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RESEARCH ARTICLE OPEN ACCESS

Increasing Global Expansion Speeds of Marine Invaders

Emily L. Richardson[1] | James M. Pringle[2] | James E. Byers[1]

[1]Odum School of Ecology, University of Georgia, Athens, Georgia, USA | [2]Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire, USA

Correspondence: Emily L. Richardson (emily.richardson2@uga.edu)

Received: 20 June 2025 | **Revised:** 19 September 2025 | **Accepted:** 12 October 2025

Editor: Elizabeta Briski

Funding: This study was supported by grants from NSF grant OCE-1947954 to J.M.P.; NSF grant 1947884 to J.E.B.; FFIRE Postdoctoral Scholars Program from the University of Georgia Office of Research.

Keywords: biogeographic boundaries | biological invasions | expansion | GBIF | jump dispersal | range distribution

ABSTRACT

Aim: Quantifying the speed of invasive species range expansion and the mechanisms behind it is a key management goal that also informs ecological theories of spread. Byers et al. found that time since first global introduction (TSI) was the strongest predictor of non-native range size of coastal marine invertebrates relative to environmental and species traits, and species were predicted to expand on average 400 km/decade along coastlines. Here, one decade later using the same 138 marine invertebrates, we repeat that analysis and test the prediction that the average invader expansion speed was 400 km from 2014 to 2024.

Methods: Using the Global Biodiversity Information Facility (GBIF), we downloaded species occurrences to estimate the non-native range size of each invader along coastlines in the northern and southern hemispheres. We calculated expansion speed as the difference between each species' 2024 range size and its 2014 range size estimated by Byers et al. We tested (Hypothesis 1) TSI is still the most important variable for explaining global invasive range size; (Hypothesis 2) Mean expansion speed is 400 km/decade; (Hypothesis 3) Expansion speed is best predicted by distributional characteristics of a species' non-native range (i.e., initial range size, initial number of coastlines occupied); and (Hypothesis 4) Expansion speeds vary across taxonomic groups.

Results: TSI was still the best predictor of non-native range size (RVI = 1, β: 0.39–0.42). However, average range expansion speed since 2014 was 3000 km/decade, ~8× the previous prediction. Species that started with large ranges and distributions across multiple coastlines exhibited the fastest expansion speeds ($R^2 = 0.4$), but there were no taxonomic patterns in expansion.

Main Conclusions: Ranges of non-native species are not at equilibrium and are still spreading rapidly, posing a challenge for coastal ecosystem management.

1 | Introduction

Quantifying the spread of invasive species is a long-standing goal of ecology, and pivotal for understanding invasion dynamics and finding management solutions (Elton 1958; Fisher 1937; Hastings et al. 2005; Skellam 1951). Invasive species are non-native species capable of spreading in their introduced range. Across species, and across spatially disjunct populations of a single species, there is enormous variation in the size of non-native ranges and how those ranges are dispersed around the world (Byers et al. 2015; Fenollosa et al. 2021). Some invasive species have successfully expanded their ranges to multiple continents, while others are found regionally, for instance, in one city or on one coastline (Byers et al. 2015; Crooks and Soulé 1999; Pyšek and Hulme 2005). Efforts to identify mechanisms that support or inhibit expansion have mostly focused on the physical characteristics of the environment (Byers 2002; Guisan and

Thuiller 2005). However, invader life history (Rejmánek and Richardson 1996), taxonomy (Padayachee et al. 2017), interactions with native species (Byers 2000; Svenning et al. 2014), evolutionary responses (Perkins et al. 2013) and dispersal pathways (Wilson et al. 2009) are also important for invasion dynamics. Empirical tests evaluating invader traits and the mechanisms important for expansion rates (i.e., Δrange size over time) can forecast which invasive species are most threatening to an ecosystem (Crooks and Soulé 1999; Ferrari et al. 2014; Lake et al. 2020).

Invasion dynamics differ across time and space (Arim et al. 2006; Hastings et al. 2005; Pyšek et al. 2008). Considering expansion in the long-term versus the short-term, or globally versus locally, may generate estimates of population growth rate and expansion speed that differ substantially across these scales, within and across species (Pyšek et al. 2008). Expansion rates at the leading edge of the range and unaided by humans (i.e., locally), are slow and more sensitive to the environment and habitat quality (Marco et al. 2013). However, spread is often accelerating following a long-distance human-mediated introduction into a favourable, novel environment (Pyšek and Hulme 2005; Wilson et al. 2009). For example, in Argentine ants (*Linepithema humile*), annual expansion rates after 'jump' dispersal (i.e., the colonisation of new areas over long distances) to new continents were three orders of magnitude greater than annual local dispersal (Suarez et al. 2001). While jump dispersal events are rare, their effect has shaped phylogenetic and biogeographic patterns via intercontinental colonisation (Givnish and Renner 2004; Petit et al. 2008; Renner 2004), and has also challenged predictions of classic spread models (Hastings et al. 2005).

The individual effects that dispersal pathway, life history and physical environmental factors have on expansion rate are intertwined, because spread can accelerate, decelerate or fail based on how each influences reproduction or movement (Ellner and Schreiber 2012). Species traits and dispersal pathway interactively determine dispersal distances—for example, jump dispersal occurs in insects with larvae that feed on imported goods (Liebhold et al. 2021; Mally et al. 2022), and also in plants with seed morphologies that are easily dispersed by wind and ocean currents (Nathan et al. 2002, 2008). Further, many successful invaders have life history traits that allow them to broaden their niche and tolerate variable environmental conditions (Atwater and Barney 2021; Pili et al. 2020). Poleward expansion of invasive crabs (*Hemigrapsus sanguineus*) was linked to temperature-driven temporal variation in the phenological window for successful larval release, development and recruitment (Giménez et al. 2020). The interconnections between dispersal pathway, life history traits and environmental conditions highlight the importance of using all three factors in tandem to understand global distributions and expansion rates.

Life history traits are phylogenetically related, so there can be patterns related to invasion pathway, establishment, and method of spread that are specific to certain taxa (van Kleunen et al. 2007). For example, plant groups (i.e., families, orders, subclasses) with mostly climbing (Daehler 1998) or tall species (van Kleunen et al. 2007) have greater invader success. Mode of introduction is also associated with taxonomic groups (Padayachee et al. 2017; Riera et al. 2021). For example, sessile marine invertebrates are often introduced through fouling on the hulls of ships where they are attached (Sylvester et al. 2011). Regardless of taxa, species that are introduced in large numbers in multiple attempts (i.e., with high propagule pressure) often have the most success establishing an invasive population (Kolar and Lodge 2001; Lonsdale 1999).

Despite the expectation of influential physical and biological factors, time since global introduction (TSI) often best explains invasive range size and expansion rate following species establishment (Wilson et al. 2007). As per Byers et al. (2015), time since global introduction (TSI) is defined for a species as the time since its first record of introduction anywhere in the world, which is extracted from the literature. Generally, range size increases with TSI for plants (Pyšek and Jarošík 2005), amphibians and reptiles (Li et al. 2014), birds (Dyer et al. 2016), and marine invertebrates (Byers et al. 2015), so TSI has been used to predict the impact of invasive species (Kulhanek et al. 2011). However, terrestrial, aquatic and marine invasive species spread in different ways and at different rates (Grosholz 1996; Padayachee et al. 2017), so the predictive power of TSI may differ across these habitats. For example, in the ocean, expansion rates are heavily affected by current transport (Marshall et al. 2012; Strathmann 1985). This is especially true for species that reproduce with larvae that must spend time in the water column while developing (Byers and Pringle 2006), so that general principles of invasion that are understood from observing terrestrial species may not apply to marine invaders.

Byers et al. (2015) compiled a database of coastal invasive marine invertebrate species to test if non-native range size was best predicted by time since first record of global introduction (TSI), physical components of the environment (temperature, salinity, current speed), or their life history (habitat, adult mobility, adult body size, development type). Physical and biological variables had little significance on invasive range size, and instead, TSI was the most important variable, explaining 20% of the variation across species (Byers et al. 2015). The slope of the relationship between TSI and range size predicted species would spread 400 km/decade. Here 10 years later, we use the same 138 marine invertebrate invaders and their current range sizes to test two hypotheses related to results in Byers et al. (2015): (Hypothesis 1) TSI is still the most important variable for explaining global invasive range size; and (Hypothesis 2) Mean expansion speed (i.e., Δrange size = 2024 range size − 2014 range size) is 400 km/decade. We also test two hypotheses regarding interspecific variation in expansion speed: (Hypothesis 3) Expansion speed is best predicted by distributional characteristics of a species' non-native range (i.e., initial range size, initial number of coastlines occupied); and (Hypothesis 4) Expansion speeds vary across taxonomy.

2 | Methods

We replicated methods from Byers et al. (2015) using the same 138 invasive coastal marine invertebrates (see Table S1.1). Here, we briefly describe how species occurrences, non-native range sizes, life history traits, physical variables, and distributional characteristics were obtained, but see 'Methods' in Supporting Information for detailed methods.

We used species occurrence data from the Global Biodiversity Information Facility database (GBIF) to quantify range sizes. GBIF archives species occurrences globally through citizen science efforts, museum contributions, etc. and is commonly used to model species distributions (Heberling et al. 2021). Using Google Earth (Web Mercator, EPSG 3857), we measured the distance in kilometres along the coastline that encompassed the non-native range. Separate range distributions were calculated for the east and west coasts of the Atlantic, Pacific and Indian Oceans, in the northern and southern hemispheres. New Zealand was measured separately as its own distribution. Thus, there were 13 possible coastlines that a species could occupy.

To assess factors that affect non-native range size and expansion speed (Δrange size = 2024 range size − 2014 range size), we obtained biological variables for each species—development type (planktonic or non-planktonic), maximum adult body size, habitat use (infaunal or epifaunal), adult mobility (mobile or sessile) and time since first global introduction (TSI) (Table S1.1). Additionally, we quantified the number of discrete coastlines occupied in 2014 and used the non-native range size in 2014 from Byers et al. (2015) (Table S1.1).

For each species occurrence in the non-native range, oceanographic data were extracted from the closest $\frac{1}{4}^{\circ}$ by $\frac{1}{4}^{\circ}$ boxes included in the World Ocean Atlas 2023 (Reagan et al. 2024) and the Drifter Data Assembly Center (Lumpkin and Centurioni 2010). Our analyses included annual means and standard deviations of temperature, salinity and current speed, except for mean temperature and current speed for which we used spring averages (spring months: April, May, June in northern hemisphere; October, November, December in southern hemisphere). Larval density in the water column is expected to peak in spring when many benthic marine invertebrates spawn (Reitzel et al. 2004)—each hemisphere's spring sea temperature and current speed averages might better predict invasion than annual averages. Finally, we averaged physical variable values for all non-native occurrences for each species.

Theoretically, because GBIF does not remove valid occurrence data, all of the occurrences in the 2014 dataset should be present in 2024, so non-native range sizes should either increase or not change. However, most of our 138 species had some occurrences that were present in 2014 but absent in the newly downloaded GBIF data. For six species (4%), range endpoints were lost, and non-native range size decreased. We analysed data with and without the six species with negative expansion speeds, and found that results did not change qualitatively, and quantitative estimates changed only slightly (except for phylum analysis; see below). We included all species to maintain a direct comparison to Byers et al. (2015).

Occurrence losses represent a consequence of using a public database, where data can be removed and edited for quality control (e.g., correction of a misidentified species or reclassification), or historically collected data can be added (e.g., occurrences from the 1970s added after 2014). Our ability to ascribe range changes due to true range expansion versus GBIF quality controls and increased sampling efforts over the last decade is limited. We remain agnostic as to the true mechanism of any invasive range changes we observe, but it is likely that both biological expansion and improved data sources are at play. At minimum, our study provides new insight into how our current knowledge of invasive species distributions compares to 10 years ago.

2.1 | Statistical Analyses

2.1.1 | Non-Native Range Size in 2024

We replicated the Byers et al. (2015) analysis of the response variable 'non-native range size' using life history traits, physical variables and TSI (i.e., TSI in 2014 + 10 years) to test if TSI was still the strongest predictor (Hypothesis 1). After centering (i.e., subtracting the mean of a variable from each data point) and scaling (i.e., dividing each centered data by the variable's standard deviation) data, we fit linear regression models to all possible combinations of predictor variables and used standardised beta (β) coefficients (i.e., model estimates, range −1 to 1) to compare the magnitude of each variable's effect against the other variables. We used subset model selection to find the top-performing models—this is an exhaustive approach that ensures we find the best global model (Burnham and Anderson 2002). We selected the four best-fit models for each number of variables up to seven, using corrected Akaike's Information Criterion (AIC_c). Lower AIC_c values reflect greater model parsimony. For the 28 candidate models and an intercept-only null model, we calculated ΔAIC_c (i.e., difference between each model and the model with the lowest AIC_c) and Akaike weights (w_i, relative likelihood). In addition to the 28 models, we also included any remaining models that had $\Delta AIC_c < 2$. Finally, we estimated the Relative Variable Importance (RVI; range 0–1) for each independent variable by calculating w_i using only the top-performing models ($\Delta AIC < 2$), and then summing w_i of all models for which the variable appeared. A variable with a high RVI appears frequently in the list of top-performing models, and thus is important for explaining the response variable.

We wanted to examine whether the relationship between non-native range size and TSI had changed appreciably over the last decade. If the relationships are the same, then the slope of non-native range size versus TSI in 2024 should match the slope in 2014. We used an analysis of covariance (ANCOVA) with 'time since global invasion', 'study year' (categorical: 2014 or 2024), and their interaction as predictors of 'non-native range size'.

2.1.2 | Non-Native Range Expansion Speed

To test the prediction from Byers et al. (2015) that average expansion speed is 400 km/decade, we calculated 'expansion speed' (Δrange size = 2024 range size − 2014 range size) for each species. We then used a one-sample t-test comparing mean 'expansion speed' to 400 km/decade (Hypothesis 2). Then, to identify what factors best explain variation in 'expansion speed', we followed the same statistical model selection protocol described for the 'Non-native range size' analysis. As predictors we included 'time since global invasion', all of the life history and physical variables, and the distributional characteristics from each species' 2014 ranges, that is, 'non-native range size' and 'number of coastlines occupied' (Hypothesis 3). Because 'time since global invasion', 'non-native range size' and 'number of coastlines occupied' may be highly correlated, we used a Pearson correlation matrix, linear models (LM) and a Poisson generalised linear model (Poisson GLM, response: 'number of coastlines occupied') to evaluate the strength of the relationships (and possible collinearity) between the three predictors and between each predictor and expansion speed. Because correlations were $r < 0.7$ for all pairings, the predictors remained in the analysis (Table S1.2; Figure S1.1).

Finally, we evaluated whether expansion speeds varied across eight phyla in our dataset (Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca and Porifera) (Hypothesis 4). The phyla Entoprocta and Xenacoelomorpha were not included, because each has only one representative species. Because sorting species into phyla reduced the sample size per group, the six species with negative changes in range size had a greater influence than in the 'Non-native range expansion speed' analysis. Their inclusion in the taxonomy analysis significantly altered results, both qualitatively and quantitatively, so they were removed. We used one-sample t-tests to check if the average expansion speed of each phylum was greater than zero. Then, we used an analysis of variance (ANOVA) to test if 'phylum' was a significant predictor of 'expansion speed'.

2.1.3 | Testing Assumptions, R Coding and Packages

We completed all analyses and visualisations in R (version 4.3.2) and RStudio (version 2023.12.0+369; R Core Team 2024). For all linear model analyses, we used histograms and Q–Q plots to check for normality, and boxplots to check for homogeneity of variances. All residuals met assumptions, so data were not transformed. For the Poisson generalised linear model, we confirmed that the mean and variance of 'coastlines occupied' were equal.

R coding was done using the 'tidyverse' package (Wickham et al. 2019). We used the 'rgbif' package to extract occurrence data from GBIF using the commands 'occ_download', 'occ_download_wait' and 'occ_download_import' (Chamberlain and Boettiger 2017; Chamberlain et al. 2025). The command 'dredge()' in the 'MuMIn' package was used to run all possible combinations of biological and physical variables for the analyses testing '2024 non-native range size' and 'expansion speed' (Bartoń 2024). We used 'cor' from the 'stats' package to build a correlation matrix between predictor variables in our 'expansion speed' model (R Core Team 2024). We extracted and statistically compared estimates from linear models using the 'emmeans' package (Lenth 2024). For data visualisation, we used 'ggplot2' (Wickham 2016), 'ggmap' (Kahle and Wickham 2013), 'ggeffects' (Lüdecke 2018), 'scales' (Wickham et al. 2023) and 'gridExtra' (Auguie 2017).

3 | Results

3.1 | Non-Native Range Size in 2024

On average, non-native range sizes doubled from 2014 to 2024 (Figure 1). Despite large increases in range sizes over the last decade, the most important variable explaining non-native range size is still time since first global introduction (from introduction to 2024: 16–223 years; Table 1; TSI). TSI was present in all of the top models (Hypothesis 1; $\beta \sim 0.4$; RVI = 1; Table 1). The relationship between range size and TSI steepened significantly (Figure 1; ANCOVA: $t = 2.1$, df = 272, $p = 0.035$). The slope increased by 81% from 2014 (ANCOVA slope: 37.3, 95% CI: ±12.9; $R^2 = 0.19$; $t = 5.7$; df = 136; $p < 0.001$) to 2024 (ANCOVA slope: 67.6, 95% CI: ±25.1; $R^2 = 0.17$; $t = 5.3$; df = 136; $p < 0.001$).

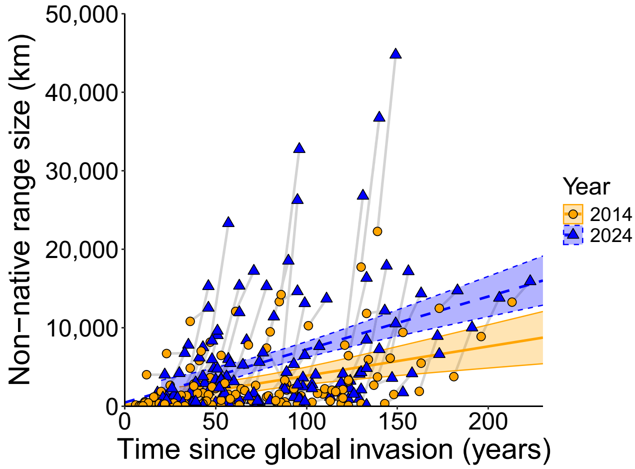

FIGURE 1 | Non-native range sizes and time since first global introduction of 138 coastal invasive marine invertebrate species. Byers et al. (2015) measured the 2014 range sizes (solid/orange), and ranges sizes were estimated ten years later for this study (blue/dashed). Grey lines connect each individual species' range size in 2014 (orange circle) and 2024 (blue triangle), so the grey slopes are expansion speeds of individual species.

Adult mobility was also important for explaining invasive range size, with sessile species having larger ranges than mobile species ($\beta \sim -0.2$; RVI = 0.95; Table 1). Further, species with large body sizes as adults (RVI = 0.56) and species that live in cooler mean spring sea temperatures (RVI = 0.28) or under variable salinities (RVI = 0.40) had larger range sizes (Table 1). However, these latter life history and physical variable β coefficients were ~0.1and not significant in any of the top models (Table 1).

3.2 | Non-Native Range Expansion Speed

In Byers et al. (2015), expansion speed (~400 km/decade) was assumed from the slope of the relationship between range size and TSI. However, the mean expansion speed estimated as the difference between each species' 2024 and 2014 range sizes (Δrange size = 2024 range size − 2014 range size), was 3075.9 km/decade (95% CI: ±789.6; one sample t-test: $\mu = 400$, $t = 6.7$, df = 137, $p < 0.001$) ~8 times the expansion speed from Byers et al. (2015) (Hypothesis 2; Figure S1.2) and ~4 times the expansion speed inferred from the 2024 range size versus TSI slope. Further, about 70% ($n = 97$) of species spread faster than 400 km/decade. Thus, the relationship that uses static non-native range size versus TSI to infer expansion speed (via the slope of that relationship) grossly underestimates the values of expansion speed measured directly for each individual species.

TABLE 1 | Models of *non-native range size* of 138 coastal marine invertebrates in 2024.

Model ID	df	R^2	AIC_c	ΔAICc	w_i	TSI	Adult mobility	Habitat	Dev. type	Max. adult body size	Current speed (spring)	Current var.	Temp. mean (spring)	Temp. SD	Salinity mean	Salinity SD
Null	2		394.7	27.3	1.9×10^{-8}											
A	6	0.21	367.4	0	0.016	**0.41**	**−0.17**			0.13						0.13
B	5	0.20	368.0	0.6	0.012	**0.41**	−0.14			0.12						
C	5	0.20	368.0	0.6	0.012	**0.41**	**−0.19**									0.12
D	5	0.20	368.0	0.6	0.012	**0.40**	**−0.17**						−0.11			
E	4	0.19	368.1	0.7	0.011	**0.41**	**−0.16**									
F	6	0.20	368.6	1.2	0.009	**0.40**	**−0.19**						−0.10			0.10
G	6	0.20	368.7	1.2	0.009	**0.40**	−0.15			0.10			−0.09			
H	7	0.20	368.7	1.3	0.008	**0.41**	−0.15	−0.07		0.14						0.13
I	6	0.20	368.8	1.3	0.008	**0.39**	**−0.16**			0.12					−0.09	
J	7	0.20	368.8	1.4	0.008	**0.40**	**−0.18**			0.11			−0.07			0.11
K	5	0.19	368.9	1.5	0.008	**0.39**	**−0.18**								−0.09	
L	4	0.18	369.3	1.9	0.006	**0.42**				0.14						
M	6	0.20	369.1	1.7	0.007	**0.42**	−0.13	−0.08		0.13						
O	5	0.19	369.4	1.9	0.006	**0.40**	**−0.17**				−0.07					
N	7	0.20	369.4	2.0	0.006	**0.42**	**−0.17**			0.12				−0.05		0.16
P	7	0.20	369.6	2.1	0.006	**0.41**	**−0.17**			0.12	−0.02					0.12
Q	8	0.20	370.2	2.7	0.004	**0.40**	**−0.18**			0.12		0.10	−0.13			0.14
R	4	0.18	370.3	2.9	0.004	**0.42**			−0.12							
S	8	0.20	370.4	2.9	0.004	**0.41**	−0.16	−0.06		0.12			−0.06			0.11
T	3	0.17	370.6	3.2	0.003	**0.42**										
U	8	0.20	370.7	3.2	0.003	**0.41**	**−0.18**			0.10			−0.08	−0.07		0.16
V	8	0.20	370.8	3.4	0.003	**0.42**	−0.15	−0.07		0.13				−0.05		0.16
W	4	0.17	371.0	3.6	0.003	**0.41**							−0.10			
X	9	0.20	371.2	3.8	0.002	**0.40**	**−0.18**			0.12	−0.17	0.26	−0.15			0.14

(Continues)

TABLE 1 | (Continued)

Model ID	df	R^2	AIC_c	$\Delta AICc$	w_i	TSI	Adult mobility	Habitat	Dev. type	Max. adult body size	Current speed (spring)	Current var.	Temp. mean (spring)	Temp. SD	Salinity mean	Salinity SD
Y	9	0.20	371.8	4.3	0.002	**0.41**	**−0.16**	−0.07		0.13		0.10	−0.12			0.14
Z	9	0.20	372.0	4.6	0.002	**0.42**	**−0.18**			0.11		0.10	−0.14	−0.08		0.19
AA	9	0.20	372.4	4.9	0.001	**0.42**	−0.16	−0.06		0.11			−0.07	−0.06		0.15
BB	3	0.02	392.4	25.0	6.1×10^{-8}		**−0.18**									
CC	3	0.02	393.3	25.8	3.9×10^{-8}										−0.16	
DD	3	0.01	394.0	26.6	2.7×10^{-8}					0.14						
					RVI	1	0.95	0.12	0	0.56	0.05	0	0.28	0	0.12	0.40

Note: Models with $AIC_c<2$, and the four best fitting models for each number of independent variables up to seven. Degrees of freedom (df) is the number of estimated model parameters (i.e., independent variables, intercept and error). Below the null model (intercept only), the models are ordered by corrected Akaike information criterion (AIC_c), with model A being the most parsimonious (lowest AIC_c). The ΔAIC_c is the difference between each model's AIC_c and the AIC_c of model A. The standardised β coefficients are shown for each variable in the model—bold and shaded β coefficients are significant ($p<0.05$). The β coefficients for adult mobility, habitat and development type (the categorical predictor variables) indicate that non-native range sizes are smaller in mobile species, species that live in epifaunal habitats and species with non-planktonic development. Akaike weight (w_i) is calculated using the models in the table and R^2 for each model is also shown. Relative variable importance (RVI) is the sum of the weights (w_i) from the models with $AIC_c<2$ (shaded and bolded Model ID).
Abbreviations: Dev., development; Max., maximum; SD, standard deviation; Temp., temperature; TSI, time since first global introduction; Var., variability.

The distributional characteristics 'initial range size in 2014' (β ~0.2; RVI = 1) and 'number of coastlines occupied in 2014' (β ~0.5; RVI = 1) were the only variables that significantly predicted expansion speed over the past decade (Hypothesis 3; Table 2). Indeed, the top model explains 40% of the variation in expansion speed—species with large ranges in 2014 and those that were dispersed on many coastlines had the largest expansion speeds (Figure 2). While TSI, initial range size, and coastlines occupied are all correlated, the model selection results suggest that phenomena related to distributional traits (e.g., rapid spread after introduction to a new coastline) supersede the importance of the time an invader has had to expand its range (Table S1.2; Figure S1.1).

Some life history and physical variables showed only slight influence on expansion speed. Species that are sessile as adults (RVI = 0.27), live in epifaunal habitats (RVI = 0.17) or have planktonic development (RVI = 0.09) had larger expansions compared to species that are mobile, occupy infaunal habitats or have non-planktonic development (Table 2). Further, species in warmer mean spring temperatures spread faster (RVI = 0.17; Table 2). However, the patterns between expansion speed and mobility, habitat, development type and spring temperature were weak (i.e., β coefficients were ~0.1) and not significant in any of the top models (Table 2).

Taxonomically all phyla showed significant range expansion over the last decade, except for Echinodermata and Porifera for which the sample size was small ($n=3$ species each; Table S1.3; Figure 3). The average expansion speed for a phylum ranged between 416 km/decade (poriferans) and 5000 km/decade (chordates). There was a trend that some phyla had faster mean expansion speeds than others (Hypothesis 4; Figure 3), but there was no significant effect of phylum on expansion speed (ANOVA: $F_{7,122}=1.2$, $p=0.303$).

4 | Discussion

Time since first global introduction (TSI) was still the most important variable predicting global invasive range size of the marine invertebrate invaders in our dataset (RVI = 1, β: 0.39–0.42), but species are spreading faster than previously predicted (Byers et al. 2015). Our estimation of mean expansion speed was almost an order of magnitude greater than 400 km/decade (Byers et al. 2015). Not only did species spread faster than 400 km/decade on average, but species with large ranges (RVI = 1, β: 0.21–0.26), and those that occupied many coastlines around the globe in 2014 spread the most (RVI = 1, β: 0.44–0.62), rejecting the notion that an average expansion speed could be applied to all species equally (Byers et al. 2015). Our finding suggests dispersal to new coastlines amplifies a species' global expansion speed via the increase in the number of range edges. For every introduction to a new coastline, a species has two new discrete range endpoints to expand from, so even when a species has a small range size, it can still have a fast expansion speed if it occupies many coastlines. Thus, we have two key findings: (1) Expansion speeds are expected to be rapid following long-distance dispersal events (e.g., jump dispersal) compared to speeds along an already-occupied coastline, and (2) The rich get richer—expansion speeds are fastest for species that already have large, widespread global ranges.

TABLE 2 | Models of *non-native range expansion speed* from 2014 to 2024 for 138 coastal marine invertebrates.

Model ID	df	R^2	AICc	ΔAICc	w_i	Coastlines occupied (2014)	Non-native range size (2014)	TSI	Adult mobility	Habitat	Dev. type	Max. adult body size	Current speed (spring)	Current var.	Temp. mean (spring)	Temp. SD	Salinity mean	Salinity SD
Null	2		394.7	67.8	3.2×10^{-17}													
A	4	0.40	326.9	0	0.017	**0.48**	**0.21**											
B	5	0.40	327.7	0.7	0.012	**0.47**	**0.21**		−0.08									
C	5	0.40	327.9	0.9	0.010	**0.46**	**0.24**								0.08			
D	5	0.40	328.3	1.3	0.009	**0.48**	**0.21**				−0.06							
E	5	0.40	328.3	1.3	0.009	**0.47**	**0.23**			0.06								
F	6	0.40	328.5	1.5	0.008	**0.46**	**0.23**		−0.10	0.08								
G	5	0.40	328.5	1.6	0.008	**0.47**	**0.21**					0.05						
H	5	0.39	328.8	1.9	0.007	**0.47**	**0.22**							0.04				
I	5	0.39	328.9	1.9	0.006	**0.48**	**0.22**						0.03					
J	5	0.39	328.9	1.9	0.006	**0.47**	**0.22**									−0.03		
K	6	0.40	328.9	1.9	0.006	**0.46**	**0.23**		−0.07						0.07			
L	6	0.40	329.1	2.1	0.006	**0.45**	**0.25**					0.07			0.09			
M	6	0.40	329.3	2.4	0.005	**0.46**	**0.26**			0.06					0.07			
N	7	0.40	329.9	2.9	0.004	**0.45**	**0.25**		−0.09	0.08					0.06			
O	7	0.40	330.4	3.5	0.003	**0.47**	**0.22**		−0.10	0.08								0.03
P	7	0.40	330.5	3.5	0.003	**0.45**	**0.24**		−0.06			0.05			0.08			
Q	7	0.40	330.5	3.6	0.003	**0.46**	**0.23**		−0.09	0.08		0.03						
R	3	0.37	331.1	4.1	0.002	**0.62**												
S	4	0.38	331.4	4.4	0.002	**0.60**			−0.09									
T	8	0.40	331.7	4.8	0.002	**0.44**	**0.25**		−0.08	0.07		0.04			0.07			
U	8	0.40	331.7	4.8	0.002	**0.45**	**0.24**		−0.10	0.08					0.07			0.04
V	4	0.38	331.8	4.9	0.001	**0.61**					−0.08							
W	8	0.40	331.9	4.9	0.001	**0.46**	**0.23**		−0.10	0.08						−0.08		0.09
X	8	0.40	332.0	5.0	0.001	**0.45**	**0.24**		−0.09	0.07					0.07		−0.03	
Y	4	0.37	332.6	5.7	0.001	**0.61**						0.05						

(Continues)

TABLE 2 | (Continued)

Model ID	df	R^2	AICc	ΔAICc	w_i	Coastlines occupied (2014)	Non-native range size (2014)	TSI	Adult mobility	Habitat	Dev. type	Max. adult body size	Current speed (spring)	Current var.	Temp. mean (spring)	Temp. SD	Salinity mean	Salinity SD
Z	9	0.40	333.4	6.4	0.001	**0.45**	**0.25**		−0.10	0.08					0.06	−0.07		0.09
AA	9	0.40	333.5	6.5	0.001	**0.45**	**0.24**		−0.09	0.07		0.05			0.08			0.05
BB	9	0.39	333.8	6.9	0.001	**0.45**	**0.25**		−0.08	0.07		0.05			0.08		−0.03	
CC	9	0.39	333.8	6.9	0.001	**0.46**	**0.23**		−0.10	0.08			0.04			−0.09		0.11
DD	3	0.26	353.6	26.6	2.7×10^{-8}		**0.52**											
EE	3	0.08	384.0	57.0	6.9×10^{-15}			**0.30**										
FF	3	0.02	392.8	65.8	8.5×10^{-17}				**−0.17**									
					RVI	1	1	0	0.27	0.17	0.09	0.08	0.07	0.07	0.17	0.07	0	0

Note: Models with $AIC_c < 2$, and the four best fitting models for each number of independent variables up to seven are included. Degrees of freedom (df) is the number of estimated model parameters (i.e., independent variables, intercept and error). Below the null model (intercept only), the models are ordered by corrected Akaike information criterion (AIC_c), with model A being the most parsimonious (lowest AIC_c). The ΔAIC_c is the difference between each model's AIC_c and the AIC_c of model A. The standardised β coefficients are shown for each variable in the model—bold and shaded β coefficients are significant ($p < 0.05$). The β coefficients for adult mobility, habitat and development type (the categorical predictor variables) indicate that non-native range expansion speed is slower in mobile species, species that live in infaunal habitats and species with non-planktonic development. Akaike weight (w_i) is calculated using the models in the table and R^2 for each model is also shown. Relative variable importance (RVI) is the sum of the weights (w_i) from the models with the $AIC_c < 2$ (shaded and bolded Model ID).
Abbreviations: Dev., development; Max., maximum; SD, standard deviation; Temp., temperature; TSI, time since first global introduction; Var., variability.

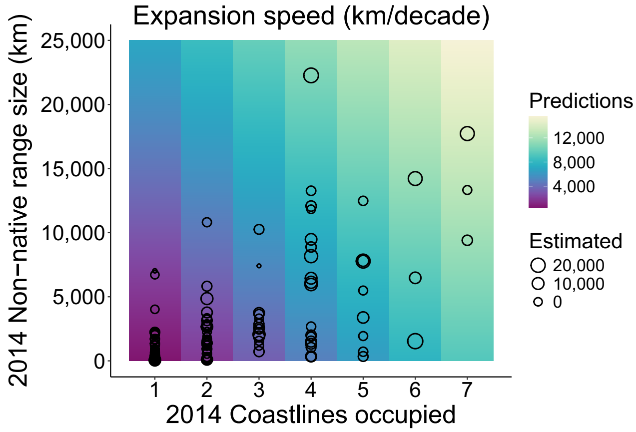

FIGURE 2 | Non-native range expansion speed of 138 coastal invasive marine invertebrate species from 2014 to 2024, predicted by each species' initial non-native range size and the number of coastlines the species occupied in 2014. Species could occupy a maximum of 13 coastlines. Circle size increases with increasing estimated expansion speeds. Background colours are predictions from the top model in Table 2—the species with the fastest expansion speeds had the largest range sizes and occupied the most coastlines (yellow, top right corner). Small circles are species with negative expansion speeds ($n = 6$), likely due to corrections made in the Global Biodiversity Information Facility (GBIF) since Byers et al. (2015) was published.

Our finding agrees with Byers et al. (2015) that TSI is useful for understanding current range sizes. In 2024, two species that were introduced 1 year apart had ranges that on average differed by 70 km (see blue dashed slope in Figure 1). However, using the slope from range size versus TSI to predict future expansion assumes that the range of one species predicts the future range of another. Importantly, the assumption undermines the importance of species-specific range characteristics and intrinsic components that yielded the massive variation in expansion speed we observed (0–25,000 km/decade). However, crucially, Byers et al. (2015) provided the foundation for estimating invasive species' range sizes, as well as providing the first point in a time series for estimating range expansion speeds; our work builds on and improves these methods by estimating expansion speeds using temporal data.

As the world's largest biodiversity network, GBIF provides a unique opportunity to study species globally. Data available in GBIF has increased rapidly over the last 20 years (Heberling et al. 2021), introducing taxonomic, spatial and temporal biases that ultimately shape our perspective of biodiversity (Heberling et al. 2021; Hughes et al. 2021). For example, data are more likely to be entered for areas of the coastline that are better sampled, for example, near marine labs. Also, certain species may be more likely to be entered because they are more identifiable or detectable. Therefore, the efficacy of parameterizing models with GBIF data has come into question for spatial and temporal studies (Beck et al. 2013, 2014; Hortal et al. 2008; Hughes et al. 2021). However, temporal analyses using GBIF are still common in ecological studies of communities (Duchenne et al. 2021; Lajeunesse and Fourcade 2023), species distributions (Callaghan et al. 2023) and invasion rates (Bonnamour et al. 2021). Inevitably, our data likely contain some spatial, taxonomic and temporal biases. For example, coastlines in the Indian Ocean are not well sampled compared to the Atlantic and Pacific coasts; the species with the most records in their non-native ranges are high profile (*Mya arenaria*, *Crepidula fornicata*, *Carcinus maenas*); and expansion speed is fastest for species with the most occurrences. As more data are added to GBIF and range estimates improve, it can be difficult to tease apart sampling bias from the biology, and we propose both factors are at play. We have two key takeaways: (1) The large range expansions we observed emphasise the importance of continuing to report invasive species abundances to publicly available databases like GBIF and (2) GBIF allowed us to quickly estimate non-native range sizes and expansions for over 100 species, across the globe and through time, highlighting a potentially important tool for invasive species management.

In both 2014 and 2024 TSI was an important predictor variable for non-native range size, but TSI did not predict range expansion speed. Furthermore, the use of the TSI—range size relationship in 2014 to infer expansion speed led to a disparity with the direct calculation of expansion speed (Δrange size = 2024 range size − 2014 range size). Such a discrepancy is an example of Simpson's Paradox—a mismatch of estimates that results when data at different scales are aggregated or analysed (Simpson 1951). In this case, the relationship across all species collectively (i.e., range size vs. TSI) is not congruent with the pattern of range expansion speeds calculated and analysed separately, i.e., for each species individually (Figure 4). Our finding is important given that TSI is a metric used frequently in invasive species management (Byers et al. 2015; Kulhanek et al. 2011).

A strength of our approach is that we captured dispersal pathways along a continuum. A species in our dataset that occupied many coastlines likely means it was spread via long-distance, jump dispersal before 2014, while a species on just one coastline had primarily been spreading by dispersal from the leading edge of the range (i.e., locally). Both local and jump dispersal may occur simultaneously for a single species (Pyšek and Hulme 2005; Suarez et al. 2001), so classic spread models that do not account for both generally do not perform well (Hastings 1996; Hengeveld 1994). Jump dispersal usually occurs after human-mediated introduction and results in more rapid spread compared to diffusion expansion (Pyšek and Hulme 2005; Wilson et al. 2009). Because marine invertebrates are commonly spread via hitchhiking mechanisms (i.e., hull fouling, ballast water, etc.), jump dispersal is likely an important pathway for their expansion, and may explain why we observed the fastest expansion speeds in species with large, widespread distributions (Padayachee et al. 2017; Sylvester et al. 2011; Wilson et al. 2009).

The strong effect of coastlines can be explained in terms of spread from occurrences at either end of the range along a coastline (e.g., northern-most and southern-most occurrences)—for example, seven coastlines provide 14 end points to spread from, while one coastline provides two. For two species with the mean 2014 non-native range size (~2500 km), expansion speed was 10 times faster for a species that occupied seven coastlines (the maximum in 2014) compared to a species that was on a single coastline (Figure 2). Non-native range size was also important and present in all models. Range size is important for expansion speed because large ranges yield large population densities and strong propagule pressure, so the chances of successful establishment and invasion are high (Kolar and Lodge 2001; Sylvester et al. 2011). Coastlines occupied and range size are causal variables that directly predict the *rate* of spread. Even though TSI is correlated with those two predictors and expansion speed (Table S1; Figure S1.1), the strong effects of distributional characteristics diminished any signal of TSI in the model (Table 2). Our findings are consistent with previous work showing the most geographically widespread species have higher expansion rates (Pyšek and Hulme 2005; Suarez et al. 2001), suggesting that how species

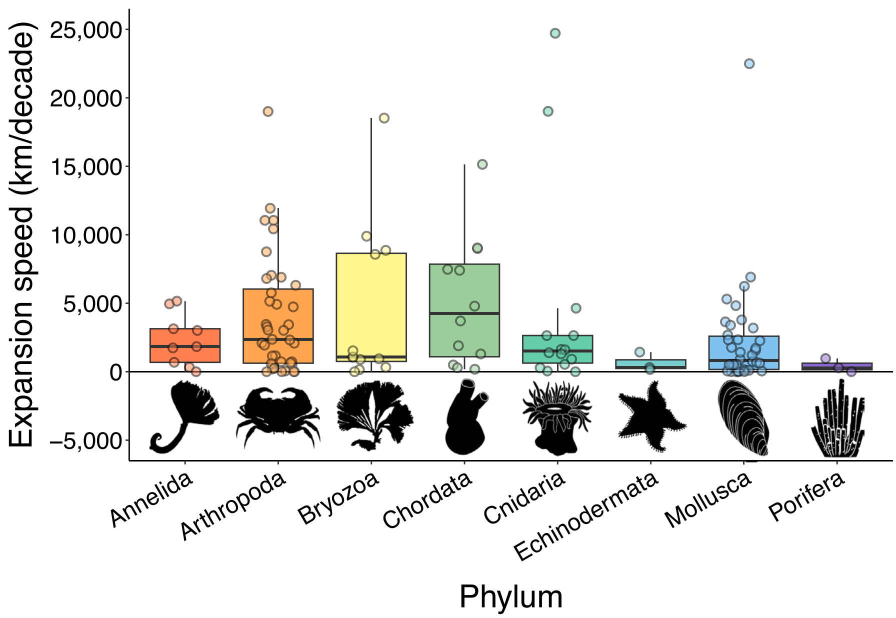

FIGURE 3 | Boxplot of non-native range expansion speed of 130 coastal invasive marine invertebrate species from 2014 to 2024, by phylum. The lower and upper hinges of the interquartile range (IQR, box) are the first (25th percentile) and third (75th percentile) quartiles, and the bold black line is the median (second quartile, 50th percentile). Whiskers mark the smallest and largest values no further than 1.5 × IQR—points beyond the whiskers are outliers. Each point is a species.

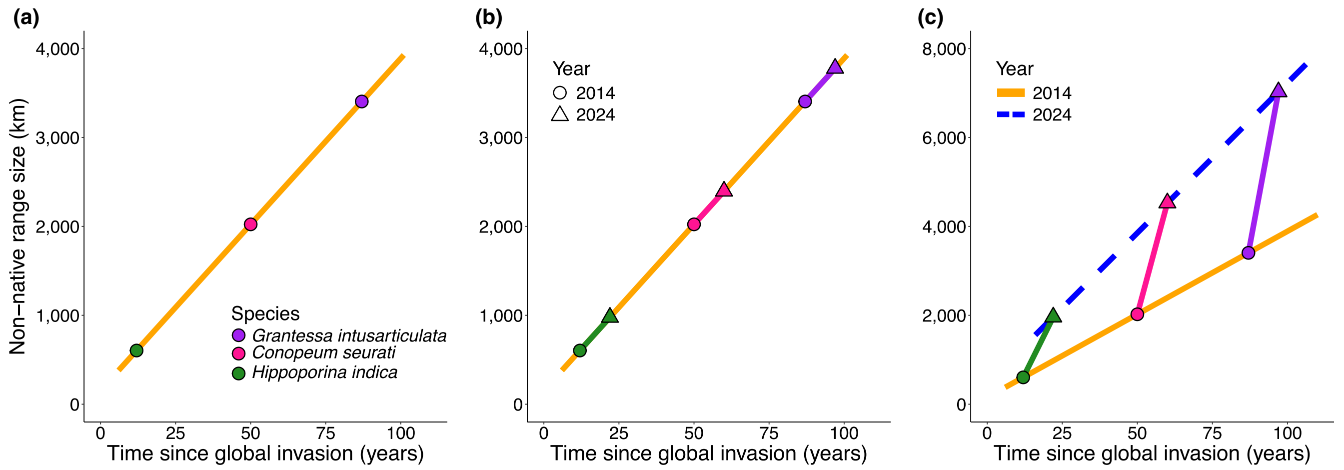

FIGURE 4 | Schematic comparing non-native range size versus time since first global introduction (TSI) model predictions to estimate of non-native range expansion speed. (a) The orange/solid slope (400 km/decade) is from Byers et al. (2015) and Figure 1. Circles are predicted 2014 range sizes for three selected species: *Grantessa intusarticulata* (large range, purple), *Conopeum seurati* (middle range, pink) and *Hippoporina indica* (small range, green). (b) Predicting 2024 range size (triangles) using the 2014 range size versus TSI slope in panel (a)—that is, expansion speed is 400 km/decade for all species. (c) Discrepancy between 2024 range size predictions in panel (b) and estimates of expansion speed. The significantly steeper 2024 blue/dashed slope (700 km/decade; Figure 1) is underpinned by interspecific variation in expansion speed (purple, pink, green slopes).

are distributed (i.e., the number of disparate range endpoints) is the most important factor for expansion speed.

Life history, environmental variables and taxonomy showed little to no importance for range size and expansion speed. We found considerable variation in expansion speed across phyla and a trend that chordates spread faster than other phyla, but the effect was not significant. Adult mobility was minimally important for both response variables—sessile species had larger sizes and faster expansion speeds, which could indicate that hitchhiking on ships disperses species to ports around the world (Padayachee et al. 2017; Sylvester et al. 2011; Wilson et al. 2009). We were surprised that current speed and variability were not important for expansion speed. In the ocean, mass dispersal can occur via current transport. Advection plays a key role in introducing invasive marine larvae to new coastlines (Byers and Pringle 2024; Marshall et al. 2012; Strathmann 1985). Namely, larvae with long larval durations are more likely to be introduced, as long as currents are not overly advective (Byers and Pringle 2006; Byers and Pringle 2024). Recent work has quantified how currents can transport larvae asymmetrically in the downstream direction from their point of origin (Byers and Pringle 2006; Pringle et al. 2011). Also, when currents become constrained, for example by impinging on a cape, this can stop range boundary spreading by breaking the alongshore flow and forcing water offshore into regions uninhabitable by coastal larvae (Pappalardo et al. 2015; Pringle et al. 2017). This process is thought to be responsible for the formation of major biogeographic breaks in the ocean (Gaylord and Gaines 2000; Pappalardo et al. 2015). However, current means used in our study are averaged across all invasive occurrences, and a global average over thousands of kilometres may not be informative for characterising expansion speed, which occurs only at the end points of the range. Therefore, coastlines occupied and 2014 range size have more explanatory power compared to mechanistic variables (i.e., life history, currents).

Of course there are other factors that could affect expansion speed, but we needed to avoid overparameterization of the model. Importantly, most other variables that we could hypothesize might be influential could not be tested because of incomplete data or because they vary too much throughout the latitudinal range. Two such examples are latitude-dependent larval duration (Alvarez-Noriega et al. 2020) and intraspecific variation in fecundity (Álvarez-Noriega et al. 2023).

In conclusion, time since first global introduction remains the most significant predictor of non-native range size (Byers et al. 2015). Byers et al. (2015) discuss that using TSI as a preventative model of spread may not be useful, because it only predicts post-invasion range size and probably underestimates expansion. We found that the range size against TSI model does in fact underestimate expansion speed, but does effectively describe the difference in current range size between species that were introduced in different years. We build on Byers et al. (2015) by improving the predictive model and estimating expansion speed directly. We again advocate for more temporal studies following invasive species distributions so that we can continue to model expansion trajectories through time and across taxonomic groups. From an applied ecology perspective, research like ours can inform invasive species management tactics, but also link life history and oceanographic principles for understanding models and theory of spread. Importantly, non-native species' ranges are not at equilibrium; their continued, accelerating spread poses a major challenge for management of coastal ecosystems.

Author Contributions

E.L.R and J.E.B. conceptualized the study. J.M.P. collected oceanographic data. E.L.R estimated range expansions, analyzed and visualized data and led the writing of the manuscript. J.E.B. and J.M.P made minor contributions to writing. All authors contributed to reviewing and editing the manuscript.

Acknowledgements

We thank P. Pappalardo, W. Lush, C. Osenberg, E. Hall, M. Pierce, K. Vaughn, A. Primo and D. Cryan for valuable feedback on the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and R code are available on Dryad, https://doi.org/10.5061/dryad.c2fqz61np.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70111.

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Biosketch

Emily Richardson is an evolutionary ecologist interested in marine life histories. Jeb Byers is a population and community ecologist who works frequently on marine biological invasions. His interests also include parasite ecology, ecosystem engineers and the biogeography of range boundaries. James Pringle is a physical oceanographer who works primarily on coastal circulation and how that circulation modulates genetic and species level diversity in the global ocean. His recent work has focused on the dynamics of storm surges and the introduction of novel/invasive diversity into coastal populations.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70111-sup-0001-AppendixS1.zip.