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Shipping and water diversion pathways expand the global area at risk from invasive freshwater bivalves

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Abstract

Invasive species affect freshwater ecosystems and economies worldwide, with their dispersal facilitated by human activities such as shipping and large water transfer projects. Here, we use the golden mussel (*Limnoperna fortunei*) as a model species and develop an integrated framework that combines a dispersal model for introduction risk with a species distribution model for establishment risk, using global shipping routes and water diversion projects as the main pathways. Our simulations reveal a expansion of high-risk basins over time, particularly after the 1990s, with coastal basins acting as invasion bridgeheads from which populations can spread inland. Several basins in North America, Europe, Australia, the Indochina Peninsula and the Amazon basin, although not yet invaded, emerge as environmentally suitable and increasingly connected, indicating elevated future invasion risk. Our study highlights the importance of implementing management strategies for invasive species, such as ballast water treatment and installing prevention measures in water diversion/transfer schemes.

Keywords: Invasive species, Biofouling, Global shipping, Inter-basin water diversion/transfer, Risk assessment

1 Introduction

Invasive species pose a remarkable and widespread threat to the environment, ecology, economy, and even human societal development on a global scale [1]. These species have the capacity to profoundly disrupt habitats and nutrient cycles, leading to biodiversity loss and even extinctions among already threatened species [2]. The estimated global cost of invasive species from 1970 to 2017 reached a staggering US$1.288 trillion, including both damage and management costs[3], quadrupling with each decade since 1970 [4]. Aquatic ecosystems, especially freshwater habitats, are particularly sensitive to biological invasions due to their high biodiversity, ecological connectivity, and intense human-mediated species exchange [5, 6, 7]. The introduction of aquatic invasive species, whether intentionally or accidentally, is often the result of human activities such as canal construction, maritime trade, tourism, and aquaculture [8, 9, 10, 11, 12]. These activities have contributed to an unprecedented rate of invasive species introductions into aquatic ecosystems, with the number of invasive species increasing by approximately 300% over the past 50 years [13]. For example, in the Laurentian Great Lakes, a new invader is detected approximately every 28 weeks [14].

Studies of biological invasions typically focus on particular stages within a broader invasion sequence that is often described as transportation, introduction, establishment and spread [15]. Among these stages, the establishment phase has received considerable attention in invasion biology, with numerous studies employing Species Distribution Models (SDMs). By correlating known occurrences with environmental variables, SDMs offer valuable insights into the potential range of invasive species and are widely used for establishment risk assessment[16, 17, 18]. However, SDMs primarily characterize the establishment component of invasion risk and generally do not explicitly represent the transport, introduction or spread stages of the invasion process, which are more directly linked to invasion pathways. These pathways have been analyzed using models such as network analysis [19, 20, 21] and probabilistic models [22, 23, 24] to quantify invasion risk along transport and introduction and subsequent spread. The pathway-focused models have provided important insights into how individual vectors contribute to invasion. But they often focus solely on specific pathways (e.g., ship cargo, ballast water, or aquaculture trade) or isolate a single stage of the invasion process, such as defining species survival probabilities during transport, without integrating the full sequence of invasion stages. Because the different stages of invasion are closely interdependent and their boundaries are often blurred in practice [25], there is a need for an integrated modelling framework that explicitly combines environmental conditions in recipient areas with the facilitating effects of multiple invasion pathways.

The pathways for the dispersal of aquatic invasive species encompass both intentional and unintentional vectors. But long-distance dispersal is dominated by a few pathways- commercial shipping and inter-basin water transfers (IBWTs) [26, 27], especially for inconspicuous water-borne species that are transported as unintentional stowaways. And both of these two pathways have increased markedly since the 1950s, in parallel with a rise in the proportion of invasive species capable of aquatic transfer (Fig. 1e). Commercial shipping, accounting for around 90% of global trade [28], is a main vector for introducing invasive species into aquatic ecosystems, with approximately 69% of aquatic non-indigenous species attributed to shipping-related pathways such as ballast water discharge and hull fouling [29]. By forming an intricate global network across continents (Fig. 1b), the commercial fleet serves as the primary vector for the intercontinental transfer of marine non-indigenous species [30]. Meanwhile, IBWTs within continents play a pivotal role in invasive species dispersal by artificially establishing direct connections between previously isolated basins, leading to substantial water transfer volumes across basins (Fig. 1c). By removing biogeographic barriers, IBWTs effectively create invasion highways [31] and thereby accelerate the dispersal of invasive species [32]. Moreover, they can modify the ecological conditions of recipient water bodies [33], enhancing the potential for invasive species to establish and thrive. makes it possible to capture both long-distance introductions and subsequent spread, in which invaded basins can act as secondary sources for new invasions. A clearer understanding of these pathway-driven dynamics can, in turn, inform more effective prevention and management strategies for aquatic invasive species.

In this study, we developed an integrated model that combines habitat suitability with artificial pathways to assess the invasion risk posed by the golden mussel (*Limnoperna fortunei*), a representative invasive freshwater bivalve. The golden mussel shares the transferring mode with many other aquatic invasive species, including mollusks and crustaceans with planktonic larvae, fishes with buoyant eggs, and various microbiomes, which collectively account for an increasing proportion of recorded aquatic invasions (Fig. 1d, f; Supplementary Notes 1). Unlike many ornamental or commercially valuable species, the golden mussel is neither attractive nor economically important, and thus human-mediated movement predominantly occurs through unintentional transport rather than deliberate release. Its life history, particularly the planktonic larval stage, has enabled it to establish in Hong Kong since 1965 and in South America since the 1990s primarily through ballast water discharge [34] and to expand inland *via* IBWTs and waterways [35, 36]. However, its absence in North America raises questions about potential limiting factors that have so far prevented its invasion process. Understanding these factors is crucial for predicting and managing the future spread of golden mussels and other water-borne invasive species.

Using invasive golden mussels as a model system, we aim to (1) construct a model that couples artificial transport pathways with habitat suitability to estimate invasion risk arising from the introduction and establishment stages; (2) create a global risk map based on artificial inter-basin connections, ballast water management, and environmental factors; and further (3) discuss control strategies informed by the distribution of risk derived from our modelling results and specific case scenarios.

2 Results

2.1 Global distribution of golden mussel invasion risk

The invasion risk of the golden mussel displayed temporal and spatial variability across global river basins (Fig. 2a–f). Before the Industrial Revolution, maritime transportation was limited to small sailing vessels primarily navigating coastlines. As a result, invasion risk remained largely confined to the its native distribution areas till 1960s, including the Pearl River basin, the Yangtze River basin, and Southeast Asia. A major turning point occurred with the advent of containerized shipping in 1956. By 1966, container vessels had become the dominant mode of maritime transport, catalyzed by rapid post-World War II growth in global trade and shipbuilding. Although global seaborne trade was still under one billion tons during this initial phase, the increased volume and reach of shipping led to a marked expansion in high-risk areas. Initially, these areas were concentrated in Asia, but as globalization progressed, risk basins extended to North America, Europe, Australia, and the Indochina Peninsula (Fig. 2a–f).

This temporal trend in invasion risk aligns with a general upward trajectory observed in invasive mollusks globally (Fig. 2g), reflecting the intensifying connectivity brought about by global maritime networks. However, the rate of risk increase varied by continent. Asia experienced broad risk expansion, largely due to the availability of suitable habitats and the short distance to the native habitat of golden mussel. Therefore, it exhibited the highest proportion of invaded areas, rising from 12.97% in 1960 to 16.25% in 2020. In North and South America, high-risk areas emerged predominantly along the east coast of the United States and in central South America after the 1950s. Both continents showed increasing trends beginning in the 1980s, reaching 1.44% and 1.09%

invaded area by 2020, respectively. Europe followed a similar trajectory but with a lower level of invasion (0.18%). In contrast, Africa and Australia remained largely unaffected, with invaded proportions remaining below 1.1% and 0.12% by 2020, respectively, likely due to limited exposure or less favorable environmental conditions. Across all continents, the proportion of suitable but uninvaded habitats declined modestly as more areas transitioned into exposed or invaded states, highlighting the ongoing dispersal of species driven by expanding global trade and maritime connectivity. Notably, the model identified several regions with high predicted invasion risk that have yet to be invaded, emphasizing the importance of early detection and biosecurity measures (see section 3 for details).

2.2 Invasion risk in coastal and inland basins

The pathways of golden mussel invasion varied between coastal and inland basins. Spatially, invasion risk showed pronounced geographic clustering, with high-risk basins tending to occur near other high-risk basins and low-risk basins near other low-risk basins as indicated by a significantly positive Moran's I ($p < 0.001$; Table S1; Supplementary Notes 2). Against this background of risk aggregation, invasion risk consistently exhibited an outward pattern—spreading from coastal regions toward inland areas. This trend is evident in regions such as the eastern and western coasts of the United States, Australia, and South America, where coastal areas first show elevated risk that later expands inland (Fig. 3). To better compare the differences between coastal and inland regions, three representative years were selected: the initial ship trade year (1950), the present (2000), and the future projection (2040). In 1950, although overall invasion risk was low, coastal regions already showed significantly elevated risk compared to inland areas ($p = 1.85 \times 10^{-6}$), indicating their early vulnerability. By 2000, this disparity had widened markedly ($p = 2.65 \times 10^{-12}$), and the trend continued into 2040, with an even greater difference observed between the two groups ($p = 1.62 \times 10^{-27}$). And under both global and within-continent permutations, the observed coastal–inland mean difference remained more extreme than expected by chance (all $p < 0.001$), supporting the robustness of the contrast (Fig. S1). Coastal basins consistently showed higher invasion risk than inland basins across all examined years, primarily due to their direct exposure to maritime shipping and higher likelihood of serving as initial entry points. In contrast, invasion risk in inland basins increased more gradually, driven by secondary dispersal through inland navigation networks and IBWTs.

2.3 Invasion processes in the main infected regions

The dispersal of the golden mussel to Japan, South America, and northern China from the 1990s onward corresponds with the modeled increase in invasion risk in these regions (Fig. 4). While the general invasion trend followed risk projections, regional variations in invasion process reflect differences in introduction pathways, biogeographical connectivity and habitat suitability.

In Japan, the species was first reported in 1990 in the Ibi River [37], with early populations concentrated in western parts of the country. By the 2000s, the mussel had expanded its range into eastern Japan and additional river systems, indicating progressive spatial expansion. In South America, the dispersal trajectory similarly followed increasing risk zones, particularly within central and southeastern regions. Initial introductions likely occurred *via* ballast water discharge in major port cities, followed by secondary dispersal along navigable rivers and artificial canals. In northern China, rising invasion risk coincided with the rapid development of large-scale water infrastructure. A notable example is the >1400 km long middle route of South-to-North Water Transfer Project (SNWTP) in China, which was completed and began supply water in 2014.

Across different regions, there is often a temporal lag between the model-predicted invasion risk and the actual detection of golden mussel populations (Fig. 3c), reflecting the species' latent phase after initial introduction. For example, in China's South-to-North Water Transfer Project (SNWTP), no immediate biofouling was observed following the project's operation. However, larvae introduced from the Danjiangkou Reservoir gradually established populations, with densities reaching 4000 ind. m^{-2} upstream and midstream by 2015, and 1000 ind. m^{-2} downstream by 2018 [36]. Visible biofouling and infrastructure impacts typically emerge only once mussel populations surpass a critical threshold, which reflect the importance of early risk forecasting and proactive management. And invasion dynamics vary across regions, with the rate of population growth strongly influenced by local environmental factors.

3 Discussion

3.1 Drivers and dynamics of golden mussel invasion under globalization

The temporal expansion of golden mussel invasion risk is closely linked to the evolution of global maritime transport. Prior to the 19th century, limited ship size and slow transoceanic travel confined the mussel's dispersal to its native range in East and Southeast Asia. The mid-20th century introduction of containerized shipping transformed this dynamic by drastically increasing cargo volume, reducing travel time, and broadening intercontinental connectivity. This shift enabled more frequent and geographically widespread unintentional introductions, primarily through ballast water discharge and hull fouling. As trade routes expanded, so did the risk of biological invasions, particularly in coastal basins that served as initial entry points. Genetic and historical evidence from multiple invaded regions further suggests that maritime shipping has played a dominant role in mediating long-distance dispersal of the golden mussel [38, 39,40]. In addition, the structure of modern shipping routes facilitates not only cross-ocean dispersal but also upstream movement along inland navigation systems. The attachment of adult golden mussels to ship hulls and other vectors led to jump dispersal with a rate of approximately 240 km per year in the Plata basin [41].

In contrast to maritime shipping, IBWTs facilitate sustained inland dispersal rather than initial coastal introductions. These engineered systems create long-distance hydrological links that enable continuous transport of golden mussel larvae from infested source basins. During the breeding season, regular water transfers generate a recurrent, reproductively driven flux of larvae. For instance, in the SNWTP, whose >1400 km middle route began operation in 2014, larvae from the Danjiangkou Reservoir are consistently conveyed downstream, forming a persistent source of propagules. Additionally, the concrete-lined channels of IBWTs offer favorable settlement surfaces, turning the infrastructure itself into a secondary source for local colonization. As a result, golden mussel populations have grown and adapted to northern conditions, including the cold winters in the Beijing region [35, 42].

Maritime shipping and IBWTs play dominant roles at broad spatial scales, but individual invasions can involve multiple overlapping pathways that are not fully captured by our model. For example, although most golden mussel records in Japan occur near commercial ports, one hypothesized introduction pathway was incidental co-transport with edible freshwater clams [43]. Given that the golden mussel is a small-bodied species with negligible food or ornamental value and is therefore unlikely to be moved deliberately, treating it primarily as a stowaway associated with shipping and IBWTs is a reasonable simplification. The analysis from Europe invasion records also supports such simplification [44]. However, for other taxonomic groups, such as many freshwater fishes whose introductions are strongly driven by aquarium and ornamental trade [45], important pathways are not explicitly represented in our transport layer. For such species, pathway-specific extensions of the framework would be needed to provide a more complete assessment of invasion risk.

3.2 Invasion in South America but not in North America

Our modeling results indicate a high invasion risk in both North and South America, which is consistent with the high suitability suggested by previous species distribution model projections [46, 47]. However, golden mussels have not yet been recorded in North America as of 2024. In contrast, two other mussel species, the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis*), have successfully spread across North America (Fig. 5) [48]. These two invasive bivalves were originally introduced to North America through ballast water from Europe in the mid-1980s [48] and were the targets of efforts by managers in both the USA and Canada to develop better invasive species management strategies. The US Congress, for instance, has enacted legislation for preventing future spread and eradicating existing invasive populations[49] (Fig. 5). Concurrently, in South America, an extensive network of navigable waterways has been developed, spanning approximately 1930 km on the Parana River, 2260 km on the Paraguay River, and 500 km on the Uruguay River. These waterways include approximately 85% of navigable waters within impounded reaches, associated with 13 dams and a sequence of 10 locks designed to accommodate an elevation difference of approximately 230 m. They form a network that plays a crucial role in connecting major Brazilian industrial and urban areas in Sao Paulo State, facilitating the transportation of approximately 10 million tons of cargo annually. However, this extensive waterway construction has also inadvertently provided a pathway for the invasion of golden mussels into the hinterland.

Individuals that manage to evade control strategies and reach North America still confront a highly competitive environment. Dreissenid mussels occupy niches similar to those of golden mussels and exhibit remarkable competitiveness (Fig. 5). Both zebra and golden mussels typically avoid pure mud, showing a preference for isolated hard substrates such as wood fragments, shells, stones, and artificial structures. In contrast, the quagga mussel can colonize silty sediments, particularly in the profoundal zones of deep, large lakes. In lakes with large profoundal zones, quagga mussels may thrive in higher numbers across the entire lake compared to zebra or golden mussels. Additionally, unexpected niche shifts have been observed among dreissenid mussels. Zebra mussels have been recorded on silty substrates adjacent to the original hard substrates [50], while quagga mussels have been observed moving inshore and displacing zebra mussels from rocky littoral zones [51]. Given that these two dreissenid mussels were introduced to North America earlier and have established stable populations, it may be challenging for golden mussels to outcompete them, as demonstrated in competitive interactions between zebra and quagga mussels [48].

Therefore, ballast water management and strong biotic competition from established dreissenid mussels may act as a dual defense, substantially slowing the invasion process of the golden mussel in North America. This highlights the importance of fully implementing and further strengthening ballast water management policies, particularly in regions that are currently uninvaded but environmentally suitable, including strict compliance with the D-1 and D-2 standards established by the IMO Ballast Water Management Convention. In parallel, exploring management approaches that make use of biotic resistance may provide an additional, environmentally friendly component of invasion management. For example, conserving native predators and competitors, or in some cases using them under carefully controlled conditions, could help reduce the risk of future invasions.

3.3 Invasions through South-to-North Water Transfer Project but not in Beijing-Hangzhou Grand Canal

While inter-basin connection projects have a long history in China (Supplementary Notes3), dating back to ancient endeavors like the Beijing-Hangzhou Grand Canal (BHGC), established in 466 B.C., and more recent initiatives such as the South-to-North Water Transfer Project (SNWTP), our model reveals an increased invasion risk in northern China due to recent and ongoing projects. Notably, historical records do not document the presence of golden mussels in northern China, suggesting that neither invasion nor biofouling incidents were detected in the connection with the BHGC. Several key factors explain the differences. Firstly, these projects operate differently - water flows spontaneously under gravity in both projects, but the BHGC includes alternate sections with opposite flow directions (Fig. 6a), which hinders the northward migration of larvae. Additionally, the BHGC was designed to cross natural river systems, including the Yangtze and Yellow rivers, acting as natural barriers to golden mussels. The high sediment concentration in the rivers inhibited the filtration capacity of golden mussels [52]. When crossing major rivers, ships passed through a series of structures in the canal, such as locks and dams, sailed on the river, and then returned to the BHGC (Fig. 6c). Due to differing flow conditions in the Yellow River, Yangtze River, and the canal itself, vessels were sometimes changed along the route rather than traveling continuously through the entire system. This frequent switching of ships, combined with the fact that early shipping did not use water for ballast, significantly reduced the probability of species dispersal via hull fouling or ballast water. Furthermore, blockage of the BHGC due to avulsion of the Yellow River led to water transportation being predominantly by sea after 1831 (Supplementary Notes3; Table S2; Fig. S2). Moreover, the period from the 1500s to the 1900s was one of the coldest in ancient China [53], likely preventing any golden mussel that did reach northern areas from surviving harsh winters. In contrast, conditions in the SNWTP are conducive to the transfer of golden mussels. A steady supply of water with flow discharges up to 420 $m^3 s^{-1}$ brings numerous larvae from the donor basin. The relatively enclosed concrete-lined channels of the SNWTP (Fig. 6b) not only provide a suitable habitat for golden mussel attachment but also protect them from predators.

Drawing insights from the experiences of the BHGC and SNWTP, several effective strategies can be implemented in IBWTs. One strategy is the reconstruction of sedimentation pools up stream of the intake points of IBWTs. These structures can create conditions for larvae to settle, reducing their migration downstream.

Another approach is adjustment of scheduling during breeding period. For example, utilizing high-concentration sediment-laden water during peak reproduction periods may deactivate golden mussel larvae and curb their proliferation. In mega-projects, reservoir regulation can offer dual benefits. Besides their primary function in water storage and regulation, reservoir can provide an opportunity to settle larvae without compromising water quality. Additionally, introducing or promoting native predators in source regions or along transfer routes presents a sustainable method for population suppression. Native species that prey on golden mussels can help contain their expansion with minimal ecological disruption. Implementing these strategies within IBWTs can significantly reduce the risk of golden mussel invasions, thereby safeguard aquatic ecosystems and ensure the long-term security and functionality of water infrastructure.

4 Conclusions

We developed an integrated model that takes environmental requirements (establishment stage) and invasion pathways (introduction stage) into account to study the effect of artificial pathways in golden mussel invasion. We collected global shipping and inter-basin water diversion/transfer project data for our simulations, and our results unveiled a significant expansion in the areas of high invasion risk basins, especially after the 1990s. Coastal basins emerged as pivotal bridgeheads for golden mussel invasions. These regions served as initial introduction points, where golden mussels first established before dispersing to other basins *via* inland shipping or IBWTs. Intercontinental shipping plays a dominant role in promoting the intercontinental dispersal of golden mussels, a trend that is intensified with the growth of international trade and containerization after 1950s. Simultaneously, inter-basin water transfer projects emerged as crucial vectors, facilitating the dispersal of golden mussels within continental interiors. Despite not yet being invaded by golden mussels, several basins, including those in North America, Europe, Australia, the Indochina Peninsula, and the Amazon basin, face increasing invasion risks as shipping pathways expand. By comparing our model results with the actual distribution of golden mussels, we have identified several effective control strategies. These strategies include inducing larvae settling, larval elimination through high sediment flows, ballast water management, and biotic control measures. These interventions have already proven efficient in managing golden mussel invasions within IBWTs and shipping pathways. Implementing these strategies proactively can help mitigate the risks associated with golden mussel invasions in vulnerable regions worldwide.

5 Material and methods

5.1 Data compilation

(1) Hydrological data

This study focuses on the invasion risk of golden mussel globally, primarily relying on the HydroATLAS level 5 water basin database, which provides comprehensive global geographic coverage of river basins and hydrological networks [54], as a fundamental source of information. Specifically, the annual runoff data for each basin served as a representation of the available water volume. Furthermore, we constructed a natural river system by establishing the relationships between the upstream and downstream components of each basin. For the species distribution data of the golden mussel, we compiled a comprehensive database that encompassed occurrences in both its native and invasive ranges (Supplementary Methods 1). Basins containing confirmed native golden mussel populations were assigned a value of 1 (presence), while all others were assigned 0 (absence), representing the species' initial distribution status prior to the influence of human activities.

(2) Water transfer projects data

To account for anthropogenic hydrological connectivity, we incorporated data on inter-basin water transfer megaprojects from the global database developed by Shumilova et al. [55]. This dataset includes 34 existing projects and 76 future schemes, each meeting at least one of the following criteria: construction cost exceeding US$1 billion, transfer distance greater than 190 km, or water volume exceeding 0.23 km³ annually. Key project attributes—such as geographic location, water volume transferred, infrastructure length, construction year, and intended use—were included. We also conducted literature searches using keywords such as “water transfer”, “water diversion”, and “water redistribution schemes” in both Web of Science and Google Scholar. This additional effort allowed us to gather data on each project’s geographical location, total water transfer distance, and the year of construction (Supplementary Methods 2).

(3) Shipping data

To capture global maritime connectivity, we utilized commercial maritime schedules published by shipping companies to construct a representative shipping network. This approach mitigates biases associated with Automatic Identification System (AIS) data, which can vary with ship types and coverage. Ship tonnage data—critical for understanding ballast water discharge patterns—were sourced from reports by the International Maritime Organization (IMO) (Fig. S3). Furthermore, we determined the ballast management policies in each port based on the regulations of the authorized country (Supplementary Methods 3). A visual representation of this data is presented in Fig. 1a.

(4) Environmental factors

To assess the suitability of the golden mussel in each basin, we obtained the current and future climatic data from the WorldClim database (www.worldclim.org), with a spatial resolution of 30 arc-seconds (~1 km²). Slope was also included as proxy for flow velocity because direct hydrodynamic measurements are not available globally. In cases where there was a high covariance (>0.7) between variables, we made the selection of one variable for use in our simulations . Consequently, we chose a total of ten layers, which included annual average temperature, isothermality, minimum temperature of the coldest month, annual temperature range, mean temperature of the warmest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest quarter, and slope (Fig. S4).

5.2 Model development

Taking into consideration the biological characteristics of golden mussels, our analysis of the invasion risk focused on river basins. By integrating artificial and natural pathways that drive both first introductions and subsequent introductions between basins habitat suitability, which reflects the potential for populations to establish, the newly developed model comprises three distinct data layers (Fig. 7). The water body layer provides a standardized compilation of hydro-environmental attributes for all basins and rivers worldwide at high spatial resolution and the species occurrence. The pathway layer defines the various types of connections among basins, incorporating natural downstream flow, inter-basin water transfer projects and shipping connections and thus represents the introduction pathways. The suitability layer, derived from the species distribution model, represents habitat suitability relevant to the establishment of golden mussels. Utilizing these layers, we simulated the stages of golden mussel invasion following: (1) its presence in the source region as either the native or invasive species, (2) its introduction to a new habitat from native and already invaded basins through transfers, and (3) the establishment of a self-sustaining population during the colonization process.

The source region was defined as the river basins where the golden mussel is distributed (Supplementary Methods 1). The potential for dispersal was contingent upon the proportion of water bodies within these basins that have been invaded. The transfer of infectious water took place through either natural or artificial pathways, originating from these source basins and extending to other basins, and thus represents the introduction stage of the invasion process at the basin scale. In the natural river system, golden mussel larvae are transported downstream by the water flow. Additionally, golden mussel can also dispersal upstream by fishing equipment or animals from basins with alien populations of golden mussel. The flux is determined by the discharge between basins, the proportion of invaded water in the source basin, and a coefficient indicating the difficulty of dispersal. Consequently, the natural flux from basin *i* to basin *j* is show as equation (1):

$$\text{Natural flux}_{ij} = \begin{cases} \alpha_d P(\text{invaded})_i Q_{ij} & \text{basin } i \text{ is the upsteam of } j \\ \alpha_u P(\text{invaded})_i Q_{ij} & \text{basin } i \text{ is the downsteam of } j \end{cases} \quad (1)$$

, where α_d is the downstream coefficient, α_u is the upstream coefficient, $P(invaded)_i$ is the proportion of invaded water in basin *i*, Q_{ij} is the discharge from the basin *i* to basin *j*.

IBWTs involve the dispersal of freshwater from a donor basin to a recipient basin, effectively provide introduction pathways within river systems. The golden mussel demonstrates exceptional adaptability within IBWT systems, primarily because of the absence of natural predators and the presence of conducive environmental conditions [31]. Furthermore, this adaptability is amplified by water transfer projects that can continuously introduce mussel larvae into the recipient basin, irrespective of the scale of a project. Moreover, the relatively short duration of water transfer is sufficient to ensure the survival of mussel larvae [42]. Consequently, the primary limiting factor for the introduction flux in this context is the supply discharge of the IBWTs:

$$\text{IBWT flux}_{ij} = \alpha_s P(\text{invaded})_i Q_{s,ij} \quad (2)$$

, where α_s is the supply coefficient, $Q_{s,ij}$ is the supply discharge from the basin *i* to basin *j*.

Another main introduction pathway for the introduction of golden mussels is the ballast water or hulls of maritime and inland shipping vessels. The ballast tanks within vessels constitute harsh environments, characterized by fluctuating temperatures, varying salinity levels, fluctuating oxygen concentrations, and mechanical stress due to the vessel's movement. Field studies demonstrated that population densities of phyto- and zooplankton within ballast water tanks tended to decline exponentially over time [56]. Notably, golden mussels exhibit limited tolerance to continuous salinities exceeding 2 or 3‰ and discontinuous salinities exceeding 23‰ [57, 58]. This implies that settled adult golden mussels on the hulls of maritime ships are unlikely to survive. Larvae present in the ballast water tanks upon arrival at the recipient port can also be adversely affected by the varying salinity levels. Furthermore, many countries have implemented ballast water policies for preventing the introduction of invasive species. Consequently, the flux introduced by ships hinges on the survival of the species during transport:

$$\text{Ship flux}_{ij} = \begin{cases} \alpha_h P(\text{invaded})_i & \text{(inland ship)} \\ \alpha_{dis}\alpha_{ss}\alpha_m P(\text{invaded})_i B_{ij} & \text{(maritime ship)} \end{cases} \tag{3}$$

, where α_h is the dispersal coefficient in inland waterways, α_{dis} is the distance coefficient, α_{ss} is the sea salinity coefficient, α_m is the ballast water management coefficient, B_{ij} is the ballast water discharge from the basin i to basin j.

Once larva-carrying water, whether through natural or artificial flux, reaches a new basin, the invasion dynamics within the recipient basin are modeled through transitions between Susceptible, Exposed, and Invaded states. Susceptible water bodies are those that have not yet received viable propagules. Exposed water bodies are those that have received propagules through natural or human-mediated dispersal (e.g., river flow, IBWTs, shipping), but where mussels have not yet established self-sustaining populations. Invaded compartments contain populations that are established and capable of reproduction. The creation of new exposures is driven by the dissemination of golden mussels within and between basins. Concerning intra-basin dispersal, the rate at which susceptible water bodies in basin transition to the exposed state is contingent upon the suitability of the environment for the golden mussel. In the case of inter-basin dispersal, the quantity of exposed water bodies is determined by the total infectious flux originating from other basins.

Subsequently, these exposed water bodies transition to the invaded compartment with a probability that is proportional to the suitability of the basin. The suitability of the recipient basin is influenced by various biotic and abiotic factors that influence the likelihood of establishment. To quantify this, MaxEnt model [59]was applied for *L. fortunei* using presence-only distribution data compiled from its native and already invaded ranges, consistent with the source-region definition given above. Occurrence records were first spatially thinned with the spThin package to reduce sampling bias [60], and model complexity (feature class combinations and regularization multipliers) was tuned with ENMeval based on AUC (Fig. S5) values followed the previous studies [61, 62], while all other MaxEnt settings were kept at their default values [63]. These cell-level predictions were then aggregated to the basin scale to derive a suitability index (Fig. S6) for each basin, which in turn was used to parameterize the establishment component of the invasion model (Supplementary Methods 4). The resulting suitability values were used to parameterize the coefficients governing intra-basin dispersal and establishment in recipient basins. The invasion risk of basin *i* is defined as the proportion of water bodies within that basin that have transitioned to the invaded compartment, thereby integrating both the likelihood of introduction via pathways and the probability of successful establishment given local environmental conditions.

$$\begin{cases} \text{Susceptible}_{t+1} - \text{Susceptible}_t = -\lambda \cdot \text{Invaded}_t - \text{flux}_t \\ \text{Exposed}_{t+1} - \text{Exposed}_t = \lambda \cdot \text{Invaded}_t + \text{flux}_t - \beta \cdot \text{Exposed}_t \\ \text{Invaded}_{t+1} - \text{Invaded}_t = \beta \cdot \text{Exposed}_t \\ \text{Susceptible} + \text{Exposed} + \text{Invaded} = \text{Total} \\ R(\text{invasion})_i = P(\text{invaded})_i = \text{Invaded}_i / \text{Total}_i \end{cases} \tag{4}$$

, where β is the establishment coefficient, λ is intra-basin spread coefficient.

Data availability

All relevant data used in this study, including occurrence records of *Limnoperna fortunei*, global shipping routes and inter-basin water diversion/transfer project data, have been deposited in Figshare (https://doi.org/10.6084/m9.figshare.30938933).

Code availability

The R code used to implement the invasion risk model and to generate the main analyses and figures has been deposited in Figshare (https://doi.org/10.6084/m9.figshare.30938933).

References

1. Galil, B. S., H. K. Mienis, R. Hoffman & M. Goren, 2021. Non-indigenous species along the Israeli Mediterranean coast: tally, policy, outlook. Hydrobiologia, 848(9):2031-2031, doi:10.1007/s10750-020-04502-9.
2. Gallardo, B., M. Clavero, M. I. Sánchez & M. Vilà, 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology, 22(1):151-163 doi:10.1111/gcb.13004.
3. Diagne, C., B. Leroy, A. C. Vaissière, R. E. Gozlan, D. Roiz, I. Jaric, J. M. Salles, C. J. A. Bradshaw & F. Courchamp, 2021. High and rising economic costs of biological invasions worldwide. Nature, 592(7855):571-+ doi:10.1038/s41586-021-03405-6.
4. Roy, H. E. P., A.; Stoett, P.; Renard Truong, T.; Bacher, S.; Galil, B. S.; Hulme, P. E.; Ikeda, T.; Sankaran, K. V.; McGeoch, M. A.; Meyerson, L. A.; Nuñez, M. A.; Ordonez, A.; Rahlao, S. J.; Schwindt, E.; Seebens, H.; Sheppard, A. W.; Vandvik, V., 2023. Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control. In: Roy, H. E. P., A.; Stoett, P.; Renard Truong, T.; Bacher, S.; Galil, B. S.; Hulme, P. E.; Ikeda, T.; Sankaran, K. V.; McGeoch, M. A.; Meyerson, L. A.; Nuñez, M. A.; Ordonez, A.; Rahlao, S. J.; Schwindt, E.; Seebens, H.; Sheppard, A. W.; Vandvik, V. (ed). Bonn, Germany.
5. Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker & D. H. Wall, 2000. Global biodiversity scenarios for the year 2100. Science, 287(5459): 1770-1774.
6. Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges[J]. Biological reviews, 81(2): 163-182.
7. Moorhouse T. P. & D. W. Macdonald, 2015. Are invasives worse in freshwater than terrestrial ecosystems?[J]. Wiley Interdisciplinary Reviews: Water 2(1): 1-8.
8. Floerl, O. & G. J. Inglis, 2005. Starting the invasion pathway: the interaction between source populations and human transport vectors. Biological Invasions, 7(4):589-606, doi:10.1007/s10530-004-0952-8.
9. Hulme, P. E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46(1):10-18, doi:10.1111/j.1365-2664.2008.01600.x.
10. Leuven, R. S. E. W., G. van der Velde, I. Baijens, J. Snijders, C. van der Zwart, H. J. R. Lenders & A. B. de Vaate, 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. Biological Invasions, 11(9):1989-2008, doi:10.1007/s10530-009-9491-7.

11. Lin, Y., Z. X. Gao & A. Zhan, 2015. Introduction and use of non-native species for aquaculture in China: status, risks and management solutions. Reviews in Aquaculture, 7:28-58.
12. Prié, V., 2023. How was France invaded? 170 years of colonisation of metropolitan France by freshwater mussels. Hydrobiologia, 852(5): 1323-1337.
13. Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pysek, M. Winter, M. Arianoutsou, S. Bacher, B. Blasius, G. Brundu, C. Capinha, L. Celesti-Grapow, W. Dawson, S. Dullinger, N. Fuentes, H. Jäger, J. Kartesz, M. Kenis, H. Kreft, I. Kühn, B. Lenzner, A. Liebhold, A. Mosena, D. Moser, M. Nishino, D. Pearman, J. Pergl, W. Rabitsch, J. Rojas-Sandoval, A. Roques, S. Rorke, S. Rossinelli, H. E. Roy, R. Scalera, S. Schindler, K. Stajerová, B. Tokarska-Guzik, M. van Kleunen, K. Walker, P. Weigelt, T. Yamanaka & F. Essl, 2017. No saturation in the accumulation of alien species worldwide. Nature Communications, 8:14435, doi:ARTN 1443510.1038/ncomms14435.
14. Ricciardi A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity[J]. Diversity and Distributions, 12(4): 425-433.
15. Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson & D. M. Richardson, 2011. A proposed unified framework for biological invasions[J]. Trends in ecology & evolution, 26(7): 333-339.
16. Elith, J. & J. R. Leathwick, 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual review of ecology, evolution, and systematics, 40:677-697, doi:10.1146/annurev.ecolsys.110308.120159.
17. Melo-Merino, S. M., H. Reyes-Bonilla & A. Lira-Noriega, 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecological Modelling, 415: 108837, doi:ARTN 10883710.1016/j.ecolmodel.2019.108837.
18. Blanco, A., A. R. Larrinaga, J. M. Neto, J. Troncoso, G. Mendez, P. Dominguez-Lapido, A. Ovejero, L. Pereira, T. M. Mouga, R. Gaspar, B. Martinez, M. F. L. Lemos & C. Olabarria, 2021. Spotting intruders: Species distribution models for managing invasive intertidal macroalgae. Journal of Environmental Management, 281: 111861, doi:ARTN 11186110.1016/j.jenvman.2020.111861.
19. Kaluza, P., A. Kölzsch, M. T. Gastner & B. Blasius, 2010. The complex network of global cargo ship movements. Journal of the Royal Society Interface, 7(48):1093-1103, doi:10.1098/rsif.2009.0495.
20. Keller, R. P., J. M. Drake, M. B. Drew & D. M. Lodge, 2011. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. Diversity and Distributions, 17: 93–102.
21. Tavasszy, L., M. Minderhoud, J. F. Perrin & T. Notteboom, 2011. A strategic network choice model for global container flows: specification, estimation and application. Journal of transport geography, 19(6):1163-1172, doi:10.1016/j.jtrangeo.2011.05.005.
22. Rosvall, M., A. V. Esquivel, A. Lancichinetti, J. D. West & R. Lambiotte, 2014. Memory in network flows and its effects on spreading dynamics and community detection. Nature Communications, 5(1): 4630, doi:ARTN 463010.1038/ncomms5630.
23. Saebi, M., J. Xu, S. R. Curasi, E. K. Grey, N. V. Chawla & D. M. Lodge, 2020. Network analysis of ballast-mediated species transfer reveals important introduction and dispersal patterns in the Arctic. Scientific Reports, 10(1): 19558, doi:ARTN 1955810.1038/s41598-020-76602-4.
24. Saebi, M., J. Xu, E. K. Grey, D. M. Lodge, J. J. Corbett & N. Chawla, 2020. Higher-order patterns of aquatic

species spread through the global shipping network. Plos One, 15(7): e0220353, doi:ARTN e022035310.1371/journal.pone.0220353.

25. Soto, I., P. Balzani, L. Carneiro, R. N. Cuthbert, R. Macêdo, A. Serhan Tarkan, D. A. Ahmed, A. Bang, K. Bacela-Spychalska, S. A. Bailey, T. Baudry, L. Ballesteros-Mejia, A. Bortolus, E. Briski, J. R. Britton, M. Buřič, M. Camacho-Cervantes, C. Cano-Barbacil, D. Copilaș-Ciocianu, N. E. Coughlan, P. Courtois, Z. Csabai, T. Dalu, V. De Santis, J. W. E. Dickey, R. D. Dimarco, J. Falk-Andersson, R. D. Fernandez, M. Florencio, A. C. S. Franco, E. García-Berthou, D. Giannetto, M. M. Glavendekic, M. Grabowski, G. Heringer, I. Herrera, W. Huang, K. L. Kamelamela, N. I. Kirichenko, A. Kouba, M. Kourantidou, I. Kurtul, G. Laufer, B. Lipták, C. Liu, E. López-López, V. Lozano, S. Mammola, A. Marchini, V. Meshkova, M. Milardi, D. L. Musolin, M. A. Nuñez, F. J. Oficialdegui, J. Patoka, Z. Pattison, D. Pincheira-Donoso, M. Piria, A. F. Probert, J. J. Rasmussen, D. Renault, F. Ribeiro, G. Rilov, T. B. Robinson, A. E. Sanchez, E. Schwindt, J. South, P. Stoett, H. Verreycken, L. Vilizzi, Y.-J. Wang, Y. Watari, P. M. Wehi, A. Weiperth, P. Wiberg-Larsen, S. Yapıcı, B. Yoğurtçuoğlu, R. D. Zenni, B. S. Galil, J. T. A. Dick, J. C. Russell, A. Ricciardi, D. Simberloff, C. J. A. Bradshaw & P. J. Haubrock, 2024. Taming the terminological tempest in invasion science. Biological Reviews, 99:1357–1390.
26. Cole, E., R. P. Keller & K. Garbach, 2019. Risk of invasive species spread by recreational boaters remains high despite widespread adoption of conservation behaviors. Journal of Environmental Management, 229:112-119, doi:10.1016/j.jenvman.2018.06.078.
27. Ludwig, S., E. H. R. Sari, H. Paixao, L. C. Montresor, J. Araujo, C. F. A. Brito, G. Darrigran, A. R. Pepato, T. H. D. A. Vidigal & C. B. Martinez, 2021. High connectivity and migration potentiate the invasion of Limnoperna fortunei (Mollusca: Mytilidae) in South America. Hydrobiologia, 848(2):499-513, doi:10.1007/s10750-020-04458-w.
28. Li, Z., M. Xu & Y. Shi, 2014. Centrality in global shipping network basing on worldwide shipping areas. GeoJournal, 80(1):47-60, doi:10.1007/s10708-014-9524-3.
29. Molnar, J. L., R. L. Gamboa, C. Revenga & M. D. Spalding, 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment, 6(9):485-492, doi:10.1890/070064.
30. Davidson, I. C., C. Scianni, M. S. Minton & G. M. Ruiz, 2018. A history of ship specialization and consequences for marine invasions, management and policy. Journal of Applied Ecology, 55(4):1799-1811, doi:10.1111/1365-2664.13114.
31. Zhan, A. B., L. Zhang, Z. Q. Xia, P. Ni, W. Xiong, Y. Y. Chen, G. D. Haffner & H. J. MacIsaac, 2015. Water diversions facilitate spread of non-native species. Biological Invasions, 17(11):3073-3080, doi:10.1007/s10530-015-0940-1.
32. Zhuang, W., 2016. Eco-environmental impact of inter-basin water transfer projects: a review. Environmental Science and Pollution Research, 23(13):12867-12879, doi:10.1007/s11356-016-6854-3.
33. Zeng, Q., L. Qin & X. Li, 2015. The potential impact of an inter-basin water transfer project on nutrients (nitrogen and phosphorous) and chlorophyll a of the receiving water system. Science of the Total Environment, 536:675-686.
34. Boltovskoy, D., E. Paolucci, H. J. MacIsaac, A. B. Zhan, Z. Q. Xia & N. Correa, 2022. What we know and don't know about the invasive golden mussel Limnoperna fortunei. Hydrobiologia, 852(5): 1275-1322, doi:10.1007/s10750-022-04988-5.
35. Xia, Z. Q., J. R. Barker, A. B. Zhan, G. D. Haffner & H. J. MacIsaac, 2021. Golden mussel (Limnoperna fortunei) survival during winter at the northern invasion front implies a potential high-latitude distribution. Diversity and

Distributions, 27(8):1422-1434, doi:10.1111/ddi.13289.

36. Zhao, N., M. Z. Xu, K. Blanckaert, C. H. Qiao, H. M. Zhou & X. L. Niu, 2019. Study of factors influencing the invasion of Golden Mussels (Limnoperna fortune) in water transfer projects. Aquatic Ecosystem Health & Management 22(4):385-395, doi:10.1080/14634988.2019.1698860.
37. Kimura T., 1994 The earliest record of Limnoperna fortunei (Dunker) from Japan. Chiribotan (Journal of the Malacological Society of Japan), 25:34–35 [In Japanese]
38. Tominaga, A., K. Goka, T. Kimura & K. Ito, 2009. Genetic structure of Japanese introduced populations of the Golden Mussel, Limnoperna fortunei, and the estimation of their range expansion process. Biodiversity, 10(2-3):61-66.
39. Zhan, A. B., P. V. Perepelizin, S. Ghabooli, E. Paolucci, F. Sylvester, P. Sardina, M. E. Cristescu & H. J. MacIsaac, 2012. Scale-dependent post-establishment spread and genetic diversity in an invading mollusc in South America. Diversity and Distributions, 18(10):1042-1055 doi:10.1111/j.1472-4642.2012.00894.x.
40. Ghabooli, S., A. B. Zhan, P. Sardina, E. Paolucci, F. Sylvester, P. V. Perepelizin, E. Briski, M. E. Cristescu & H. J. MacIsaac, 2013. Genetic Diversity in Introduced Golden Mussel Populations Corresponds to Vector Activity. Plos One, 8(3): e59328.
41. Darrigran, G. & C. Damborenea, 2005. A South American bioinvasion case history: Limnoperna fortunei (Dunker, 1857), the golden mussel. American Malacological Bulletin, 20(1-2):105-112.
42. Wang, C. C., M. Z. Xu, J. H. Zhang & X. D. Zhou, 2024. High-latitude invasion and environmental adaptability of the freshwater mussel Limnoperna fortunei in Beijing, China. Ecological Applications, 34(1): e2887, doi:ARTN e288710.1002/eap.2887.
43. Magara, Y., Y. Matsui, Y. Goto & A. Yuasa, 2001. Invasion of the non-indigenous nuisance mussel, Limnoperna fortunei, into water supply facilities in Japan. Journal of Water Supply: Research and Technology—AQUA, 50(3):113-124, doi:DOI 10.2166/aqua.2001.0011.
44. Nunes A. L., E. Tricarico, V. E. Panov, A. C. Cardoso & S. Katsanevakis, 2015. Pathways and gateways of freshwater invasions in Europe. Aquatic invasions, 10(4): 359-370.
45. García-Díaz, P., A. Kerezsy, P. J. Unmack, M. Lintermans, S. J. Beatty, G. L. Butler, R. Freeman, M. P. Hammer, S. Hardie, M. J. Kennard, D. L. Morgan, B. J. Pusey, T. A. Raadik, J. D. Thiem, N. S. Whiterod, P. Cassey & R. P. Duncan, 2018. Transport pathways shape the biogeography of alien freshwater fishes in Australia. Diversity and Distributions, 24:1405–1415.
46. Oliveira M. D., Hamilton S. K. & C. M. Jacobi, 2010. Forecasting the expansion of the invasive golden mussel limnopernafortunei in brazilian and north american rivers based on its occurrence in the paraguay river and pantanal wetland of brazil. Aquatic Invasions, 5(1): 59-73.
47. Campos, M. C. S., A. F. A. de Andrade, B. Kunzmann, D. D. Galvão, F. A. Silva, A. V. Cardoso, M. D. Carvalho & H. R. Mota, 2014. Modelling of the potential distribution of Limnoperna fortunei (Dunker, 1857) on a global scale. Aquatic Invasions, 9(3): 253-265.
48. Karatayev, A. Y., L. E. Burlakova & D. K. Padilla, 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia, 746(1):97-112, doi:10.1007/s10750-014-1901-x.
49. Campara, L., V. Francic, L. Maglic & N. Hasanspahic, 2019. Overview and Comparison of the IMO and the US Maritime Administration Ballast Water Management Regulations. Journal of marine science and engineering, 7(9):283, doi:ARTN 28310.3390/jmse7090283.

50. Berkman, P. A., D. W. Garton, M. A. Haltuch, G. W. Kennedy & L. R. Febo, 2000. Habitat Shift in Invading Species: Zebra and Quagga Mussel Population Characteristics on Shallow Soft Substrates. Biological Invasions, 2(1):1-6, doi:10.1023/a:1010088925713.
51. Cuhel, R. L. & C. Aguilar, 2013. Ecosystem Transformations of the Laurentian Great Lake Michigan by Nonindigenous Biological Invaders. Annual review of marine science, 5(1): 289-320, doi:10.1146/annurev-marine-120710-100952.
52. Darrigran, G., C. Damborenea, E. C. Drago, I. E. de Drago & A. Paira, 2011. Environmental factors restrict the invasion process of Limnoperna fortunei (Mytilidae) in the Neotropical region: A case study from the Andean tributaries. Annales De Limnologie-International Journal of Limnology, 47(3):221-229, doi:10.1051/limn/2011025.
53. Chu, C., 1973. A prelimininary study on the climate change of China in the past 5000 years. Scientia Sinica, 1(2):15-38.
54. Linke, S., B. Lehner, C. O. Dallaire, J. Ariwi, G. Grill, M. Anand, P. Beames, V. Burchard-Levine, S. Maxwell, H. Moidu, F. Tan & M. Thieme, 2019. Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. Scientific Data, 6(1), 283, doi:ARTN 28310.1038/s41597-019-0300-6.
55. Shumilova, O., K. Tockner, M. Thieme, A. Koska & C. Zarfl, 2018. Global Water Transfer Megaprojects: A Potential Solution for the Water-Food-Energy Nexus? Frontiers in Environmental Science, 6: 150.
56. Gollasch, S., J. Lenz, M. Dammer & H. G. Andres, 2000. Survival of tropical ballast water organisms during a cruise from the Indian Ocean to the North Sea. Journal of Plankton Research,, 22(5):923-937, doi:DOI 10.1093/plankt/22.5.923.
57. Angonesi, L. G., N. G. da Rosa & C. E. Berrivenuti, 2008. Tolerance to salinities shocks of the invasive mussel under experimental conditions. Iheringia Serie Zoologia, 98(1):66-69, doi:Doi 10.1590/S0073-47212008000100009.
58. Sylvester, F., D. H. Cataldo, C. Notaro & D. Boltovskoy, 2013. Fluctuating salinity improves survival of the invasive freshwater golden mussel at high salinity: Implications for the introduction of aquatic species through estuarine ports. Biological Invasions, 15(6): 1355–1366.
59. Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling, 190(3-4):231-259, doi:10.1016/j.ecolmodel.2005.03.026.
60. Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & R. P. Anderson, 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38(5), 541-545.
61. Merow C., M. J. Smith, & J. A. Jr Silander, 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography, 36(10): 1058-1069.
62. Low, B. W., Y. Zeng, H. H. Tan , & D. C. Yeo, 2021. Predictor complexity and feature selection affect Maxent model transferability: Evidence from global freshwater invasive species. Diversity and Distributions, 27(3), 497-511.
63. Phillips S J, & M. Dudík, 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31(2): 161-175.

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Contributions

Jiahao Zhang performed data analysis and visualization and wrote the first draft of the manuscript. Mengzhen Xu designed the study, carried out data analysis and revised the manuscript. Aibin Zhan carried out data analysis and revised the manuscript. Chunlong Liu analysed invasion records and revised the manuscript. He Tian revised the manuscript. Gustavo Darrigran provided and curated data from South America and revised the manuscript. Zhaoyin Wang and Xudong Fu designed the study.

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Ethics declarations

Competing interests

The authors declare no competing interests.

Figure Captions

Figure 1. Overview of invasive species and anthropogenic water-Borne pathways

a Depicts key ports, major waterways, inter-basin water transfer projects, occurrences of the golden mussel, and environmental factors (with runoff data shown here as an illustrative example). **b** The current global shipping network, with nodes representing different countries. **c** The total water transferred volume of different continent (TWTV, km^3). **d** Invasive species records categorized by group. **e** The progression of cumulative water transfer volume (CWTV, km^3) alongside world shipping tonnage (measured in 10^3 gross register tons [grt]). **f** The evolution of invasive species, classified by their aquatic transfer capabilities, with a pie chart summarizing the total species count for each 50-year interval.

Figure 2. The global invasion risk of the golden mussel.

a-f Presents spatial distribution maps depicting the global risk levels in typical years, pie plots illustrating the proportion of susceptible, exposed and invaded water bodies in each continent. **g** Temporal changes in world shipping and the global invasion risk of golden mussel, mmt: million tons, grt: gross registered tons. And the lines of risk show the average trend in different continents. Data on invasive species records are sourced from Seebens et al. [13].

Figure 3. Comparison of invasion risk between coastal and inland basins.

Boxplots show the median (central line), interquartile range (boxes, 25th–75th percentiles), and the full range of the data (whiskers).

Figure 4. Dispersal and invasion risk of the golden mussel in the main infected regions.

a East Asia. **b** South America. **c** The evolving invasion risk within these infected basins over time.

Figure 5. Contrasting ballast water management and invasion pathways of three invasive mussels across North and South America.

Figure 6. Inter-basin water transfer schemes in China.

a Middle route of the South-to-North Water Transfer Project (put into operation in 2014) and Beijing-Hangzhou Grand Canal (established in the C13–19th). **b** The concrete surface of the middle route of the SNWTP is amenable to golden mussel attachment. **c** The BHGC route crosses major rivers with high sediment load that acts as a natural barrier to golden mussel as it inhibits filtration.

Figure 7. Schematic illustration of the model.

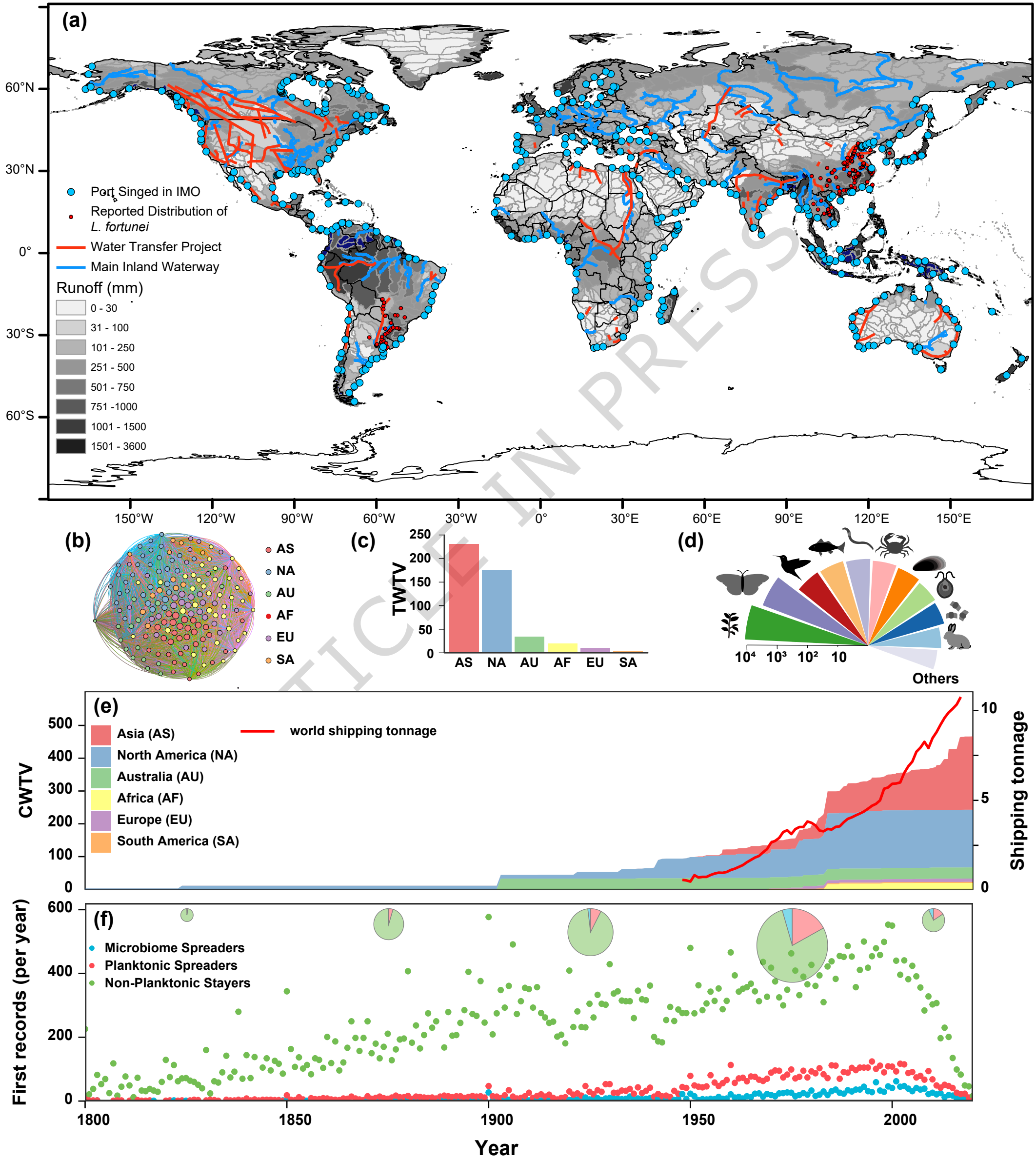
Water body layer shows the average runoff and other parameters of different basins; pathway layers define the various types of the connections among the basins (natural, water transfer project and shipping connections); suitability layer shows the suitability derived from species distribution model which influences the establishment of golden mussel.

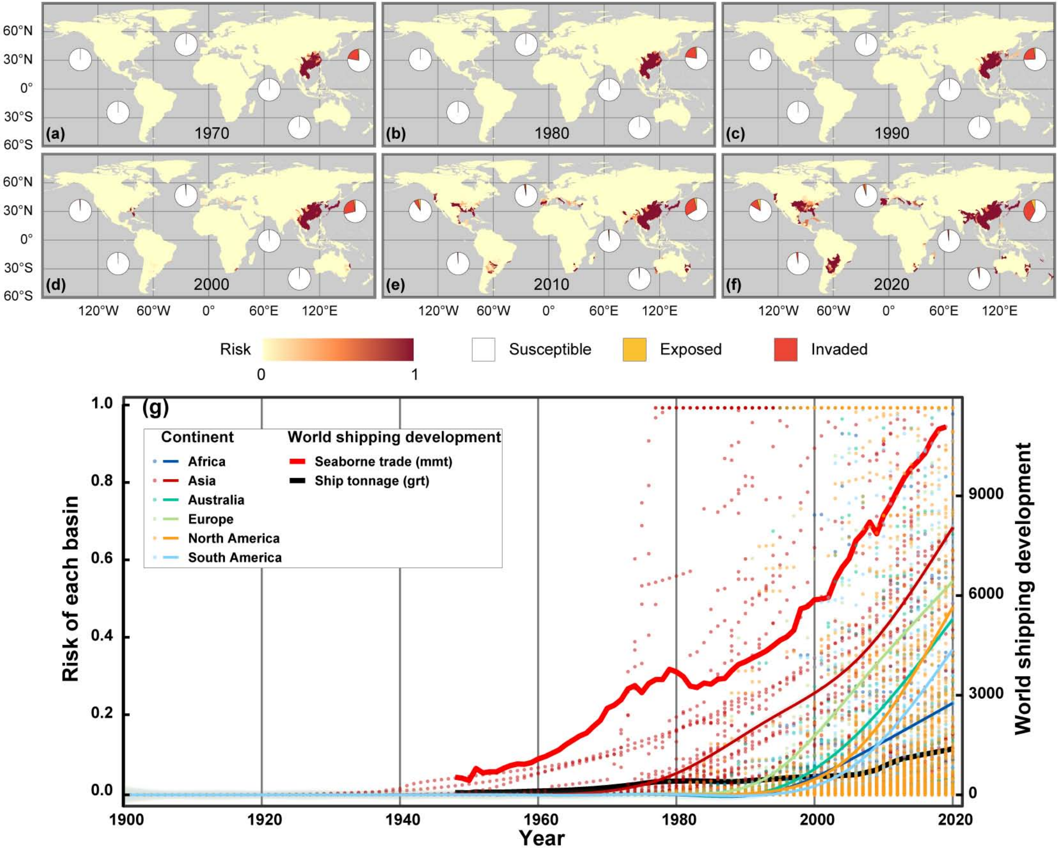
Editorial Summary:

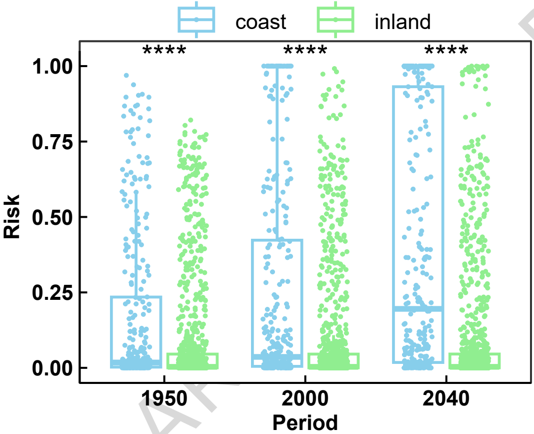
Water-borne invasions of the golden mussel, *Limnoperna fortunei*, can become more widely distributed where inland basins are connected by humanmediated channels, according to an ensemble framework combining niche and dispersal models.

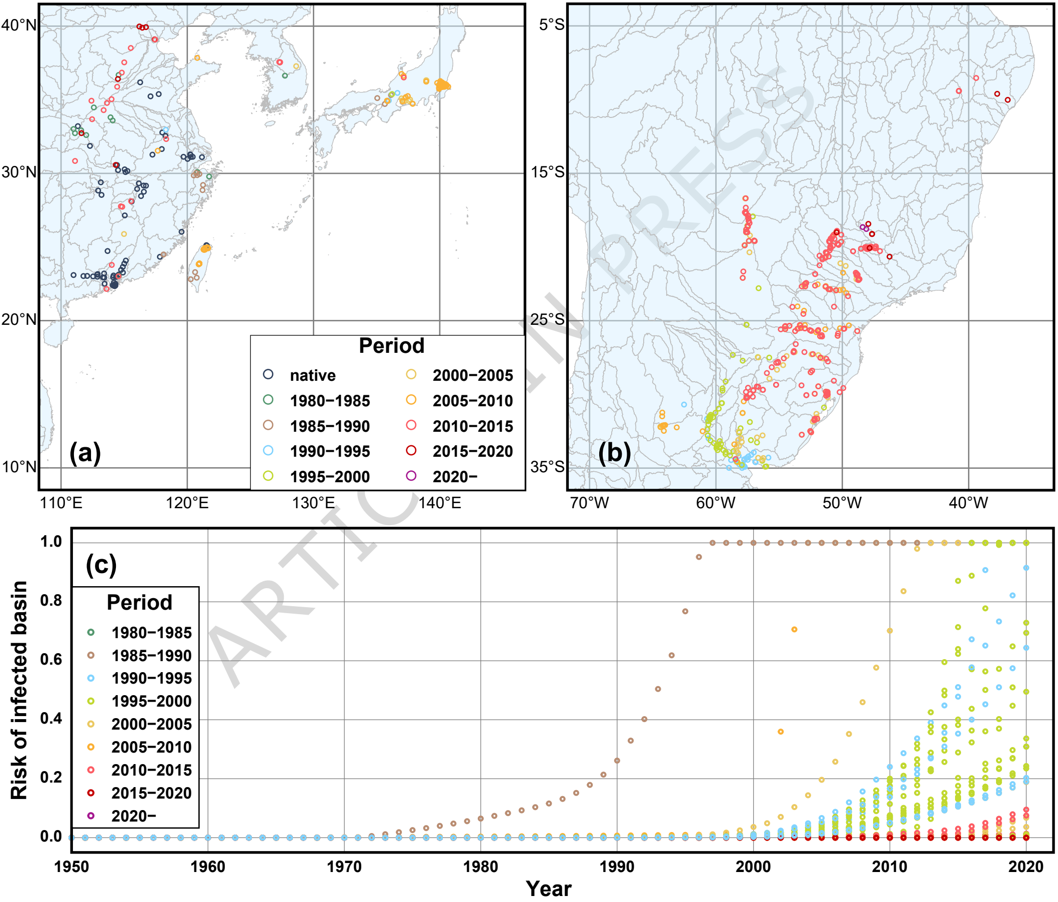
Peer Review Information:

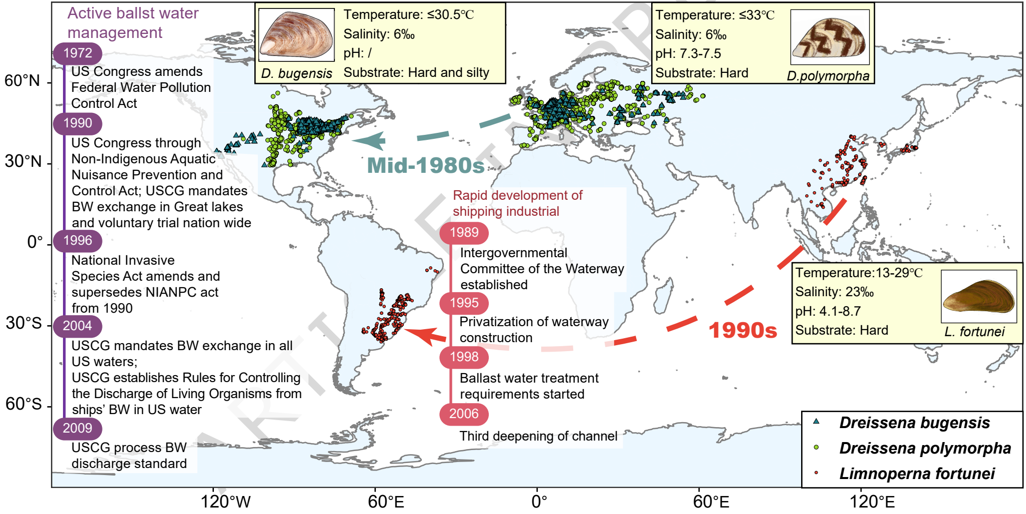
Communications Earth and Environment thanks the anonymous reviewers for their contribution to the peer review of this work. Primary Handling Editors: Haihan Zhang and Joseph Aslin. A peer review file is available.


(a)
Port Singed in IMO
Reported Distribution of *L. fortunei*
Water Transfer Project
Main Inland Waterway
Runoff (mm)
0 - 30
31 - 100
101 - 250
251 - 500
501 - 750
751 -1000
1001 - 1500
1501 - 3600
60°N
30°N
0°
30°S
60°S
150°W
120°W
90°W
60°W
30°W
0°
30°E
60°E
90°E
120°E
150°E
(b)
AS
NA
AU
AF
EU
SA
(c)
TWTV
250
200
150
100
50
0
AS
NA
AU
AF
EU
SA
(d)
10⁴
10³
10²
10
Others
(e)
CWTV
500
400
300
200
100
0
Asia (AS)
North America (NA)
Australia (AU)
Africa (AF)
Europe (EU)
South America (SA)
world shipping tonnage
Shipping tonnage
10
5
0
(f)
First records (per year)
600
400
200
0
Microbiome Spreaders
Planktonic Spreaders
Non-Planktonic Stayers
1800
1850
1900
1950
2000
Year


60°N
30°N
0°
30°S
60°S
(a) 1970
(b) 1980
(c) 1990
(d) 2000
(e) 2010
(f) 2020
120°W
60°W
0°
60°E
120°E
Risk
0
1
Susceptible
Exposed
Invaded
(g)
Continent
Africa
Asia
Australia
Europe
North America
South America
World shipping development
Seaborne trade (mmt)
Ship tonnage (grt)
Risk of each basin
0.0
0.2
0.4
0.6
0.8
1.0
World shipping development
0
3000
6000
9000
Year
1900
1920
1940
1960
1980
2000
2020


coast
inland
****
****
****
1.00
0.75
0.50
0.25
0.00
Risk
1950
2000
2040
Period


40°N
30°N
20°N
10°N
110°E
120°E
130°E
140°E
5°S
15°S
25°S
35°S
70°W
60°W
50°W
40°W
(a)
(b)
Period
native
1980–1985
1985–1990
1990–1995
1995–2000
2000–2005
2005–2010
2010–2015
2015–2020
2020–
(c)
Risk of infected basin
0.0
0.2
0.4
0.6
0.8
1.0
Year
1950
1960
1970
1980
1990
2000
2010
2020
Period
1980–1985
1985–1990
1990–1995
1995–2000
2000–2005
2005–2010
2010–2015
2015–2020
2020–



Active ballst water management

1972 US Congress amends Federal Water Pollution Control Act

1990 US Congress through Non-Indigenous Aquatic Nuisance Prevention and Control Act; USCG mandates BW exchange in Great lakes and voluntary trial nation wide

1996 National Invasive Species Act amends and supersedes NIANPC act from 1990

2004 USCG mandates BW exchange in all US waters;
USCG establishes Rules for Controlling the Discharge of Living Organisms from ships' BW in US water

2009 USCG process BW discharge standard

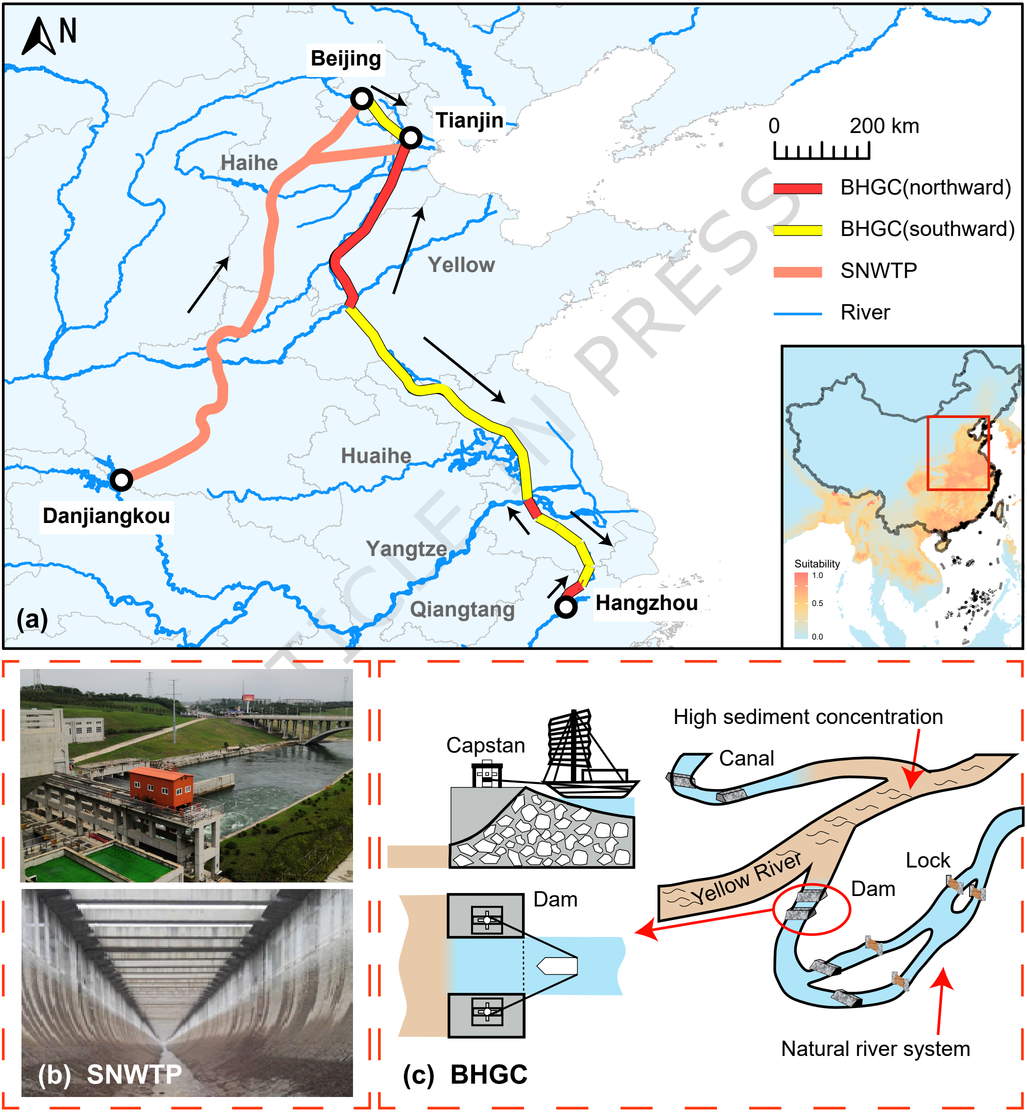
Rapid development of shipping industrial

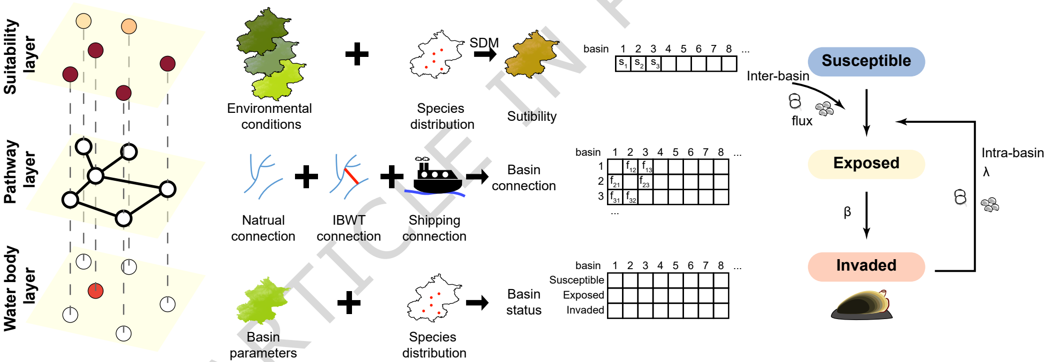
1989 Intergovernmental Committee of the Waterway established

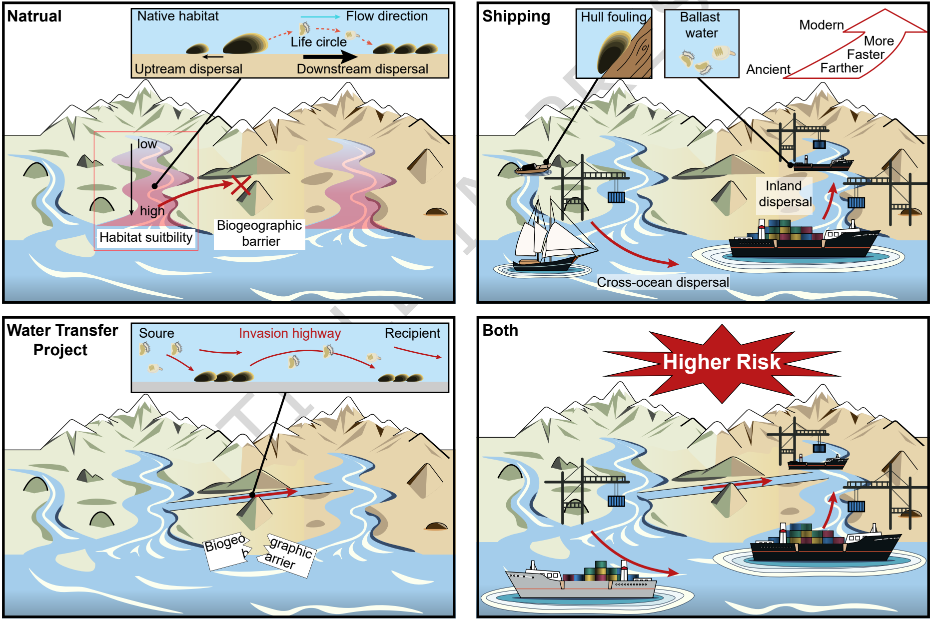
1995 Privatization of waterway construction

1998 Ballast water treatment requirements started

2006 Third deepening of channel


N
Beijing
Tianjin
Haihe
Yellow
Huaihe
Danjiangkou
Yangtze
Qiangtang
Hangzhou
(a)
0
200 km
🟥 BHGC(northward)
🟨 BHGC(southward)
SNWTP
River
Suitability
1.0
0.5
0.0
(b) SNWTP
Capstan
Dam
High sediment concentration
Canal
Yellow River
Lock
Dam
Natural river system
(c) BHGC


Suitability layer
Pathway layer
Water body layer
Environmental conditions
+
Species distribution
SDM
Sutibility
basin 1 2 3 4 5 6 7 8 ...
s_1 s_2 s_3
Susceptible
Inter-basin
flux
Natrual connection
+
IBWT connection
+
Shipping connection
Basin connection
basin 1 2 3 4 5 6 7 8 ...
1 f_{12} f_{13}
2 f_{21} f_{23}
3 f_{31} f_{32}
...
Exposed
Intra-basin
λ
β
Basin parameters
+
Species distribution
Basin status
basin 1 2 3 4 5 6 7 8 ...
Susceptible
Exposed
Invaded
Invaded


Natrual
Native habitat
Flow direction
Life circle
Uptream dispersal
Downstream dispersal
low
high
Habitat suitbility
Biogeographic barrier
Shipping
Hull fouling
Ballast water
Modern
Ancient
More
Faster
Farther
Inland dispersal
Cross-ocean dispersal
Water Transfer Project
Soure
Invasion highway
Recipient
Biogeo b
graphic arrier
Both
Higher Risk