



Determining environmental drivers of global mud snail invasions using climate and hydroclimate models

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Abstract Climate change and invasive species represent two intertwined global environmental challenges profoundly affecting freshwater ecosystems. This study uses Ecological Niche Modeling along with risk screening to delve into the preferences and potential distribution of *Potamopyrgus antipodarum*, an invasive species, in relation to climate zones and habitat types, shedding light on the critical importance of coastal wetlands and high soil organic carbon

content in shaping habitat suitability. Our findings underscore that *P. antipodarum* exhibits a distinct affinity for cool temperate, moist climates, as well as temperate floodplain rivers, wetlands, and coastal areas. Notably, coastal wetlands, endowed with elevated soil organic carbon levels, emerged as pivotal habitats for this species. Projections indicated a significant expansion in North America, potentially extending into South America. Türkiye reveals an

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intriguing alignment between its habitat and the natural distribution areas of *P. antipodarum*, presenting potential for habitat contraction while still retaining a broader range compared to other regions. These potential expansions were predominantly driven by climate suitability, playing a pivotal role in the invasiveness of *P. antipodarum*, with anticipated future climate regimes exerting substantial influence on its dispersal capabilities.

Keywords New Zealand mud snail · Climate change · Ecological Niche Model · Coastal wetlands · Hydro-environmental characteristics

Introduction

Invasive species pose a growing threat by contributing to the escalating biodiversity crisis (Simberloff, 2013). They are a major driver to the loss of biodiversity, as their environmental adaptability and unique characteristics often allow them to outcompete native species (Bellard et al., 2016; Haubrock et al., 2021). Furthermore, invasive species can have substantial socioeconomic impacts on ecosystem services, such as diminishing the cultural benefits to humankind, and can negatively affect the global economy (Vilá et al., 2010; Cuthbert et al., 2021), exacerbating the need for ecological conservation efforts. The impacts of invasive species are particularly important on freshwater ecosystems due to the interconnected nature of freshwater systems facilitating the movement of invasive species across different regions (Reid et al., 2019; Soto et al., 2023). Furthermore, human activities, such as commerce and recreation that lead to hydromorphological alterations, can inadvertently facilitate the spread of invasive species in freshwater ecosystems (Hulme, 2009; Haubrock et al., 2020, 2022).

Global production and the arising economic competition have intensified as new markets and trade routes have emerged (Van Agtmael, 2007). The emergence of these new trade routes is paralleled by new economic developments and new products and goods transported globally (Hulme, 2009). Recent studies have shown that species have been transported to new habitats, directly or indirectly, through these novel trade routes (Alexandre da Silva et al., 2019; Balzani et al., 2022). Consequently,

these introductions have often resulted in species becoming invasive in their new habitats (Dukes and Mooney, 2004), enabled and facilitated by climatic and environmental changes modulating their ecological impact (Emiroğlu et al., 2023; Soto et al., 2023; Haubrock et al., 2024) as temperature increases and precipitation regimes change, leading to the formation of new suitable habitats (Rahel and Olden, 2008). Together, these factors contribute to the heightened risk of invasive species establishment and proliferation worldwide.

One case of an invasive species with a broad ecological tolerance is the New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843), which is a caenogastropod native to the freshwater lakes and streams of New Zealand and listed among the “100 worst invasive species” and ranked as the second worst invasive gastropod in Europe (Lowe et al., 2000). It has the ability to rapidly adapt to external stressors through an advantageous reproductive strategy and competitive traits (Duft et al., 2003; Alonso and Castro-Díez, 2008), which encompass both sexual and parthenogenetic reproduction (Zaranko et al., 1997; Dybdahl and Kane, 2005). *Potamopyrgus antipodarum* has successfully spread across vast parts of Europe, North America, South America, Australia, Asia, and Africa (Alonso and Castro-Díez, 2008; Taybi et al., 2021; Haubrock et al., 2022) where substantial ecological impacts on aquatic ecosystems have been observed. These successful invasions are facilitated by its ability to be transported through several taxa such as migratory birds (Boycott, 1936; Lassen, 1975; Ponder, 1988) and fish (trout and perch) (Bondesen and Kaiser, 1949; Haynes et al., 1985; Richards, 2002), surviving the passage through the digestive tract of fish and tolerating air exposure during transportation by waterfowl or fishing tools (Richards et al. 2004; Alonso and Castro-Díez, 2008; Vinson and Baker, 2008). These mechanisms contribute to *P. antipodarum*’s ability to successfully establish itself in new environments (Alexandre da Silva et al., 2019). While its long-distance transportation to Europe and America was through aquaculture products and recreation (Haynes et al., 1985; Geist et al., 2022), it can regionally disperse through algae and macrophytes (Alonso and Castro-Díez, 2008; Ribi and Arter, 1986). It has also been demonstrated by Alonso et al. (2019) that it has spread throughout the entire Iberian Peninsula and

is clearly in a spreading phase, making it extremely challenging to control, especially given its non-water mediated dispersion mechanisms (such as mud or birds).

To prevent an ecological pandemonium (Elton, 1942) and to protect natural habitats and endemic species, it is crucial to take proactive measures and prioritize the allocation of resources (Tarkan et al., 2022). One effective approach is to identify suitable habitats for non-native species and to assess potential risks. Risk screening methods, such as the AS-ISK (Copp et al., 2016), provide a valuable tool for evaluating the potential impact of non-native species in a given area (Tarkan et al., 2017). By conducting comprehensive risk screenings, we can acquire valuable insights into the potential invasiveness posed by non-native species, enabling us to prioritize appropriate preventive measures. These measures may entail implementing enhanced biosecurity protocols, enacting legislation to prohibit introductions, and identifying specific economic, cultural, or other aspects that are susceptible to threats from the invader, regardless of its current establishment status (Vilizzi et al., 2021). Leveraging risk assessments, conservation, or management efforts can concentrate on targeted interventions, thus safeguarding the delicate natural ecological equilibrium of ecosystems and the well-being of the species reliant on these ecosystems.

Potamopyrgus antipodarum has been brought to Europe and North America attached to ornamental plants, aquaculture products, recreational craft, and fishing gear (Haynes et al., 1985; Alexandre da Silva et al., 2019). In Türkiye, where the species has been introduced relatively recently, *P. antipodarum* was firstly recorded in the Aegean and Mediterranean regions (Bilgin, 1980), being reported from different Aegean freshwater ecosystems and one coastal marine area, West Mediterranean and Marmara to West Anatolia and the Black Sea (Odabaşı and Arslan, 2015; Odabaşı et al., 2019; Yıldırım et al., 2022). Until today, *P. antipodarum* has been reported from eighteen different Turkish localities, and according to Turkish records, it has spread from the west to the east of Türkiye, yet no comprehensive risk assessment has been conducted (Tarkan et al., 2021).

Understanding the ecological needs of invasive species with detrimental impacts like *P. antipodarum* is essential for their effective management (Stohlgren

and Schnase, 2006; Tobin, 2018). During the initial invasion phase, the most appropriate type of management aims to limit the invader's potential to spread, thus focusing on eradication programs (Haubrock et al., 2022). These limitations are usually based on the ecological characteristics and tolerance level of the invader. Determining the ecological requirements of the species in new habitat areas is limited to regions with very large and different climatic structures. Hence, to build a reliable Ecological Niche Model (ENM), which is widely regarded as an effective method for predicting the impact of climate change on the species distribution species in both marine and freshwater ecosystems (Elliot et al., 2015), it is crucial to use bioclimatic and environmental data to assess in which geographical areas a possibly very harmful invasive species can occur (Elith et al., 2010; Pili et al., 2020). In this study, we aimed to (1) utilize Ecological Niche Models (ENMs) to determine the potential distribution of the highly invasive species *P. antipodarum* in both its non-native ranges (Australia, Africa, North America, South America, Europe) and native range (New Zealand), with a focus on Türkiye where the species has recently been colonizing, (2) linking it to the outcome of a Türkiye-based risk screening, and to (3) determine whether measures could be taken to prevent or limit the distribution of the species following the indicated ecological niche of *P. antipodarum*. We also estimated the extent of climatically suitable potential areas worldwide by testing the hypotheses of reciprocal niche shift and conservatism to better understand potential invasion areas better, which could inform so-called deny and blacklists (Soto et al., 2023). Here, Ecological Niche Modeling is considered suitable for testing these hypotheses as it is a powerful tool to predict how climate change will influence the species distributions in freshwater ecosystems (Rahel and Olden 2008; Elliott et al. 2015), especially where the distributions of these species are strongly temperature driven and so influenced by latitudinal and altitudinal gradients (Forister et al. 2010; Chen et al. 2011).

Methods

Species occurrence records

For the analyses performed in this manuscript, we used occurrence and field sampling data compiled by the *Global Biodiversity Information Facility* (GBIF). In total, 154,151 global occurrence points were identified in the study, 154,114 from GBIF and 37 from literature, reported from different freshwater ecosystems and one coastal marine area from regions of Aegean, West Mediterranean and Marmara to West Anatolia and Black Sea (Yıldırım et al., 2022). We removed duplicate records and those without coordinates using the Wallace-2-shiny application (Kass et al., 2022). We continued with the remaining 30,002 GBIF and 37 sampling records (Fig. S1). The spatial scale of the selected predictors plays a crucial role in modeling; we specifically chose a grid of 2.5 arc minutes wide or about 5 km across at the equator (Deichmann et al., 2001; Hui 2022). Since we used 2.5-arc minutes climatic data in our study, we downscaled the occurrence data to 5 km. We rarefied records at 5-km intervals using the SDMtoolbox (Brown et al., 2017) in ArcGIS version 10.8.2 to eliminate duplicate points and prevent sampling bias occurrence and redundant information. Therefore, we retain a total of 8,189 occurrence points downscaled in the 5-km distance plane (Fig. S1).

Environmental variables and scenarios

We downloaded climate data for 1970–2000 encompassing 19 bioclimatic variables (Table S1) from WorldClim version 2.1 at a spatial resolution of 2.5 min (~5 km at the equator; Fick and Hijmans 2017). We obtained hydrological, physiographic, land cover, and soil data from HYDROATLAS (Linke et al., 2019; Lehner et al., 2022) using the ArcGIS version 10.8.2 conversion tool feature (Table S1). We extracted the Shared Socioeconomic Pathways (SSPs), low greenhouse gas emissions (SSPs126), and very high greenhouse gas emissions (SSPs585) (IPCC 2021; Riahi et al., 2017) from the sixth version of the Model for Interdisciplinary Research on Climate (MIROC), called MIROC6 climate models (Tatebe et al., 2019) to estimate future climate change for the 20-year intervals 2041–2060 (2050) and 2081–2100 (2100). Data for www.worldclim.org were

obtained from the Coupled Model Intercomparison Project Phase 6 (CMIP 6) (Eyring et al., 2016).

In Maxent (Maximum Entropy)—a machine learning modeling which can handle presence-only data—a set of scenarios is utilized to represent different future projections. These scenarios are designed to simulate various potential conditions or circumstances that may arise, such as different socio-economic pathways, climate change scenarios, or land use patterns. By incorporating these scenarios, the modeling process captures the range of possible environmental and socio-economic factors that could influence the species' distribution. This approach allows for a comprehensive analysis of how the species' habitat suitability may change in response to different future conditions, aiding in understanding its potential distribution patterns and informing conservation and management strategies.

Environmental Niche Modeling

We developed two models in this study: a climate and a hydroclimate model. Using only climatic variables, the climatic model determined the species' current and future habitat suitability. The hydroclimatic model determines habitat suitability by combining climate, hydrology, physiography, land cover, and soil data. Species distribution models are used to predict distribution changes due to climate change. When making predictions, it is essential to know how current and future changes will occur. For this purpose, we created a vector file (based on the centroids of the species ranges) by calculating the distribution changes between current and future Species Distribution Models, showing the magnitude and direction of the change. With these vector data, the direction in which the species will change its distribution in the future was determined (SDMtoolbox) (Brown et al., 2017). Also, based on habitat suitability maps for the species, this study calculated the mean Levins' B1 (inverse concentration) and B2 (uncertainty values) using ENMTools v1.3. (Warren et al., 2008). Levins' B2 value ranges from 0 to 1, with values near 0 indicating narrower niche breadths and values near 1 indicating broader niche breadths (Slatyer et al., 2013; Cai et al., 2021; Evans and Jacquemyn, 2022). Additionally, we used two indices Schoener's D (Schoener, 1968) and Hellinger's I (Warren et al., 2008) to evaluate niche

overlap with ENMTools. The values of Schoener's D and Hellinger's I range between 0 and 1, with 0 indicating a small degree of niche overlap and 1 indicating a high degree of niche overlap (Jiang et al., 2022).

The change in the distribution area of species within each region was measured in square kilometers. This measurement was then used to assess the future threat size to the species, based on the changes in their habitat area using the formula:

$$\text{HabitatChangeIndex} = f/c$$

where f is the future range expansion (range expansion km^2 + no change km^2) and c the current range (no change km^2 + range contraction km^2).

For invasion habitats, a value of zero indicates a stable threat, positive values indicate an increase in threat, and negative values indicate a decrease in threat. In case of native habitats, negative values start at -100 while positive values have no limit.

To reduce multicollinearity, we clipped the data to the study area (ArcGIS version 10.8.2) and tested for correlations using the variance inflation factor (VIF; Naimi et al., 2014), excluding variables with a $\text{VIF} > 10$. A total of 48 environmental variables (19 bioclim, hydrological, physiographic, land cover, and soil data) were correlated and thus excluded from the final models (Hydroclimatic model), retaining a total of 32 variables (Table S2, S3). We used eight bioclimatic variables to determine the future projection of the species (Table S2, S3). Maxent version 3.4.4 estimated the dispersal potential of the *P. antipodarum* (Phillips et al., 2023). In the settings section, we implemented automatic features with ten replicates with threshold rules, randomized tests, a maximum of 1000 repeated iterations, cross-validation using repeated runs, and maximum training sensitivity and specificity. Response curves show how each environmental variable affects the Maxent prediction. These graphs reflect the predicted suitability's dependence on the selected variable and the dependencies caused by correlations between the selected variable and other variables. By creating response curves in the model, the ranges of influence of environmental variables were determined. The evaluation of the models used the area under the curve (AUC). The AUC values range between 0 and 1; AUC values of less than 0.6 imply low

predicting ability, AUC values of 0.6 to 0.70 imply medium, between 0.7 and 0.8 indicate good result, and AUC value of 0.8 to 0.9 is considered excellent performance, 1 indicates 100% accuracy (Araújo et al 2005; Alexandre da Silva et al., 2019; Marchessaux et al., 2021; Alqadhi et al., 2022). All variables were transferred via ArcMap 10.8.2 to ASCII format for use in Maxent.

Risk screening

To assess the potential invasiveness of *P. antipodarum* in Türkiye, which was designated as a risk assessment (RA) area, we employed the Aquatic Species Invasiveness Screening Kit (AS-ISK v2.3.3). This tool is recognized for its reliability in assessing non-native species and has been proved effective in screening potential invasive aquatic organisms in various RA areas worldwide (Vilizzi et al., 2021). The screening process was carried out by Ali Serhan Tarkan and Naime Arslan, adhering to the "minimum standards" outlined in the European Commission Regulation on the prevention and management of invasive alien species (Roy et al., 2018). The AS-ISK screening protocol consists of 55 questions (Copp et al., 2016). The initial 49 questions focus on the Basic Risk Assessment (BRA) and examine the biogeographical and biological aspects of the species under assessment. The remaining six questions pertain to the Climate Change Assessment (CCA) and require the assessor to evaluate how future climate conditions may impact the risks associated with the introduction, establishment, dispersal, and impact of the species. Each screening question necessitates a response, a level of confidence in the response, and a justification.

Upon completing the screening, the species is assigned a BRA score and a BRA + CCA (composite) score, ranging from -20 to 70 and -32 to 82 , respectively. Scores below 1 indicate a low risk of invasiveness, while higher scores classify the species as posing a medium or high risk. The differentiation between medium- and high-risk levels is determined by a predefined threshold value. In this study, the threshold is based on the calibrated global BRA score of 13.25 for freshwater invertebrates (Vilizzi et al., 2021). The AS-ISK utilizes confidence levels associated with each question-related response, ranked as follows: 1 = low, 2 = medium, 3 = high, and

4 = very high. These confidence rankings align with those recommended by the International Programme on Climate Change (IPCC, 2005). Overall confidence levels CL_{Total} , as well as CL_{BRA} and CL_{CCA} , are calculated based on the allocated confidence level for each response across all 55 questions.

Results

Environmental Niche Modelling

The AUC value of the climatic modeling was 0.783%, while the AUC value of the hydro-environmental modeling was 0.785%. In this sense, all models are considered as “good.” In the hydro-environmental habitat suitability model, the most suitable habitats for the species were New Zealand, Europe, North America, South America, and Australia. Hydro-environmental characteristics modeling for Türkiye showed habitat suitability close to the natural distribution areas of the species (Table S4). With the outputs obtained as a result of climatological modeling, the current and future niche width change of the species was calculated. The species’ habitat suitability was accordingly highest in the native area, North America, and globally according to the SSPs 585_2100 scenario, in Europe according to the SSPs 585_2050 scenario, and in Türkiye, Australia, and South America according to the current scenario (Table S5).

Habitat areas where the species will gain, lose, and remain in the future were determined. The species distribution area, especially in North America, was determined to expand (Table 1). The species will

experience the highest habitat area contraction in Türkiye, but the suitability (niche breadth) of possible habitats for the species in Türkiye is higher than in other regions (Tables S4, S5).

Environmental Niche Modeling revealed the presence of suitable habitats for the species in South America (Fig. S3), although GBIF reported no records for this continent. The future distribution direction of the species was determined to follow a distribution route in the eastern Black Sea basin in Türkiye, northward in Europe, northwestward in North America, and southward in South America (Fig. 1). In future projections, the invasive range of *P. antipodarum* experienced both habitat loss and habitat expansions (Fig. 2). In North America, there is a noticeable northward shift in the species’ centroid, combined with a reduction in the overall suitable habitat similar to Europe but with a substantial habitat expansion. In Türkiye, the centroid shift is minimal, but there is a discernible expansion in habitat. South America showed a marked southward shift with habitat loss while for Australia the shift is mostly eastward, with the species gaining new suitable habitat areas. Lastly, in New Zealand (native range), the species experienced minimal habitat change with a slight gain in suitable areas.

The most influential environmental variables driving the distribution of *Potamopyrgus antipodarum* were Min Temperature of Coldest Month (BIO6), Precipitation Seasonality (Coefficient of Variation) (BIO15), and Precipitation of Coldest Quarter (BIO19) (Table S5). Among these variables, Min Temperature of Coldest Month (BIO6) had the highest impact on reducing the model’s predictive performance when omitted. Suitable habitat areas of the

Table 1 Changes in future distribution rate (%) suitable habitat area ratios of the species

Area	SSPs_126_2050	SSPs_126_2100	SSPs_585_2050	SSPs_585_2100
Australia	−17.3	−14.2	−30.9	−61.7
North America	9.3	5.6	21.8	50.9
South America	−8.9	−9.2	−8.7	−6.0
Europe	−22.8	−24.9	−26.9	−40.6
Türkiye	−20.8	−24.0	−36.8	−79.4
New Zealand	3.4	3.1	3.2	2.5
Globally	−0.02	−18.7	−18.8	−25.71

SSPs_126_2050—Shared Socioeconomic Pathways (SSPs): Optimistic scenario for 2050; SSPs_126_2100—Shared Socioeconomic Pathways (SSPs): Optimistic scenario for 2100; SSPs_585_2050—Shared Socioeconomic Pathways (SSPs): Pessimistic scenario for 2050—SSPs_585_2100—Shared Socioeconomic Pathways (SSPs): Pessimistic scenario for 2100

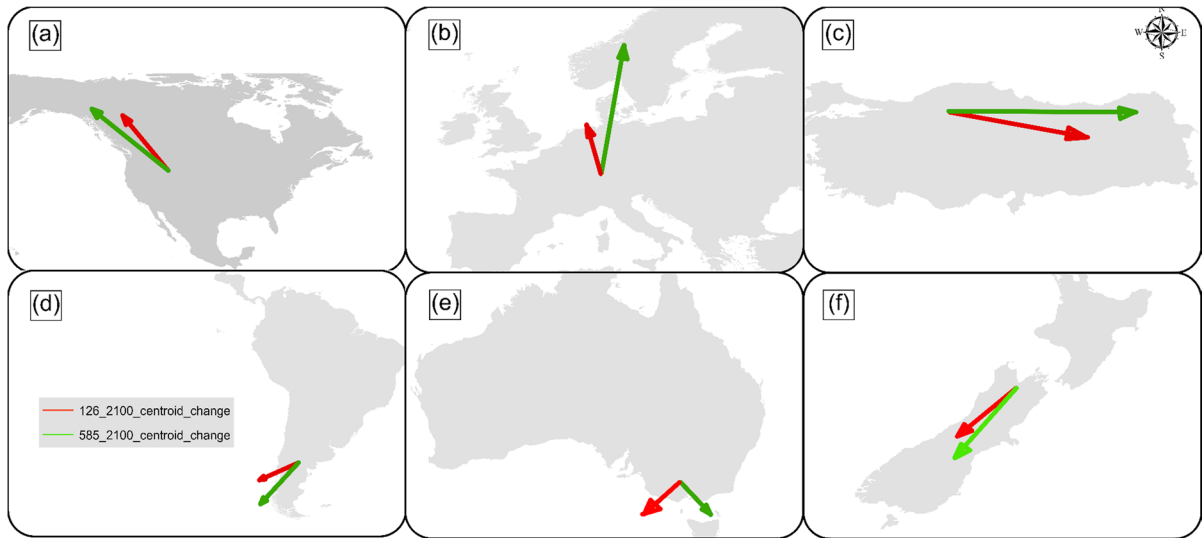


Fig. 1 Centroid shift of *Potamopyrgus antipodarum* climatic niche for two future SSPs scenarios 126 and 585 (2080_2100) in North America (a), Europe (b), Türkiye (c), South America (d), Australia (e), and New Zealand (f)

species were mostly the cool temperate and moist climatic zone, warm temperate and mesic climatic zone as well as temperate floodplain rivers, wetlands, and temperate coastal rivers (Fig. 3).

The calculated ROC curve showed how each environmental variable affected the Maxent prediction and determined the effect of each environmental variable on the habitat suitability of the species (Figs. S4a, b, S5a–f). Among the lithologic classes with the highest distribution of the species were Carbonate Sedimentary Rocks (SC) (Fig. S6). The most important wetland class was Coastal wetland (incl. mangrove, estuary, delta, and lagoon), and the most important soil structure variable was Organic Carbon Content in Soil. Habitat suitability for *P. antipodarum* was found to increase in areas with higher soil organic carbon content. Soil organic carbon content of 200 tons/hectare is the optimum amount for habitat suitability (Fig. S5a–f). The stream gradient was calculated as the ratio between the elevation drop within a given river stretch. The species is concentrated in rivers with low river gradient values, with decimeters per kilometer reaching a maximum at 0–200 and decreasing thereafter 400. The species does not prefer high volume rivers, high volume lakes, high volume lakes, and reservoirs and river habitats with a stream gradient greater than 200 dm (Fig. S5a–f).

Risk screening

Based on the calibrated global threshold value (i.e., 13.25), the Basic Risk Assessment (BRA) score for *P. antipodarum* in Türkiye indicates a high-risk category, with a score of 23 (Table S7). Considering the potential impact of climate change, the BRA score increases to 33, indicating an even higher risk for the species to become invasive in this risk assessment (RA) area under predicted climate change conditions (Table S7). Several factors and traits contribute to the increase in the BRA score, including a history of invasiveness in other regions, ecological persistence traits, and mechanisms of reproduction and dispersal. On the other hand, the absence of cultivation, resource exploitation, and tolerance attributed to the species in the RA area resulted in a decrease in the overall score. The mean confidence levels (CL) associated with responses to the BRA, Climate Change Assessment (CCA), and BRA+CCA questions are as follows: $CL_{BRA} = 2.55 \pm 0.09$, $CL_{CCA} = 2.17 \pm 0.17$, and $CL_{TOTAL} = 2.51 \pm 0.09$. These values indicate a medium-to-high level of confidence in all cases.

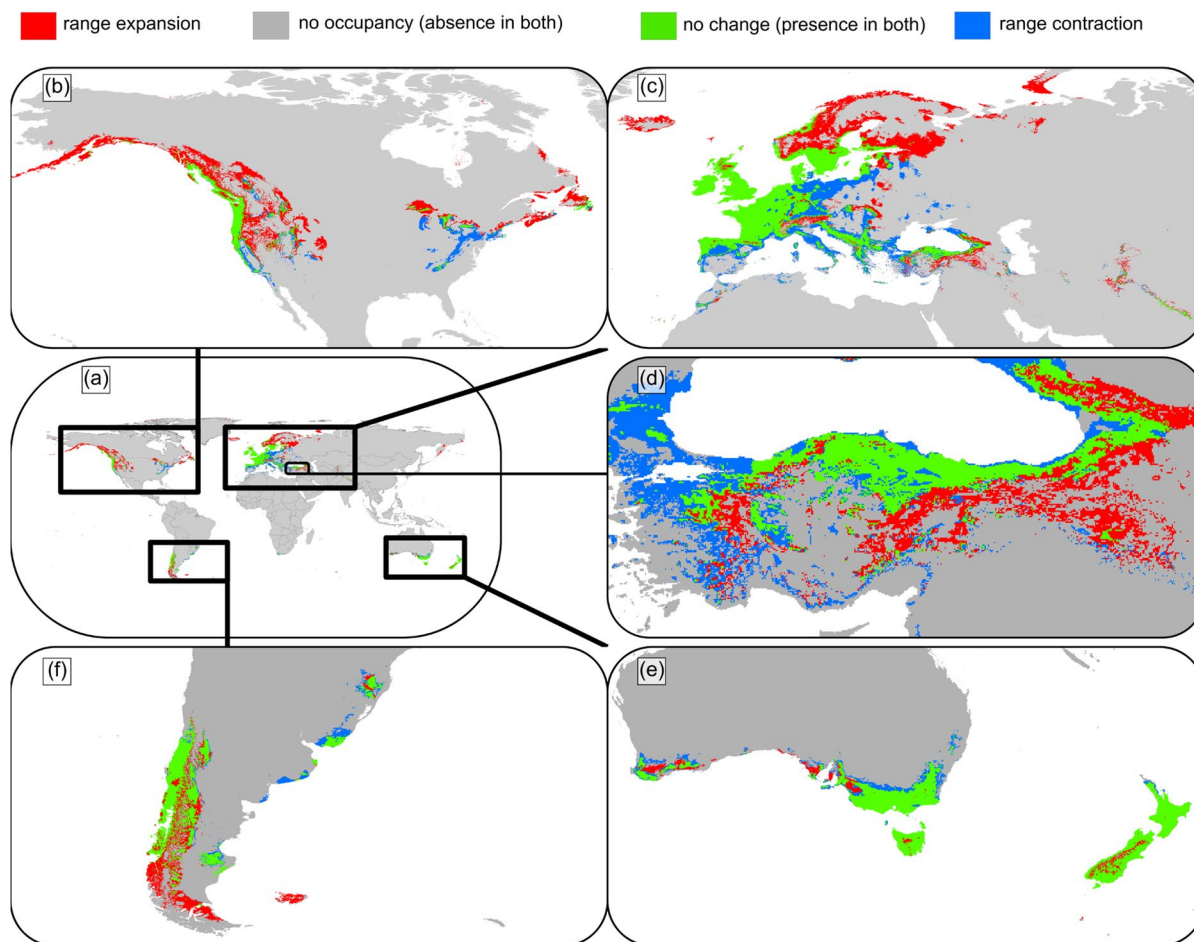


Fig. 2 Future habitat changes of *Potamopyrgus antipodarum* globally (a), focusing specifically on North America (b), Europe (c), Türkiye (d), Australia (e), and South America (f)

Discussion

Invasive species may be impacted by several aspects of climate change such as altered heat regimes, decreased lake ice cover, increased salinity, altered stream flow regimes, and increased water development activities such as canal and reservoir construction (Poff et al., 2002; Emiroğlu et al., 2023). Research on the evolution of river thermal regimes in various parts of the world to date indicates severe inclines, albeit to different extends (Marszelewski and Pius, 2016; Ptak and Nowak, 2017), advancing more quickly in European freshwaters than marine waters (EEA 2017), driven by a combination of human pressure and climate change (Gizinkas and Sojka, 2023). Here, our study sheds light on

the environmental preference of *P. antipodarum* for specific climatic zones and habitat types, emphasizing the importance of coastal wetlands and high soil organic carbon content in determining habitat suitability. Previous local studies on *P. antipodarum* have been conducted in the American West/Northwest, as well as in the other areas around the globe. These findings are congruent with our results and demonstrate the reliability of the selected variables used to predict the spread of *P. antipodarum* (Geist et al., 2022). The projections for its future distribution and the alignment between Türkiye's habitat and the species' natural distribution areas contribute to our understanding of potential range expansion and dispersal patterns. These findings are crucial for informing conservation strategies and

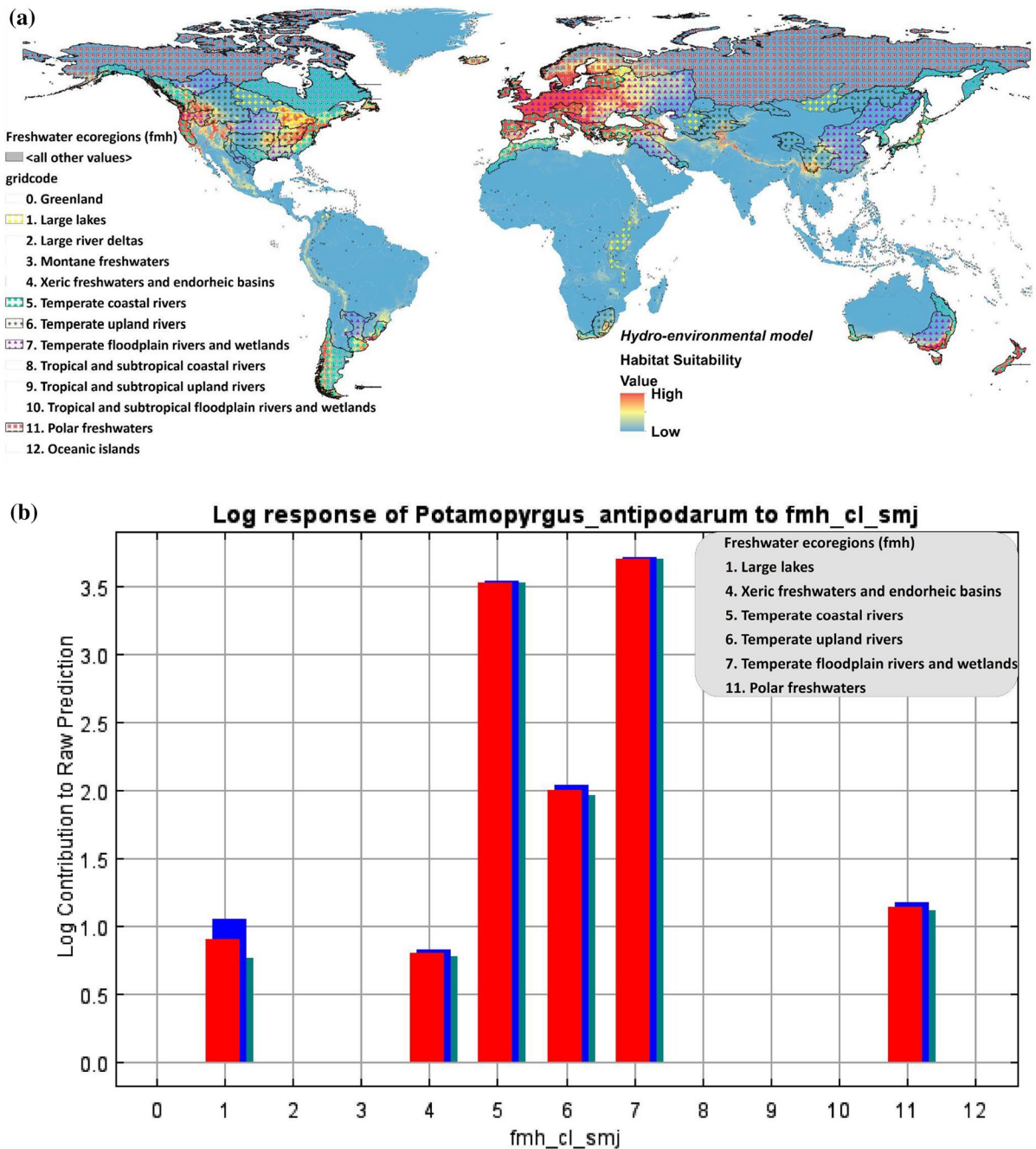


Fig. 3 Freshwater ecoregion and *Potamopyrgus antipodarum* hydro-environmental model distribution areas **(a)** and freshwater ecoregion classes of suitable habitat areas of *Potamopyrgus antipodarum* **(b)** (fmh_cl_smj; 1: large lakes, 2: large river deltas, 3: montane freshwaters, 4: xeric freshwaters and endorheic basins, 5: temperate coastal rivers, 6: temperate upland rivers,

7: temperate floodplain rivers and wetlands, 8: tropical and subtropical coastal rivers, 9: tropical and subtropical upland rivers, 10: tropical and subtropical floodplain rivers and wetlands, 11: polar freshwaters, 12: oceanic islands)

management actions aimed at mitigating the impacts of *P. antipodarum* in different geographic regions and preventing the spread through, e.g., deny lists as well as local or regional legislation targeting relevant pathways (Geist et al., 2022).

Recent studies have focused on assessing potential distribution areas and modeling habitat suitability for various species, including *P. antipodarum* (Alexandre da Silva et al. 2019; Low et al., 2021; Vythalingam et al., 2022). These studies consistently indicate an expanding global distribution for *P. antipodarum*, with its range continuing to increase over time (Alexandre da Silva et al., 2019; Geist et al., 2022; Alonso et al., 2023). The recorded occurrences of *P. antipodarum* have shown a steady increase over time. In 2022, the Global Biodiversity Information Facility recorded 142,297 occurrences, which rose to 154,114 records by 2023 (GBIF.org, December 14, 2022; GBIF.org, May 26, 2023). This upward trend in both species range and recording points indicates the ongoing expansion of its distribution. Our study identified suitable habitats for *P. antipodarum* in previously unrecorded areas, aligning with previous research findings (Alexandre da Silva et al., 2019). Although the potential suitable habitat areas within Türkiye have narrowed (Table 1), the remaining habitats still exhibit relatively high suitability, comparable to the species' natural distribution area (Table S3, S4). There are significant implications for biosecurity and biodiversity (Geist et al., 2022; Alonso et al., 2023), as our results suggest that more suitable habitats for *P. antipodarum* exist than previously assumed, making it likely that this invader may establish robust populations in these new areas (Geist et al., 2022), suggesting that managers need to be vigilant about spread prevention and proactively minimizing potential impacts of the invasive species. Indeed, in terms of its distribution, our study projects significant expansion for *P. antipodarum*, primarily focused on North America. Moreover, the species' range is expected to extend northwestward in North America and eventually southward in South America. The adaptability of an invasive species within its habitat is of greater concern than the mere expansion of its distribution range, emphasizing the potential ecological impacts of *P. antipodarum*'s presence (Alonso et al., 2023).

Our study indicates that *P. antipodarum* exhibits a clear preference for specific climatic zones and habitat

types, including cool temperate and moist climatic zones, warm temperate and mesic climatic zones, as well as temperate floodplain rivers, wetlands, and coastal rivers. Notably, the Coastal wetland category, encompassing mangrove, estuary, delta, and lagoon habitats, emerges as the most crucial wetland class for the species. While *P. antipodarum* is commonly regarded as a freshwater invader in North America, there is an observed increase in its presence in brackish estuarine habitats and nearby aquatic environments (Gerard et al. 2003, Bersine et al. 2008, Davidson et al. 2008, Brenneis et al. 2011). Our analysis reveals that habitat suitability for *P. antipodarum* increases in areas characterized by high soil organic carbon content, with an optimum of 200 tons/hectare identified. As it pertains to the high organic content in the soil predicting the occurrence of *P. antipodarum*, we believe that high organic matter facilitates the establishment due to the excessive availability of nutrients. These specific habitat types provide the essential environmental conditions and resources necessary for the species' growth, reproduction, and overall survival (Kearney and Porter, 2009; Theuerkauf et al., 2022).

The case of Türkiye

Hydro-environmental drivers are important, especially in Türkiye where sensitive habitats are already threatened by pollution and habitat modification (Aksu et al., 2021). Our hydro-environmental modeling for Türkiye revealed a significant convergence between Türkiye's habitat and the natural distribution areas of *P. antipodarum* (Table S4, S5, Fig. S2, S3). However, it is important to note that while Türkiye is expected to face considerable habitat contraction, it exhibits higher suitability and a broader range of potential habitats compared to other regions (Emiroğlu et al., 2023). This projected distribution direction provides valuable insights into the species' potential for range expansion and dispersal. Considering future implications of the species, it is further projected that the invasive range will undergo a combination of habitat loss and acquisition of novel habitats. Conversely, minimal habitat attrition is anticipated in the native range while it augments appropriate habitats through the colonization of previously unexplored territories.

The elevated habitat compatibility in Türkiye can be primarily attributed to the freshwater and saltwater interfaces and disconnections, geographical, topographical, and climatic changes that occurred during the time it took for Türkiye to acquire its current landmass, which led to increased ecosystem diversity at the microhabitat and microclimate levels (Gümüþ et al., 2022). Our modeling outputs suggest that the Eastern Black Sea Basin in Türkiye could act as a potential future distribution direction (as a stepping stone) for the species. This interpretation stems from the historical isolation of this region as a basin during Türkiye's geological transformations. The Eastern Black Sea Basin, encompassing the provinces of Giresun, Trabzon, Rize, and Artvin, has been identified as one of the potential future distribution directions for *P. antipodarum*. Previous studies conducted on the upper layers of drilling in this region has provided evidence of a dominant and stable hydrology with a humid climate, indicated by the prevalence of *Picea* pollen and the retreat of mixed forests such as *Castanea* and *Fagus* in favor of spruce over the past 2000 years (Aytuğ et al., 1975). This ecological context aligns with the requirements of *P. antipodarum*, an opportunistic and invasive species known for its broad tolerance to environmental adaptability (Alonso and Castro-Díez, 2008). Our risk screening further supports its invasive potential in Türkiye, underscoring its high ecological adaptability and the consequent elevated invasion risk (Table S7).

Notably, climate suitability was identified as the most influential factor for the invasion success of *P. antipodarum*, especially projected future climate conditions which can significantly impact the species' dispersal capacity. In a study based on the analysis of 245 articles related to the ecological impacts, spatial distribution, population dynamics, dispersal vectors, and invasion success of *P. antipodarum*, it was noted that the conditions facilitating the species' invasion and colonization include stable hydrology, low stream velocity, high specific conductivity and moderate salinity (Geist et al., 2022). The North Anatolian Mountain Ranges, which comprise the entirety of the Black Sea coastal mountains and include the Eastern Black Sea region, are the most ancient mountains in Türkiye. These mountain ranges, which extend parallel to the coast, prevent the moist sea air from the Black Sea from reaching the inland areas in

this region. Hence, the distinct climatic disparities observed between the coastal and inland areas, particularly in the Eastern Anatolia Region located in the southern part of the Eastern Black Sea, along with the persistent influence of orographic rainfall along the coast, provide an explanation for the potential preference of *P. antipodarum* for the Black Sea region characterized by a humid and rainy climate. Furthermore, the variations in elevation within the Eastern Black Sea region (peaking at 4000 m) differ significantly from the elevations found in the Central (up to 1000 m) and Western Black Sea (around 2000 m) regions. Additionally, the presence of coastal plains and the continental shelf further contributes to the unique environmental characteristics of the Eastern Black Sea region.

Geist et al. (2022) reported that *P. antipodarum* has parthenogenetic reproduction strategy. The main event that distinguishes parthenogenetic reproduction from other forms of asexual reproduction is that the egg is activated by a variable other than sperm that acts like it. The known stimulator of this activation in surface waters is the increase in the amount of Ca and alkalinization (Tabakoğlu-Oğuz, 2001). Being high CaCO_3 content of the mountain streams in the Eastern Black Sea region of Turkey (Akin and Akin, 2007; Gültekin et al., 2012; Verép et al., 2020) explains the reason why these areas are preferred by the species as one of the future distribution directions. Also, stable hydrology and moderate salinity are suitable environmental conditions for facilitating the species invasion and colonization as mentioned in the study by Geist et al. (2022). Streams located in the Eastern Black Sea region are suitable habitats with these optimal conditions. In the research conducted in the upper layers of the Eastern Black Sea Region drillings, *Picea* pollen has become widespread and *Castanea* and *Fagus* have retreated in favor of *Picea* as a mixed forest in the last 2000 years (Aytuğ et al., 1975). This situation is considered to be an indication that a humid climate has a dominant and stable hydrology in line with the ecological demands of *P. antipodarum*, which is an opportunistic and invasive species with broad tolerance to environmental conditions.

Conclusion

Our projections provide valuable insights into the potential range expansion and dispersal patterns of *P. antipodarum*. This invasive species adaptability and spread pose potential risks to biosecurity globally (Gallardo et al., 2022). Our study emphasizes the intricate relationship between climate change, hydro-environmental characteristics, and the potential distribution and range expansion of the invasive species *P. antipodarum*. Our results suggested that the potential distribution and range expansion of *P. antipodarum* are closely linked to climate shift and hydro-environmental characteristics. Understanding these dynamics is essential for predicting and managing the impacts of invasive species on aquatic ecosystems. Although our search of the existing literature yielded limited studies on the impact of the species in Türkiye, the available data align with previous studies (Geist et al., 2022) in demonstrating the risk of *P. antipodarum* causing significant impact (Table S7). In non-native environments, high densities of *P. antipodarum* alter benthic communities, reducing native biodiversity, and competing with native molluscs for space and food (Riley et al., 2008; Geist et al., 2022). It also disrupts the ecosystem's nitrogen cycle by promoting nitrogen-fixing diatoms through substantial green algae consumption (Arango et al., 2009). These effects pose a severe threat to the rich and unique ecosystems of Anatolia, where endemic species are already at risk. Thus, the impact of climate change on invasive species spread calls for increased vigilance, rigorous research, and targeted conservation to safeguard vulnerable ecosystems. This study thus underscores the urgency of developing effective and sustainable strategies to manage the challenges presented by invasive species in the face of rapidly changing environmental conditions.

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Ethical approval and consent to participate Not applicable.

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