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Original Research

Non-native species in marine protected areas: Global distribution patterns

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ABSTRACT

Marine protected areas (MPAs) across various countries have contributed to safeguarding coastal and marine environments. Despite these efforts, marine non-native species (NNS) continue to threaten biodiversity and ecosystems, even within MPAs. Currently, there is a lack of comprehensive studies on the inventories, distribution patterns, and effect factors of NNS within MPAs. Here we show a database containing over 15,000 occurrence records of 2714 marine NNS across 16,401 national or regional MPAs worldwide. To identify the primary mechanisms driving the occurrence of NNS, we utilize model selection with proxies representing colonization pressure, environmental variables, and MPA characteristics. Among the environmental predictors analyzed, sea surface temperature emerged as the sole factor strongly associated with NNS richness. Higher sea surface temperatures are linked to increased NNS richness, aligning with global marine biodiversity trends. Furthermore, human activities help species overcome geographical barriers and migration constraints. Consequently, this influences the distribution patterns of marine introduced species and associated environmental factors. As global climate change continues to alter sea temperatures, it is crucial to protect marine regions that are increasingly vulnerable to intense human activities and biological invasions.

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1. Introduction

Globalization and climate change contribute to the rise in the introduction and establishment of non-native species (NNS) [1,2]. Approximately one-fifth of Earth's surface is threatened by species invasion, one of the five direct drivers with the largest impact on natural change [3]. Due to the open and continuous nature of Earth's marine systems and their expanding interconnectedness, marine species can more easily overcome biogeographical barriers and migrate — intentionally and unintentionally — beyond their native habitats [4]. In marine systems, NNS cause ecological and economic harm [5]; for example, they can diminish the ecological

quality of native marine communities [6], spread disease [7,8], and deplete commercial fish stocks [9,10].

As a result of the negative impacts of NNS, they have been identified as a serious threat to global terrestrial protected areas [11–13]. Marine protected areas (MPAs) play a pivotal role in marine conservation by offering refuge to harvested species and mitigating the impact of human activities [14,15]. They are an effective tool for maintaining marine biodiversity and are vital for achieving biodiversity goals; thus, MPAs are instrumental in fulfilling the Sustainable Development Goals of the United Nations [16,17]. However, the biological invasion of MPAs is an important issue that is garnering increasing attention. Many countries are intensifying their efforts to protect marine environments to achieve the global conservation goals agreed upon under the Convention on Biological Diversity (CBD) [18]. While current studies reportedly demonstrate that MPAs resist biological invasions [19,20], the findings must be interpreted cautiously due to the limited data available on this crucial topic [21,22]. A questionnaire-based study

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conducted with MPA practitioners and scientists worldwide showed that NNS were present in 62.9% of the associated MPAs [23]. Additionally, marine NNS have been reported to disrupt biodiversity and broader ecosystems, including within MPAs [5,23].

Despite the growing interest in studying the distribution patterns of NNS to broad geographical extents, the influence of human activities and environmental factors on these patterns remains poorly understood for many taxonomic groups. As a result of anthropogenic stressors, the drivers of marine biological invasions have become increasingly global in nature [5,24,25]. Understanding the patterns and drivers of MPA invasion by marine NNS is an urgent challenge and essential for developing protection and management strategies and early warning systems in global MPAs. Based on the available knowledge about various regions and non-native taxa, the hypotheses generated to explain the biogeography and invasion drivers of marine NNS can be grouped into three general categories, as described below. The hypotheses within the first category involve high propagule supply pressures linked to intense human activities, such as shipping, the aquarium trade, and mariculture, increasing the risk of invasion by marine NNS [26,27]. Studies indicate that 60–90% of marine invasive species and most aquatic NNS are translocated via ballast water or biofouling of ships [5,28,29]. The hypotheses in the second category focus on interactions with native species, especially biotic resistance, with the success of an invasion depending on whether the native community resists or succumbs to the invader [30,31]. Meta-analyses have shown that marine biotic resistance varies and is influenced by latitude, habitat, and the invader taxon [32]. Differentiating between competition with and consumption of native species is also crucial. Finally, an environment's suitability, particularly the climate compatibility between the source and target regions, is likely an important factor for determining invasiveness [33]. While the similarity between the environmental conditions of the source and recipient climates is a key determinant of the performance of NNS in terrestrial, freshwater, and marine ecosystems [34,35], there has been limited investigation into the contributions that such correlations make to the diversity of NNS across marine MPAs worldwide.

In this study, we compiled a comprehensive global database that details the occurrence of marine non-native animal species across 19 taxonomic groups. We identified 2714 species (698 Chordata, 606 Arthropoda, 573 Mollusca, 328 Annelida, and 15 other taxa) after collecting relevant information about marine NNS from four global databases and 234 documents. We mapped the distribution pattern of these marine NNS in MPAs and explored the introduction network of each species across different regions using 444,696 occurrence records of these species. We integrated data on abiotic, biotic, and anthropogenic factors, considering area variations and sampling efforts, to determine which factors most influenced the variation in NNS richness in MPAs worldwide (see [Supplementary Material Table S3](#)). Our analysis shows that MPAs are vulnerable to the threat of NNS due to the intensification of climate change and human activities worldwide.

2. Methods

2.1. Global MPA data

We gathered information on global MPAs from the World Database on Protected Areas (WDPA; version dated April 2022), including their location and boundaries. We also collected information on and included 400 marine-related protected areas in China to address the significant data gap in Chinese MPAs ([Supplementary Material Table S1](#)). We used ArcMap 10.5 to

intersect the MPAs and sea boundary layers [36]. All MPAs located exclusively on land and not extending into the sea were excluded. Ultimately, 16,401 MPAs were included in the analysis.

2.2. Species and occurrence data

We compiled a list of 2714 marine NNS belonging to 19 different phyla (i.e., Acanthocephala, Annelida, Arthropoda, Brachiopoda, Bryozoa, Chaetognatha, Chordata, Cnidaria, Ctenophora, Echinodermata, Entoprocta, Mollusca, Nematoda, Nemertea, Phoronida, Platyhelminthes, Porifera, Rotifera, and Sipuncula; [Supplementary Material Table S2](#)). Information on each species was extracted from different references identified using the Google Scholar search engine (see the Reference list in [Supplementary Material Table S2](#)) and the following NNS online databases: the World Register of Introduced Marine Species (WRiMS, <https://www.marinespecies.org/introduced/>) [37]; the Information System on Aquatic Non-Indigenous Species (AquaNIS, www.corpi.ku.lt/databases/aquanis) [38]; and the United States Geological Survey's (USGS) repository of Nonindigenous Aquatic Species (NAS, <http://nas.er.usgs.gov/>) [39]. For each species, the searches included all known synonyms and were conducted from January 13 to May 15, 2022.

Initially, we cross-referenced the species taxonomies with the World Register of Marine Species (WoRMS, <http://www.marinespecies.org/index.php>) [40]. This database ensured an authoritative taxonomic classification and identification of the marine species and obtained their accepted names and corresponding synonyms. Then, we deleted species whose environment is strictly freshwater or terrestrial, whose status is cryptogenic or doubtful, with a *nomen dubium*, or of uncertain origin. Finally, each marine nonindigenous animal included in our study was assigned a valid AphiaID.

The occurrence data of marine NNS within each taxon were collected from additional references (see the Reference list in [Supplementary Material Table S2](#)), as well as the Global Biodiversity Information Facility (GBIF), the Ocean "Biogeographic" Information System (OBIS), the USGS's Biodiversity Information Serving Our Nation (BISON) resource, the Atlas of Living Australia (ALA), iNaturalist, the Integrated Digitized Biocollections (iDigBio), and VertNet using the *spocc* package in R [41]. Researchers have commonly used these resources to depict the existence, origin, establishment, and spatial patterns of various taxa worldwide [42,43]. We utilized the *CoordinateCleaner* package to filter out invalid and outlier records [44] and to guarantee the accuracy and reliability of coordinate data. Records with identical latitude and longitude values and those within a 0.5-degree radius of the 0/0 point were excluded. Occurrences within a one-degree radius of the GBIF headquarters in Copenhagen, 100 m of biodiversity institutions, and 10,000 m of capital cities were removed. Furthermore, records lacking information on the year or source of the observation and those of unlikely geographical locations (such as incorrect political borders or on land) were also removed.

Coordinates marked as "origin: alien" in marine areas were considered by comparing the distribution points of the NNS with their documented distribution areas in the WoRMS database since their non-native distribution points, whereas other marine areas in the database were classified as their native habitats. We plotted a chord diagram to quantify the global migration patterns of these NNS found in MPAs based on native and exotic range data. This approach enabled us to determine the main origin and recipient regions. The analysis was conducted using the *circlize* package in R (version 4.2.1) [45], following the methodologies used in previous studies [13,46].

2.3. Explanatory variable data

A set of anthropogenic and environmental (including abiotic and biotic) explanatory variables were chosen for the model construction, guided by their appropriateness for hypothesis testing. The descriptions and sources of the available raw data for each candidate variable are listed in [Supplementary Material Table S3](#). Our analysis used four variables — MPA characteristics, abiotic factors, biotic factors, and human interference — to explain the variation in the number of marine NNS per MPA. We excluded the land area for each MPA and used only the ocean area. Variation among the sea regions regarding the sampling effort for detecting marine NNS can potentially introduce bias in assessing global NNS patterns. Given that data on the sampling effort for detecting NNS in each sea region were unavailable, we used the number of published studies conducted in each sea region as a surrogate measure for the sampling effort for detecting marine NNS, following Watkins et al. [47].

We collected data on climatic and environmental factors, such as temperature, salinity, current velocity, dissolved oxygen, and primary productivity, from the Bio-ORACLE website at a spatial resolution of 5 arc-min [48]. The model did not consider dissolved oxygen due to its contribution to multicollinearity. The correlation coefficients obtained from the Pearson rank correlation analyses revealed that the remaining predictor variables did not exhibit high collinearity, showing values under 0.75 ([Supplementary Material Fig. S1](#)). The destructive fishing and shipping indexes were used as proxies to reflect human pressures based on a previous study of human impacts on oceans worldwide [49,50]. Additionally, the native species richness data for Arthropoda, Chordata, Mollusca, and all marine animals were extracted from the AquaMaps website [51], a resource for creating model-based, broad-scale forecasts of natural occurrences of marine species. We excluded Annelida, Bryozoa, and Cnidaria from our model analysis because global richness maps for these groups were unavailable. The averages of these variables were calculated for all the grids within each MPA. We used the nearest available grid for calculations when specific MPAs in coastal regions lacked precise grid coverage.

2.4. Statistical analyses

We fitted a generalized linear mixed-effect model (GLMM) with a zero-inflated negative binomial distribution (ZINB) to examine the correlates of cross-taxon marine NNS richness patterns across all MPAs. The GLMM was used as a function of the following fixed effects: true ocean area, sampling effort, distance to land, surface temperature, salinity, current velocity, primary productivity, native species richness, destructive fishing, and shipping. The *z*-score standardization (subtracting the mean and dividing it by the standard deviation) was applied to all continuous predictor variables before they were incorporated into the model. This procedure ensured numerical stability and that parameter estimates of the models were on a comparable scale. We took the administrative region where the MPA was located as a random effect. We added a random effect at the sample level due to the variance in the investigation efforts and capabilities across countries or regions.

We performed a multi-model comparison with all candidate sub-models (total: $2^{10} - 1 = 1023$ models). We ranked the set of models based on the corrected Akaike's Information Criterion (AICc), and we performed a model averaging for the best models within 2 AICc units ($\Delta\text{AICc} \leq 2$) to calculate model-averaged coefficients of all predictors [52]. Finally, fixed-effect coefficients were converted into variance components, following the methodology described by Nakagawa and Schielzeth [53]. The relative importance of each predictor to the number of marine NNS was expressed

as a percentage of the explained variance, calculated by dividing the standardized parameter estimate of each predictor by the sum of all standardized parameter estimates in the models. We conducted all analyses in R version 4.2.1, using the `glmmTMB` function in the `glmmTMB` package [54] and the `dredge` and `model.avg` functions in the `MuMIn` package [55].

3. Results

Taxonomic variation in marine NNS in MPAs. We found that 31.2% (846/2714) of marine NNS were observed in 4017 MPAs, representing 24.5% of the 16,401 MPAs analyzed. The six most prevalent groups in the MPAs were Mollusca (2539 MPAs, 157 species), Arthropoda (2031 MPAs, 196 species), Chordata (1660 MPAs, 208 species), Annelida (955 MPAs, 105 species), Cnidaria (663 MPAs, 71 species), and Bryozoa (405 MPAs, 65 species). The three most widespread marine NNS in the MPAs were mollusks, namely, the soft-shell clam (*Mya arenaria*, 1114 MPAs), the Pacific oyster (*Magallana gigas*, 747 MPAs), and the American slipper limpet (*Crepidula fornicata*, 670 MPAs). Additionally, the most prevalent species from other groups included the bay barnacle (*Amphibalanus improvisus*, 478 MPAs) and modest barnacle (*Austrominius modestus*, 347 MPAs) from Arthropoda, the Asian tunicate (*Styela clava*, 316 MPAs) and star tunicate (*Botryllus schlosseri*, 313 MPAs) from Chordata, the red-gilled mudworm (*Marenzelleria viridis*, 163 MPAs) and bristleworm (*Aphelochaeta marioni*, 153 MPAs) from Annelida, the orange-striped anemone (*Diadumene lineata*, 127 MPAs) and freshwater hydroid (*Cordylophora caspia*, 108 MPAs) from Cnidaria, and the brown bryozoan (*Bugula neritina*, 128 MPAs) and bryozoans (*Tricellaria inopinata*, 80 MPAs) from Bryozoa.

Distribution patterns of marine NNS in MPAs. Among the 154,394 non-native distribution records of marine NNS in MPAs we collected, the northwest Atlantic Ocean and northeast Atlantic Ocean accounted for 41.65% and 37.14% of the records, respectively. In contrast, the southeast Atlantic Ocean and southeast Pacific Ocean accounted for only 0.21% and 0.07% of the total, respectively ([Supplementary Material Table S4](#)). We mapped the Mollusca, Arthropoda, Chordata, Annelida, Cnidaria, and Bryozoa distribution patterns. These selected taxa comprise a significant proportion of marine NNS, accounting for 94.8%. We performed Kruskal–Wallis H tests and the results revealed significant heterogeneity in the richness of NNS across MPAs in various International Union for Conservation of Nature (IUCN) categories and sea regions (all $P < 0.001$; see [Supplementary Material Table S5](#)). High concentrations of NNS are found in the United States (along the West Coast, in the Chesapeake Bay, and the coastal waters of Florida), the North Sea of Europe, the Galapagos Islands, and the Pelagos Sanctuary (see [Fig. 1](#) and [Supplementary Material Fig. S2](#)).

Our analysis of the origin–recipient network of all the marine NNS in MPAs showed that the primary flows consist of exchanges within specific sea regions in the northeast and northwest Atlantic Ocean and the Mediterranean Sea. The exchange of NNS among these three regions is also the most frequent. Furthermore, the North Atlantic Ocean and the Mediterranean Sea contribute significantly to species input in many other regions ([Fig. 2](#)). Studies across various groups have led to similar conclusions ([Supplementary Material Fig. S2](#)). However, in contrast, the export of Chordata species from the Indian Ocean and Bryozoa species from the southwest Pacific Ocean significantly surpasses that of other groups.

Driving factors of marine NNS in MPAs. Unreported or unregistered protected areas (falling under the IUCN categories of “Not Reported,” “Not Assigned,” and “Not Applicable”), where human–nature interactions are more prevalent, tend to harbor more NNS. The prevalence of NNS was lower in MPAs classified in

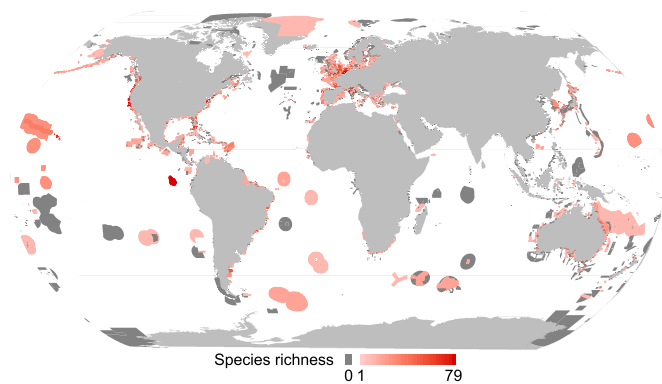


Fig. 1. The species richness of non-native species (NNS) in 16,401 global marine protected areas (MPAs). A high number (deep red shades) indicates that an MPA has relatively more NNS, while a low number (light red shades) indicates the opposite. MPAs without data are colored deep gray. The map focuses on the distribution patterns of all 2714 marine NNS.

the first IUCN category. However, the correlation between the quantity of marine NNS in an MPA and its IUCN conservation category is not straightforward (Supplementary Material Fig. S4). Area, shipping activities, and sea surface temperature were identified as consistent predictors of marine NNS richness across all groups in the GLMM (Supplementary Material Fig. S5 and Table S6). The larger the area of an MPA, the more marine NNS were found to exist. Moreover, high surface temperatures, primary productivity, proximity to land, and increased shipping were found to positively impact marine NNS, whereas a rich native species presence in an MPA tended to harm marine NNS (Fig. 3). Overall, similar trends were observed across the different studied groups; however, the effects of surface salinity, current velocity, primary productivity, and distance to land were not completely consistent (Supplementary Material Fig. S5).

4. Discussion and conclusion

This study assessed the distribution patterns and associated factors of marine NNS in MPAs globally; over 2700 species across 19 taxonomic groups were included. Mollusca and Arthropoda were the most widely distributed groups in MPAs, a finding that aligns with those of previous research [25,56]. We found that most NNS hotspots are located on the east and west coasts of the United States and in the North Sea of Europe. Conversely, coldspots were found to occur in the Arctic and northwest Pacific Oceans as well as in the South China and Eastern Archipelagic Seas. Marine NNS richness was consistently linked to surface temperature, shipping intensity, and the area of MPAs across different taxa, although these factors accounted for a small proportion of the R^2 values.

The fundamental niche of a species is dictated by abiotic factors, which set the range of environmental conditions that facilitate or impede population maintenance. Consequently, the physical environment significantly influences the success or failure of the introduction and potential spread of NNS into new regions [57]. A previous study demonstrated that sea surface temperature was the only environmental factor positively correlated with marine biodiversity across all 13 major species groups [58]. Our results also indicate that sea surface temperature is the primary predictor influencing the distribution pattern of all three taxonomic groups of NNS in MPAs (Supplementary Material Fig. S5). According to the kinetic energy or temperature hypothesis, increased metabolic rates at high temperatures may result in high speciation rates and, consequently, high biodiversity. Hence, based on our results, it may

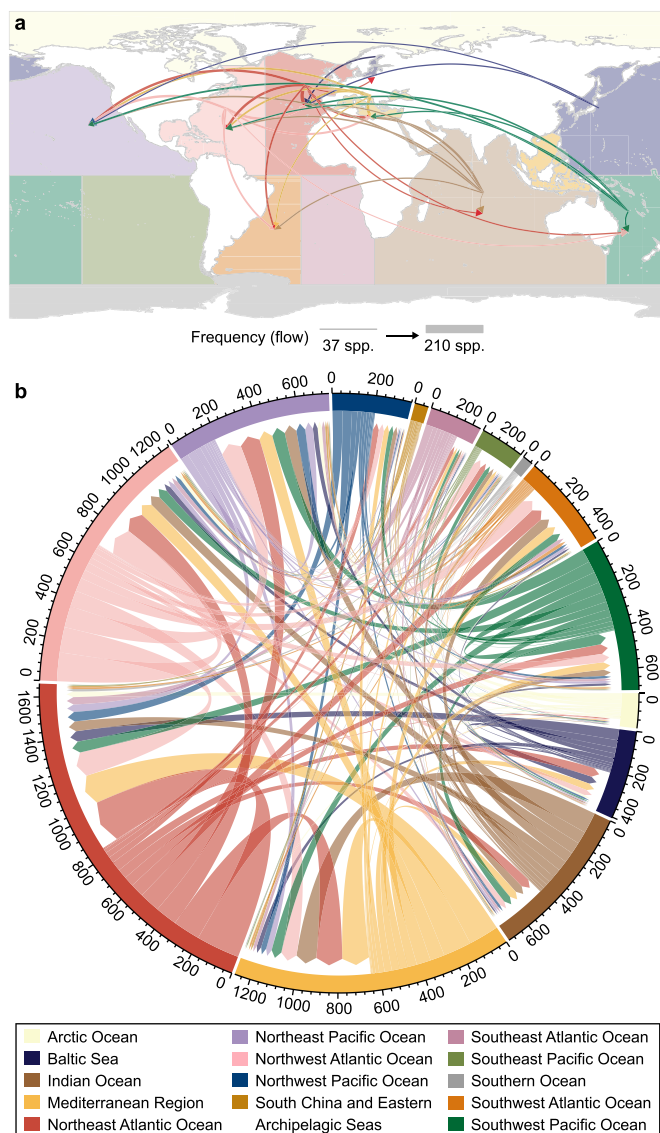


Fig. 2. The global flow network of non-native species (NNS) in marine protected areas (MPAs). **a**, The top 61.8% of the total marine NNS exchanges. The line width represents the frequency of the NNS exchange between the two sea regions. **b**, Chord diagram showing global flows from native to exotic sea regions. The colors signify the various sea regions where the species are indigenous. The chord width denotes the frequency of the NNS. The magnitude of the outer circle segments represents the overall quantity of introductions from those sea regions. The diagram illustrates the exchange patterns of all 2714 marine NNS.

be concluded that the distance to highly connected regions and environmental similarity are key drivers of the introduction of NNS, as these species are more likely to become established in recipient areas with temperatures that fall within their original thermal range [59,60]. This finding explains the high volume of NNS exchanged within sea regions.

Climate studies, such as that conducted by Barnett et al. [61], have identified a clear correlation between the warming of the upper ocean layers and greenhouse gas forcing worldwide. This anthropogenic climate change has been observed to significantly affect marine life [62]. Global warming could intensify the diffusion of marine organisms, as demonstrated by the results obtained with our GLMM. Studies have confirmed that climate change, interacting with broad biogeographical patterns, can increase species richness

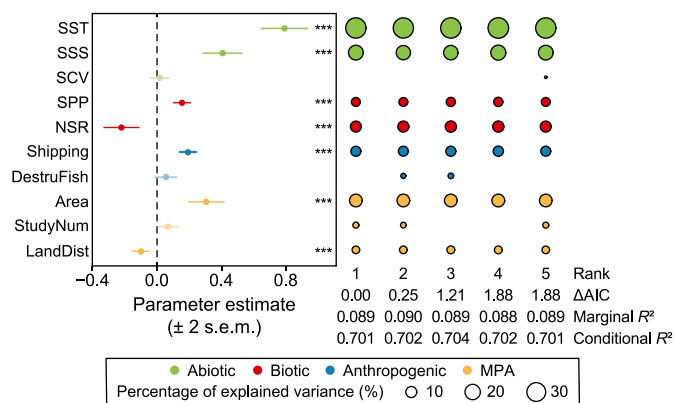


Fig. 3. Model-averaged estimates and relative importance of inherent attributes, human effects, and biotic and abiotic factors on the richness of marine non-native species (NNS). The dashed line indicates an effect equal to zero. Positive effects (the ± 2 standard error intervals do not include zero) suggest a higher likelihood of establishment with rising values of predictive variables, while the negative effects indicate the converse. Light colors indicate non-significant effects. The marginal R^2 values, indicating the explained variance by fixed effects, and the conditional R^2 values, encompassing both fixed and random effects, are provided. Abbreviations: SST, sea surface temperature; SSS, sea surface salinity; SCV, surface current velocity; SPP, surface primary productivity; NSR, native species richness; DestruFish, destructive fishing; Area, total ocean area; StudyNum, study number; LandDist, distance to land. All 2714 marine NNS are considered in the figure.

in temperate regions, including in the North Sea [63], the Mediterranean Sea [64], and North America [65,66], where relatively more NNS were identified in MPAs in this study. There is mounting evidence that global climate change has wide-ranging consequences for marine ecosystems, including that it facilitates biological invasions and has greater negative impacts on native species than on NNS [67–71]. Regrettably, none of the 20 2011–2020 Aichi Biodiversity Targets, nor the milestones for limiting global warming to 1.5 °C, have been achieved [72]. Effectively managed MPAs, especially no-take reserves, can mitigate some of these threats and help partially restore marine biodiversity, although they are not a complete solution.

Although favorable abiotic conditions exist in some regions for certain species, their absence is often due to biotic resistance or dispersal limitations. Human-mediated translocation of these species can help overcome the latter constraint. Occurrence data examined in this study displayed marked geographical bias, which may have stemmed from potential bias in sampling efforts, as discussed subsequently. However, it is more likely that the introduction of NNS is linked to an increase in the volume of commercial transactions in developed nations [73]. Our results indicated a robust positive correlation between shipping intensity and NNS richness across all three taxa (Supplementary Material Fig. S5). The global shipping network, responsible for over 80% of the international trade volume [74], enhances global connectivity, including with Antarctica [75]. The northeast Atlantic Ocean and northern European seas border many developed countries with high trade volumes [76]. Consequently, exchange within and between the northeast Pacific Ocean, northeast Atlantic Ocean, northwest Atlantic Ocean, and Mediterranean Sea accounts for a substantial proportion (37.3%) of the total exchange of marine NNS.

Given that shipping intensity does not account for a large percentage of the explained variance, it is conceivable that it may not adequately reflect the colonization pressure. The distance to land, which negatively affects all taxa, also reflects the pressures of human effects, such as ballast water releases and aquaculture. Additionally, variations in shipping practices, such as ballasting operations and the duration of port stays, can impact the supply of

propagules across oceans, regardless of the number of vessel arrivals [77,78]. Shipping corridors, such as the Suez Canal and Panama Canal, also contribute to the convenient transportation of marine NNS [25]. Numerous NNS, typically from temperate regions, have been observed in the western Mediterranean Sea. In contrast, NNS from tropical regions has been observed in the eastern Mediterranean Sea due to the proximity of tropical regions to the Suez Canal [35]. Rapid coastal development during the Anthropocene era has also resulted in the associated coastal infrastructure providing new habitats for marine NNS [23].

The surface area of an MPA also significantly correlates with alien richness across taxa; this finding aligns with those of other studies that have shown that surface area is a strong determinant of invasive species richness in terrestrial protected areas [13,20]. Notwithstanding these fixed effects, the explanation of NNS richness variation was found to increase by more than 60% when the sea region and sample-level random effects were considered, as evidenced by the marginal versus conditional R^2 values shown in Fig. 3. This implies that marine NNS richness may be influenced by additional spatially related socioeconomic, historical, or political factors not considered in this analysis. For instance, European occupation and trade influenced regional fisheries, maritime environments, and traffic during the colonial era [79,80]. Today, the food and aquarium industries primarily transport live animals by ship, which may result in the introduction of NNS via the escape or accidental release of such animals [81]. Shipping traffic is a significant vector for introducing species into aquatic ecosystems by releasing ballast water and biofouling [82]. However, applying antifouling treatments to boat hulls typically counteracts the latter issue in developed countries [83]. Therefore, the anthropogenic factors analyzed in this study may not be a robust and complete proxy for colonization pressure.

Our study is subject to two noteworthy limitations. First, due to the high sampling coverage found in developed countries [84], occurrence data examined in this study may exhibit a bias resulting from varying survey efforts. Only two of the 30 marine realms accounted for 47% of the records, yet they represented just 10% of the genera. In contrast, the two most genera-rich realms comprised 17% of the genera and contributed just 9% of the records [85]. Deep-sea areas remain unexplored globally, with 30–50% of marine taxa primarily recorded in coastal areas (within 5 km of the shore) [85]. In addition, even though we included easily studied and well-known species (e.g., the lionfish, *Pterois miles*), the impact information of many marine NNS is still poorly understood [86]. Second, our data set contained more NNS than the data sets of Bailey et al. [25] and Watkins et al. [47]. This result was primarily due to the lack of reliable distribution data for established marine NNS. Our attention was not directed toward such established species. Consequently, we could not definitively confirm the presence of biotic resistance using the native biodiversity variable across all groups. An observed negative association between native and exotic species richness may indicate high colonization pressure in areas with low native species richness [87].

Our observation that the first and third IUCN categories host fewer marine NNS than the other categories (Supplementary Material Fig. S4) deviates from the global pattern identified across all the IUCN categories for terrestrial protected areas. In these terrestrial areas, a higher richness of NNS was notably observed in the second IUCN category [13]. Therefore, increased efforts are necessary to safeguard MPAs with high IUCN category levels from biological invasion. Specifically, developing standardized monitoring protocols and implementing long-term programs are crucial for assessing the effects of NNS on marine ecosystems. Standardized methods must be implemented across all sea regions to ensure the precision of data and the evaluation of the invasion period of

NNS. Integrating multiple invasion models with additional available occurrence data can also significantly improve predictions of invasion probabilities [66].

Transport, climate change, and socioeconomic shifts are likely the main drivers of biological invasion, and it is anticipated that the impact of introduced species on biodiversity will be significant in the future, even under favorable conditions [88,89]. It is worth noting that some NNS may have contributed to achieving conservation targets by ensuring ecosystem functions and the flow of ecosystem services [10,90], particularly in areas facing various human pressures and global warming [91,92]. Nevertheless, the pre- and post-impact ecological states may differ [93], and NNS have rarely been considered in marine conservation and management planning [21,94–96]. Additionally, many benthic fish, including NNS, may migrate to deeper waters as climate change progresses [97]. Thus, future research should be conducted on the capacity of exotic benthic species in MPAs to adapt to deeper environments and to develop appropriate monitoring systems. For instance, image-based monitoring using cabled video observatories and underwater cameras has already proven to be beneficial in the monitoring of fish within MPAs [98,99] and has the potential to be extended to more species groups and various ocean depths.

Only 7.74% of global ocean areas are currently protected; however, this figure is likely overestimated, as it includes areas not actively protected [100]. In addition, 33.9% of marine and coastal Key Biodiversity Areas still lack protection. These facts are concerning, given the critical role of MPAs in maintaining biodiversity and providing continuous ecosystem services [101,102], and the persistent positive effect they are expected to have during future climate change [103]. A substantial augmentation of MPAs is necessary to attain the “30 × 30 target” [104]. Considering the risk posed by invasive marine NNS, selecting and protecting areas vital to biodiversity restoration and ecosystem services is a complex matter that will require increasing attention in the future.

CRediT authorship contribution statement

Tianjian Song: Writing - Original Draft, Visualization, Methodology, Formal Analysis, Conceptualization. **Yuxin Huang:** Methodology, Formal analysis, Visualization. **Lei Fang:** Methodology. **Yonghua Li:** Methodology. **Junsheng Li:** Writing - Review & Editing, Validation, Supervision, Conceptualization. **Jiang Chang:** Writing - Review & Editing, Validation, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The author is an Editorial Board Member/Editor-in-Chief/Associate Editor/Guest Editor for [*Environmental Science and Ecotechnology*] and was not involved in the editorial review or the decision to publish this article.

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Appendix A. Supplementary data

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