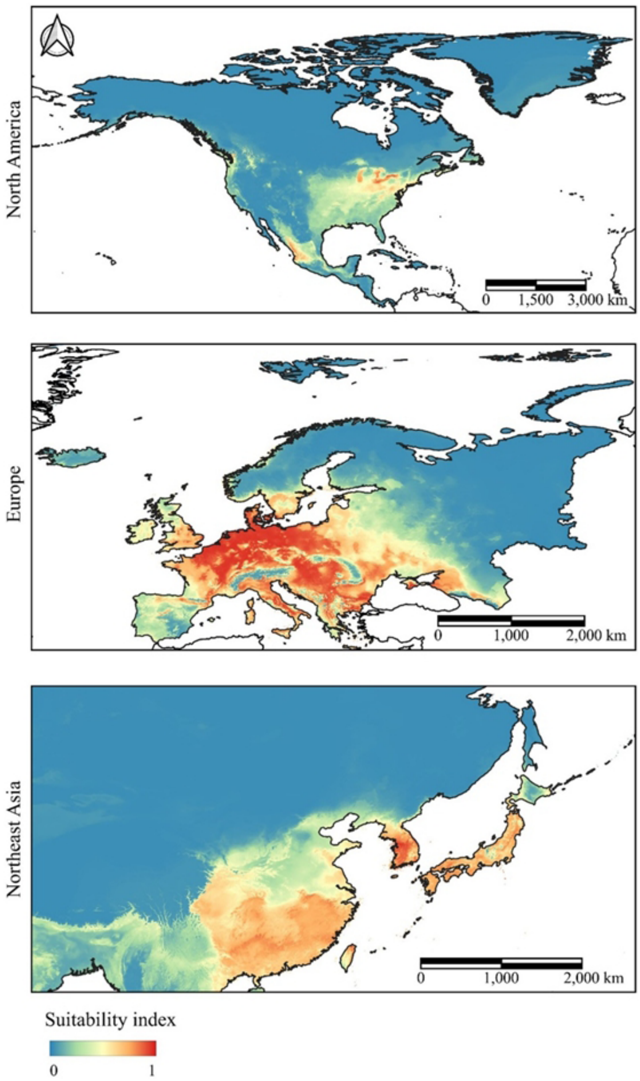

Fig. 2 Habitat suitability map for *Procambarus virginalis*, produced by the ensemble species distribution model projections on the current climate using six bioclimatic variables. The scale represents the habitat suitability index, ranging from 0 (least-suitable) to 1 (most-suitable habitat).

the largest in the EU (2,610,446 km^2), covering 14.8% of the total EU region. ASIA region also showed a large area of high habitat suitability (480,585 km^2). In particular, South Korea (74.5%) had a higher suitable area ratio relative to its total area than Japan (22.2%) and China (2.4%). In the NA region, it showed high suitability in the eastern region, including Florida (119,109 km^2). NA is limited to the eastern region, making up 0.3% of the total area, which is smaller than EU region.

Risk of *P. virginalis* invasion into South Korea

Considering individual models for South Korea, the GLM model had the best performance (TSS = 0.978 and ROC = 0.989). The CTA model showed the lowest TSS and ROC values (TSS = 0.978 and ROC = 0.981, respectively), and all eight models that met the criteria were used. In most models measuring the invasion risk in South Korea, the HII was identified as the most critical component, with a relative importance between 0.129 and 0.832 (Table 2). Important precipitation-related bioclimatic variables were BIO13 (precipitation of the wettest month) and BIO14 (precipitation of the driest month). BIO4 (temperature seasonality) was shown to have an importance score comparable to precipitation in several models. In the FDA model, the temperature during the coldest month was deemed the most important variable.

The suitability from ensemble models (ranging from 0 to 1) was considered as the probability of invasion, and the risk was classified at 0.25 intervals (Fig. 3). In the current climate, sub-regions at high risk of *P. virginalis* invasion are densely populated, including Seoul, the capital of Korea (Fig. 3). Moreover, the southern coastal and island locations where *P. virginalis* has not yet been confirmed were assessed as risky. The risky sub-region gradually increased in models that used SSP 2-4.5 and SSP 5-8.5 scenarios. By 2050, the areas at moderate and low risk expanded by 57% (SSP 2-4.5) and 69% (SSP 5-8.5), respectively, compared to the current model. Under the SSP 5-8.5 scenario in 2070,

Table 2 Importance of the selected variables by algorithm in governing the distribution of *Procambarus virginalis*

	GAM	GBM	GLM	CTA	RF	ANN	FDA	MARS	MaxEnt
BIO1	0.160	0.000	0.116	0.002	0.022	0.012	0.178	0.122	0.001
BIO3	0.066	0.031	0.141	0.127	0.092	0.022	0.079	0.118	0.015
BIO4	0.134	0.001	0.017	0.005	0.005	0.188	0.181	0.133	0.010
BIO12	0.108	0.093	0.019	0.157	0.111	0.064	0.036	0.028	0.043
BIO13	0.172	0.006	0.151	0.007	0.064	0.269	0.150	0.139	0.042
BIO14	0.082	0.031	0.094	0.040	0.054	0.029	0.036	0.069	0.334
HII	0.129	0.832	0.272	0.639	0.513	0.278	0.132	0.221	0.472
Distance	0.025	0.000	0.007	0.002	0.003	0.073	0.008	0.015	0.012
WTC	0.124	0.006	0.182	0.020	0.118	0.064	0.200	0.155	0.071

The relative importance of each variable was presented.
GAM: General Additive Models; GBM: General Boosted Models; GLM: General Linear Models; CTA: Classification Tree Analysis; RF: Random Forests; ANN: Artificial Neural Networks; FDA: Flexible Discriminant Analysis; MARS: Multiple Adaptive Regression, Splines; MaxEnt: Maximum Entropy Model; HII: human influence index; WTC: water temperature of coldest month.

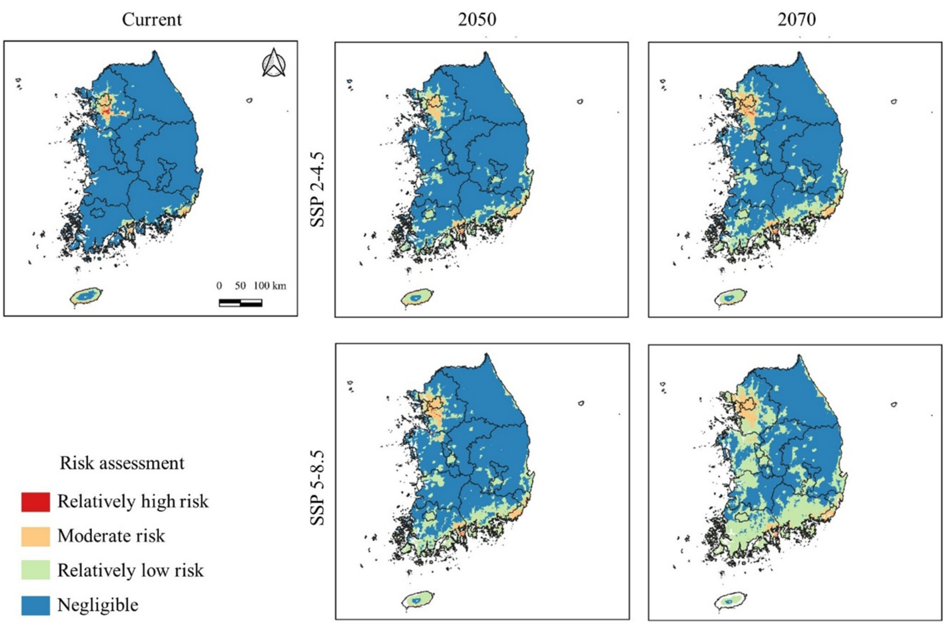

Fig. 3 Risk assessment of *Procambarus virginalis* introduction into Korean peninsula under climate scenarios. Distribution maps for 2050 and 2070 are shown under SSP2-4.5 or SSP5-8.5 scenarios. In the ensemble species distribution models applied with the nine variables in Table 1, the risk was divided into four levels.

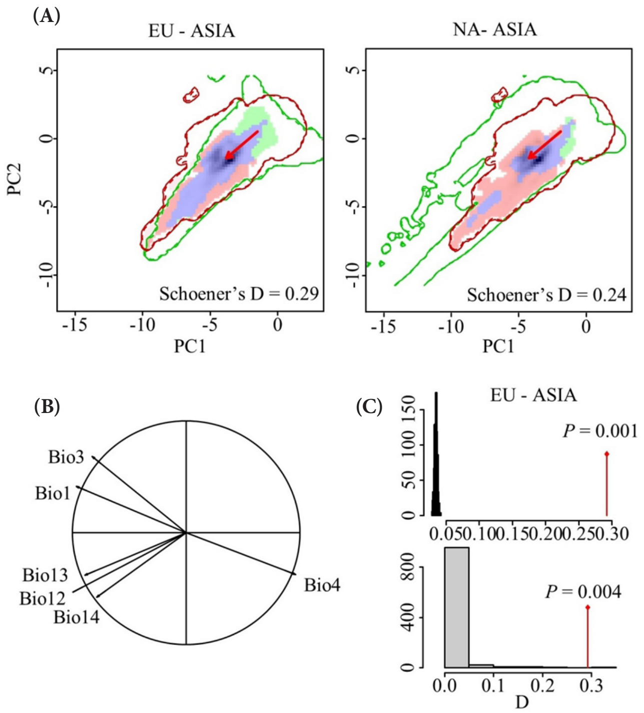

Fig. 4 Ecological niche comparison of *Procambarus virginalis* in three regions: Europe (EU); North America (NA); Northeast Asia (ASIA). (A) Niche overlap between EU, NA and ASIA. Red and green range indicate expansion and unfiling area, respectively. Purple range indicate overlapping niches, and red arrow represented shift of niche centroid. (B) The correlation circle shows the variable importance along the first two principle axes. (C) Niche equivalency and similarity tests each with 1,000 replications of EU-ASIA comparison. Red line indicated observed Schoener's D.

Table 3 Results of niche comparison test for *Procambarus virginalis* between regions

	D	Expansion (E)	Stability (S)	Unfilling (U)
ASIA-EU	0.292	0.036	0.964	0.289
BIO1	0.329	0.137	0.863	0.025
BIO3	0.315	0.001	0.999	0.059
BIO4	0.818	0.000	1.000	0.002
BIO12	0.438	0.001	0.999	0.494
BIO13	0.326	0.019	0.981	0.944
BIO14	0.607	0.003	0.997	0.001
ASIA-NA	0.240	0.188	0.812	0.292
BIO1	0.201	0.489	0.512	0.000
BIO3	0.505	0.015	0.985	0.000
BIO4	0.372	0.011	0.989	0.000
BIO12	0.271	0.164	0.836	0.005
BIO13	0.210	0.453	0.547	0.896
BIO14	0.593	0.019	0.981	0.000

Values of niche overlap (Schoener's D index) and niche dynamics indices (Expansion, Stability, and Unfilling) in Europe (EU), North America (NA), and Northeast Asia (ASIA) regions, considering each climatic variable separately.

the sub-region at risk expanded the most, accounting for 38% of South Korea's total geographic range (100,266 km^2). However, the sub-region at relatively high risk was reduced under these scenarios.

Niche overlap between the primary regions and Northeast Asia

According to the PCA of the three regions, the first two components explained 62.9% (PC1) and 19.5% (PC2) of the variability in the six bioclimatic variables (Fig. 4C). PC1 was strongly and negatively related to BIO1 and BIO3 but positively related to BIO4. In contrast, PC2 was negatively related to the precipitation variables (BIO12, BIO13, and BIO14).

The niche overlap between the primary regions (EU and NA) and the recently introduced region (AISA) of *P. virginalis* was modest (Schoener's D = 0.29 and 0.24), following the classification scheme of Rödder and Engler (2011) (Table 3, Fig. 4). The similarity test revealed that *P. virginalis*' climatic niche in AISA is more similar to its niche in EU than would be expected by chance ($p = 0.004$; Fig. 4). The equivalency test also adopted the alternative hypothesis that the observed overlap between the native and invaded niche is higher than if the two niches are randomized ($p = 0.001$; Fig. 4). The niche shift from EU to AISA had a conservative tendency, with S = 0.964 and E = 0.036 (Table 3). Niche conservatism in NA and AISA showed no significant similarity or equivalence, indicating climatic niche variations between the two regions. The niche stability of NA and AISA was also relatively low (0.812), implying that the overlap between NA and AISA was not strict. The niche centroid from EU and NA to AISA shifts to places with smaller seasonal temperature fluctuations and higher precipitation (Fig. 4A).

The results comparing the niches for each of the six bioclimatic variables confirmed high overlap between regions in BIO4 and BIO14. In the EU and ASIA, Schoener's D was the highest at 0.818 in BIO4, and moderate overlap was also confirmed in the variables related to precipitation (BIO12, BIO13, and BIO14). These variables showed conservative niche changes with stability higher than 0.980. The results compared to NA were similar, but relatively low Schoener's D indices were calculated.

Discussion

Habitat suitability of *P. virginalis*

P. virginalis is a decapod believed to have originated in EU or NA (Martin et al. 2007; Sanna et al. 2021). Its extensive habitable environment and parthenogenetic reproduction allow it to be aggressively invasive (Martin et al. 2016). This study used a SDM and a niche comparison to evaluate the likelihood of *P. virginalis* invasion and establishment in South Korea. *P. virginalis* displayed great adaptability in EU, its primary habitat, as well as South Korea, where survey data were included (Fig. 2). Although reports and news of *P. virginalis* occurrences are available in many countries, they are frequently not included in existing databases (Chucholl and Pfriffer 2010). As a result, the suitability of *P. virginalis* for AISA may have been underestimated. Nevertheless, this study confirms that *P. virginalis* can be introduced and established in AISA.

When invasive species are introduced into new ranges, their environmental niches typically shift (Aravind et al. 2022). On the other hand, *P. virginalis* is a parthenogenetic species with very simple genetic diversity, but it has been successfully established in several European countries and other climatic regions, such as Madagascar (Andriantsoa et al. 2019; Feria and Faulkes 2011). Although the niche overlap between EU and AISA was low in the current study, the equivalence and similarity tests revealed significant niche overlap. The environmental niche in NA is extensive, yet there is no significant niche overlap (Fig. 4, Table 3). However, NA's relatively high unfilling (U = 0.292) indicates an imbalance between genuine occurrence data and suitable habitats, implying that *P. virginalis* has a high potential for expansion (Cunze et al. 2018). As a result, we suggest that *P. virginalis* has a broad fundamental niche rather than a niche shift.

Although *P. virginalis* is found in the invaded region outside its native range, the invaded region may also be within the fundamental niche range where *P. virginalis* can survive and reproduce (Qiao et al. 2017). Therefore, global information on the realized niche where *P. virginalis* are identified is still needed to determine niche shift in the invaded region (Aravind et al. 2022). We argue that many countries need to share information on *P. virginalis* occurrence.

The expansion of *P. virginalis* by human activity

In South Korea, there is a high risk of release into the natural ecosystem owing to human activity. HII was very important in ensemble models (Table 2), and most *P. virginalis* were raised as ornamental animals by individual breeders. Also, *P. virginalis* are mainly sold and traded personally. In particular, they are traded mainly in cities, including metropolitan areas, and the possibility of their introduction seems to be higher as the number of people who can purchase ornamental species increases. The release of *P. virginalis* due to the abandonment of breeding by humans is likely to occur primarily in rivers and lakes in megacities. Furthermore, human activities can increase the risk of establishment. The successful reproduction and establishment of *P. virginalis* rely heavily on water temperature during winter. The FDA, GAM, GLM, and MARS models also identified water temperature in the coldest month as an important variable (Table 2). However, *P. virginalis* is found near Jukdangcheon in South Korea, near a factory discharging warm water. This drainage system is well known as a habitat where tropical fish species (Poecilia reticulata) have been successfully established. If *P. virginalis* can survive the warm water discharged by the factory, it will show rapid population growth via parthenogenesis. Human-related factors indeed play an important role in the spread of invasive species (Gallardo and Aldridge 2013; Hulme 2009; Rodríguez-Rey et al. 2019). Therefore, it seems essential to consider human-related variables to improve the explanatory and predictive accuracy of models (Menuz et al. 2015; Rodríguez-Rey et al. 2019). Given that the introduction and establishment of *P. virginalis* are influenced by human activity, regulations and education on the import and release of alien species should prevent this issue.

Risk of invasion and establishment in South Korea

There is concern about the risk of *P. virginalis* invasion into South Korea due to climate change. Given the uncertainty of climate change, this may be an overblown concern, but increasing the area of suitable habitat could increase the likelihood of establishment upon release. The sub-regions of the Korean peninsula with intermediate and low invasion threats increased significantly in both SSP2-4.5 and SSP5-8.5 scenarios, and they expanded over time (Fig. 3, Table S1). The increased risk was visible not only in the sub-regions where individuals were confirmed but also in the southern seas and islands (Fig. 3). The precipitation and river water temperature on the Korean peninsula are projected to rise. Precipitation is related to the climatic conditions that increase the niche centroid movement of *P. virginalis* (Fig. 4A, C). However, owing to the limited occurrence data, sub-regions with relatively high risks were fewer in the climatic scenarios. Data in small sub-regions underestimated the risk (Mainali et al. 2015). Nevertheless, we contend that the climate of South Korea is more suitable for the survival and reproduction of *P. virginalis*. Therefore, the alien SDM should prioritize sub-regions with a high risk of future *P. virginalis* invasion and conduct efficient monitoring. Although human behavior in releasing *P. virginalis* into the wild is unpredictable, the risk of invasion should be assessed, and regular on-site surveys should be conducted to prevent its establishment.

In this study, the southern parts of the Korean peninsula were designated as sub-regions at risk of invasion based on their actual occurrence. Because *P. virginalis* is a freshwater species, the total area assessment will likely be more comprehensive than the actual range. There are few rivers or ponds where it can live in southern Korea and on the islands, but it was assessed as a risk area. Therefore, further studies are needed based on additional survey sites and small river maps. However, we aimed to assess the invasion potential of *P. virginalis* in a broad range and propose priority survey areas, and we consider these sub-regions to be cautious.

Conclusions

In this study, the distribution of *P. virginalis* was forecast using an ESDM to assess the rate of alien species invasion in South Korea. An ensemble model can forecast species distribution more accurately than a single model in a small region (Guo et al. 2015). However, habitat suitability for alien species may be underestimated due to a lack of occurrence data in the region being invaded. Therefore, we compared the niche with the primary habitat regions and determined the extent to which the climatic niches overlapped. AISA, which includes the Korean peninsula, has a climate comparable to that of EU. Even with the current climate, the Korean peninsula is a suitable habitat for *P. virginalis*, and the invaded range is expected to increase in the future. A limitation of this study is that the occurrence data of *P. virginalis* may be insufficient when compared to the true distribution. There could be numerous regions where it is habitable but has not yet been examined, such as NA, where the "Unfilling" range is extensive. Furthermore, the effective invasion of *P. virginalis* has been documented in Madagascar, a country with a climate distinct from that of EU (Feria and Faulkes 2011). Therefore, regular monitoring of invasive species and sharing occurrence data are necessary to meet the common goals of preventing and eliminating the invasion of alien species.

Supplementary Information

Supplementary information accompanies this paper at https://doi.org/10.5141/jee.24.087.

Table S1. Area change (%) by habitat suitability for *Procambarus virginalis* under current and SSP scenarios for 2050 and 2070.

Abbreviations

SDM: Species distribution models
ESDM: Ensemble species distribution models
VIF: Variance inflation factor
HII: Human influence index
SSP: Shared socioeconomic pathways
ANN: Artificial Neural Networks
FDA: Flexible Discriminant Analysis
GLM: General Linear Models
GAM: General Additive Models
GBM: General Boosted Models
CTA: Classification Tree Analysis
MARS: Multiple Adaptive Regression, Splines
RF: Random Forests
MaxEnt: Maximum Entropy Model

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Author's contributions

HJ conceived the ideas, checked the database, analyzed model, visualized results, and wrote the manuscript. JHC conceived the ideas, analyzed model, visualized results, and reviewed the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

References

Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol. 2006;43(6):1223-32. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Andriantsoa R, Jones JPG, Achimescu V, Randrianarison H, Raselimanana M, Andriatsitohaina M, et al. Perceived socio-economic impacts of the marbled crayfish invasion in Madagascar. PLoS One. 2020;15(4):e0231773. https://doi.org/10.1371/journal.pone.0231773.

Andriantsoa R, Tönges S, Panteleit J, Theissinger K, Carneiro VC, Rasamy J, et al. Ecological plasticity and commercial impact of invasive marbled crayfish populations in Madagascar. BMC Ecol. 2019;19(1):8. https://doi.org/10.1186/s12898-019-0224-1.

Aravind NA, Shaanker MU, Bhat HNP, Charles B, Uma Shaanker R, Shah MA, et al. Niche shift in invasive species: is it a case of "home away from home" or finding a "new home"? Biodivers Conserv. 2022;31:2625-38. https://doi.org/10.1007/s10531-022-02447-0.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol. 2012;3(2):327-38. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Bhagwat SA, Breman E, Thekaekara T, Thornton TF, Willis KJ. A battle lost? Report on two centuries of invasion and management of Lantana camara L. in Australia, India and South Africa. PLoS One. 2012;7(3):e32407. https://doi.org/10.1371/journal.pone.0032407.

Blackburn TM, Bellard C, Ricciardi A. Alien versus native species as drivers of recent extinctions. Front Ecol Environ. 2019;17(4):203-7. https://doi.org/10.1002/fee.2020.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, et al. A proposed unified framework for biological invasions. Trends Ecol Evol. 2011;26(7):333-9. https://doi.org/10.1016/j.tree.2011.03.023.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, et al. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr. 2012;21(4):481-97. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Chucholl C, Pfeiffer M. First evidence for an established Marmorkrebs (Decapoda, Astacida, Cambaridae) population in Southwestern Germany, in syntopic occurrence with *Orconectes limosus* (Rafinesque, 1817). Aquat Invasions. 2010;5(4):405-12. https://doi.org/10.3391/ai.2010.5.4.10.

Chucholl F, Fiolka F, Segelbacher G, Epp LS. eDNA detection of native and invasive crayfish species allows for year-round monitoring and large-scale screening of lotic systems. Front Environ Sci. 2021;9:639380. https://doi.org/10.3389/fenvs.2021.639380.

Cunze S, Kochmann J, Koch LK, Klimpel S. Niche conservatism of Aedes albopictus and Aedes aegypti - two mosquito species with different invasion histories. Sci Rep. 2018;8(1):7733. https://doi.org/10.1038/s41598-018-26092-2.

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, et al. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography. 2017;40(6):774-87. https://doi.org/10.1111/ecog.02671.

Earthdata. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). 2005. https://doi.org/10.7927/H4BP00QC. Accessed 19 Jul 2024.

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, et al. Crossing frontiers in tackling pathways of biological invasions. BioScience. 2015;65(8):769-82. https://doi.org/10.1093/biosci/biv082.

Feria TP, Faulkes Z. Forecasting the distribution of Marmorkrebs, a parthenogenetic crayfish with high invasive potential, in Madagascar, Europe, and North America. Aquat Invasions. 2011;6(1):55-67. https://doi.org/10.3391/ai.2011.6.1.07.

Gallardo B, Aldridge DC. The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. J Appl Ecol. 2013;50(3):757-66. https://doi.org/10.1111/1365-2664.12079.

GBIF.org. GBIF occurrence download. 2024. https://www.gbif.org/occurrence/search. Accessed 14 Jul 2024.

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C. Unifying niche shift studies: insights from biological invasions. Trends Ecol Evol. 2014;29(5):260-9. https://doi.org/10.1016/j.tree.2014.02.009.

Guo C, Lek S, Ye S, Li W, Liu J, Li Z. Uncertainty in ensemble modelling of large-scale species distribution: effects from species characteristics and model techniques. Ecol Modell. 2015;306:67-75. https://doi.org/10.1016/j.ecolmodel.2014.08.002.

Gutekunst J, Maiakovska O, Hanna K, Provataris P, Horn H, Wolf S, et al. Phylogeographic reconstruction of the marbled crayfish origin. Commun Biol. 2021;41:1096. https://doi.org/10.1038/s42003-021-02609-w.

Hulme PE. Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol. 2009;46(1):10-8. https://doi.org/10.1111/j.1365-2664.2008.01600.x.

Khouni I, Louhichi G, Ghrabi A. Use of GIS based Inverse Distance Weighted interpolation to assess surface water quality: case of Wadi El Bey, Tunisia. Environ Technol Innov. 2021;24:101892. https://doi.org/10.1016/j.eti.2021.101892.

Lehan NE, Murphy JR, Thorburn LP, Bradley BA. Accidental introductions are an important source of invasive plants in the continental United States. Am J Bot. 2013;100(7):1287-93. https://doi.org/10.3732/ajb.1300061.

Lipták B, Mrugała A, Pekárik L, Mutkovič A, Gruľa D, Petrusek A, et al. Expansion of the marbled crayfish in Slovakia: beginning of an invasion in the Danube catchment? J Limnol. 2016;75(2). https://doi.org/10.4081/jlimnol.2016.1313.

Mainali KP, Warren DL, Dhileepan K, McConnachie A, Strathie L, Hassan G, et al. Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. Glob Chang Biol. 2015;21(12):4464-80. https://doi.org/10.1111/gcb.13038.

Martin P, Kohlmann K, Scholtz G. The parthenogenetic Marmorkrebs (marbled crayfish) produces genetically uniform offspring. Naturwissenschaften. 2007;94(10):843-6. https://doi.org/10.1007/s00114-007-0260-0.

Martin P, Thonagel S, Scholtz G. The parthenogenetic Marmorkrebs (M alacostraca: D ecapoda: C ambaridae) is a triploid organism. J Zool Syst Evol Res. 2016;54(1):13-21. https://doi.org/10.1111/jzs.12114.

McGeoch MA, Buba Y, Arlé E, Belmaker J, Clarke DA, Jetz W, et al. Invasion trends: an interpretable measure of change is needed to support policy targets. Conserv Lett. 2023;16(6):e12981. https://doi.org/10.1111/conl.12981.

Menuz DR, Kettenring KM, Hawkins CP, Cutler DR. Non-equilibrium in plant distribution models–only an issue for introduced or dispersal limited species? Ecography. 2015;38(3):231-40. https://doi.org/10.1111/ecog.00928.

Naimi B, Araújo MB. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography. 2016;39(4):368-75. https://doi.org/10.1111/ecog.01881.

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? Ecography. 2014;37(2):191-203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.

National Institute of Ecology. Investigating ecological risk of alien species. 2022. https://www.nie.re.kr/streamdocs/view/sd;streamdocsId=N0k-sGRJe6VHjAfO3uW7Tm4fe-5X0_PhPjycyi5QeKc?pType=POP. Accessed 13 Jul 2024.

Nentwig W. Pathways in animal invasions. In: Nentwig W, editor. Biological invasions. Springer, Berlin, Heidelberg; 2008. p. 11-27.

Park HR, Rahman MM, Park SM, Choi JH, Kang HJ, Sung HC. Risk assessment for the native anurans from an alien invasive species, American bullfrogs (Lithobates catesbeianus), in South Korea. Sci Rep. 2022;12(1):13143. https://doi.org/10.1038/s41598-022-17226-8.

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, et al. Scientists' warning on invasive alien species. Biol Rev Camb Philos Soc. 2020;95(6):1511-34. https://doi.org/10.1111/brv.12627.

Qiao H, Escobar LE, Peterson AT. Accessible areas in ecological niche comparisons of invasive species: recognized but still overlooked. Sci Rep. 2017;7(1):1213. https://doi.org/10.1038/s41598-017-01313-2.

R Core Team. R: a language and environment for statistical computing. 2021. https://www.r-project.org/. Accessed 14 Jul 2024.

Riahi K, van Vuuren DP, Kriegler E, Edmonds J, O'Neill BC, Fujimori S, et al. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: an overview. Global Environ Change. 2017;42:153-68. https://doi.org/10.1016/j.gloenvcha.2016.05.009.

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL. Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr. 2013;83(3):263-82. https://doi.org/10.1890/13-0183.1.

Rödder D, Engler JO. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob Ecol Biogeogr. 2011;20(6):915-27. https://doi.org/10.1111/j.1466-8238.2011.00659.x.

Rodríguez-Rey M, Consuegra S, Börger L, Garcia de Leaniz C. Improving Species Distribution Modelling of freshwater invasive species for management applications. PLoS One. 2019;14(6):e0217896. https://doi.org/10.1371/journal.pone.0217896.

Ruzzier E, Lupi D, Tirozzi P, Dondina O, Orioli V, Jucker C, et al. A two-step species distribution modeling to disentangle the effect of habitat and bioclimatic covariates on *Psacothea hilaris*, a potentially invasive species. Biol Invasions. 2024;26(6):1861-81. https://doi.org/10.1007/s10530-024-03283-9.

Sánchez O, Oficialdegui FJ, Torralba-Burrial A, Arbesú R, Valle-Artaza JM, Fernández-González Á, et al. *Procambarus virginalis* Lyko, 2017: a new threat to Iberian inland waters. Ecol Evol. 2024;14(5):e11362. https://doi.org/10.1002/ece3.11362.

Sanna D, Azzena I, Scarpa F, Cossu P, Pira A, Gagliardi F, et al. First record of the alien species *Procambarus virginalis* Lyko, 2017 in fresh waters of Sardinia and insight into its genetic variability. Life (Basel). 2021;11(7):606. https://doi.org/10.3390/life11070606.

Seitz R, Vilpoux K, Hopp U, Harzsch S, Maier G. Ontogeny of the Marmorkrebs (marbled crayfish): a parthenogenetic crayfish with unknown origin and phylogenetic position. J Exp Zool A Comp Exp Biol. 2005;303(5):393-405. https://doi.org/10.1002/jez.a.143.

Sheppard NLM, Pham J, Ricciardi A. Influence of reproductive state and temperature on the functional response of the marbled crayfish, *Procambarus virginalis*. Biol Invasions. 2024;26(1):9-16. https://doi.org/10.1007/s10530-023-03166-5.

Suarez AV, Tsutsui ND. The evolutionary consequences of biological invasions. Mol Ecol. 2008;17(1):351-60. https://doi.org/10.1111/j.1365-294X.2007.03456.x.

Thuiller W, Georges D, Gueguen M, Engler R, Breiner F, Lafourcade B, et al. biomod2: ensemble platform for species distribution modeling. R package version 4.2-6-2. 2024. https://biomodhub.github.io/biomod2/. Accessed 14 Jul 2024.

Turbelin AJ, Diagne C, Hudgins EJ, Moodley D, Kourantidou M, Novoa A, et al. Introduction pathways of economically costly invasive alien species. Biol Invasions. 2022;24(7):2061-79. https://doi.org/10.1007/s10530-022-02796-5.

Vogt G. Evaluation of the suitability of the parthenogenetic marbled crayfish for aquaculture: potential benefits versus conservation concerns. Hydrobiologia. 2021;848(2):285-98. https://doi.org/10.1007/s10750-020-04395-8.