Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER

Dynamic Environmental Niches of Marine Invasive Species Over 200 Years

Chunlong Liu[1,2] | Zeli Ruan[1] | Jiayuan Xie[3,4] | Jonathan M. Jeschke[5,6] | Lise Comte[7] | Julian D. Olden[8] | Yunwei Dong[1] | Jiansong Chu[9] | Bin Kang[1] | Brian Leung[10]

[1]The Key Laboratory of Mariculture, Ministry of Education, College of Fisheries, Ocean University of China, Qingdao, Shandong Province, People's Republic of China | [2]Key Laboratory of Aquaculture Nutrition and Feed, Ministry of Agriculture and Rural Affairs, College of Fisheries, Ocean University of China, Qingdao, Shandong Province, People's Republic of China | [3]State Key Laboratory of Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China | [4]College of Advanced Agricultural Sciences, University of Chinese Academy of Sciences, Beijing, China | [5]Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany | [6]Institute of Biology, Freie Universität Berlin, Berlin, Germany | [7]Conservation Science Partners, Truckee, California, USA | [8]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA | [9]College of Marine Life Science, Ocean University of China, Qingdao, China | [10]Department of Biology, McGill University, Montreal, Quebec, Canada

Correspondence: Jiansong Chu (oucjs@ouc.edu.cn) | Bin Kang (binkang@163.com) | Brian Leung (brian.leung2@mcgill.ca)

Received: 20 February 2025 | **Revised:** 10 June 2025 | **Accepted:** 11 June 2025

Funding: C.L. was sponsored by the Young Scientists Fund of the National Natural Science Foundation of China (No. 42306133), Mount Taishan Scholar Young Expert (No. tsqn202312093). J.C. was sponsored by the National Natural Science Foundation of China (No. 42176234).

Keywords: climate change | ecological niche | invasive species | niche breadth | niche dynamics

ABSTRACT

Anticipating the risk of species invasions in new geographical regions remains fundamental to conservation. One critical assumption is that species' environmental niches remain stable under changing environments. If native environmental drivers predict introduced distributions, we would expect high overlap in niche space between native and introduced ranges, with introduced niche increasingly resembling their native niche over time. We quantified changes in species' occupied niche space across 200 years of invasion records, for 778 marine invaders at the global scale. For species in introduced ranges, the majority of their native niche space remained unfilled, even after two centuries. As expected, overlap between native and introduced niche spaces increased with time since invasion. However, niche overlap remained low on average, never exceeding 20% across species. Our results suggest that native environmental drivers will largely fail to predict introduced species ranges in marine ecosystems within policy-relevant (decadal) time frames.

1 | Introduction

Unprecedented human actions have dramatically impacted all facets of biological diversity, leading to the extinction of local populations, the redistribution of species and the alteration of ecosystem functioning (Lembrechts et al. 2021; Sunday et al. 2012; Wallingford et al. 2020). Biological invasions are among the most important contributors to the anthropogenic upheaval facing the world (García Molinos et al. 2016; Pecl et al. 2017). Escalating trading activities and human movement have dissolved geographical barriers, resulting in thousands of species being introduced to new ranges at an unprecedented rate (Olden et al. 2018; Seebens et al. 2017). At the global scale, invasive species have caused economic costs of at least US$ 1.3 trillion in recent decades and have contributed to 60% of known extinctions of plants and animals (Diagne et al. 2021; Roy et al. 2024). As such a paramount challenge is to anticipate potential risks of invasive species, to help develop management strategies at the national and global scales (Lodge et al. 2016; Seebens et al. 2017).

https://doi.org/10.1111/ele.70164

Over the past decades, the environmental niche (hereafter, 'niche') has emerged as a crucial concept to evaluate and anticipate the redistributions of living organisms and shifts in biodiversity patterns under changing environments (Guisan et al. 2014; Sexton et al. 2017). With the accelerating availability of ecological data, niche-based models have been used as a fundamental tool to understand and predict species' invasions into non-native environments, which is projected to further intensify in the future (Liu et al. 2020b; Sardain et al. 2019). Yet, for these tools to be predictive, there is the implicit assumption that niches remain stable, and that past environmental drivers predict distributions in new areas and/or under changing environments. However, while environmental variables (typically abiotic) are often highly predictive under historical conditions (Pinsky et al. 2013), prediction under novel conditions is more challenging, because the context can change, resulting in unexpected species-environment relationships (Liu et al. 2020b). For instance, changes in biotic interactions (Araújo and Luoto 2007), community assemblies (Werkowska et al. 2017) and evolutionary response (Peterson et al. 2019) can all compromise historically strong relationships between distributional patterns and environmental factors. Here, biological invasions represent a high bar, because much of the implicit context will be broken (e.g., with biotic factors), and niche models will only be predictive if the abiotic environmental factors explicitly included in the models continue to determine occurrence patterns. Yet, given the social and economic impacts of invasive species, it is critical to assess the magnitude of niche changes of invasive species, and understand the accuracy of predicted invasion risks under new environments (Liu et al. 2020a; Yates et al. 2018).

In their introduced range, invasive species are often confronted with environmental contexts that differ from those in their native range (Sax et al. 2007; Wallingford et al. 2020). Several studies have used this opportunity to address how invasive species' realised niches shift in new environments (Abellán et al. 2017; Liu et al. 2020a; Petitpierre et al. 2012). During the invasion process, invasive species can maintain, expand, or contract their niche. Importantly, different species are at varying stages of the invasion process, with some recent invasions and others occurring centuries ago (Seebens et al. 2018). We expect that as the invasion progresses, species' realised introduced niche will change over time, potentially increasing its similarity with the native niche or broadening beyond it. Since greater overlap between native and introduced niches implies greater predictiveness of invaders' distributions (or conversely, greater magnitude of niche change corresponds to lower predictiveness), we could gain insight into how long it takes before historical environmental drivers become predictive of a species distribution under novel conditions (or whether it does at all) (Petitpierre et al. 2012). This time lag in predictiveness is an important consideration, given that policy relevant time frames are often measured in years or decades (Epanchin-Niell and Hastings 2010).

Many techniques have been developed for measuring niche changes of invasive species. Among them is the COUE scheme (Figure 1a), which is considered the gold standard, quantifying Centroid shift, Overlap, Unfilling and Expansion of species niches (Guisan et al. 2014; Liu et al. 2020a). The COUE scheme delineates species' native and introduced niches in a two-dimensional (2D) space constructed by the first two axes synthesising environmental predictors important for species distributions (Broennimann et al. 2012; Guisan et al. 2014). A species' global niche is divided into three components: Stability (S) represents the overlapped environmental space occupied in both native and introduced ranges, while Unfilling (U) and Expansion (E) represent the environmental space occupied only in the native range, and only in the introduced range, respectively. When inferring species' responses under evolving environmental conditions (e.g., climate change) through the lens of biological invasions, (i) a larger S suggests a stronger tendency of a species to occupy environmental conditions similar with its historical niche in the future (Figure 1b), (ii) a larger U could arise due to greater dispersal limitation, so that even suitable habitats remain unfilled (Figure 1c) and (iii) a larger E suggests a stronger capacity to occupy novel environments (Figure 1d).

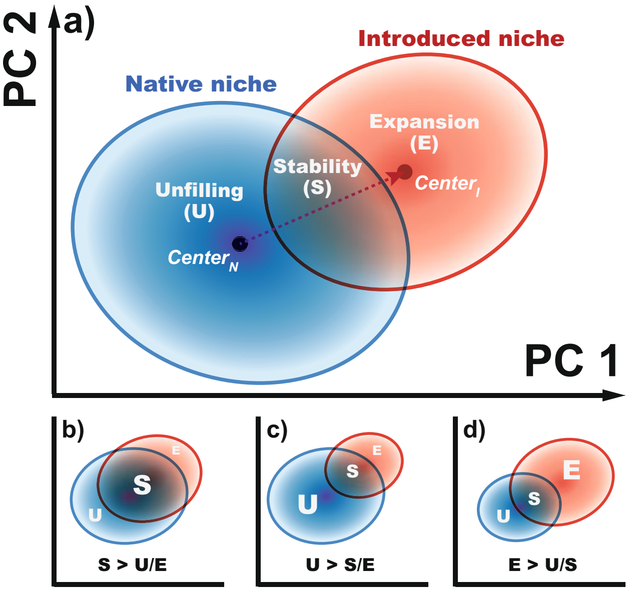

FIGURE 1 | (a) Schematic figure illustrating how species' native niche (blue) and introduced niche (red) can be decomposed using the COUE scheme based on principal components (PC) analysis into Unfilling (U), Stability (S) and Expansion (E), representing the environmental space occupied only in the native range, in both the native and introduced range, and only in the introduced range, respectively (revised from Guisan et al. 2014). The niche centre is determined as the point with the highest density in the environmental space of the native and introduced niche, respectively. Environmental conditions available across the global marine waters are used as the background region to represent where species could potentially colonise (see Section 2 for more details). (b–d) Examples illustrating three scenarios of niche change, with invasive species occupying environments similar to the native niche (S > U/E), being dispersal-limited in new environments (U > S/E), and occupying mainly novel environments (E > U/S), respectively.

In this study, we examine niche changes of biological invaders over space and time, focusing on marine ecosystems. Marine ecosystems have been subject to considerable rates of species invasions over the last half century (Molnar et al. 2008), which may be further amplified by cascading effects of anthropogenic activities and climate changes (McCarthy et al. 2019; Sardain et al. 2019). Yet, niche changes have only been occasionally assessed for species invading specific marine areas (e.g., the Mediterranean Sea; Chefaoui and Varela-Álvarez 2018;

Parravicini et al. 2015), which are poorly studied compared to terrestrial systems (Liu et al. 2020a). Insufficient knowledge of niche changes limits both the development of predictive models and management strategies for marine invaders (Anton et al. 2019).

We collated data for 778 global marine invaders across two centuries of records and compiled their occurrence data in the native and introduced ranges, and then used the COUE scheme to quantify niche changes over time. We hypothesise that niches should remain relatively empty for new invasions (i.e., large Unfilling), but environmental drivers should become more predictive for older invasions (i.e., increasing Stability), as invasive species spread. We also hypothesise that species will occupy a greater number of new environments over time (i.e., increasing Expansion). Although we predict the direction of these changes, we have no a priori expectation on *how long* these processes may take and the *relative magnitudes* of Expansion versus Stability. If historical environmental drivers are to be predictive, the degree of Expansion should be far less than Stability. Additionally, if initial invasions are largely unrelated to environmental suitability (e.g., species introductions driven by stochasticity or non-environmental factors related to human movement), we hypothesise that the deviation between Centroids of native and introduced niches would also decrease over time, as suitable habitat becomes increasingly occupied. Conversely, if initial invasions are most likely to occur in the most suitable environments (i.e., driven by environmental determinants of establishment), the deviation in centroids may remain constant or possibly even increase over time due to increasing Expansion. Finally, we hypothesise that patterns of COUE could differ regionally, and between different groups of organisms. Specifically, given that lower latitudes often have greater species richness, we expect that biotic factors, such as competition and predation, could be stronger at these latitudes (Costello and Chaudhary 2017; Freestone et al. 2021), resulting in greater Unfilling and lower Stability. We expect taxonomic groups to differ in their niche changes due to their different life history traits (e.g., dispersal mode, Wiens and Graham 2005). Taken together, this study seeks to provide insight into our ability to predict the responses of invasive species to novel conditions in policy-relevant time-frames.

2 | Materials and Methods

2.1 | Data Compilation

We assembled a global list of marine invasive species, including their native and introduced ranges, from multiple global databases, particularly the Standardising and Integrating Alien Species (SInAS) database v 2.4.2 (Seebens et al. 2020), Global Register of Introduced and Invasive Species (Pagad et al. 2018), Ocean Biodiversity Information System (OBIS; www.obis.org), IUCN Red List (IUCN; http://www.iucnredlist.org), FishBase (www.fishbase.ca) and SeaLifeBase (www.sealifebase.ca). Marine invaders were defined as non-native species that have successfully established themselves and spread in the introduced range (Jeschke and Strayer 2005). This definition of invasiveness does not refer to ecological or economic impacts caused by non-native species (Anton et al. 2019). Species names were first validated and standardised based on taxonomies of the World Register of Marine Species (https://www.marinespecies.org) for most species, and were checked manually for the remaining species. This study specifically focuses on aquatic species that spend all or most of their life in marine environments—they are classified into three taxonomic groups (algae, invertebrates and fishes). We excluded terrestrial species (e.g., birds) that spend part of their life in the marine realm.

For each species, we collected the information on their native and introduced ranges from diverse sources, such as online databases, government reports and scientific publications (see Table S1 for more details). The native and introduced status of most species are recorded for administrative regions (e.g., country or state), and the range map are lacking for most marine invasive species (International Union for Conservation of Nature; www.iucnredlist.org). We thus adopted 219 regions (105 mainland regions and 114 island regions) to determine native and introduced ranges for each invader. This information was then used for determining the continent(s) where species are native and introduced (hereafter, native continents and introduced continents), with islands and archipelagos in the Pacific Ocean and the Indian Ocean being considered separately. If a species is native to an ocean neighbouring one region but invading a different ocean also neighbouring that region (e.g., the contiguous United States borders the Pacific Ocean and the Atlantic Ocean), we considered their status in this entire region as native, according to the status recorded for administrative regions. In other words, only transnational invasions were considered here. We performed sensitivity analyses by excluding data from regions with isolated parts bordering at least two oceans and obtained similar estimates of niche changes (correlation coefficients > 0.85 for most indices; Table S2).

Species occurrences were compiled from three global databases: GBIF (Global Biodiversity Information Facility; https://www.gbif.org), OBIS (Ocean Biodiversity Information System; https://obis.org) and speciesLink (https://specieslink.net). GBIF is an international data infrastructure providing more than two billion occurrences of species across the globe, and OBIS is the most comprehensive ocean biodiversity database providing millions of marine species observations. For each species, occurrence data were carefully checked to exclude those with likely errors (e.g., not overlapping with any oceans, with both integer longitudinal and latitudinal coordinates, species were misidentified), and were geographically filtered at a resolution of 10 arc-min to only keep one occurrence per cell. For occurrences outside boundaries of all regions, the region nearest to each occurrence was used to classify occurrences into the native and introduced ranges (hereafter, native occurrences and introduced occurrences). Invasive species were then filtered based on the number of occurrences, because delineating the native/introduced niche in the environmental space required at least five occurrences in each range (Broennimann et al. 2012).

To examine temporal patterns in niche changes, data of the earliest year of species introduction were compiled from the SInAS database v2.4.2 (Seebens et al. 2020). For a minority of species missing the earliest year of introduction, we used the earliest year of occurrence reported in the introduced range. Where data existed, these estimates did not differ significantly from dates reported in the SInAS database (paired *t*-test, $\mathrm{df}=1116$, $p=0.39$). It should be noted that the year of species introduction may be earlier than the year of first record at both regional and global scales, as species may be undocumented for several years following their introduction, particularly in the case of unintentional introductions. To examine latitudinal effects, we first determined marine ecoregions (defined by Spalding et al. 2007) overlapping with occurrences in the native or introduced ranges for each species. And then, we calculated the absolute values of mean latitudes of all ecoregions in the native range and in the introduced range (hereafter, the native and introduced latitudes, respectively).

2.2 | Constructing the Environmental Space

Data of marine environmental variables under the present-day scenario (average between 2000 and 2014) at a 10 arc-min resolution were obtained from Bio-ORACLE (Assis et al. 2018). We used the environmental data for the recent period, which could introduce noise, given invasions occurred across a longer timeframe. However, we note that current conditions must be suitable to support the present-day occurrence of the species, and thus could be considered the minimum requirements necessary. Second, current environments are correlated to historic ones. Moreover, most (59%) occurrences were recorded after 1990 and 43% after 2000 in our study, supporting the use of recent environments. We selected nine widely used variables reflecting the physical, chemical and biological aspects of marine environments (Melo-Merino et al. 2020), including maximum bathymetry, mean calcite concentration, mean diffuse attenuation coefficient, mean nitrate concentration, mean phosphate concentration, mean photosynthetically available radiation, mean primary production, mean sea surface temperature and mean silicate concentration. For variables with data available for multiple depths (e.g., sea temperature data were available at the surface and bottom), we selected data recorded for the sea surface, which are often directly derived from remote sensing rather than based on bathymetric profiles (Melo-Merino et al. 2020). Assessing niche changes using the same set of environmental variables allowed us to make the findings comparable across species. To investigate whether niche changes are sensitive to the selection of variables, we further performed the same analyses using 10 additional variables related to chlorophyll, dissolved oxygen, pH, salinity and velocity (Table S2). Estimates of niche indices were significantly correlated between analyses of nine and 19 predictors (correlation coefficients >0.85 for most indices), and we only reported the findings from analyses based on nine predictors (Figure S1; Table S2). Additionally, we examined different spatial resolutions (5, 10, 30 arc-min), and found that the estimates of niche indices were robust (correlation coefficients >0.9 for most indices; Table S2). Thus, we only present findings from analyses using 10 arc-min resolution.

A principal components analysis (PCA) was used to construct a 2D environmental space based on the first two principal components (PC) synthesised from nine environmental predictors. We used the global marine environments as the background region to construct the environmental space (sensu Abellán et al. 2017), which considered the environmental availability and species occurrences across global oceans and seas. Constructing global environmental space can also facilitate the generalisation and comparison of niche changes across species (Liu et al. 2020a). The environmental space was then gridded into 250,000 cells by dividing each PC at a resolution of 500. Species' native and introduced occurrences were projected into the environmental space as points falling in the gridded cells. To account for the biases due to sampling efforts and strategies, a kernel density is applied to smooth the occurrences projected into the environmental space for delineating the native and introduced niches, respectively (Broennimann et al. 2012). To eliminate the influence of anecdotal occurrence records, we excluded 5% of cells with the lowest density in each range for each species.

2.3 | Estimating Indices of Niche Changes

Niche changes between native and introduced ranges were quantified within the framework of the COUE scheme (Broennimann et al. 2012). This study specifically focuses on changes in the realised (i.e., environmental conditions in which species can be observed in nature) rather than the fundamental niche (i.e., all environmental conditions in which species can maintain a positive population growth, assuming no negative biotic interactions or dispersal limitations), because the physiological information is lacking for most species (Guisan et al. 2014).

Based on the environmental space occupied in the native and/or introduced ranges, the relative contributions of Unfilling (U), Stability (S) and Expansion (E) to species' global niches were calculated by dividing the values of the three indices by their sum. Niche centres were determined as the cells with the highest density in the native and introduced niches, respectively (Figure 1a; Dallas et al. 2017), and the centre deviation (CD) was the distance between native and introduced niche centres. As niche changes can only be assessed for species with overlapping native and introduced niches, species with non-overlapping niches (i.e., 0 for S) were excluded from the following analyses.

2.4 | Assessing Patterns of Niche Changes

To examine temporal patterns of niche changes, we plotted a moving window of 50 years for each niche index (U, S, E and CD), for species introduced between 1800 and 2000. To investigate whether spatial and taxonomic factors influenced niche changes, we applied a Bayesian analysis, focusing on latitudinal gradients and taxonomic group, as well as the year since introduction, for each niche index. For each continuous factor, the values were standardised with a mean of 0 and a standard deviation of 1, which allows the comparisons of effects of different factors. We used weakly informative priors ($\mathrm{mean}=0$, $\mathrm{standard\ deviation}=2$) following a Gaussian distribution were used (Gelman et al. 2008). We set four chains of 10,000 iterations with the first 2000 steps as burn-in, generating a total of 32,000 posterior values for each model parameter. We confirmed good chain convergence according to values of Rhat (the potential scale-reduction factor) less than 1.01 (Bürkner 2017). Models were built using 'brms' package in R (version 4.3.1) (R Development Core Team 2023).

3 | Results

Our dataset includes a total of 2694 marine invasive species. Among these, niche changes were assessed for 778 species (234 algae, 436 invertebrates and 108 fishes) with sufficient occurrence data. The number of species were about evenly distributed among their native and introduced continents (Figure 2a,b), with Asia having relatively more native species (20.1%) and Europe having more invasive species (29.5%). More than one million native occurrences and around 0.4 million introduced occurrences were used for niche analyses. Occurrence data were heavily biased across the globe: data were more available in the northern Atlantic Ocean (e.g., eastern North America and western Europe) and western Pacific Ocean (e.g., Australia and Japan), but were less available in South America and Africa (Figure 2c).

In the environmental space, the first two PC axes accounted for 69.7% of the total variation in predictors (Figure S1; 45.9% and 23.8%, respectively). The first PC axis was positively related to the mean concentration of essential nutrients (i.e., nitrate, phosphate and silicate), and negatively related to mean sea surface temperature. The second axis was negatively related to maximum bathymetry and mean primary production.

3.1 | Niche Changes Over Time

Over the last two centuries, almost a half of marine invaders (49.9%) were introduced after 1950, with only around one fourth of species (25.8%) introduced before the 20th century (Figure S2). The magnitude of niche changes demonstrated clear temporal patterns over time, with species with longer residence time having relatively larger introduced niches (Figure 3; Figure S2). With increasing years since introduction, the magnitude of Stability consistently increased up to ~20% of the global niche, with a concomitant decrease in Unfilling. The magnitude of Expansion also generally increased over time, although it experienced a fluctuation between 150 and 200 years (Figure 3). For

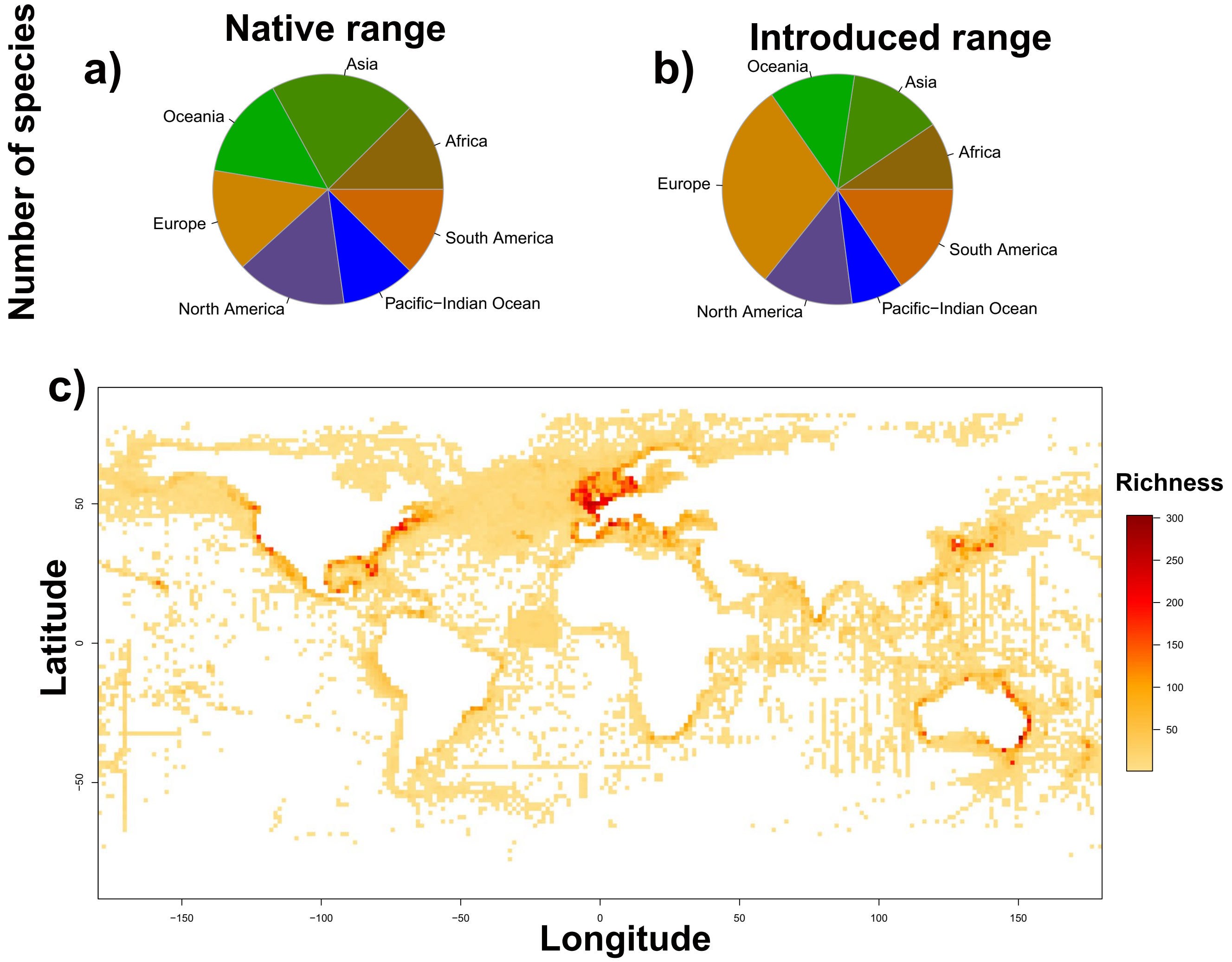

FIGURE 2 | (a, b) Proportions of marine invasive species among native and introduced continents in terms of the number of species assessed for niche changes, respectively. Islands and archipelagos in the Pacific Ocean and the Indian Ocean were considered separately as ‘Pacific-Indian Ocean’. Note that species native to and/or introduced to more than one continent were assigned to each corresponding continent. (c) The number of marine invasive species across the globe at a resolution of 1.5 arc-degree based on their occurrences. Cells with a darker colour denote higher species richness.

invaders with residence time < 100 years, more than two thirds of the global niche consisted of Unfilling, whereas Stability and Expansion only contributed 10%–20% each (Figure S2). The magnitude of niche centre changes also decreased with increasing residence time in general, despite a fluctuation between 150 and 200 years. Across taxonomic groups, the overall pattern of niche changes was evident for algae and invertebrates, with decreased Unfilling and increased Stability over time (Figure S3). However, temporal patterns of niche changes were less apparent for fishes.

3.2 | Niche Changes Across Space and Taxa

The magnitudes of niche indices were also strongly affected by organismal groups, as well as latitudinal gradients (Figure 4). Compared to invertebrates (reference group), fishes showed larger Unfilling (0.19 ± 0.04), smaller Expansion (−0.14 ± 0.04) and Stability (−0.05 ± 0.02), suggesting their relatively weaker ability to occupy introduced environments. No clear difference was found between algae and invertebrates except for a greater Stability (0.02 ± 0.02) for algae. Consistent with the

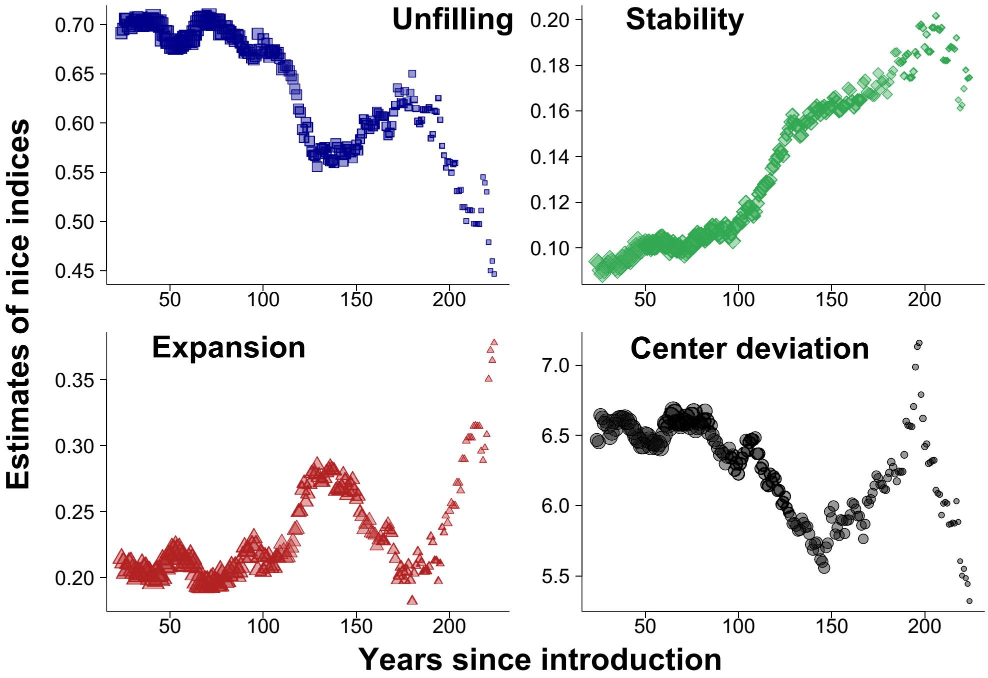

FIGURE 3 | Estimates of four niche indices for species with different years since introduction. Each niche index in each year was estimated using a moving window of 50 years. The size of points is proportional to the square-rooted transformed number of data used for estimating niche indices.

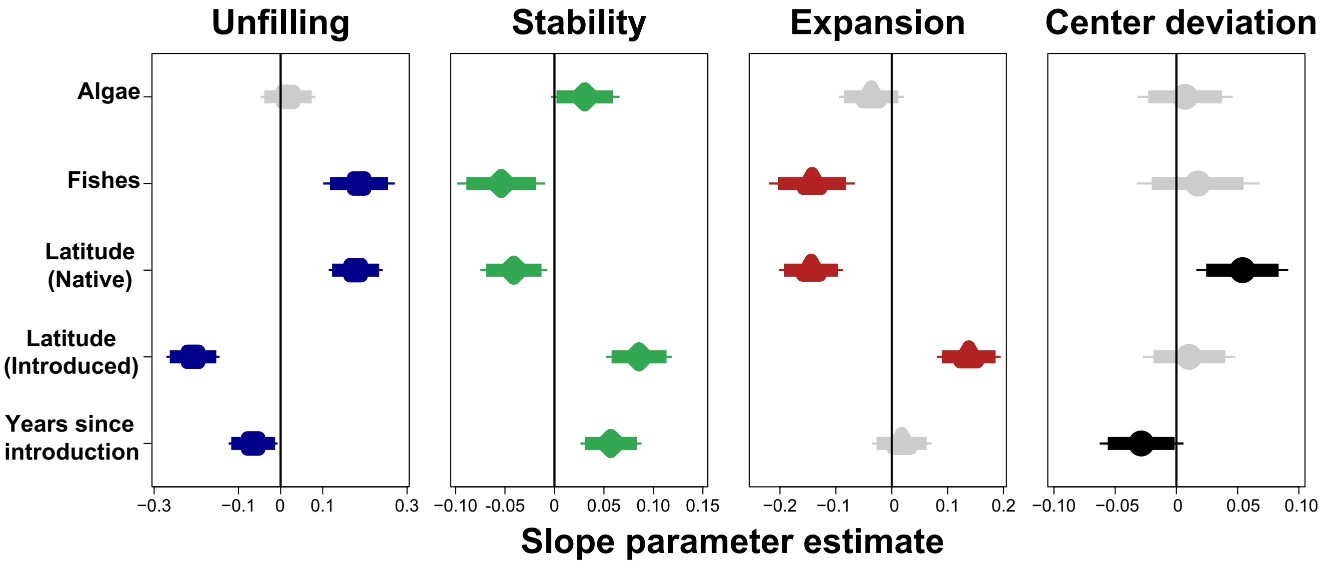

FIGURE 4 | Relationships between niche indices and focal factors for all species. The reference category selected for assessing the effects is Invertebrates for organismal groups. Points, thick lines and thin lines indicate means, 80% credible intervals (CI) and 95% CI of standardised effect sizes based on 32,000 Bayesian posterior values, respectively. Filled points indicate the 80% CI not overlapping with zero, and grey points indicate the 80% CI overlapping with zero.

moving window analysis (Figure 3), the year since introduction remained negatively related with Unfilling (−0.07 ± 0.03) and Centre deviation (−0.03 ± 0.02), and positively with Stability (0.06 ± 0.02) (Figure 4).

Niche indices were closely associated with native and introduced latitudes (Figures 4 and 5). Native latitude was positively related to Unfilling (0.18 ± 0.03) and Centre deviation (0.05 ± 0.02), but negatively related to Stability (−0.04 ± 0.02) and Expansion (−0.14 ± 0.03). This means that the introduced niche was relatively smaller for species native to high latitudes. Additionally, the positive relation between native latitude and Centre Deviation suggests that species from low latitudes had more similar native and introduced niches. By contrast, introduced latitude showed the converse relations and was negatively related to Unfilling (−0.21 ± 0.03), but positively related to Stability (0.09 ± 0.02) and Expansion (0.14 ± 0.03). Given the contrasting latitude-niche relationships between native and introduced ranges, the combined effects of latitudes tended to cancel out when species invaded within latitudes (i.e., species introduced from high to high latitudes, as well as from low to low latitudes) and showed the strongest effects for invasions across latitudes (e.g., species from high to low latitudes experience highest Unfilling, and low to high latitudes experience lowest Unfilling, Figure 5).

4 | Discussion

By leveraging a centuries-long history of marine invasions, we were able to examine patterns of niche change over time, and to gain insight into how environmental niche changes under novel contexts. As expected, Unfilling dominated the signal but decreased over time. Together with the relatively high distance between centroids of native versus introduced niches for early invasions, our results suggest that the greatest mismatch between predicted and observed occurrences should occur in the first decades of an invasion. High initial Unfilling was predicted, given that biological invasions are a dynamic process wherein species spread in the introduced range (Liu et al. 2020a; Petitpierre et al. 2012). However, species establishment in new ranges depend on the combined effect of both suitable environments and propagule pressures (Leung et al. 2012; Redding et al. 2019). Thus, one could hypothesise either that invasions are most likely to initiate in the most suitable environments (Abellán et al. 2017; Broennimann et al. 2021) or that propagule pressure, which may be driven by other factors such as human activity (Cassey et al. 2018; Sardain et al. 2019), is more important in early invasion stages (Leung et al. 2012). These alternative hypotheses correspond to either a close match between native and introduced niches in recent invasions or a large mismatch between niches, respectively. Our results support the latter hypothesis for marine invaders.

Our study suggests that patterns of niche change may strongly differ across biomes (e.g., marine vs. terrestrial), suggesting that niche changes need to be explicitly examined under different contexts. In contrast to our results of low Stability for marine invaders, a recent synthesis reported a high contribution of Stability to the global niche (> 50%) of invasive species (Liu et al. 2020a). However, only few marine species were included in this synthesis. Further, previous studies of spatial transferability between native and introduced ranges using niche-based models reported that more recent invasions were more predictable based on models calibrated to the native range (Liu et al. 2020b; Nguyen and Leung 2022). This is in contrast to our result that the distance between native and introduced niche centre was highest for recent invaders. Again, marine species were the minority in Liu et al. (2020) and were entirely absent in Nguyen and Leung (2022). Thus, it is possible that niche-based models can be used more successfully for terrestrial than marine species, and that temporal relations with shifting niches fundamentally change across biomes. In fact, the distribution of marine invaders has been shown to be harder to predict than of terrestrial invaders (e.g., Parravicini et al. 2015). Future studies should explore the mechanisms underlying these differences.

4.1 | Niche Changes Across Time

As predicted, Unfilling decreased and Stability increased over time. Importantly, however, even after two centuries, Unfilling still generally remained high (> 50% of the global niche). The magnitude of Stability remained low, whereas Expansion into new environmental conditions contributed to a higher proportion of the global niche. This suggests that marine invaders

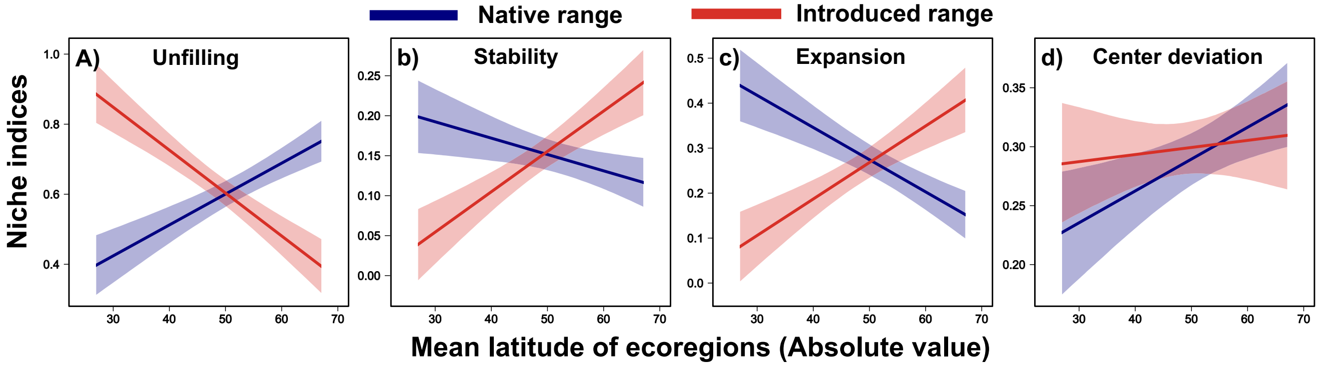

FIGURE 5 | Conditional relationships between mean latitude of ecoregions and niche indices after controlling for effects of other factors. For each niche index, the fitted relationship and 80% credible interval were assessed using Bayesian multilevel models based on 32,000 posterior values from four chains, and shown in blue (Native range) and red (Introduced range) respectively. Values of latitude were first standardised with the mean of 0 and the standard deviation of 1 to assess the effect, and then transformed to the original values for better visualisation.

are approximately 20% more likely to initially occur in new environments than historical ones in the introduced range. Furthermore, this points to the possibility that inaccurate estimation of distributions may persist under novel contexts, across policy relevant time frames. One possibility is that predictions could be improved by using integrative models that combine propagule pressure with niche-based models (e.g., Guisan and Thuiller 2005; Leung et al. 2012). However, such integrated models remain in the minority of studies (Peterson et al. 2019), and whether they actually yield improved predictive power (i.e., consistency and magnitude) requires testing.

The general increase in Expansion could be due to evolutionary adaptation or ecological effects such as the release of natural enemies in invaded ranges, facilitating invaders to occupy new environments (Levine et al. 2004). With residence time further increasing, invasive species may further expand their niche under certain circumstances, such as genetic evolution (Sax et al. 2007), genetic admixture (Sexton et al. 2009) and phenotypic plasticity (Alexander and Edwards 2010). For example, niche expansion driven by genetic adaptations has been reported for the red seaweed (*Gracilaria vermiculophylla*), which was able to invade warmer environments by evolving greater heat tolerance (Sotka et al. 2018). Likewise, phenotypic plasticity is a primary contributor of improved thermal tolerance of the Pacific oyster (*Crassostrea gigas*) by adjusting the expression of heat-shock proteins, facilitating its survival in new ranges (Hamdoun et al. 2003). However, we note that a fluctuation occurred for species introduced between 150 and 200 years. While the reasons for this fluctuation are unknown, the very long time-horizons (> 170 years) had few species and could simply reflect stochasticity (i.e., we caution not to over-interpret it). The lower expansion of other early invasions (150–170 years) had more species represented, and arguably was not due to stochasticity. Potentially, these could be due to ecological-evolutionary interactions of native species. For instance, human movement was historically much slower than in recent decades. This slower secondary spread rate could have allowed more time for native species to adapt to early invaders, thereby resulting in lower expansion. We note that these arguments are speculative, and a better understanding of mechanisms underlying niche expansion (e.g., potentially via common gardens or reciprocal transplants experiments) could improve predictive models of invasion success. Regardless, niche changes demonstrated a consistent patterns during policy relevant time frames, showing persistent high Unfilling, and although there were clear increases in Stability, these were never substantially greater than Expansion.

This study highlights the ongoing challenges to predicting marine invasions over time. Comparatively, terrestrial invasions showed higher Stability (Liu et al. 2020a). Additionally, for other anthropogenic drivers such as climate change, marine species show evidence of tracking changing conditions (Parmesan and Yohe 2003; Sunday et al. 2015), possibly because whole communities can move, thus preserving biotic interactions (whereas invasive species are inserted into distinct communities, breaking historical biotic interactions and leading to high levels of ecological novelty; Heger et al. 2019). That said, there may be critical thresholds as climate change progresses, wherein communities can no longer synchronously migrate (e.g., due to mismatched phenology, Poloczanska et al. 2013). If so, since most models use abiotic predictors (biotic relationships are often implicit, given a paucity of global community data), there is the potential risk that predictions no longer hold. Here, marine invasive species can provide some insight into the extent to which predictions may break down. By comparison, we expect less potential loss of predictiveness for terrestrial species, given the higher Stability observed (Liu et al. 2020a).

4.2 | Niche Changes Across Space and Taxa

Within the marine biome, the patterns of niche changes differed across geographical regions and organismal groups. Specifically, we found a strong latitudinal effect on the magnitude of niche changes. These effects could arguably be understood in the context of latitudinal biodiversity gradients, which show greater richness in the tropics (Costello and Chaudhary 2017). Thus, we might expect relatively stronger biotic resistance (e.g., competition and predation) at low latitudes (Freestone et al. 2021), versus enemy release of invading species (Heger et al. 2024) and relatively greater importance of abiotic fundamental niches at higher latitudes. Our findings are consistent with these hypotheses, where Unfilling was highest for species invading from high to low latitudes, potentially due to greater biotic resistance. Likewise, Expansion was greater for species invading from native low to high latitudes, consistent with greater enemy release.

We found greater Stability for species invading from low to high latitudes. At low latitudes, species occupy a narrower realised niche due to biotic constraints (Saupe et al. 2019). As biotic constraints weaken with increasing latitude, marine invaders could expand their environmental space (higher Expansion), but would also continue to survive in the historical habitats (higher Stability). Conversely, species invading from high to low latitudes could experience increasing biotic resistance, resulting in lower Stability and less opportunity for Expansion. These findings highlight the importance of predicting marine invaders in consideration of the spatial context. Given niche-based models implicitly rely on the overlap with historical environment space (Liu et al. 2022), we should expect that spatial distributions should be more accurately predicted for marine species native to low latitudes and invading high latitudes, which showed higher Stability.

Taxonomic groups also showed unequal magnitudes of niche changes. Contrary to our predictions, fishes showed higher Unfilling and lower Stability and Expansion, even though they have greater dispersal ability than invertebrates and algae (Alzate and Onstein 2022; Lester et al. 2007). As a post hoc rationale, dispersal ability might be uncoupled from geographic range size for marine species because they can colonise most suitable habitats of relatively high connectivity over evolutionary timescales (Lester et al. 2007; Sunday et al. 2012). Other possible reasons could be that fishes are likely more constrained by physiological tolerances, habitat specificity or competition with native species (Levine et al. 2004), limiting their ability to establish and spread in novel environments. Further, the stronger capacity of algae and invertebrates to expand their introduced niche could be partly attributed to the higher plasticity associated with small organisms (Soininen et al. 2013; Soininen and Luoto 2014); small organisms also have shorter generation times and greater adaptability to novel conditions (Liu et al. 2020a; Soininen and Luoto 2014). Additionally, invertebrates and algae have specific reproductive strategies, such as asexual reproduction and dispersal via propagules (Stelzer 2015). With an increasing global shipping network, invertebrates are more likely to be introduced over broader distances by means of ballast water and hull biofouling compared to fishes (Briski et al. 2012). Together, these factors could result in greater Expansion and Centre deviation of algae and invertebrates than fishes. While we expected differences in niche changes among taxonomic groups, the rationale for the specific patterns observed needs further testing and elucidation. Another intriguing question is how species characteristics (e.g., life history traits) are associated with the magnitude of niche changes.

We acknowledge the potential influence of biases in the use of species occurrence and present-day environmental data to estimate niche indices. For example, the number of occurrences was lower at tropical than at temperate latitudes, which may be due to sampling bias. Occurrence records are more available in environments with higher sampling efforts, potentially resulting in greater observational bias under water (Liu et al. 2020a; Peterson and Holt 2003). However, the COUE scheme has the advantage of controlling for sampling bias and efforts. To do so, species occurrence is first projected from geographical space to environmental space, and then a kernel function is applied to smooth occurrence density in the environmental space (Broennimann et al. 2012). The lower richness of marine invaders in tropical areas is potentially related to higher native biodiversity there, resulting in greater biotic resistance against invasive species (Briggs 2012). In addition, niche indices were estimated using data of present-day environmental conditions, without considering the historical environments in which species were recorded. Future studies could construct more complex models that incorporate temporal fluctuations in environmental conditions.

5 | Conclusion

Biological invasions are considered as the leading threat to biodiversity and economic activities of marine systems (Anton et al. 2019; Sardain et al. 2019). Anticipating invasion risks of marine species remains an urgent priority for conserving marine diversity and environments (Parravicini et al. 2015; Sardain et al. 2019). Increasing numbers of studies have applied niche-based models to anticipate potential distributions of marine invaders in new space and time (Carlos-Júnior et al. 2015; Crickenberger 2016), assuming that current correlations with environmental drivers will remain similar. However, our findings echo concerns of applying this approach, because global marine invaders demonstrated low Stability even after two-centuries of invasion history. Thus, predicting invasion risks based on models using current distributions should be viewed with caution, at least for marine species (Parravicini et al. 2015). Further, patterns vary by biome, geography and taxonomy, and thus the context dependency of predictiveness needs to be evaluated, potentially identifying where relationships may be stable and where they are not.

Author Contributions

C.L., J.C., B.K. and B.L. conceived the idea and designed the study. C.L. ran the analyses and led the writing, with substantial input from B.L. All co-authors commented on and approved the manuscript.

Acknowledgements

C.L. was sponsored by the Young Scientists Fund of the National Natural Science Foundation of China (No. 42306133), Mount Taishan Scholar Young Expert (No. tsqn202312093). J.C. was sponsored by the National Natural Science Foundation of China (No. 42176234). We thank Liuxin Qiao, Wenze Cui, Wenjuan Ouyang, Yanling Xu, Liyi Yu, Siyan Yu and Linhe Zhang for carefully checking the native and introduced ranges for marine invasive species.

Data Availability Statement

The data and R scripts generated in this study are available in the FigShare repository (https://doi.org/10.6084/m9.figshare.28440854).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70164.

References

Abellán, P., J. L. Tella, M. Carrete, L. Cardador, and J. D. Anadón. 2017. "Climate Matching Drives Spread Rate but Not Establishment Success in Recent Unintentional Bird Introductions." *Proceedings of the National Academy of Sciences* 114: 9385–9390.

Alexander, J. M., and P. J. Edwards. 2010. "Limits to the Niche and Range Margins of Alien Species." *Oikos* 119: 1377–1386.

Alzate, A., and R. E. Onstein. 2022. "Understanding the Relationship Between Dispersal and Range Size." *Ecology Letters* 25: 2303–2323.

Anton, A., N. R. Geraldi, C. E. Lovelock, et al. 2019. "Global Ecological Impacts of Marine Exotic Species." *Nature Ecology & Evolution* 3: 787–800.

Araújo, M. B., and M. Luoto. 2007. "The Importance of Biotic Interactions for Modelling Species Distributions Under Climate Change." *Global Ecology and Biogeography* 16: 743–753.

Assis, J., L. Tyberghein, S. Bosch, H. Verbruggen, E. A. Serrão, and O. De Clerck. 2018. "Bio-ORACLE v2.0: Extending Marine Data Layers for Bioclimatic Modelling." *Global Ecology and Biogeography* 27: 277–284.

Briggs, J. C. 2012. "Marine Species Invasions in Estuaries and Harbors." *Marine Ecology Progress Series* 449: 297–302.

Briski, E., S. Ghabooli, S. A. Bailey, and H. J. MacIsaac. 2012. "Invasion Risk Posed by Macroinvertebrates Transported in Ships' Ballast Tanks." *Biological Invasions* 14: 1843–1850.

Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, et al. 2012. "Measuring Ecological Niche Overlap From Occurrence and Spatial Environmental Data." *Global Ecology and Biogeography* 21: 481–497.

Broennimann, O., B. Petitpierre, M. Chevalier, et al. 2021. "Distance to Native Climatic Niche Margins Explains Establishment Success of Alien Mammals." *Nature Communications* 12: 2353.

Bürkner, P.-C. 2017. "Brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80: 1–28.

Carlos-Júnior, L. A., D. M. Neves, N. P. U. Barbosa, T. P. Moulton, and J. C. Creed. 2015. "Occurrence of an Invasive Coral in the Southwest Atlantic and Comparison With a Congener Suggest Potential Niche Expansion." *Ecology and Evolution* 5: 2162–2171.

Cassey, P., S. Delean, J. L. Lockwood, J. S. Sadowski, and T. M. Blackburn. 2018. "Dissecting the Null Model for Biological Invasions: A Meta-Analysis of the Propagule Pressure Effect." *PLoS Biology* 16: 1–15.

Chefaoui, R. M., and E. Varela-Álvarez. 2018. "Niche Conservatism and Spread of Seaweed Invasive Lineages With Different Residence Time in the Mediterranean Sea." *Biological Invasions* 20: 423–435.

Costello, M. J., and C. Chaudhary. 2017. "Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation." *Current Biology* 27: R511–R527.

Crickenberger, S. 2016. "Predicting a Range Shift and Range Limits in an Introduced Tropical Marine Invertebrate Using Species Distribution Models." *Hydrobiologia* 763: 193–205.

Dallas, T., R. R. Decker, and A. Hastings. 2017. "Species Are Not Most Abundant in the Centre of Their Geographic Range or Climatic Niche." *Ecology Letters* 20: 1526–1533.

Diagne, C., B. Leroy, A.-C. Vaissière, et al. 2021. "High and Rising Economic Costs of Biological Invasions Worldwide." *Nature* 592: 571–576.

Epanchin-Niell, R. S., and A. Hastings. 2010. "Controlling Established Invaders: Integrating Economics and Spread Dynamics to Determine Optimal Management." *Ecology Letters* 13: 528–541.

Freestone, A. L., M. E. Torchin, L. J. Jurgens, et al. 2021. "Stronger Predation Intensity and Impact on Prey Communities in the Tropics." *Ecology* 102: 1–11.

García Molinos, J., B. S. Halpern, D. S. Schoeman, et al. 2016. "Climate Velocity and the Future Global Redistribution of Marine Biodiversity." *Nature Climate Change* 6: 83–88.

Gelman, A., A. Jakulin, M. G. Pittau, and Y. S. Su. 2008. "A Weakly Informative Default Prior Distribution for Logistic and Other Regression Models." *Annals of Applied Statistics* 2: 1360–1383.

Guisan, A., B. Petitpierre, O. Broennimann, C. Daehler, and C. Kueffer. 2014. "Unifying Niche Shift Studies: Insights From Biological Invasions." *Trends in Ecology & Evolution* 29: 260–269.

Guisan, A., and W. Thuiller. 2005. "Predicting Species Distribution: Offering More Than Simple Habitat Models." *Ecology Letters* 8: 993–1009.

Hamdoun, A. M., D. P. Cheney, and G. N. Cherr. 2003. "Phenotypic Plasticity of HSP70 and HSP70 Gene Expression in the Pacific Oyster (*Crassostrea gigas*): Implications for Thermal Limits and Induction of Thermal Tolerance." *Biological Bulletin* 205: 160–169.

Heger, T., M. Bernard-Verdier, A. Gessler, et al. 2019. "Towards an Integrative, Eco-Evolutionary Understanding of Ecological Novelty: Studying and Communicating Interlinked Effects of Global Change." *Bioscience* 69: 888–899.

Heger, T., J. Jeschke, M. Bernard-Verdier, C. Musseau, and D. Mietchen. 2024. "Hypothesis Description: Enemy Release Hypothesis." *Research Ideas & Outcomes* 10: e107393.

Jeschke, J. M., and D. L. Strayer. 2005. "Invasion Success of Vertebrates in Europe and North America." *Proceedings of the National Academy of Sciences* 102: 7198–7202.

Lembrechts, J. J., J. Lenoir, R. Scheffers, and B. De Frenne. 2021. "Designing Countrywide and Regional Microclimate Networks." *Global Ecology and Biogeography* 30: 1168–1174.

Lester, S. E., B. I. Ruttenberg, S. D. Gaines, and B. P. Kinlan. 2007. "The Relationship Between Dispersal Ability and Geographic Range Size." *Ecology Letters* 10: 745–758.

Leung, B., N. Roura-Pascual, S. Bacher, et al. 2012. "TEASIng Apart Alien Species Risk Assessments: A Framework for Best Practices." *Ecology Letters* 15: 1475–1493.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. "A Meta-Analysis of Biotic Resistance to Exotic Plant Invasions." *Ecology Letters* 7: 975–989.

Liu, C., C. Wolter, F. Courchamp, N. Roura-Pascual, and J. M. Jeschke. 2022. "Biological Invasions Reveal How Niche Change Affects the Transferability of Species Distribution Models." *Ecology* 103: e3719.

Liu, C., C. Wolter, W. Xian, and J. M. Jeschke. 2020a. "Most Invasive Species Largely Conserve Their Climatic Niche." *Proceedings of the National Academy of Sciences* 117: 23643–23651.

Liu, C., C. Wolter, W. Xian, and J. M. Jeschke. 2020b. "Species Distribution Models Have Limited Spatial Transferability for Invasive Species." *Ecology Letters* 23: 1682–1692.

Lodge, D. M., P. W. Simonin, S. W. Burgiel, et al. 2016. "Risk Analysis and Bioeconomics of Invasive Species to Inform Policy and Management." *Annual Review of Environment and Resources* 41: 453–488.

McCarthy, A. H., L. S. Peck, K. A. Hughes, and D. C. Aldridge. 2019. "Antarctica: The Final Frontier for Marine Biological Invasions." *Global Change Biology* 25: 2221–2241.

Melo-Merino, S. M., H. Reyes-Bonilla, and A. Lira-Noriega. 2020. "Ecological Niche Models and Species Distribution Models in Marine Environments: A Literature Review and Spatial Analysis of Evidence." *Ecological Modelling* 415: 108837.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. "Assessing the Global Threat of Invasive Species to Marine Biodiversity." *Frontiers in Ecology and the Environment* 6: 485–492.

Nguyen, D., and B. Leung. 2022. "How Well Do Species Distribution Models Predict Occurrences in Exotic Ranges?" *Global Ecology and Biogeography* 31: 1051–1065.

Olden, J. D., L. Comte, and X. Giam. 2018. "The Homogocene: A Research Prospectus for the Study of Biotic Homogenisation." *NeoBiota* 37: 23–36.

Pagad, S., P. Genovesi, L. Carnevali, D. Schigel, and M. A. McGeoch. 2018. "Introducing the Global Register of Introduced and Invasive Species." *Scientific Data* 5: 170202.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems." *Nature* 421: 37–42.

Parravicini, V., E. Azzurro, M. Kulbicki, and J. Belmaker. 2015. "Niche Shift Can Impair the Ability to Predict Invasion Risk in the Marine Realm: An Illustration Using Mediterranean Fish Invaders." *Ecology Letters* 18: 246–253.

Pecl, G. T., M. B. Araújo, J. D. Bell, et al. 2017. "Biodiversity Redistribution Under Climate Change: Impacts on Ecosystems and Human Well-Being." *Science* 355: eaai9214.

Peterson, A. T., and R. D. Holt. 2003. "Niche Differentiation in Mexican Birds: Using Point Occurrences to Detect Ecological Innovation." *Ecology Letters* 6: 774–782.

Peterson, M. L., D. F. Doak, and W. F. Morris. 2019. "Incorporating Local Adaptation Into Forecasts of Species' Distribution and Abundance Under Climate Change." *Global Change Biology* 25: 775–793.

Petitpierre, B., C. Kueffer, O. Broennimann, C. Randin, C. Daehler, and A. Guisan. 2012. "Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders." *Science* 335: 1344–1348.

Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. "Marine Taxa Track Local Climate Velocities." *Science* 341: 1239–1242.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3: 919–925.

R Development Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. http://Rproject.org.

Redding, D. W., A. L. Pigot, E. E. Dyer, Ç. H. Şekercioğlu, S. Kark, and T. M. Blackburn. 2019. "Location-Level Processes Drive the Establishment of Alien Bird Populations Worldwide." *Nature* 571: 103–106.

Roy, H. E., A. Pauchard, P. J. Stoett, et al. 2024. "Curbing the Major and Growing Threats From Invasive Alien Species Is Urgent and Achievable." *Nature Ecology & Evolution* 8: 1216–1223.

Sardain, A., E. Sardain, and B. Leung. 2019. "Global Forecasts of Shipping Traffic and Biological Invasions to 2050." *Nature Sustainability* 2: 274–282.

Saupe, E. E., C. E. Myers, A. Townsend Peterson, et al. 2019. "Spatio-Temporal Climate Change Contributes to Latitudinal Diversity Gradients." *Nature Ecology & Evolution* 3: 1419–1429.

Sax, D. F., J. J. Stachowicz, J. H. Brown, et al. 2007. "Ecological and Evolutionary Insights From Species Invasions." *Trends in Ecology & Evolution* 22: 465–471.

Seebens, H., T. M. Blackburn, E. E. Dyer, et al. 2018. "Global Rise in Emerging Alien Species Results From Increased Accessibility of New Source Pools." *Proceedings of the National Academy of Sciences* 115: E2264–E2273.

Seebens, H., T. M. Blackburn, E. E. Dyer, et al. 2017. "No Saturation in the Accumulation of Alien Species Worldwide." *Nature Communications* 8: 14435.

Seebens, H., D. A. Clarke, Q. Groom, et al. 2020. "A Workflow for Standardising and Integrating Alien Species Distribution Data." *NeoBiota* 59: 39–59.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. "Evolution and Ecology of Species Range Limits." *Annual Review of Ecology, Evolution, and Systematics* 40: 415–436.

Sexton, J. P., J. Montiel, J. E. Shay, M. R. Stephens, and R. A. Slatyer. 2017. "Evolution of Ecological Niche Breadth." *Annual Review of Ecology, Evolution, and Systematics* 48: 183–206.

Soininen, J., J. J. Korhonen, and M. Luoto. 2013. "Stochastic Species Distributions Are Driven by Organism Size." *Ecology* 94: 660–670.

Soininen, J., and M. Luoto. 2014. "Predictability in Species Distributions: A Global Analysis Across Organisms and Ecosystems." *Global Ecology and Biogeography* 23: 1264–1274.

Sotka, E. E., A. W. Baumgardner, P. M. Bippus, et al. 2018. "Combining Niche Shift and Population Genetic Analyses Predicts Rapid Phenotypic Evolution During Invasion." *Evolutionary Applications* 11: 781–793.

Spalding, M. D., H. E. Fox, G. R. Allen, et al. 2007. "Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas." *Bioscience* 57: 573–583.

Stelzer, C. P. 2015. "Does the Avoidance of Sexual Costs Increase Fitness in Asexual Invaders?" *Proceedings of the National Academy of Sciences* 112: 8851–8858.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. "Thermal Tolerance and the Global Redistribution of Animals." *Nature Climate Change* 2: 686–690.

Sunday, J. M., G. T. Pecl, S. Frusher, et al. 2015. "Species Traits and Climate Velocity Explain Geographic Range Shifts in an Ocean-Warming Hotspot." *Ecology Letters* 18: 944–953.

Wallingford, P. D., T. L. Morelli, J. M. Allen, et al. 2020. "Adjusting the Lens of Invasion Biology to Focus on the Impacts of Climate-Driven Range Shifts." *Nature Climate Change* 10: 398–405.

Werkowska, W., A. L. Márquez, R. Real, and P. Acevedo. 2017. "A Practical Overview of Transferability in Species Distribution Modeling." *Environmental Reviews* 25: 127–133.

Wiens, J. J., and C. H. Graham. 2005. "Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology." *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539.

Yates, K. L., P. J. Bouchet, M. J. Caley, et al. 2018. "Outstanding Challenges in the Transferability of Ecological Models." *Trends in Ecology & Evolution* 33: 790–802.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.