

Global forecasts of shipping traffic and biological invasions to 2050

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Socioeconomic factors, including population growth, global trade and the worldwide transport of materials, interact with environmental drivers to determine the sustainability of natural systems. We focus on the global shipping network, which is central to invasive species spread worldwide. We explain 90% of the variation in global shipping traffic and a twofold increase in shipping using basic socioeconomic indicators and a temporal validation set. Combining our model with global economic development scenarios, we project global maritime traffic to increase by 240–1,209% by 2050. Integrating our predictions with global climate change projections and shipping-mediated invasion models, we forecast invasion risk to surge in middle-income countries, particularly in Northeast Asia. Shipping growth will have a far greater effect on marine invasions than climate-driven environmental changes: while climate change might actually decrease the average probability of invasion, the emerging global shipping network could yield a 3- to 20-fold increase in global invasion risk.

There is an increasing awareness that human activities in one region are connected to broader, often global effects on conservation and sustainability¹. Simultaneously, substantial social changes are anticipated over the coming decades, with increasing population sizes and different potential socioeconomic trajectories². Thus, to understand sustainability, we must map the ways in which different regions are interconnected globally³, and consider the interplay between these connections, anticipated socioeconomic changes and their environmental effects.

One of clearest ways in which regions are connected is via transportation networks. In particular, the global shipping network (GSN) is the primary means by which materials and goods are moved worldwide, accounting for over 80% of world trade⁴. Thus, to understand changing global physical connectivity, changing shipping traffic is an obvious choice for analyses.

From a sustainability standpoint, the GSN is responsible for the introduction of non-indigenous species (NIS), which can have detrimental ecological and economic impacts⁵. For instance, ships may transport living organisms through ballast water, which is taken up to stabilize the vessel, and biofouling, whereby species attach on the hulls of ships. Together, these two pathways are believed to account for 60–90% of marine bioinvasions⁶. Likewise, terrestrial pests are moved as a by-product of shipping (for example, infestations of wood packing material⁷), where the characteristics at arrival ports could influence the pest spread rates across a continent⁸.

In recent years, data on global shipping movements have become available with vessel-tracking automatic identification systems technology, allowing for reconstruction of the GSN⁹ and, subsequently, forecasting of global invasions through the network^{10,11}. Most of these forecasts focus on the effects of climate change on NIS spread^{10–12}, and for good reason: global climate change is expected to alter the range and distribution of many species, such that the risk of invasion of certain areas linked through the GSN may also change¹³. However, as global climate projections are undertaken at the scale of multiple decades, one must consider that perhaps the GSN itself will also change. To date, however, no study has factored in potential changes to the GSN, either in shipping intensity or distribution.

To assume that the GSN will remain static over the coming decades goes against the historical trend. Indeed, between 1992 and 2012, shipping traffic grew fourfold¹⁴. As an added complication, global shipping growth occurs non-uniformly across space. For instance, although both Western Europe and Japan experienced dramatic increases in shipping traffic between 1960 and 1970 followed by a period of stagnation, only Western Europe experienced another boom in traffic two decades later, while Japan has continued to experience marginal growth to the present day¹⁵. Growth in maritime traffic also differs between ships: between 2000 and 2007, the annual growth rate of the global fleet of liquefied natural gas tankers (in deadweight tonnes) was 11%, 5% for roll-on/roll-off cargo ships and 2% for bulk carriers¹⁵.

Socioeconomic factors largely underlie the changes in the GSN⁴. As wealth and population increase, so too comes a growing need for goods and services that are not locally available. Imbalances between supply and demand create conditions for trade and interdependence between nations. The transport of goods traded between global commercial partners is the GSN's *raison d'être*. These close links between economy and shipping underlie the 25% drop in global shipping during the 1930s recession and 640% increase over the 25 years of post-World War II economic boom¹⁵. More recently, China's share of global container throughput surged from 1.4–20.1% between 1990 and 2013, reflecting the country's economy growing 830% in the same time period¹⁶. In view of this variability in trade and shipping patterns in recent decades—both in terms of magnitude and distribution—it is clear that the assumption of an unchanging GSN warrants greater scrutiny when venturing to forecast shipping-mediated invasion into the next century.

Moreover, given the importance of socioeconomic factors in driving change in global shipping, it is logical to investigate how well traditional socioeconomic indicators predict changes in shipping patterns, as well as what other factors should be considered towards this end. For instance, all other things being equal, trade between nations has been found to increase proportionally with the product of their gross domestic products (GDPs), and to be greater still if they share a common language (for example, refs. ^{17–19}). One may

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Table 1 | Parameter values and predictive accuracy for the proposed model

	Bulk carrier	Chemical tanker	Container ship	Crude oil/oil products tanker	General cargo ship	LNG tanker	Ro-ro cargo ship	All ships
Intercept	3.63 (0.0319)	2.31 (0.0316)	2.89 (0.0451)	2.23 (0.0316)	2.71 (0.0295)	1.48 (0.0297)	2.04 (0.0340)	4.67 (0.0345)
GDP_I	1.40 (0.0610)	1.19 (0.0613)	1.07 (0.0875)	0.929 (0.0618)	1.26 (0.0570)	0.622 (0.0573)	0.991 (0.0348)	1.53 (0.0353)
GDP_J	1.16 (0.0610)	1.03 (0.0323)	1.27 (0.0461)	0.889 (0.0618)	1.13 (0.0570)	0.685 (0.0574)	0.992 (0.0348)	1.40 (0.0663)
Pop_I	-0.123 (0.0615)	-0.185 (0.0617)	0.204 (0.0880)	0.181 (0.0624)	-0.209 (0.0574)	0.0205 (0.0578)	NA	NA
Pop_J	0.167 (0.0615)	NA	NA	0.253 (0.0624)	-0.128 (0.0574)	0.148 (0.0578)	NA	0.140 (0.0666)
Distance	-0.385 (0.0347)	-0.956 (0.0390)	-0.704 (0.0520)	-0.870 (0.0372)	-1.15 (0.0370)	-0.687 (0.0372)	-0.829 (0.0386)	-0.671 (0.0425)
CB	NA	-0.151 (0.0588)	NA	NA	0.150 (0.0345)	-0.271 (0.0347)	NA	0.156 (0.0400)
CL	0.277 (0.0336)	0.302 (0.0330)	0.632 (0.0471)	0.0327 (0.0334)	0.326 (0.0312)	0.249 (0.0313)	0.525 (0.0352)	0.455 (0.0360)
CCH	NA	0.190 (0.0566)	0.115 (0.0502)	0.213 (0.0361)	NA	NA	0.0944 (0.0372)	NA
RTA	0.393 (0.0344)	0.407 (0.0349)	0.440 (0.0486)	0.163 (0.0342)	0.367 (0.0320)	0.453 (0.0321)	0.295 (0.0366)	0.454 (0.0371)
R²_{MSE}	0.678	0.835	0.875	0.741	0.931	0.595	0.752	0.897

Parameter values are based on vessel traffic data and rescaled driver data for 2006–2014. Predictive accuracy is measured as R^2_{MSE} applied to 2014 validation data, using fits on 2006–2009 data. Standard errors are listed in brackets. The subscripts I and J denote source and destination SERs, respectively. CB, common border; CCH, common colonial history; CL, common official language; LNG, liquefied natural gas; NA, non-significant variable at $\alpha=0.05$ and $n=210$ (15×14); pop, population; ro-ro, roll-on/roll-off; RTA, regional trade agreement.

expect similar relationships to hold for shipping traffic, although to what extent remains an open question. Furthermore, given that different ship types carry different cargoes, we should expect the relationships between socioeconomic development and maritime traffic to vary by ship type. This is particularly important from the perspective of biological invasion, as different ships have different associated invasion risks. For instance, bulk cargo ships generally release more ballast water than roll-on/roll-off cargo ships, resulting in a greater likelihood of species introduction²⁰.

Linking changes in shipping traffic to socioeconomic drivers also allows us to benefit from, and build on, extensive research on socioeconomic scenarios^{21,22}. The shared socioeconomic pathways (SSPs) are among the most recent set of comprehensive forecasts of global development. Developed by the International Institute for Applied Systems Analysis (IIASA) as part of the International Panel on Climate Change's (IPCC's) Fifth Assessment Report, the SSPs present five possible global futures, matched with qualitative narratives and corresponding quantitative pathways of socio-economic variables, such as GDP and population². In addition to forming the basis for the IPCC forecasts of global greenhouse gas emissions and mitigation recommendations, the SSPs have been used in forecasting studies in the domains of land use² and agricultural production²³, water consumption²⁴, public health²⁵ and vulnerability to extreme weather events²⁶. To add global shipping, and concomitant biological invasions, to this list further advances the scenarios by adding to their dimensionality, thereby contributing to a higher-resolution image of the possible future.

In this manuscript, we provide: (1) a novel synthesis, integrating data and research across disciplines, including maritime traffic, socioeconomic indicators, quantitative projections of global development and climate change, and probability models of ship-mediated invasion; (2) global projections of shipping traffic, demonstrating that forecasting is possible, and providing novel forecasts to 2050; and (3) as an outcome of 1 and 2, forecasting of global marine biological invasions, projecting both the magnitude and changing hot spots of invasion risk. These will form quantitative, predictive building blocks, with which new, more advanced,

sustainability models can be constructed, incorporating a central mechanism of global, physical connectivity.

Results

In the Methods, we describe our approach to predicting global maritime traffic and its impact on biological invasions. As an overview, we integrated global data on >50 million ship voyages across 9 years, and historical variables and socioeconomic predictors, to build our model, hereafter referred to as the residual-adjusted unconstrained gravity (RAUG) model. We then integrated the RAUG model with global socioeconomic development scenarios, IPCC global climate change projections and shipping-mediated marine invasion models to forecast traffic and marine invasions across socio-ecoregions (SERs; see Methods).

Model validation and predictor variables. The RAUG model predicted 90% of variation in shipping traffic in 2014 based on training data from 2006–2009 when aggregating across ship types, as well as predicting the twofold increase in shipping observed between fitting and validation years (actual increase: 2.03×; RAUG prediction: 1.81×). When separating by ship types, the RAUG model predicted between 59 and 93% of variation in traffic (Table 1). RAUG consistently outperformed three alternative models for all ship types (Supplementary Table 1). Interestingly, inclusion of autocorrelation terms (alternative model IV) yielded virtually identical fits, indicating that residual adjustment accounts for autocorrelation. We thus proceeded with the simpler version of the RAUG model.

Across all ship types, GDP, distance, common language and regional trade agreements were found to be important predictors (Table 1). In all cases, source GDP, destination GDP, common language and regional trade agreements had positive relationships with vessel traffic, while distance had a negative relationship. Other variables were only predictive for some ship types. Where these variables were significant, shipping traffic had a positive relationship with common colonial history and an ambivalent relationship with source population, destination population and contiguity.

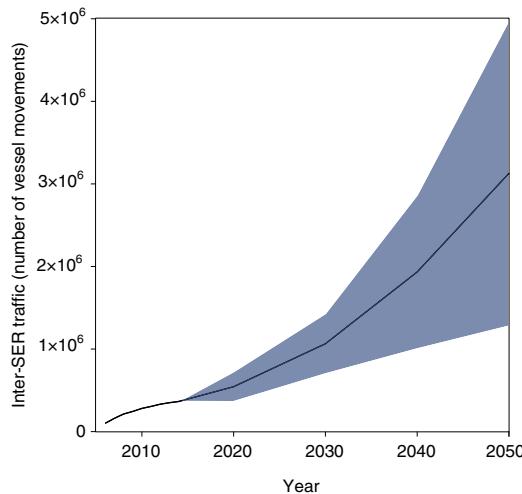


Fig. 1 | Decadal projections of total inter-SER traffic. The error envelope represents the combined error due to scenario uncertainty (SSP), as well as parameter estimation for the gravity model (PI_{gm}) and residual adjustment (PI_{ra}).

Of all these predictors, GDP consistently had the strongest effect on shipping traffic. In some cases, GDP's positive effect on traffic was tempered by a negative relationship with population, suggesting that GDP per capita could be the driving factor. In all cases, both source and destination GDPs affected shipping, sometimes with a combined effect greater than unity. Distance was the next strongest determinant of shipping traffic, followed by socio-political factors.

Forecasting to 2050. We predict that the number of vessel movements between SERs will be between 240 and 1,209% greater in 2050 than in 2014 (Fig. 1). In comparison, we found that inter-SER traffic increased by 258% between 2006 and 2014. However, this growth will not be uniform (Fig. 2 and Supplementary Fig. 2). Increases in shipping traffic will be highest along connections with large, fast-growing economies, notably Northeast Asia. Connections with large, developed economies (for example, around the Mediterranean) or fast-growing, but less-developed economies (African and southern South American SERs) will experience more moderate increases. Meanwhile, smaller, slow-growing economies, such as those in the Eastern Indo-Pacific, will remain relatively low traffic through to 2050.

Although shipping traffic growth is projected to differ between scenarios, all five SSPs project increases in shipping traffic from 2014 levels for the vast majority of areas (Fig. 2 and Supplementary Fig. 2). This growth will be most pronounced for environmentally sustainable (SSP1) or unsustainable (SSP5) scenarios, due to global trajectories in both increased magnitudes of GDP and decreased cross-national inequality. In contrast, trajectories that result in greater global inequality—evidenced most strongly in SSP3—will see lower rates of shipping growth, and therefore lower invasion risk, through the mid-century.

Furthermore, we predict a dramatic, global increase in invasion risk by 2050, regardless of the development scenario. Our analysis suggests that this increase will primarily be due to shipping traffic (Fig. 3). In comparison, environmental change will have a marginal effect on invasion risk, and may in fact reduce it in most areas. This is true whether or not future environmental distances are calculated with respect to a source port's current or future environmental conditions (Supplementary Fig. 3). When only factoring in environmental change, the mean expected number of annual invasions at the SER level is anticipated to drop from 1.18 ($\sigma=1.12$) in 2014 to 1.14 ($\sigma=1.08$) in 2050, with 14 of 15 SERs experiencing slight

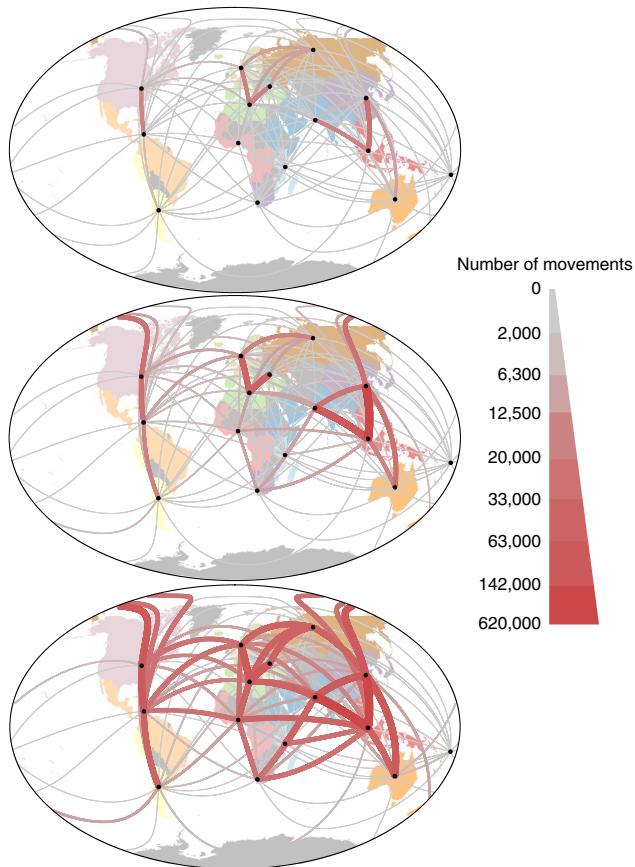


Fig. 2 | Shipping vessel movements. Number of shipping vessel movements between SERs in 2014 (top), and 2050 under lowest-case traffic growth and lowest $PI_{gm} + PI_{ra}$ error bound (middle; SSP3: 'regional rivalry') and highest-case traffic growth and highest $PI_{gm} + PI_{ra}$ error bound (bottom; SSP5: 'fossil-fuelled development').

decreases in invasions. When also factoring in change in shipping traffic, the mean expected number of annual invasions is expected to increase to between 3.91 ($\sigma=3.89$) and 23.40 ($\sigma=21.16$)—a 3- to 20-fold increase.

The major sources of invasions will thus be areas generating high amounts of shipping traffic, with Northeast Asia being the most important invasion source for most SERs by a considerable margin (Fig. 4 and Supplementary Fig. 4). Nonetheless, environmental differences will continue to play a decisive filtering role, dictating the relative importance of certain SERs as sources of invasion. For instance, despite forecasted traffic to the Mediterranean from Northern Europe being six to nine times greater than from the Central America region, the expected number of invasions will be eight to ten times less. However, in comparison with the anticipated growth in shipping traffic, change in environmental conditions over the coming decades is not expected to result in significant changes in the relative importance of areas as sources of invasion (Supplementary Fig. 4).

Discussion

Our results suggest that the GSN in 2050 will differ substantially from current patterns, for all global development scenarios. Previous invasion forecasts have done well incorporating change with respect to some important abiotic factors^{11,12,20}; however, they have assumed that shipping dynamics will remain static over the coming decades, despite historical evidence suggesting this is highly unlikely¹⁴. Our results show that this assumption could lead to a

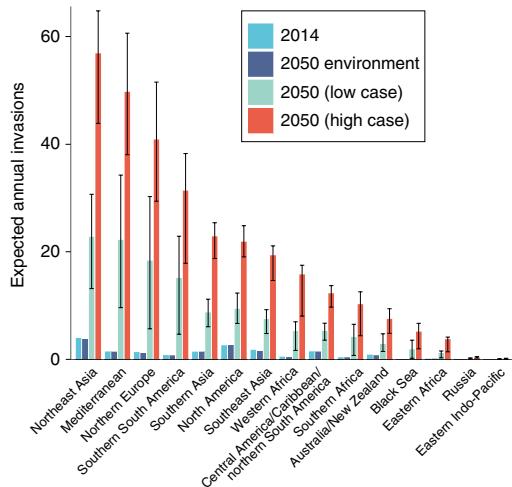


Fig. 3 | Invasions into each SER under different conditions. Expected annual number of invasions into each SER in 2014 under 2014 environmental conditions, forecasted 2050 environmental conditions with 2014 levels of shipping traffic, and forecasted 2050 environmental conditions with low- (SSP3: ‘regional rivalry’) and high-case (SSP5: ‘fossil-fuelled development’) shipping projections (see equation (12)). Error bars represent the combined error due to parameter estimation for the gravity model and residual adjustment (PI_{gm} and PI_{ra} ; see equation (5)).

drastic underestimation of global invasion risk, and suggest that quantitative estimates of shipping growth are critical to forecasting marine biological invasions. Using 2014 (our last year of data) as our baseline, consideration of only environmental change yields roughly the same overall invasion risk, whereas inclusion of GSN growth yields a 3- to 20-fold increase.

Forecasting efforts in the invasion literature have primarily focused on climate-driven environmental change. While environment plays an undeniable role in biological invasion, more precisely, it is the difference in environmental conditions between source and destination (that is, environmental distance) that matters for species establishment²⁷. It is not clear that environmental distances will systematically decrease with climate change; in contrast, we expect shipping traffic to generally and greatly increase by 2050. However, we note two caveats. First, we analysed temperature and salinity—the most common environmental variables for marine studies and those used in previous forecasting efforts^{10,12,28}. Other factors could conceivably have a more systematic effect increasing invasion success (for example, habitat disturbance). Unfortunately, data on such variables are less available. Second, the relative importance of propagule pressure (which is related to traffic) versus environmental distance probably differs across systems. For instance, for aquarium fish introductions into the USA, changes in environment had a greater effect than changes in propagule pressure²⁹, which arguably reflects the tropical origins of popular aquarium fish, and the anticipated climate-driven change towards more similar environments in the USA. Nonetheless, in the global context, where NIS can come from worldwide sources and potentially invade worldwide destinations, propagule pressure appears to be the dominant, consistent force, given anticipated socioeconomic changes.

Given the importance of shipping, it is encouraging that socioeconomic predictors capture much of the variation in global shipping. We found that the most important determinant was GDP. However, while previous studies have used GDP as a linear predictor of propagule pressure^{30,31}, we found a nonlinear relation, with parameters mostly greater than 1 (that is, shipping increases at a rate greater than GDP). Moreover, it was not just the GDP of the destination, but the multiplicative effect between source and

destination GDPs that mattered. The implication of this is that: (1) using a given region’s GDP as a proportional surrogate of invasion pressure will probably underestimate the true change; and (2) the relationship between GDP and traffic (propagule pressure) cannot be understood in isolation, but needs to be considered within the larger context of all trading partners of a given nation.

Shipping was not solely determined by GDP, however. Population exhibited both positive and negative relationships with maritime traffic. Furthermore, these relationships were generally relatively weak in nature. These findings may seem counterintuitive as larger populations tend to consume more materials³². However, two factors may be counteracting this effect, explaining the variable’s ambivalence. First, a larger market size may incentivize domestic production (‘import substitution’)³³, resulting in greater self-sufficiency and decreased reliance on international trade³⁴. Second, in the context of positive relationships with GDP, a negative population parameter yields a metric of GDP per capita ($\text{GDP} \times \text{Population}^{-b}$). Conceivably, GDP per capita, which is related to standard of living, could be a relevant measure of economic development affecting trade.

Beyond GDP and population size, other significant factors included subtler social determinants that might facilitate trade (for example, common language, common colonial history and trade agreements) and other factors that might hinder it, such as distance. Meanwhile, contiguity exhibited both positive and negative relationships with shipping. This surprising result might also be explained by the interaction of opposing forces: on the one hand, contiguous regions might engage in more trade because they are physically closer to one another, while on the other hand, contiguous areas have opportunities for overland transport, which would reduce reliance on shipping as a transport medium. Sure enough, when significant, contiguity—much like population—had a relatively weak effect. Together, these socioeconomic predictors helped explain 90% of variation in shipping, substantially outperforming comparative ‘naïve’ models (Supplementary Table 1).

Given the predictability of the GSN based on socioeconomic predictors, we could investigate the implications of alternative global socioeconomic scenarios on biological invasions. First, our analyses suggested that ‘sustainability’ and ‘fossil-fuelled development’ scenarios both had the highest increase in invasions. This was because both increasing economic development and decreasing social inequality result in increased shipping traffic. Pursuing a trajectory of sustainability and equality is obviously of common interest; however, it is important to have a complete accounting of the costs and benefits of policies, to identify unintended consequences, and to potentially identify solutions.

A further consequence of these socioeconomic processes is that areas experiencing pronounced economic growth will simultaneously experience surges in invasion risk. This is reflected in the growth in the expected number of invasions in some already developed areas, but also in middle-income areas whose economies are anticipated to continue to develop over the coming decades. However, unlike the already developed group, the middle-income group is rarely the focus of invasion studies³⁵, which, our results suggest, appears to be a substantive oversight. In particular, Northeast Asia, which is anticipated to be the primary invasion hotspot—both as a source and sink—over the coming decades, warrants greater attention in the invasion literature. Interestingly, North America has been the traditional source of marine invasions to Northern Europe (40–50% of invasion risk) compared with Northeast Asia (15–20%)²⁰. In contrast, our forecasts suggest that Northeast Asia could account for 80% of invasion risk to Northern Europe by 2050. These differences are logically consistent. The results of Seebens et al.²⁰ were based on 2007–2008 shipping. Between 2008 and 2014, North American GDP barely changed, whereas Northeast Asia’s increased by 250%. Likewise,

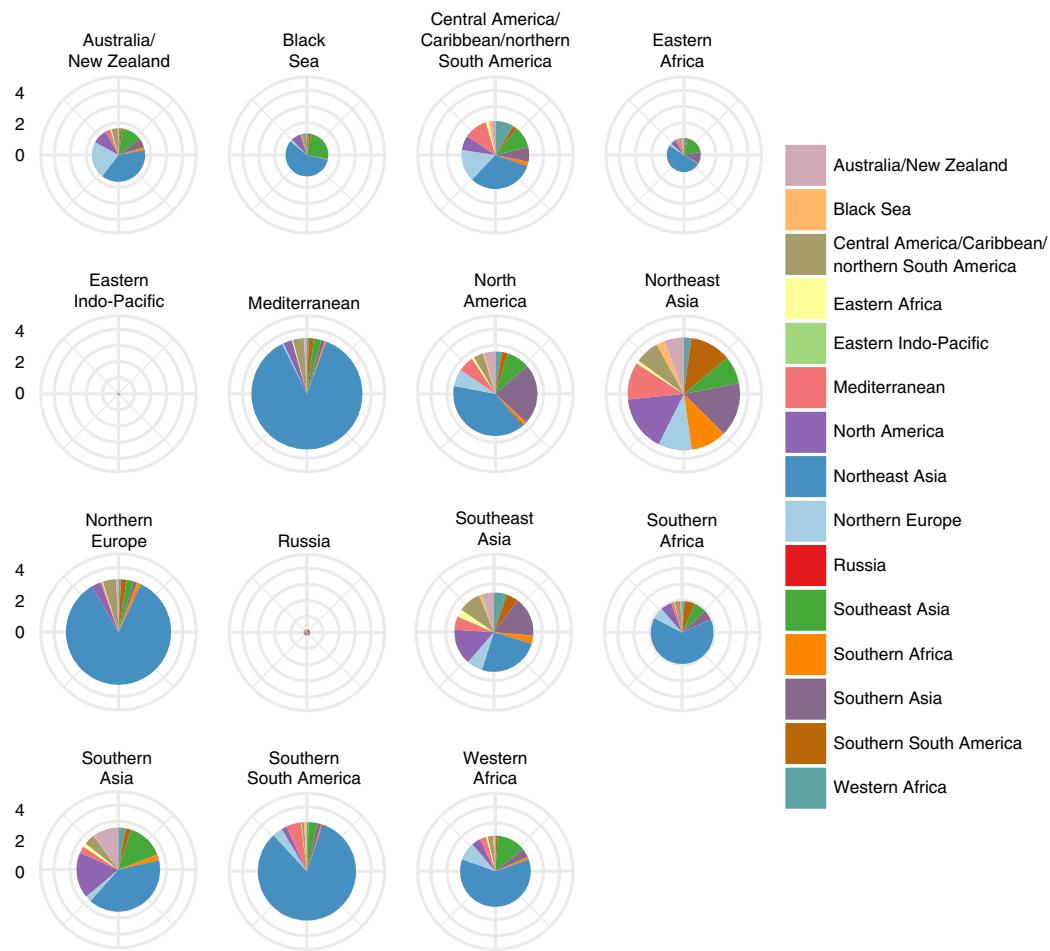


Fig. 4 | Breakdown of invasion risk by source SER for each destination SER in 2050 under ‘status-quo’ shipping projections (SSP2: ‘middle-of-the-road’). Source SERs are defined by colour, while destination SERs are labelled above each pie chart. A pie chart’s radius represents the log-scaled expected annual number of invasions (see equation (11)). See Supplementary Fig. 5 for upper and lower 95% prediction intervals.

invasion risk to Northern Europe from Northeast Asia (26%) overtook North America (22%) by 2014. In 2050, North America GDP is projected to increase by 2 \times , while Northeast Asia is projected to increase by 21 \times , explaining the dramatic shift in invasion risk. In comparison, although the world’s least developed regions will continue to face numerous sustainability challenges over the coming decades^{36,37}, we expect these regions to continue to experience comparatively fewer invasions (although this does not speak to their potential impact).

This study focused primarily on economic drivers of change; however, the GSN has also historically been influenced by political, technological and geophysical factors (see Supplementary Information). We excluded the first two factors from the model as these are inherently unpredictable on the time scale of this study (but see Supplementary Information), and we purposefully omitted the last category as only two potential changes are on the horizon. The first is the construction of the Nicaragua Inter-oceanic Canal, which is unlikely to significantly impact global shipping patterns³⁸, if it is to be completed at all³⁹. The second is the opening of Arctic passages due to the melting of polar ice caps, which has garnered much attention in recent years^{40–42}. However, despite studies showing that Arctic avenues may open up by the mid-century^{43,44}, sea-ice irregularity will pose significant problems for shipping, which is an industry dominated by logistical constraints and strict delivery schedules. The substantial increase in navigation risks and associated insurance premiums means that Arctic maritime traffic is

likely to remain largely destinational rather than navigational until the mid- to late-century^{45,46}.

As with all models, there are assumptions and potential improvements. For one, the regionalization of shipping traffic means intra-regional movements are excluded from consideration. Focusing on broad geographical scales is most appropriate for analyses of global biological invasions, emphasizing meaningful regional biotic composition⁴⁷, limiting secondary dispersal effects, and minimizing other forms of human travel (that is, overland) and transshipments, which can decouple macroeconomics from shipping (for example, entry through hub-ports, then subsequent secondary transport to other countries⁴⁸). For researchers interested in intraregional dynamics (for example, at the country level), we recommend our regional model, which is highly predictive, followed by a second intraregional submodel. Notably, other factors (for example, transshipments or neighbourhood effects), which are damped by the aggregation of traffic into large multi-country SERs, may be more important at smaller scales, potentially requiring other model formulations (for example, explicitly mechanistic trade models⁴⁹, spatial autocorrelative models⁵⁰ and network models⁵¹). Second, certain spatiotemporal effects may also affect invasion risks, such as differences in regional species richness⁵², and the seasonality of transport cycles and reproduction⁵³. Third, other model formulations are possible. We constructed our model using Seebens et al.²⁰ as our invasion model structure; however, alternative models of invasion probability exist (for example, ref. ⁵⁴), have different properties

and might be worth developing. Likewise, our understanding of climate change and socioeconomic scenarios continues to evolve, and could change the projections from this paper. Fourth, our index of risk was measured as the sum of invasion probabilities. This is arguably the simplest formulation, and while relaxing this assumption would be interesting, it would require knowledge of species compositions across ports, which are currently unknown in a global context. For all of these reasons, our forecasts serve principally to highlight differential invasion risk, between both regions and scenarios, rather than to provide a precise estimation of the number of future invasions. Finally, our forecast does not consider changes to vessel hygiene protocols, which may lead to lower risks of invasion than those forecast in this study. We omitted this factor as biosecurity standards have hitherto been highly variable across locations, and their biological efficacy, in many cases, is uncertain⁵⁵. While these additional factors offer avenues for future research, the current effort arguably establishes an estimate of how the GSN will evolve, and a new baseline for global biological invasions over the coming decades.

Importantly, these baseline projections for invasions should not be viewed as inalterable; environmental policies, as is their purpose, could moderate them. Our work here intersects with, and is largely commendatory of, current policy initiatives, such as the international Ballast Water Management Convention. The Convention, which entered into force in 2017, represents the latest global effort to control ballast-mediated bioinvasions; for instance, using ballast exchange—a measure that has been effective at reducing invasion rates in the freshwater Laurentian Great Lakes⁵⁶. While it is too soon to assess the Convention's effectiveness globally, this study highlights the necessity for concerted measures targeting marine bioinvasions, which otherwise are at risk of increasing to unprecedented proportions. The Convention targets the most relevant driver, given that increased global shipping (that is, propagule pressure), and not environmental change (that is, environmental suitability), was found to be the key factor driving the increase in invasion risk. Furthermore, if efficacy in reducing the per-ship probability of introduction could be estimated, this study could be a key piece in quantifying the averted damages and benefit of the Convention.

Here, we have posited that the GSN will not remain static, that changes are predictable by socioeconomic factors, and that these may result in dramatic increases in biological invasions, far beyond those that might be caused by environmental changes. As human societies and their environment continue to transform at accelerating rates⁵⁷, understanding the potential implications of such changes on sustainability, and the benefits of environmental policy, becomes an increasingly important task. Although applied to invasive species, our methods could be applied directly to other sustainability issues, such as forecasting transport-related emissions or energy demand. Beyond environmental sciences and invasion biology, this work may also contribute to disciplines such as trade economics, by emphasizing potential collateral environmental consequences associated with economic growth (that is, invasive species), providing a highly predictive regional model, which could be followed by intraregional country submodels, and introducing residual adjustments as a simple approach to incorporate variation due to unmeasured factors affecting trade and transport (for example, spatial autocorrelation). Regardless of the application, forecasting the GSN provides a substantive layer in understanding the global transport systems, movement of materials across the world, and modelling of sustainability science.

Methods

Data. We acquired data on ship movements from IHS Sea-web. Sea-web provides data on movements (port-of-call, arrival and departure dates, and hours in port) and ship attributes (for example, size and type). For fitting of the RAUG model, we collected data on all movements occurring between 2006 and 2014 inclusive,

consisting of voyages of 81,305 ships separated into 7 ship types (accounting for 95% of shipping traffic), between 3,872 ports.

We obtained GDP and population data from the World Bank, and data on inter-country distance, regional trade agreements, common language, common border and common colonial history through the Centre d'Études Prospectives et d'Informations Internationales research centre^{58,59}. We obtained forecasted GDP and population values from the IIASA's SSP projections database.

As different ships release different amounts of ballast, we collected data on ballast water releases from the National Ballast Information Clearinghouse (NBIC) Database⁶⁰. The NBIC collects data on ballast water discharge for all ships calling at US ports and is the most comprehensive database of its sort available globally. We collected data on all ballast releases recorded by the NBIC between 1 January 2006 and 31 December 2014.

We obtained current and forecasted environmental conditions for all ports from the AquaMaps Environmental Dataset⁶¹. AquaMaps lists temperature and salinity values at a scale of 0.5° latitude × 0.5° longitude cells worldwide, providing forecasted values based on IPCC Scenario A2. We matched each port with the nearest AquaMaps environmental cell.

Before RAUG model parameterization, we applied a number of filtering steps on the data. First, we interpreted all port calls lasting less than 2 h (the minimum recorded time window) as a passage through a port's detection zone and discarded these. We also discarded voyages that required a mean speed exceeding 65 km h⁻¹ (twice the average speed for merchant ships; <http://worldceanreview.com/en/wor-1/transport/global-shipping/2/>). Finally, for the purposes of our model, we disregarded ship movements to Panama and Egypt as the data did not allow us to distinguish between canal passages and true port visits. Instead, the previous and subsequent ports of call were taken as the source and destination, respectively.

We then categorized the world's marine-coastal countries into 15 different SERs (Supplementary Table 2). We define SERs as regions displaying marine biogeographic and ecological similarity, roughly matching the 'realm' bioregionalization by Spalding et al.⁴⁷, but also incorporating socioeconomic regionalization. Considering socioeconomic, geographic and ecological groupings allowed for meaningful regional biotic composition, minimization of other forms of human travel (for example, overland) and minimization of secondary dispersal, and also allowed linkages to macroeconomic variables, which were the predictors in the RAUG model.

In addition to excluding non-coastal countries, we also omitted countries for which data were missing in any of the four aforementioned datasets. This filtering step resulted in the exclusion of 40 coastal countries, most of which were small island states. The remaining 140 countries accounted for 99.3% of all port calls.

Building and testing the predictive model. The model we used is an adaptation of the gravity model of trade. Inspired by Newton's law of universal gravitation, the gravity model of trade's original formulation states that bilateral trade flows between two countries are proportional to the product of the size of their economies and inversely proportional to the distance between them⁶². Since then, this model has been adapted to include more variables that may affect trade resistance, such as common colonial ties or contiguity^{18,19,49}, and used to explore other types of bilateral flows, such as migration⁶³ and commuting behaviour⁶⁴. Given the close link between trade and shipping, the application of gravity models to predict shipping traffic is logical.

We used the following gravity model formulation:

$$\begin{aligned} \log[X_{Ijst}] = & \beta_{s0} + \beta_{s1} \log[\text{GDP}_{It}] + \beta_{s2} \log[\text{GDP}_{jt}] + \beta_{s3} \log[\text{pop}_{It}] \\ & + \beta_{s4} \log[\text{pop}_{jt}] + \beta_{s5} \log[\text{dist}_{Ij}] \\ & + \beta_{s6} \text{CL}_{Ij} + \beta_{s7} \text{CB}_{Ij} + \beta_{s8} \text{CCH}_{Ij} + \beta_{s9} \text{RTA}_{Ij} + \varepsilon \end{aligned} \quad (1)$$

where X_{Ijst} designates ship movements of ship type s from source SER I to destination SER J in year t , pop is population, dist is the great-circle distance between SERs (calculation below), and CL, CB, CCH and RTA are values from 0–1 denoting the proportion of pairs between each of I and J 's member countries that share a common official language, common border, common colonial history and regional trade agreement, respectively. The residual term ε reflects unmeasured factors, such as differential trade infrastructure⁶⁵, historical preferences⁶⁶, neighbourhood effects⁶⁷, trade costs and multilateral resistance⁴⁹. Where these factors reflect systematic, repeatable differences between inter-regional pairs, explicitly modelling the residuals could offer a simple means of incorporating diverse, unmeasured processes (as discussed below).

GDP and pop are the sum of the GDP and population, respectively, of all countries within a SER. Because we were interested in SER-level invasions, dist was calculated based on the mean latitude and longitude of all countries within an SER, weighted by each country's population; for example:

$$\text{Latitude}_I = \sum_{i \in I} \text{Latitude}_i \times \frac{\text{Population}_i}{\sum_{i \in I} \text{Population}_i} \quad (2)$$

where i is a country in SER I , and population_i is the average population of country i over the course of the RAUG model's fitting years. With each SER's

latitude and longitude values, we calculated inter-SER distances as great-circle distances on an ellipsoid between geographical point locations⁴⁸. We utilized this metric—rather than true ship distance—as the RAUG model uses national-level indicators, and it is not obvious how to include true ship distance (a port-level measure). Since we do not anticipate shipping distances to change over the forecasting period (see Supplementary Information), we expect the residual adjustment (see below) to largely correct for any error due to the use of great-circle distance. Common official language, common border, common colonial history and regional trade agreement are typically binary values for each country pair. To convert these to SER-level variables, we calculated the mean of binary values for each combination of countries present in each pair of SERs. We fit the model separately for each ship type, using forward selection to determine which variables should be retained.

Our model accounts for variation in each of the predictor variables; however, myriad other factors intrinsic to each bilateral connection could also impact movement flows. To account for this, we incorporated inter-regional residual effects (that is, the ‘residual-adjustment’ component of the RAUG model). If deviations from the mean expectation reflect systematic, repeatable differences between regional pairs, the residual structure would contain predictive information and should be preserved (for example, if traffic between Northeast Asia and Southeast Asia were higher than expected based on equation (1) in 2009, we might expect it to remain higher in 2014 or 2050). The effect of this is similar to using dummy variables for each region, but has important consequences for forecasting. First, region-specific dummy variables would capture much of the variation due to macroeconomic variables, which could yield a good fit, but would result in poorer predictions if these macroeconomic variables have a real effect and change in the future. Second, using dummy variables requires additional parameters to be fit for each region, whereas residuals do not. In notation, the final predicted traffic values with residual adjustment (\hat{X}'_{Ijs}) were calculated as follows:

$$\hat{X}'_{Ijs} = \frac{X_{Ijs0}}{\hat{X}_{Ijs0}} \times \hat{X}_{Ijs} \quad (3)$$

Here, X_{Ijs0} refers to actual mean historical traffic values, and \hat{X}_{Ijs} denotes predicted mean values without residual adjustment for historical (\hat{X}_{Ijs0}) and forecasted (\hat{X}'_{Ijs}) traffic (see Supplementary Table 3 for residual adjustments by SER). Equivalently, one can conceptualize the effect of the macroeconomic predictors used in the gravity model as a scaling factor for the proportional change in shipping, given all of the background factors determining shipping between regions. Given the gravity model’s log-linear formulation, this back-transformed offset was multiplicative.

We performed model validation by fitting model parameters to four years of data (2006–2009) and predicting ship movements in 2014. Prediction strength was evaluated using the squared deviation from the 1:1 line of predicted values (\hat{y}) versus observed values (y)—that is, the mean squared error (MSE) as a proportion of the variation in observed values, R^2_{MSE} :

$$R^2_{\text{MSE}} = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2} \quad (4)$$

This measure will always be less than or equal to the conventional coefficient of determination R^2 , which generates residuals from the best-fitting regression line. As this was applied to temporally distinct validation data, the unexplained variation ($1 - R^2_{\text{MSE}}$) represents prediction error, which is an outcome of all of the underlying forms of uncertainty (for example, epistemic uncertainty (model and parameter) and stochasticity (for example, spatiotemporal fluctuations)).

We compared the RAUG model against four alternative models. Alternative model I was a ‘naïve history’ model that assumed that shipping traffic would remain unchanged from mean values between 2006 and 2009. The naïve history model is identical to basing predictions only on residuals; thus, improvements from using RAUG are due to the effects of macroeconomic predictors. Alternative model II was a historical model with a fitted scalar to adjust for growth. Here, we used mean traffic between 2006 and 2008 as the historical baseline and traffic data for 2009 to calculate an annual growth rate. We then applied this annual rate of growth each year to 2014. Alternative model III resembled our proposed model, but did not use residual adjustment. Instead, we added dummy variables to equation (1) for each source and destination SER. This formulation of the gravity model is widely used^{17,69} and attempts to capture multilateral resistance⁴⁹. The use of dummy variables is a more traditional approach than our RAUG model, but, as explained above, can capture much of the variation due to macroeconomic predictors. Alternative model IV considered spatial autocorrelation. Although SERs represented broad geographical scales, autocorrelation could still occur. We tested whether the residual adjustment accounts for autocorrelation by modifying equation (1) to include GDP and the population of the nearest neighbouring SER as additional predictors.

Forecasting to 2050. To forecast ship movements to 2050, we refit the RAUG model to all nine years of historical data (2006–2014; equations (1)–(3)), using GDP and population projections under each of the five SSPs. Common official

language, common border, common colonial history and regional trade agreement were kept constant at the 2014 levels.

The IIASA’s SSPs—developed as part of the IPCC’s Fifth Assessment Report—present five different narratives of future socioeconomic developments². SSP1 (‘sustainability’) foresees a global emphasis shift from economic growth to human well-being, and lower resource and energy intensity, leading to lower inter- and intra-country inequality. SSP2 (‘middle-of-the-road’) projects a continuation of the historical trend: uneven global development, moderate population growth, and slow progress in mitigating environmental degradation and reducing resource and energy intensity. SSP3 (‘regional rivalry’) forecasts a rise in global protectionism, resulting in slow economic development and current levels of inequality or worse, where population growth is low in developed nations and high in developing ones. SSP4 (‘inequality’) is characterized by high intra- and international stratification of power, wealth and opportunity, split between a capital-intensive, well-connected society and a fragmented collection of lower-income societies. SSP5 (‘fossil-fuelled development’) proposes a world that embraces resource- and energy-intensive practices coupled with effective management of social and ecological systems, resulting in rapid global economic growth and increasingly integrated global markets.

Associated with each of the five SSPs are decadal GDP and population forecasts to 2100, covering 181 countries. Each SSP presents a single population projection and three different GDP projections, one of which is designated the representative ‘marker’ for that SSP. Here, we used the population and marker GDP projections for each SSP.

The alternative SSPs yielded the main source of uncertainty in our forecasts. These were combined with uncertainty estimates for the RAUG model to obtain upper and lower bounds of our projections. For RAUG uncertainty, we first used the predict function setting interval = ‘prediction’ with the lm object in R, to obtain upper and lower 95% prediction intervals for the gravity model (PI_{gm}) (equation (1)), passing each bound through the remainder of the RAUG procedure. Uncertainty could also occur in the residual adjustment. The residuals included context-specific factors determining trade between region pairs, but would also contain interannual variability. The prediction interval was thus calculated comparing observed and predicted traffic in the fitting years:

$$\text{PI}_{\text{ra}} = s \times t_{0.05(2), n-1} \times \left(1 + \frac{1}{n}\right)^{0.5} \quad (5)$$

Where PI_{ra} is the 95% prediction interval, s is the standard deviation between observation and expected values ($X_{Ijs} - \hat{X}'_{Ijs}$), calculated across fitted years, t is the critical value from the t distribution, and n is the number of fitted years used in estimating the residual adjustment (equation (3)). To obtain the overall upper bound of our forecasts, we took each SSP and passed the socioeconomic projections as predictors into upper prediction intervals of the RAUG model (PI_{gm} and PI_{ra}), and then took the highest traffic projection. We repeated this with the lower bounds.

Probability of invasion. Next, RAUG-SSP projections of global shipping were integrated into a shipping-mediated marine biological invasion model, using the methodology outlined by Seebens et al.²⁰. The model decomposes the probability of a species invading a certain port due to a given vessel movement into independent probabilities of a species being alien to the destination port, the species being introduced by the vessel, and that species successfully establishing. For every inter-port movement, we calculated the probability of that movement leading to species invasion from the origin port to the destination port.

As the GSN dataset that we derived was not identical to that of Seebens et al., we recalibrated invasion model parameters to match their published probabilities of port-level invasion risk²⁰. We used the same years as those used to fit their model, and adjusted the parameters in our establishment model to minimize deviation between our model’s output and the published probabilities. The resulting parameter values (defined below) were: $\alpha = 0.0000928$, $\sigma_t = 14.02^\circ\text{C}$, $\sigma_s = 23.88 \text{ ppt}$, $\beta = 14.72$, $\gamma = 1,020.18 \text{ km}$, $\lambda = 45.74 \text{ m}^{-3}$ and $\mu = 0.023 \text{ d}^{-1}$, and a correlation coefficient of $r = 0.85$ fit to their probabilities of establishment. Thus, our models generally produced the same patterns for 2007–2008, which were the fitting years used by Seebens et al.²⁰.

Following Seebens et al., the likelihood that a native species in donor port i is non-native in recipient port j is a function of biogeographical dissimilarity:

$$P(\text{alien}) = \left(1 + \frac{\gamma}{d_{ij}}\right)^{-\beta} \quad (6)$$

where d_{ij} is the inter-port distance, and γ and β are constants. The likelihood that a species is introduced from source i to destination j on ship route r is:

$$P(\text{introduction}) = (1 - e^{-\lambda B_r}) e^{-\mu \Delta t_r} \quad (7)$$

In this formulation, the probability of introduction increases with the amount of released ballast water B_r that is taken up at source port i and released at destination port j , and decreases with the mortality rate of the species μ and travel time Δt_r . λ is

a constant. For each set of connections, Δt_r was set as the number of days between port calls.

Ballast water released for a given ship route r (that is, from a source port i to a destination port j) was calculated as follows:

$$B_r = z W_r \left(1 - \frac{z W_r}{V_r} \right)^{\delta_r} \quad (8)$$

where W_r represents the amount of ballast a given ship releases, V_r denotes the volume of a ship's ballast tank, δ_r is the number of intermediate stopover routes on route r , and z is the fraction of zero releases a ship makes. We estimated ship-type-specific values of z using US ballast water release data from the NBIC. We estimated values of W_r by applying regressions on non-zero releases from the same dataset, using ship size (deadweight tonnes) and ship type as predictors (Supplementary Table 4), and calculated V_r as one-quarter of a ship's carrying capacity²⁰.

The probability of establishment follows a Gaussian function of standardized differences of water temperature and salinity between donor and recipient ports²⁰:

$$P(\text{establishment}) = \alpha e^{-0.5 \left[\left(\frac{\Delta T_{ij}}{\sigma_T} \right)^2 + \left(\frac{\Delta S_{ij}}{\sigma_S} \right)^2 \right]} \quad (9)$$

where $\frac{\Delta T_{ij}}{\sigma_T}$ and $\frac{\Delta S_{ij}}{\sigma_S}$ represent standardized differences in temperature and salinity, respectively, between the source port i and destination port j , α is the basic probability of establishment, and σ_T and σ_S are scaling parameters for temperature and salinity, respectively.

We combined the above equations to calculate invasion probabilities between any two ports:

$$P(\text{invasion})_{ij} = 1 - \prod_{r_{ij}} [1 - P(\text{alien})_{ij} P(\text{introduction})_r P(\text{establishment})_{ij}] \quad (10)$$

where r_{ij} denotes each vessel movement from port i to port j . We then aggregated invasion probabilities across all ports i contained in SER I to port j in SER J as an index of invasion risk between SERs:

$$E(\text{invasion})_{IJ} = \sum_{i \in I} \sum_{j \in J} P(\text{invasion})_{ij} \quad (11)$$

$E(\text{invasion})_{IJ}$ is analogous to the expected number of invasions, with the simplifying assumption that invasions from different ports are independent (necessary given the absence of species-specific information).

To forecast inter-port invasion risk to 2050, we recalculated invasion probabilities using forecasted environmental values, then applied an exponential coefficient based on the RAUG-SSP-projected increase in traffic for the corresponding SER pair:

$$n_{IJ2050} = \hat{X}'_{IJ2050} / X_{IJ2014} \quad (12)$$

where again \hat{X}' denotes the predicted traffic with residual adjustment, and X refers to actual traffic. These calculations yielded the following forecasted values:

$$E(\text{invasion})_{IJ2050} = \sum_{i \in I} \sum_{j \in J} [1 - [1 - P(\text{invasion})_{ij2014}]^{n_{IJ2050}}] \quad (13)$$

where again port i is located in SER I , port j is located in SER J , and n_{IJ2050} represents the ratio of traffic between SERs I and J in 2050 compared with 2014, and was used to scale traffic with their ports. Given that $P(\text{invasion})$ incorporates higher-order connections, our forecasts will as well. This assumes that higher-order connections increase proportionally with primary traffic predicted from the RAUG model. Using the output of these models, we present how the expected number of invasions may vary under the different socioeconomic scenarios, and compare the effects of climate-driven environmental change and prospective growth in shipping traffic on global invasion probabilities.

Code availability

Code underlying the results will be made available upon request.

Data availability

Historical GDP and population data were obtained from the World Bank Databank (<http://databank.worldbank.org/>), and forecasted values are accessible through the IIASA SSP database (<https://tntcat.iiasa.ac.at/SspDb/>). Data on inter-country distance, trade agreements, common language, common border and common colonial history are obtainable through the CEPPII research centre's GeoDist and Gravity datasets (http://www.cepii.fr/CEPII/en/bdd_modele/bdd_modele.asp). Data on historical ballast releases can be accessed through the NBIC Database (<https://invasions.si.edu/nbic/search.html>). Current and forecasted environmental variables used in this study are available from the AquaMaps Environmental

Dataset (https://www.aquamaps.org/main/envt_data.php). Data on ship movements and attributes were purchased from IHS Sea-web, are used under license and cannot be publicly shared by the authors. However, these data can be purchased from IHS (<https://maritime.ihs.com>).

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Author contributions

A.S. and B.L. designed the study, analysed the data and wrote the manuscript. E.S. contributed experience and perspectives relating to socioeconomic, shipping and trade components. All of the authors reviewed and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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