Potential spreading risk of an invasive snail species (*Pomacea canaliculata*) in freshwater habitats of Asia

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The invasive success of the freshwater snail species (*Pomacea canaliculata*) continues to wreak havoc around the world. The present study was initiated to analyse spatial trend and associated environmental conditions related to the invasive success of *P. canaliculata* in Asia. Systematic searches were performed to identify relevant studies through different databases, and appropriate statistical methods like spatial autocorrelation, standard deviational ellipse method and PCA were used to generate new knowledge on this species. The potential invasive range of this species is between 40°N and 40°S lat. The present study reveals that the spatial distribution of *P. canaliculata* is most significantly correlated with human population density, followed by humidity, temperature and precipitation. Moreover, the grazing rates are dramatically affected by nutrient content of freshwater macrophytes. Spatial autocorrelation analysis result indicates clustered dispersion pattern of this snail, and standard deviational ellipse depicts the invasion trend of *P. canaliculata* moving from East Asia to potential areas in South and West Asia. We therefore conclude that *P. canaliculata* is likely to be the ‘next harmful visitor’ to South and West Asian countries.

Keywords. Freshwater macrophytes, invasive species, *Pomacea canaliculata*, spreading risk.

*POMACEA CANALICULATA* (also known as golden apple snail) is a native species of South America1–3, and was first introduced to Asia in 1980 through South China from Argentina for aquaculture purposes4. Later, *P. canaliculata* was introduced to southeast Asia primarily for aquaculture and food purposes5–7. After introduction, this species thrived in freshwater habitats of marshes, ponds and ditches5 and has become a significant pest in its non-native ranges causing severe impacts on freshwater ecosystems4,8,9. As a macrophyte grazer, this species has caused serious damage to freshwater wetlands in terms of diminishing wetland functions and services10. This invasive species has caused substantial economic loss to countries in Southeast and East Asia in particular3. Furthermore, *P. canaliculata* is also an intermediate host for *Angiostrongylus vasorum*, which causes infectious disease of human eosinophilic encephalitis6. Based on the damage caused to freshwater ecosystems, *P. canaliculata* is considered as one of the worst invasive species in the world1 (Figure 1).

The high rate of survival and fecundity enables successful establishment of a species in a new environment11. In Thailand, *P. canaliculata* was able to survive in the new environment by outcompeting the native species, i.e. Thai native snail (*Pila scutata*), and thus become a successful invader throughout that country10. Rapid growth and distribution of *P. canaliculata* in Southeast Asia suggest that phenotypic plasticity of this species could support its successful invasion in this region12. As phenotypic plasticity is a result of natural selection, we can identify the areas with high risk of being invaded by this species by summarizing the general characteristics of invaded habitats. Such identification and prediction of potential areas of invasion of this snail will be important for a better understanding to implement management activities and policies.

In this study we used quantitative forecasting methods that link with spatial statistics to predict the directional trend to spatial distribution of this snail. As such, we focus on several aspects: (1) the dispersal pattern of *P. canaliculata* in the global range; (2) the distribution variation in recent years; (3) the key environmental factors that will affect invasion success and regulate spatial distribution pattern, and (4) the potential habitats of the snail.

Methods

A systematic survey was carried out using scientific databases and search engines, followed by relevant analysis. The keyword combinations of *P. canaliculata* OR apple snail AND distribution* AND freshwater* AND vegetation* OR macrophytes* AND growth* AND plasticity* in the title were used. By this method, comprehensive
studies (88 scientific articles and reports) which were carried out from 1994 through 2017 were identified. Approximately 82.56% of the published studies was carried out between 2010 and 2015, of which 37% was primarily done in East Asian counties.

Data extraction method

Based on the vast data of this species, we reveal the global distribution pattern of P. canaliculata and crucial factors responsible for its drastic distribution in Southeast and East Asia. Locations of the snails collected from different articles and web pages which cited them were used to identify habitats of snails and hence to prepare snail distribution maps. Google Earth was used to identify latitudes and longitudes, when such data were not provided. Arc Map software (version 10.2.2) was used to draw distribution maps. Maps available on ArcGIS on-line and satellite images were used to extract statistics on human population density, rainfall, average temperature and minimum temperature of the habitats of this snail. Elevation data were extracted using ASTER GDEM of USGS Earth Explorer13. Average annual relative humidity of the identified habitats was extracted from Climate Research unit, University of East Anglia, UK14. Further, data extraction from figures in peer-reviewed publications was carried out using Plot Digitizer software15.

Statistical analysis

Principle component analysis (PCA) was performed on environmental parameters and further on properties of plants related to feeding preference of this snail to explore the major factors that determine the invasive success of the snail. Spatial autocorrelation, if any, out in the distribution of this snail was determined using Moran I statistics. Thus, Moran’s I value was used to determine whether the pattern was clustered, dispersed or random. The Moran’s I index for spatial autocorrelation for a given variable is defined as

\[ I = \frac{n}{S_0} \sum \frac{\sum w_{ij}(x_i - \bar{x})(x_j - \bar{x})}{\sum (x_j - \bar{x})^2}, \]

where \( n \) is the total number of features indexed by \( i \) and \( j \), \( x \) the variable of interest; \( \bar{x} \) the mean of \( x \), \( S_0 \) the aggregation of all spatial weights and \( w_{ij} \) is the spatial weight between features \( i \) and \( j \).

Standard deviational ellipse (SDE) method was used to reveal directional trend and hence degree of spatial dispersion of invasion of P. canaliculata across different geographical areas. In the present study, we considered one standard deviation to demonstrate the distribution that accounted for 68% of all input variables of snail densities and environmental conditions.
SDE is represented as

\[ SDE_x = \sqrt{\frac{\sum_{i=1}^{n} (x_i - \bar{x})^2}{n}}, \quad (2) \]

\[ SDE_y = \sqrt{\frac{\sum_{i=1}^{n} (y_i - \bar{y})^2}{n}}, \quad (3) \]

where \( x_i \) and \( y_i \) are the coordinates of feature \( i \), \( \{\bar{x}, \bar{y}\} \) depicts mean centre of the features, and \( n \) depicts the total number of features.

The angle rotation of SDE is given by the following equations

\[ \tan \theta = \frac{A + B}{C}, \quad (4) \]

\[ A = \left( \sum_{i=1}^{n} \bar{x}_i^2 - \sum_{i=1}^{n} \bar{y}_i^2 \right), \quad (5) \]

\[ B = \left( \sum_{i=1}^{n} \bar{x}_i^2 - \sum_{i=1}^{n} \bar{y}_i^2 \right) + 4(\bar{x}_i, \bar{y}_i)^2, \quad (6) \]

\[ C = 2 \sum_{i=1}^{n} \bar{x}_i, \bar{y}_i, \quad (7) \]

where \( \bar{x}_i \) and \( \bar{y}_i \) are deviations of the \( x \) and \( y \) coordinates from the mean centre.

The standard deviation for the \( x \) and \( y \) coordinates is given as

\[ \sigma_x = \sqrt{\frac{\sum_{i=1}^{n} (\bar{x}_i \cos \theta - \bar{y}_i \sin \theta)^2}{n}}, \quad (8) \]

\[ \sigma_y = \sqrt{\frac{\sum_{i=1}^{n} (\bar{x}_i \sin \theta - \bar{y}_i \cos \theta)^2}{n}}. \quad (9) \]

**Results**

Figure 2 shows the distribution pattern of \( P. canaliculata \) across the world. It is preferentially distributed across regions with an average temperature of 20–25°C, and minimum temperature of 10–15°C (Figure 3). Moreover, noticeable snail population density was observed in areas of average annual precipitation of 1500 mm.

In Figure 4, the first three axes explain 96% (49.39% + 30.57% + 16.68%) of the total variation in environmental data. There is significant positive correlation between snail density and human population density. Furthermore, snail density is also positively correlated with humidity, temperature and precipitation. The result of spatial autocorrelation statistics shows significant spatial correlation in snail density in different geographical regions. The Moran’s I value is 1.36 (> 0.5; \( P < 0.5 \)), suggesting that distribution of \( P. canaliculata \) was more spatially clustered.

Figure 5 shows the directional trend and dispersion pattern of \( P. canaliculata \) in different geographical regions. SDE reveals directional trends of how snails are spreading based on environmental conditions. The orientation of the ellipse indicates that the direction of \( P. canaliculata \) is more likely to be established in freshwater areas of tropical and subtropical regions in South and West Asia.

Feeding preference of the snail on various plant species differs. Certain plant properties are important in determining feeding preference of the snail (Figures 6 and 7). In Figure 7, the first two axes explain 91% (0.7423 + 0.1683) of the total variation in the considered properties of plants. Feeding rates of snails are highly influenced by phosphorus content, followed by nitrogen content in plants. The grazing rates are dramatically affected by the phenolic and dry matter content of plants (Figure 7).

**Discussion**

Environmental factors are key determinants of the spatial distribution of species all over the world. Climate change is one of the leading factors determining the distribution pattern of species across the world. So changes in temperature and rainfall influence the spreading of biological invaders.

According to our results, \( P. canaliculata \) invaded and thrived in ecoc regions of temperate coastal rivers and floodplain rivers in some areas of Europe and East Asia, and tropical floodplain rivers and wetlands in East Asia. However, native distribution of snails is mostly confined to areas of temperate coastal rivers, and tropical and subtropical upland rivers, i.e. between 20°S and 40°S lat. However, invasion was also recorded between 40°N and 40°S lat (Figure 2). And its invasion prefers to low elevation (<50 m) areas (Figure 3 e). Comparing with its native distribution (tropical, subtropical and temperate wetlands in South America), its invasion expands to tropical, subtropical and temperate wetlands both in south and north hemisphere.

The significant positive correlation between snail density and human population density indicated that introduction, colonization and dispersal of the snail are highly affected by human activities. A few freshwater snails are traditionally delicious cuisine in some countries. \( P. canaliculata \) was also introduced into East Asia in 1980 as a supplementary protein source. Our analysis of the
distribution pattern is also in accordance with this result. Another factor crucial to invasive success of this species is relative humidity (Figures 3d and 4). Dramatically high densities of snail occurred in habitats with relative humidity of 60–80%. It has been reported that the survival of this snail is significantly correlated with relative humidity, and the optimal value is 59.8–77.1% (mean 69.3%)\(^8\).

The present study revealed that snail density is correlated with temperature. This snail species can tolerate a wide range of temperatures, from 10°C to 28°C. An earlier study also indicated that survival of this snail was correlated with temperature, and significant growth was observed at temperature between 16.6°C and 28.3°C (mean 22.4°C)\(^8\). It was reported that survival rates of these snails were negatively correlated with temperature (100% for 15°C and 20°C, 95.83% for 25°C and 87.5% for 30°C)\(^9\). Although this snail generally grows at 10°–28°C (Figure 3a)\(^20\), a few previous studies revealed that this snail can even survive in dramatic low temperatures, i.e. below 0°C (Figure 3b)\(^9\). Such a result indicates the overwintering ability of this species in subtropical and temperate regions. Potential distribution of high biomass of \textit{P. canaliculata} was predicted at coastal and inland Mediterranean areas in Europe (Figure 2)\(^7\). Interestingly, they have the adaptive capability of resistance to warmer climate to a certain extent by inducing several proteins to repair damage caused by heat stress\(^21\).

The maturity ages of \textit{P. canaliculata} present variation according to different environments. A laboratory experiment done in Hawaii, USA, revealed that maturity age of \textit{P. canaliculata} was 10 months, while it was 2 years...
The maturity age in Southeast Asian countries such as Philippines and Malaysia was 3–7 months. These results indicate that the maturity age could be self-regulated according to different environments and the changed maturity period induced population explosion in the invaded habitats rather than the native habitats. Breeding in *Pomacea* species could be influenced by temperature and relative humidity. In Southeast Asia, the fecundity of *P. canaliculata* was higher with 2400–8700 eggs/year (ref. 3), while in the US fecundity was about 4355 eggs/year (ref. 24). The average number of eggs in per clutch is highly variable in the native and invaded ranges, i.e. 42 eggs/clutch in the eastern coast of Uruguay, 68–208 eggs/clutch in the Philippines, and 97 eggs/clutch in both Hawaii and Taiwan Island.
According to IPCC\textsuperscript{26}, by the end of this century, global mean temperature will increase by 2.6°–4.8°C. It is evident that the Indian sub-continent will face more warming impact and hence there will be relatively high temperature in winter\textsuperscript{27}. As temperature increases, the species will move from their original ranges\textsuperscript{28,29}. Based on our results, this species shows enhanced ability of growth and distribution in the invaded areas, especially with greater capacity to spread in tropical and subtropical areas of Asia. Considering the climate change trend and environment characters, we further speculate that \textit{P. canaliculata} will have a trend of moving to potential habitats in South and West Asian countries (Figure 5).

The population size of the species could be determined by its consumption of food types and proportion of its consumption\textsuperscript{30}. \textit{P. canaliculata} is a macro-phytophagous snail. Its nutrient utilization ability varies with the type of nutrients available in plants. Chemical factors, such as the amount of phenolic compound, dry matter content, nitrogen and phosphorus content affect the feeding of this snail\textsuperscript{17,32}. The feeding rates were dramatically influenced by phosphorus content, followed by nitrogen content in plants. Macrophytes containing more phenolic and dry matter, and greater physical toughness in terms of more lignin and cellulose are less palatable\textsuperscript{16,31,32}. Freshwater plants like \textit{Ipomoea}, \textit{Amaranthus} and \textit{Apium} (Figures 6 and 7) are generally higher in nutrient content in terms of nitrogen and phosphorus, while lesser in physical toughness. Hence these macrophyte species are more palatable to \textit{P. canaliculata}. Furthermore, \textit{Eichornia} and \textit{Amaranthus} are also invasive weeds which have cosmopolitan distribution in freshwater bodies around the world. Our results indicated the potential damages by \textit{P. canaliculata} to wetlands rely on the macrophyte community composition\textsuperscript{16}. Previous studies further revealed that nitrogen and phosphorus contents in edible plants were positively correlated with growth and fecundity of the snail\textsuperscript{31}. Additionally, females can adjust the spawning time based on

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image1.png}
\caption{Directional trend of \textit{P. canaliculata} distribution in different geographical areas. (Map drawn using freely available GIS data\textsuperscript{16} with Arc GIS version 10.2.2.)}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image2.png}
\caption{Properties of freshwater macrophytes: (a) nutrients, (b) toughness and (c) dry matter content and feeding rates of \textit{P. canaliculata}.}
\end{figure}
Figure 7. PCA bi-plot showing axes 1 and 2 of PCA ordination of properties of plants (black arrows) and feeding rates (red arrow). Filled circles show the considered plant species.

the feeding nutrient level, which indicates that dietary flexibility also attributes to their rapid and successful distribution. The present study therefore ascertains the current spatial variation and future trend of invasion of *P. canaliculata* in Asia.

Conclusion

Growth and survival of *P. canaliculata* vary considerably with environmental factors and hence these factors determine the spatial distribution pattern of *P. canaliculata* across different regions in the world. Feeding preference of this species is determined by some traits of plants. Interestingly, the results of this study suggest that human population density, followed by relative humidity, temperature and precipitation affect snail density and thus facilitate its distribution. Thus, rapid distribution of *P. canaliculata* has occurred across the regions in humid Asia compared to other species living in the same habitats. Furthermore, *P. canaliculata* has the ability to invade rapidly in South and West Asia, in particular.

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