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Non-Native Species in Aquaculture: Burgeoning Production and Environmental Sustainability Risks

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ABSTRACT

Rising global food demands and technological advancements have led to unprecedented growth in the aquaculture industry. This rapid expansion has facilitated the translocation of species beyond their native ranges. While farming non-native species boosts global food supply, it also poses environmental and socio-economic risks when escapees establish in non-native ecosystems. Using FAO data, we quantified and analysed global non-native aquaculture production, economic value, and monetary costs over space and time. Since 1950, one-third of the 560 species used in aquaculture ($n = 160$) have been farmed outside of their native ranges, totaling 571.6 million tonnes valued at USD 1.2 trillion. Both native and non-native production increased over time, with non-native species showing greater interannual variability. Fishes largely dominated total aquaculture production with 940 million tonnes, of which 182 million tonnes were non-native production (19%). Non-native algae and crustacean production exceeded that of native species, accounting for 67% and 55% of total production, respectively. Notably, non-native crustacean production has grown enormously in recent years, with a rate of change of over 11,000% since 2000, compared to the previous two decades. According to the InvaCost database, 27 non-native species have been associated with reported monetary costs due to their impacts as invasive species. Among them, nine major aquaculture species documented at least USD 6.4 billion in global

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total costs. To address the rising threats of biological invasions triggered by aquaculture escapees, enhanced biosecurity, stakeholder awareness, and promotion of sustainable use of native resource alternatives are needed.

1 | Introduction

The projected increase in food demand by 2050 presents a major sustainability challenge, particularly for global supply chains [1, 2]. With ongoing global food insecurity, uneven resource distribution, and widespread malnutrition—driven not only by availability but also by affordability constraints [3], ensuring the sustainable production of food for a human population exceeding 8.2 billion is of paramount importance [4]. This rapidly increasing demand has, however, exacerbated the exploitation of natural resources across environments [5], driving a necessary shift toward more sustainable practices away from the current “business-as-usual” scenario to align with the Sustainable Development Goals for 2030 [6]. In 2022, aquaculture surpassed capture fisheries as the primary source of aquatic animal production for the first time [7]. Ensuring the sustainability of both fisheries and aquaculture is therefore essential [8].

Aquatic ecosystems harbor particularly high levels of biodiversity and productivity [9], motivating the exploitation of numerous wild species [10] and the captive breeding of several others [11]. Aquaculture production has exhibited tremendous growth in both quantity and the number of farmed species [7, 12], spanning over 190 countries across various biogeographic regions [13]. While it has underpinned poverty alleviation, food security, and important socio-economic values (e.g., generation of 22 million jobs [14]) in low- and middle-income countries [15], the growth of aquaculture poses environmental and ecological risks, as well as socio-economic costs, particularly the escape of non-native species into the wild [16–18]. Balancing sustainable food production with environmental protection and biodiversity conservation thus stands as a critical challenge aligned with the United Nations Sustainable Development Goals [19, 20].

Aquaculture has become one of the main introduction pathways for non-native species [21], mainly due to unintentional escapes from facilities [22]. Species selected for aquaculture often possess biological and physiological traits, such as rapid growth, early maturation, high fecundity, and high environmental tolerance, which can enhance production by achieving marketable sizes earlier [23]. The same traits that enhance production may simultaneously promote invasion success of the farmed species should they escape, by facilitating their establishment in the wild and reaching of high abundances or biomass [24, 25]. The term “invasive” when referring to non-native species is often based on either their capacity to spread beyond initial introduction sites, their ecological or economic impact, or a combination of both [26]. Consequently, if non-native farmed species escape to the wild and successfully establish self-sustaining populations, they can become invasive, spreading and causing severe impacts [16, 27, 28]. Mechanisms through which non-native species exert their impacts include the spread of pathogens, such as those introduced through non-native farmed bivalves [29] and hybridization with native species (e.g., between non-native and native carps [30]). Non-native species can also disrupt biotic interactions (e.g., through predation, competition or grazing) and induce physical and chemical alteration of

invaded habitats [31]. Additionally, they can have socio-economic impacts, such as the negative effect of the Nile tilapia (*Oreochromis niloticus*) on traditional inland fisheries in China, [32] as well as incurring management costs due to the damage they can cause [33].

Due to the interplay of societal benefits and environmental costs, the use of non-native species in aquaculture is a controversial issue [34, 35]. For example, Abate et al. [36] used a cross-country regression model encompassing 95 countries worldwide to illustrate how the growth of aquaculture has at times been hindered by stringent environmental regulations, while being positively associated with Gross Domestic Product and population growth. Aquaculture policies in more industrialized countries, such as the EU Member States or the USA, have generally focused on environmental protection, resulting in numerous constraints and rigid regulations, and consequently, a slower growth of the aquaculture sector [37]. More lenient environmental policies in low- and middle-income countries have likely driven aquaculture growth to a higher level than in developed nations, highlighting, to some extent, the role of food demand and job creation as drivers of aquaculture development. Similarly, within countries, stricter restrictions are often implemented in protected areas (e.g., national parks) compared to heavily human-modified areas, where environmental regulations are generally more lenient. This disparity reflects differences in the assessment of ecological risk versus (for instance) economic and socio-cultural benefits. Stringent environmental regulations often prioritize conservation goals, whereas more flexible policies can favor economic interests. Risk–benefit trade-off is debated, as the ecological consequences of escapees are generally not immediately perceived but are typically long-lasting. In contrast, the economic gains and food production benefits derived from aquaculture are direct, with socio-economic advantages, such as job creation and industry development, being more immediate and sustained [38]. In the past, international codes of practice for non-native species have been used in aquaculture [39] and detailed risk analyses performed to raise awareness of the ecological and socio-economic damages they may cause (e.g., in the European Union [16]).

The prospects for aquaculture sustainability are contingent upon effectively mitigating environmental risks. In this context, our study provides a comprehensive global analysis of non-native species in global aquaculture production. We used species production metrics from the *Food and Agriculture Organization of the United Nations* (FAO) database [40], analyzed their global distribution and biogeographic origins, and assessed monetary costs from aquaculture species using the *InvaCost* database [41]. We aimed to (1) examine the production quantity (metric tonnes) and economic value (2017 USD) of aquaculture species in both their native and non-native ranges over time and space; and (2) quantify the associated monetary costs that the major aquaculture species can incur in terms of their typology and the affected sectors. Finally, we draw attention to the farming of non-native species that are classified as invasive, whose escapes into the wild could pose environmental and socio-economic harm.

2 | Materials and Methods

2.1 | Data Sources

2.1.1 | Aquaculture Production—FAO Database

We accessed the FAO Fisheries and Aquaculture statistics using *FishStatJ* software 4.04.00 [40] as of September 2024. In particular, we used the FAO *Global Fishery and Aquaculture Production Statistics* v2024.1.0 workspace, which contains global aquaculture production for (a) quantity and (b) economic value. Both datasets contain data on aquaculture production by species (or group of species), country, fishing area, and aquatic environment. Aquaculture production specifically refers to outputs from aquaculture activities, which are designated for final harvest for consumption but not for ornamental purposes (<https://www.fao.org/fishery/en/collection/aquaculture>). For production quantity, the time series spans from 1950 to 2022, whereas it extends from 1984 to 2022 for economic value expressed in United States dollars (USD) [40]. Although amphibians and reptiles have rarely been considered in aquaculture production, the FAO database documents some production (this study; and see for example Table S10 in [14]). We decided to retain amphibians and reptiles in our general analysis because their inclusion does not affect the main results as they represent only a marginal fraction of the total. Moreover, the purpose of their production (whether for aquaculture or ornamental trade) is likely irrelevant to the likelihood of these species establishing in the wild and their resulting ecological impacts.

2.1.2 | Distribution Databases

Once we retrieved the species included in the FAO database, we searched for their distribution (both native and non-native countries) in the global databases *FishBase* [42] and *SeaLifeBase* [43]. To do this, we used the `rfishbase` R package [44] using the function `country` to extract information about the country where species are present and their status (native or non-native). For those species or countries lacking information in global databases, particularly noticeable with freshwater crayfish, amphibians, algae, and bivalves, we supplemented our data using CABI Compendia datasheets (<https://www.cabidigitallibrary.org/product/QI>), *AmphibianWeb*, *AlgaeBase* [45], *Global Invasive Species Database* [46], and relevant scientific literature. This procedure aimed to enhance distribution accuracy and determine whether production occurred in the native or non-native range. In cases where a species was found to be both native and introduced in the same country, we considered the whole country as native to avoid overestimation in our calculations.

2.1.3 | Economic Costs—InvaCost Database

To analyse the documented monetary costs that species used in aquaculture caused outside of their native ranges, we retrieved data from the *InvaCost* database (version 4.1), which is the most comprehensive global database of monetary costs associated with biological invasions [47]. Cost entries in the *InvaCost* database were standardized to 2017 USD dollars using market exchange rates provided by the World Bank and adjusted for

inflation based on the Consumer Price Index corresponding to the year in which each cost was originally estimated [41]. Every cost entry recorded in *InvaCost* is characterized by various descriptors specifying the method reliability and implementation, type of cost and impacted sector, country and temporal duration, among others (see [41] and online “Descriptors” document at doi.org/10.6084/m9.figshare.12668570 for further information). Method reliability refers to the reliability of the publication type and the cost estimation methodology. Specifically, entries with cost estimates from peer-reviewed articles and official reports, or from gray literature with documented, reproducible, and traceable methods were classified as having “high” reliability, whereas all other entries were designated as “low” reliability. Implementation relates to whether the cost was observed (i.e., realized or empirically incurred) or potential (i.e., based on predictions or expected costs over time or space). Regarding the type of cost, it classifies expenditures into three categories: “damage”, which includes losses or damage caused by biological invasions (e.g., restoration actions, resource losses); “management”, which covers expenditures related to control, early warning and rapid responses, monitoring, and eradication; and “mixed”, which applies to cases where the categories cannot be clearly distinguished. The impacted sector identifies the sector affected by each cost (e.g., “agriculture”, “fisheries”, “forestry”, “health”, “authorities-stakeholders”). If the information is unclear or if the cost affects multiple sectors, the costs are classified as “diverse/unspecified”. Finally, to calculate the total cumulative cost over time, it is necessary to account for the duration of each documented cost, which is derived from the “Probable starting year adjusted” and “Probable ending year adjusted” columns. *InvaCost* is a dynamic database allowing for corrections and additions of new cost entries as they develop or are reported. The current version of *InvaCost* comprises 13,123 cost entries of invasive non-native species retrieved from published peer-reviewed and gray literature.

2.2 | Data Handling, Standardization and Filtering

To avoid inconsistencies between the FAO, data distribution, and *InvaCost* databases, we carried out several steps to standardize the obtained information, thereby making them comparable. First, scientific names were updated (e.g., *Lithobates catesbeianus* formerly called *Rana catesbeiana*, or *Magallana gigas* formerly called *Crassostrea gigas*). To do that, we compared the resulting species list with the *Global Biodiversity Information Facility* (GBIF) using the `taxize` R package [48], which also served to obtain taxonomic information (e.g., family, order). Second, particularly for the FAO database, entries associated with old names of states (e.g., Union of Soviet Socialist Republics, Czechoslovakia) were discarded because they were incomparable with present-day countries. Third, only entries specifically attributed to species were considered, thus discarding entire genera, subspecies, hybrids, or entries attributed to multiple species. Focusing exclusively on species makes the dataset more accurate, but it could lead to lower figures compared to the FAO’s official reports. Species were categorized into nine taxonomic groups (fishes, crustaceans, algae, mollusks, amphibians, reptiles, ascidians, cnidarians, and echinoderms). The database is detailed in <https://github.com/IsmaSA/Aquaculture>.

As the FAO database provides entries from different fishing areas and/or different environments, but sometimes belonging to the same country and species, we summed their quantity and economic value to include them as a single entry (i.e., one entry per species and country). This allowed further comparisons between species' distribution (attribution of a species as native or non-native to a country) and the *InvaCost* database, which does not consider economic costs within native countries. We further ensured that there were no discrepancies regarding the native or non-native ranges of the species between databases. Also, the annual economic values of aquaculture-produced species present in the FAO database are reported in US dollars (USD) with their nominal values for the year of production. To ensure that these were comparable with *InvaCost* values, which are in 2017 USD, we converted all of the FAO values into 2017 USD following Diagne et al. [41].

In addition to the analyses conducted for the nine taxonomic groups mentioned above, we filtered a subset of species (or species groups) from the main database, focusing on the major aquaculture species [as listed in Table 10 of FAO [14]]. This approach allowed us to quantify the share of total production—both in native and non-native ranges—attributable to the major aquaculture species, as well as to illustrate their potential harm in invaded areas. Note that we selected *The State of World Fisheries and Aquaculture 2022* [14] instead of the 2024 version because the previous version principally includes specific species rather than groups, which allows for a more detailed real analysis of production quantity and economic value, as well as monetary costs associated at the species level (see below).

To quantify the monetary costs of non-native species used in aquaculture, we matched the *InvaCost* database with the major aquaculture species farmed globally. In a subsequent step, we classified the monetary costs of non-native species present in both databases according to their method reliability (high or low) and implementation (observed or potential). Although we first report estimates for total costs (including both observed and potential costs with high and low reliability), for our main analysis we adopted a conservative approach by focusing on the highly reliable observed costs. This decision, while considerably reducing the cost estimates, provides more accurate real estimates. Also, we analysed other descriptors including the country where monetary costs have been incurred, the type of cost, and the impacted sector. Finally, by using duration (in years) and standardized costs in 2017 USD, we annualized the data, assigning each cost entry to a single year. This approach allowed for the comparison of cost entries over time. To assess the documented monetary costs of invasive non-native species through the aforementioned descriptors, we used the *invacost* R package [49].

2.3 | Analyses

The annual growth rate was calculated for the entire available period for both native and non-native aquaculture production (1950–2022) and economic value (1984–2022) as follows:

$$\text{Annual growth rate} = (V_{t+1} - V_t) / V_t$$

where the V is the production quantity or the economic value, and the t is the year. For better visualization, a Loess Regression method was applied to smooth the volatile time series. The rate of change (ROC) for the volume of aquaculture production between periods pre-2000 and post-2000 was calculated based on the formula below. Due to distinct time frames in the datasets for production quantity and economic value, 20-year (1980–1999 and 2000–2019) and 15-year (1985–1999 and 2000–2014) periods were established respectively. For the calculation of both ROCs, we used the following equation:

$$\text{Rate of Change} = ((V_{\text{Post2000}} / V_{\text{Pre2000}}) - 1) \times 100$$

We selected these equal periods based on the availability of data reported, the notable increase in the volume of aquaculture production over the last four decades, and the surge of invasion science since approximately 2000 (e.g., evidenced by the launch of the *Biological Invasions* journal in 1999; or the NEOBIOA publication series founded in 2002).

Country-level species origins for those non-native species with aquaculture production were retrieved from the above-mentioned global databases as well as GBIF and web-scraping techniques. Each country was assigned to its respective continent, and overseas territories were associated with the continent that corresponded to their geographic, rather than political, designation. Countries in Central America were assigned to North America. For species with native ranges spanning multiple continents, we estimated the relative importance of different origin regions by dividing the number of species or production quantity by the number of continents to which the species is native, thus preventing inflated economic values (see [33]). Chord diagrams depicting the number of species and production quantity (in million tonnes) were generated using the *circlize* R package [50]. All analyses were carried out using R version 4.4.1 [51].

3 | Results

3.1 | Volume and Economic Value of Aquaculture Production in Native and Non-Native Ranges

From 1950 to 2022, a total of 560 species spanning 204 territories/countries have contributed to the aquaculture production of 1731.65 million tonnes, amounting to USD 3.92 trillion (1984–2022, when economic value was available). This total production has been mainly based on four taxonomic groups, including fishes, algae, mollusks, and crustaceans, with a minor representation of the other groups (see Figure S1 for shares in number of species, volume of production and economic value). These total figures have not been evenly distributed over time or space (see Sections 3.2 and 3.3, respectively).

Of the total farmed species, 71.4% (400 species) of aquaculture species were exclusively produced in countries within their native ranges, but 8.8% (49 species) were farmed exclusively in their non-native ranges, and 19.8% (111 species) in countries within both native and non-native ranges (Table 1; for full list of species see Table S1). While the majority of production quantity has come from farming species within their native range (67.0%

TABLE 1 | Summary of the number of species, global production quantity, and economic value depending on whether they are farmed in their native, non-native ranges or both. Species farmed exclusively within their native range are highlighted in green, those farmed in non-native regions in orange, while species farmed in both native and non-native countries are shown in grey. Their global production quantity and economic value are allocated according to the specific country where they have been farmed (Table S1).

Status	Farmed species	Global production (million tonnes)	Economic value (USD trillion)
Native range	400	1 160.1	2.74
Non-native range	111	49	571.6
Total	560	1 731.65	3.92

of the total global production; 1160.1 million tonnes), 33.0% of aquaculture production (571.6 million tonnes) has stemmed from the species farmed outside their native range, amounting to USD 1.17 trillion (Table 1).

The most commonly farmed aquaculture species globally, according to FAO [14], included 23 fish species (and five fish groups), eight crustacean species, five mollusk species (and three mollusk groups), three species (and two groups) of other aquatic animals, and five algae species (and three algae groups) (Table 2). Together, these accounted for 92.8% of the total production (1606.89 million tonnes) and 87.5% of the total economic value (USD 3.42 trillion) from the entire available period. Focusing exclusively on non-native production, these major aquaculture species accounted for 97.9% of the global non-native production reported in the FAO database, totaling 559.5 million tonnes. For all groups except fish, the list of the most commonly farmed aquaculture species accounted for nearly the entirety of their production and economic value (Figure 1). Some highly farmed fishes, with production in both native and non-native ranges, but not included in the list of major aquaculture species, were the ray-finned fish *Cirrhinus mrigala* with 15.4 million tonnes, the Japanese eel *Anguilla japonica* with 8.8 million tonnes, and the northern snakehead *Channa argus* with 7.9 million tonnes, most of which were produced within its native range. In contrast, the channel catfish *Ictalurus punctatus* had over one-third of its total production (12.7 million tonnes) farmed outside its native range.

3.2 | Trends in Global Aquaculture

Despite a general increase in the total volume of aquaculture production and economic value (Figure 2) and across the taxonomic groups (Figure S2), the annual growth rate for both native and non-native species' production has fluctuated over time. Over the past decades, production volumes have risen rapidly, with native production being several orders of magnitude higher than its non-native counterpart (Figure 2a). While the annual growth rate of native species production has experienced an abrupt decline from approximately 10% to 2% from 1990s to 2020s, it still exhibits positive values in annual growth (Figure 2b). In contrast, while the rate of growth in non-native species production has also witnessed a reduction, the decline has been more moderate, with the annual growth rate actually

surpassing that of native production since approximately 2000 (Figure 2b). Regarding the total economic value, it has increased more gradually in both categories, particularly in native species production, which appears to have reached a plateau since the late 2010s (Figure 2c). However, the annual growth rates of economic value differed markedly from those of production. Both native and non-native species' economic value exhibited similar trends, with the latter consistently growing at higher rates since 1990 (Figure 2d). Since 2019, the annual growth rate of native species' value has declined, reaching -5% by 2022, mirroring the recent economic plateau. A similar trend is observed in the annual growth rate of the economic value of non-native species production, although it has still maintained positive growth in recent years (Figure 2d).

When examining the number of species farmed within their native and non-native ranges over time, we observed a growing trend in both groups. Specifically, the number of native species has increased at an average annual rate of approximately 2.9% (ranging from 46 species in 1950 to 341 in 2022), with two marked peaks in 1984 and 2021, when the number of species increased by 22.8% (from 114 to 140 species) and 19.3% (from 321 to 383), respectively. In comparison, the number of non-native species farmed in aquaculture has increased at an average annual rate of approximately 3.1% from 1950, when 12 species were farmed, to a total of 102 non-native species in 2022. Interannual variation in the number of non-native species farmed was more pronounced than that of native species over time, with peaks of 19.0% in 1986 (from 42 to 50) but also declines of -8.1% in 2022 (from 111 to 102), likely due to the discontinuous production of certain species in recent decades (Figure S3).

The rate of change between periods 1980–1999 and 2000–2019 (see Methods for the period selection) for both native and non-native production differed among taxonomic groups (Figure 3a,b). Focusing on the most important taxonomic groups in terms of production quantity (i.e., fishes, algae, mollusks, and crustaceans; Figures 1 and S4), the rate of change for production in non-native ranges exceeded that of native production for fishes and crustaceans. For example, the production of fish in their non-native range was nearly 500% higher in the past two decades compared to the last 20 years of the 20th century, thereby doubling the increase observed in native production. The percentage of change for crustaceans within their non-native range was enormous, i.e., 11,209%, with a production lower than

TABLE 2 | Major aquaculture species farmed globally according to FAO [14], with volume of production (in million tonnes) and economic value (in 2017 USD billion) for both native and non-native ranges, along with examples of their ecological and socio-economic impacts (both mechanisms and types of impacts). Asterisks denote species groups with their species included in the FAO data base are listed in the table note. †Indicates the most up-to-date scientific name of the species. The Nile tilapia and the rainbow trout are exclusively present in inland aquaculture, although they are also present in marine and coastal aquaculture.

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
Finfish in inland aquaculture							
Silver carp	<i>Hypophthalmichthys molitrix</i>	117.74	16.49	191.63	25.88	<ul style="list-style-type: none"> Decline in zooplankton Alteration of water quality Negative effect on native sport fish 	[52, 53]
Grass carp	<i>Ctenopharyngodon idella</i> †	123.62	4.91	221.17	9.22	<ul style="list-style-type: none"> Decline of macrophyte abundance and biomass Alteration of abiotic environment 	[54]
Common carp	<i>Cyprinus carpio</i>	77.36	25.21	131.73	50.38	<ul style="list-style-type: none"> Decline of phytoplankton and zooplankton biomass, macrophytes, fish, benthic invertebrates Indirect effects on waterfowl and fish populations (reducing chironomids) Alteration of suspended solids, sedimentation, erosion Alteration to nutrient cycling Increase to water turbidity 	[55, 56]
Bighead carp	<i>Hypophthalmichthys nobilis</i>	74.91	1.92	132.23	2.87	<ul style="list-style-type: none"> Displacement of native fishes Hybridization 	[57]
Nile tilapia	<i>Oreochromis niloticus</i>	16.49	58.75	28.19	112.99	<ul style="list-style-type: none"> Effect on biomass of native fish Reduced growth and survival of native species Alteration of water quality Disruption of trophic positions and destabilizing food web Effect on commercially valuable fishes and prawns 	[32, 58, 59]
Catla	<i>Gibelion catla</i> †	55.34	0.15	89.15	0.26	<i>Unclear</i>	
Roho labeo	<i>Labeo rohita</i>	42.69	0.29	76.73	0.44	<i>Unclear</i>	
Striped catfish	<i>Pangasianodon hypophthalmus</i>	22.98	12.74	36.66	17.06	<ul style="list-style-type: none"> Competition with native fauna Hybridization 	[60]

(Continues)

TABLE 2 | (Continued)

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
Rainbow trout	<i>Oncorhynchus mykiss</i>	1.93	22.43	8.56	98.09	<ul style="list-style-type: none"> • Alteration to behavior, growth rate and dominance of fish • Predation on amphibians • Competition with native trouts • Hybridization • Disease transmission • Cascading effects at community-level • Alteration to food web structure 	[61]
Wuchang bream	<i>Megalobrama amblycephala</i>	19.43	0.00	44.19	0.00	<i>Unclear</i>	
Black carp	<i>Mylopharyngodon piceus</i>	12.29	0.02	41.53	0.07	<ul style="list-style-type: none"> • Predation on snails, mussels, insect larvae; 	[62]
Largemouth black bass	<i>Micropterus salmoides</i>	0.01	6.41	0.03	16.14	<ul style="list-style-type: none"> • Predation on fishes and macroinvertebrates • Interspecific competition • Changes in habitat selection of native fishes • Local extirpation at community-level • Alteration in food web and community structure 	[63]
Clarias catfishes	<i>Clarias</i> spp.*	3.43	0.43	9.98	1.38	<ul style="list-style-type: none"> • Predation on native fishes • Alteration of invertebrate density • Disrupting community composition 	[64]
Tilapias nei	<i>Oreochromis</i> spp.*	0.21	1.91	0.65	3.73	<ul style="list-style-type: none"> • Predation on native fish, invertebrates and macrophytes • Competitive displacement of native fish • Aquaculture species collapse 	[65, 66]
Carassius carps	<i>Carassius</i> spp.*	0.21	0.29	0.41	0.57	<ul style="list-style-type: none"> • Decline of aquatic fauna and flora • Competition for resources (food/space) • Hybridization • Host of parasites 	[67]

(Continues)

TABLE 2 | (Continued)

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
Finfish in marine and coastal aquaculture							
Atlantic salmon	<i>Salmo salar</i>	35.77	11.85	189.97	88.01	<ul style="list-style-type: none"> • Unsuccessful hybridization affecting reproductive output of Pacific salmon • Competition with native species for prey, habitat and mating • Pathogen transmission 	[68, 69]
Milkfish	<i>Chanos chanos</i>	31.68	0.00	48.80	0.01	<i>Unclear</i>	
Japanese amberjack	<i>Seriola quinqueradiata</i>	7.47	—	57.46	—	<i>Unclear</i>	
Coho Salmon	<i>Oncorhynchus kisutch</i>	0.59	3.72	4.11	20.94	<ul style="list-style-type: none"> • Habitat disturbance with reduction in number and weight of invertebrates • Outcompeting native salmonids for food and space 	[70, 71]
Gilthead seabream	<i>Sparus aurata</i>	4.00	0.08	24.69	0.55	<ul style="list-style-type: none"> • Competition for resources (food/space) • Pathogen transmission 	[72]
European seabass	<i>Dicentrarchus labrax</i>	3.73	0.03	24.57	0.16	<ul style="list-style-type: none"> • Predation on piscivore fishes and macroinvertebrates • Competition for natural resources 	[73, 74]
Japanese seabass	<i>Lateolabrax japonicus</i>	2.64	0.00	5.45	0.00	<i>Unclear</i>	
Large yellow croaker	<i>Larimichthys crocea</i> [†]	2.57	—	4.99	—	<i>Unclear</i>	
Pompano	<i>Trachinotus ovatus</i>	—	2.01	—	13.47	<i>Unclear</i>	
Barramundi	<i>Lates calcarifer</i>	1.65	0.09	6.99	0.60	<ul style="list-style-type: none"> • Pathogen transmission • Interbreeding with native stocks 	[75, 76]
Red drum	<i>Sciaenops ocellatus</i>	0.04	1.20	0.23	2.46	<ul style="list-style-type: none"> • Predation on crustaceans, mollusks, fishes • Competition for resources (food/space) • Impact on nursery grounds • Market competition-conflict with wild fisheries 	[77, 78]
Mulletts nei	Mugilidae*	0.38	0.01	1.34	0.02	<ul style="list-style-type: none"> • Pathogen transmission • Predation on wild stocks • Competition for resources (food/space) 	[79, 80]

(Continues)

TABLE 2 | (Continued)

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
Groupers nei Crustaceans	<i>Epinephelus</i> spp.*	0.06	0.00	0.79	0.00	<i>Unclear</i>	
Whiteleg shrimp	<i>Penaeus vannamei</i>	14.36	59.38	77.13	337.81	<ul style="list-style-type: none"> • Predation on native species • Competition for resources (food/space) • Host of pathogens (Taura syndrome virus, TSV) • Gene introgression • Modification of natural benthic communities • Modification of nutrient regime • Negative impact on aquaculture/fisheries 	[81-83]
Giant tiger prawn	<i>Penaeus monodon</i>	21.66	0.15	173.74	1.21	<ul style="list-style-type: none"> • Predation on native prawns, gastropods, bivalves, crustaceans, polychaetes, fish, plant material, echinoderms, hydroids • Transmission of viral diseases • Modification of natural benthic communities • Modification of nutrient regime • Impacts on aquaculture and fisheries 	[82, 84]
Red swamp crayfish	<i>Procambarus clarkii</i>	1.73	18.41	4.34	145.15	<ul style="list-style-type: none"> • Predation on amphibians, mollusks, macroinvertebrates, macrophytes • Host of pathogens (<i>Aphanomyces astaci</i>) • Modification of ecological communities • Habitat alteration (water quality) • Reduction in valued edible native species 	[82, 85]
Chinese mitten crab	<i>Eriocheir sinensis</i>	13.75	—	146.48	—	<ul style="list-style-type: none"> • Alteration of native food web dynamics • Competition for limited resources • Competitive interactions • River bank erosion • Impacts on ecosystem services 	[82, 86]
Giant river prawn	<i>Macrobrachium rosenbergii</i>	2.38	3.30	16.74	23.84	<ul style="list-style-type: none"> • Competition for habitat and food with native prawns • Host of pathogens (white spot syndrome virus, WSSV) 	[82, 87]
Oriental river prawn	<i>Macrobrachium nipponense</i>	4.56	—	31.98	—	<i>Unclear</i>	

(Continues)

TABLE 2 | (Continued)

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
Green mud crab	<i>Scylla paramamosain</i>	2.54	—	9.49	—	Unclear	
Indo-pacific swamp crab	<i>Scylla serrata</i>	1.30	—	10.72	—	<ul style="list-style-type: none"> • Competition for food • Crossbreeding with <i>S. olivacea</i> • Alter intertidal communities 	[88]
Mollusks							
Japanese carpet shell	<i>Ruditapes philippinarum</i>	86.72	1.39	131.47	6.79	<ul style="list-style-type: none"> • Replacement of native clams 	[89]
Pacific cupped oyster	<i>Magallana gigas</i>	15.88	22.01	21.39	28.24	<ul style="list-style-type: none"> • Predation on invertebrates • Reduction of native oyster populations • Reef competence • Sediment alteration 	[90]
Sea mussels	Mytilidae*	28.06	0.05	28.51	0.08	<ul style="list-style-type: none"> • Competition with native bivalves for habitat and resources • Hybridization • Effects on native aquaculture 	[91]
Constricted tagelus							
	<i>Sinonovacula constricta</i>	20.53	—	28.11	—	Unclear	
Blood cockle	<i>Tegillarca granosa</i>	5.38	8.28	3.10	17.54	<ul style="list-style-type: none"> • Human health 	[92]
Scallops nei	Pectinidae*	9.55	0.00	27.07	0.00	Unclear	
Cupped oysters	<i>Crassostrea</i> spp.*	6.89	0.00	4.00	0.00	Unclear	
Chilean mussel	<i>Mytilus chilensis</i>	5.11	—	26.17	—	Unclear	
Other aquatic animals							
Chinese softshell turtle	<i>Pelodiscus sinensis</i> †	5.91	0.07	47.42	0.90	Unclear	[93]
Japanese sea cucumber	<i>Apostichopus japonicus</i>	2.94	—	16.83	—	Unclear	
Edible red jellyfish	<i>Rhopilema esculentum</i>	1.26	—	4.75	—	Unclear	
Frogs	<i>Rana</i> spp.‡*	—	0.07	—	0.29	<ul style="list-style-type: none"> • Displacement of native species • Decline in populations of native amphibians • Predation on endangered waterfowl • Host of pathogens (<i>Batrachochytrium dendrobatidis</i>) • Allergic reactions 	[94]

(Continues)

TABLE 2 | (Continued)

Common name	Scientific name	Quantity production		Economic value		Impact mechanisms and types	References
		Native	Non-native	Native	Non-native		
River and lake turtles	Testudinata*	0.00		0.02			
Algae							
Japanese kelp	<i>Laminaria japonica</i>	2.15	272.32	4.58	101.76	<ul style="list-style-type: none"> • Structural change and displacement of native species • Altered abundance and diversity of benthic organisms • Hybridization • Changes in local community composition 	[95]
Wakame	<i>Undaria pinnatifida</i>	56.77	0.00	33.14	0.00	<ul style="list-style-type: none"> • Modified community composition • Alter trophic interactions • Structural change of ecosystems • Reduced water movements 	[96]
Elkhorn sea moss	<i>Kappaphycus alvarezii</i>	40.38	0.25	5.75	0.03	<ul style="list-style-type: none"> • Declines to endemic corals • Reduction of species diversity • Alteration of benthic reef habitats • Habitat competition with native corals 	[97, 98]
Nori nei	<i>Pyropia</i> spp.†.*	31.44	0.00	60.42	0.02	<i>Unclear</i>	
Spiny eucheuma	<i>Eucheuma denticulatum</i>	2.40	2.86	0.18	0.05	<ul style="list-style-type: none"> • Reduction of seagrass biomass, shoot density and bed coverage 	[99]
Fusiform sargassum	<i>Sargassum fusiforme</i>	4.15		3.20		<i>Unclear</i>	
Gracilaria seaweeds	<i>Gracilaria</i> spp.*	0.38		0.22		<i>Unclear</i>	
Eucheuma seaweeds	<i>Eucheuma</i> spp.*		0.00		0.00	<i>Unclear</i>	

Note: **Clarias* spp. (*C. anguillaris*, *C. bairachius*, *C. fuscus*, *C. gariepinus*, and *C. ngamensis*); *Oreochromis* spp. (*O. andersonii*, *O. aureus*, *O. macrochir*, *O. mossambicus*, *O. shiranus*, *O. spilurus*, and *O. tanganica*); *Carassius* spp. (*C. auratus*, *C. carassius*, and *C. gibelio*); *Mugilidae* (*Chelon ramada*, *Crenimugil seheitii*, *Ellochelon vaigiensis*†, *Mugil cephalus*, *M. litza*, *Planiliza haematocheila*†, and *P. subviridis*); *Epinephelus* spp. (*E. aeneus*, *E. akaara*, *E. amblecephalus*, *E. areolatus*, *E. bleekeri*, *E. coioides*, *E. cyanopterus*, *E. fasciatus*, *E. faveatus*, *E. fuscoguttatus*, *E. lanceolatus*, *E. longispinus*, *E. maculatus*, *E. malabaricus*, *E. spilotoceps*, *E. tauvina*, and *E. tukula*); *Mytilidae* (*Aulacomya atra*†, *Choromytilus chorus*, *Mytilus edulis*, *Mytilus galloprovincialis*, *Mytilus planulatus*, *Mytilus unguiculatus*, *Mytilus unguiculatus*, *Perna canaliculus*, *Perna perna*, and *Perna viridis*); *Pectinidae* (*Aequipecten opercularis*, *Argopecten purpuratus*, *Argopecten ventricosus*, *Mimachlamys varia*, *Mizuhopecten yessoensis*, *Nodipecten nodosus*†, *Pecten fumatus*, *Pecten jacobaeus*, *Pecten maximus*); *Crassostrea* spp. (*C. corieziensis*, *C. rhizophorae*, *C. tulipa*, *C. virginica*, *Magallana bilineata*); *Rana* spp.† (*Lithobates catesbeianus*†, and *Pelophylax ridibundus*); *Testudinata* (*Chelonia mydas*); *Pyropia* spp.† (*P. columbina*, and *P. tenera*); *Gracilaria* spp. (*G. gracilis*, and *Gracilaria topsis longissima*†); and *Eucheuma* spp. (*E. isiforme*).

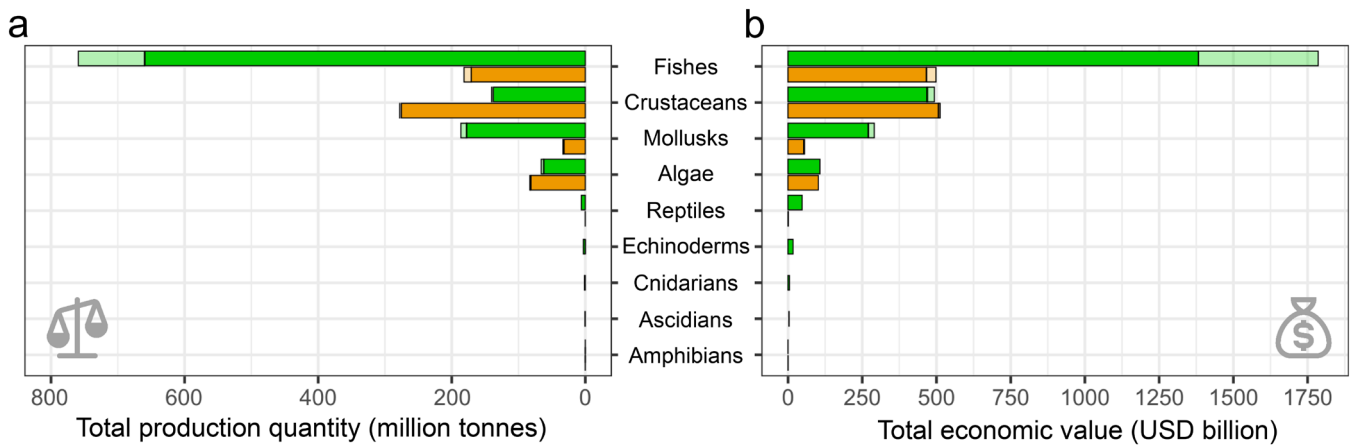


FIGURE 1 | World production of major aquaculture species (including species groups) by production quantity (a) and economic value (b). Bars in green represent production in native ranges, while those in orange indicate production in non-native ranges. The shaded areas in the bar plots represents the global production of other species not classified among the most commonly farmed in aquaculture.

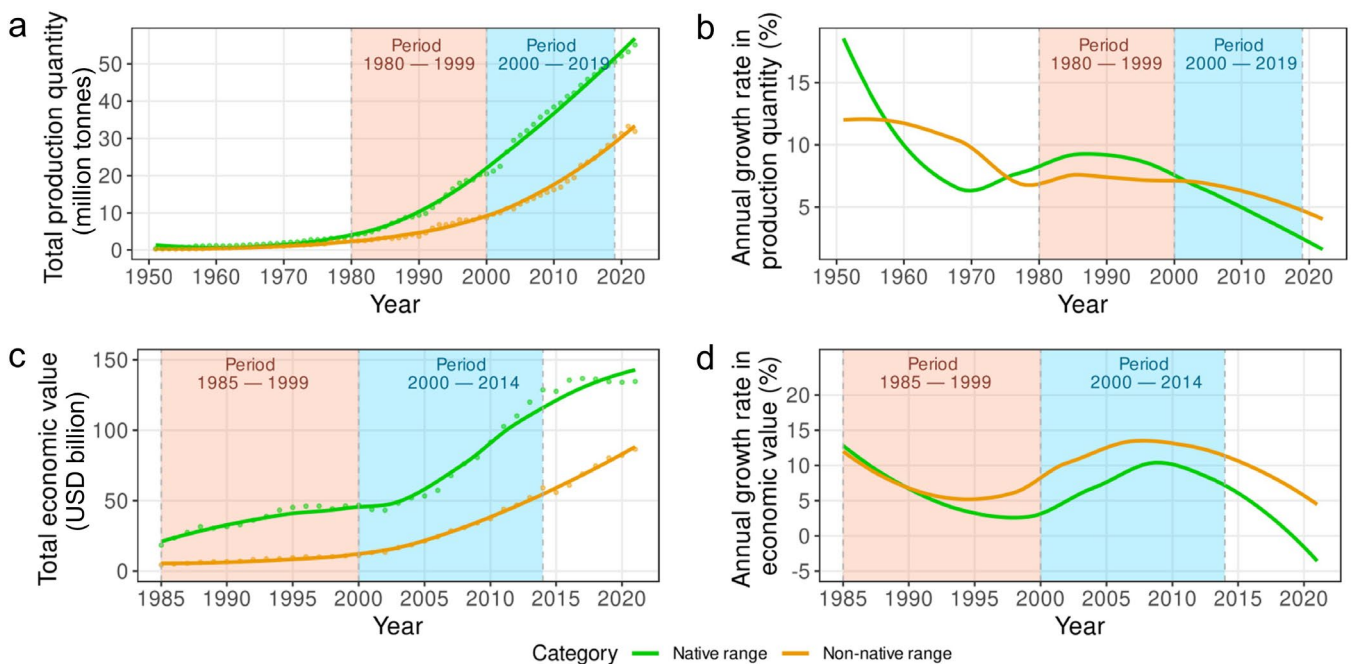


FIGURE 2 | Total production quantity per year (a) and its annual growth rate (b) for native (green) and non-native (orange) species, along with the total economic value (c) and its annual growth rate (d). Note that the analysed periods differ due to the absence of economic data prior to 1984 (see Section 2). While trends are estimated using LOESS regression to smooth volatile time series, dots in panels (a) and (c) represent the raw total aquaculture production and economic values, respectively.

0.5 million tonnes between 1980 and 1999, but exceeding 58 million tonnes from 2000 to 2019 (Figure S2). When comparing the rate of change in crustacean production between non-native and native ranges, the former was over 32 times higher, indicating a strong current bias toward the farming of non-native crustacean species. In contrast, non-native mollusk production was only 59% higher in the first two decades of the 21st century compared to the last two decades of the 20th century, whereas this increase was more than threefold (209%) in the case of native mollusk production. Notably, although non-native algae production exceeds that of native species (Figure 1a), the rate of change in non-native algae production was half that of native algae production (Figure 3a,b). This is attributable to non-native production surpassing native production since the 1960s, combined

with the sudden increase in native algae production during the 2000s (Figure S2). Although on a smaller order of magnitude, the rate of change for economic value in non-native ranges followed a similar trend across all major taxonomic groups, particularly substantial for crustaceans (4276%) compared to native production rates (Figure 3c,d).

3.3 | Aquaculture Producing Countries Around the World

Non-native aquaculture production is particularly prominent in countries of South America, Europe, the Near East, Southeastern Asia, and Oceania. Overall, the production volume of non-native

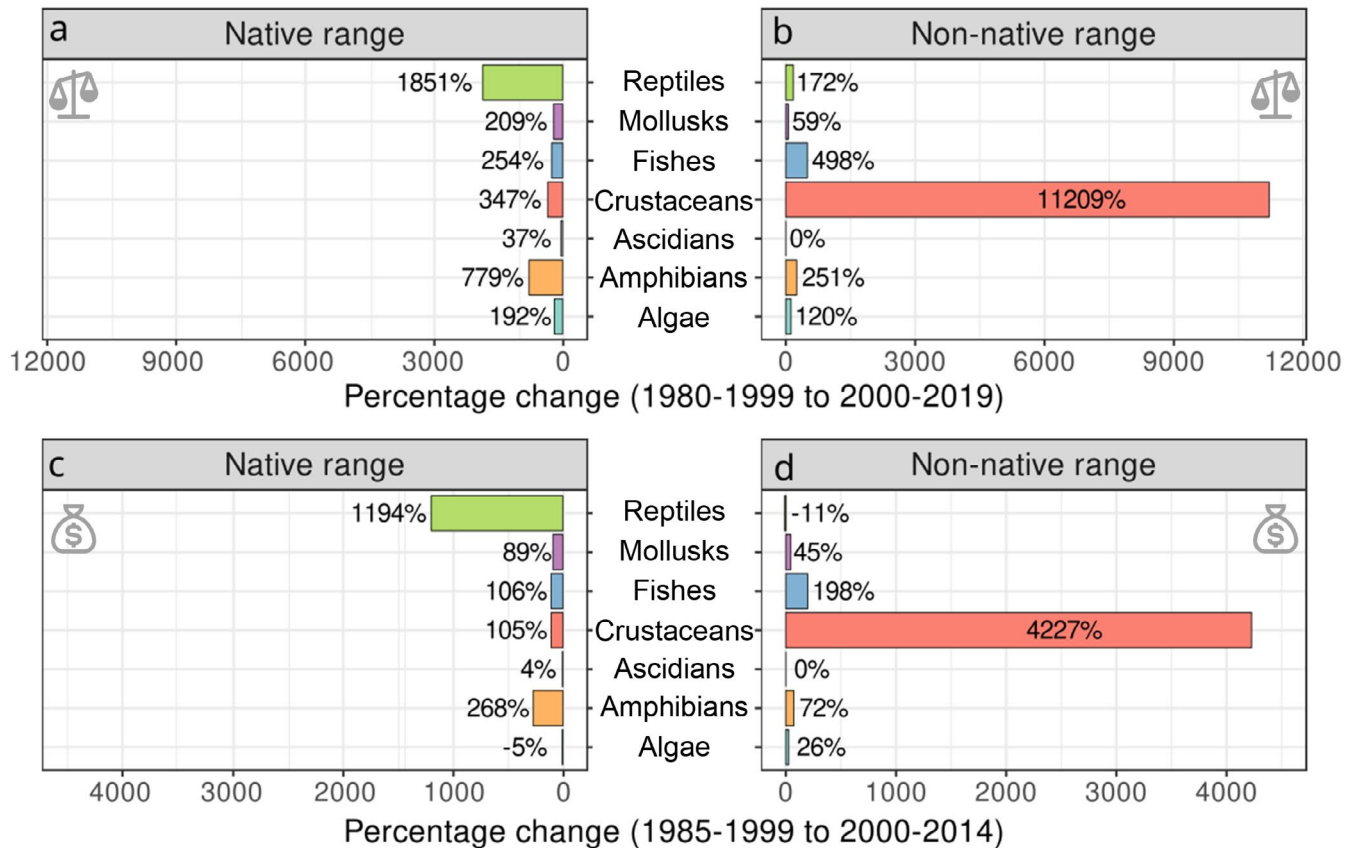


FIGURE 3 | Percentage change in production quantity and economic value for each taxonomic group in native and non-native ranges. Percentage change in production quantity between 1980–1999 and 2000–2019 (a, b). Percentage change in economic value between 1985–1999 and 2000–2014 (c, d). Ascidians, cnidarians, and echinoderms had only native aquaculture production. Cnidarians and echinoderms were documented only after 2000, and thus these two groups were excluded from the analysis.

species exceeded that of native species in 56% ($n = 115$) of territories/countries worldwide. However, many of these countries are relatively small aquaculture producers, with the notable exception of several top 20 global producers, including Indonesia (58% non-native production out of 62.1 million tonnes), North Korea (90% of 27.5 million tonnes), Chile (77% of 23.6 million tonnes), France (66% of 13.2 million tonnes), and Brazil (72% of 8.9 million tonnes). The proportion of non-native production varied not only among countries but also over time and across taxonomic groups within countries (Figures 4 and S5). For instance, among all territories/countries engaged in fish farming ($n = 202$), 115 reported higher non-native production than natives. Similarly, non-native production of crustaceans surpassed native production in 68 out of 111 territories/countries, and non-native algae in 20 out of 41. In contrast, only 14 out of 77 countries produced more non-native mollusks than native ones (see left panels in Figure 4). When analysing the proportion of non-native production over time for all countries together, we found that algae production was almost exclusively composed of native species in the 1950s, but a sudden increase in non-native production occurred from the 1960s onwards, maintaining levels between 60% and 80% to the present. In crustaceans, the proportion of non-native production rose sharply in the 2000s, increasing from 10% in 2000 to nearly 70% by 2022. Different trends have been observed in the production of non-native fishes and non-native mollusks. Non-native fish production has fluctuated between 10% and 20% since the 1950s, although there has been a slight upward trend

toward non-native production since the 1990s. In contrast, non-native mollusk production declined from 40% to 15% between 1950 and 1970, then rose again to nearly 30%, but currently stands at around 10% (see right panels in Figure 4). These global patterns in the proportion of non-native production for the four taxonomic groups result from the emergence or disappearance of non-native production, as well as shifts between native and non-native production in specific countries over the decades (Figure S5).

Although the number of non-native species farmed and the count of non-native producing countries have increased over time, 88.6% of the total non-native production, representing 83.7% of the economic value, was attributed to only 10 producing countries. While Asian countries predominantly led in non-native species production (in decreasing order, China, Indonesia, North Korea, India, South Korea, Thailand, Bangladesh, and Viet Nam), non-Asian countries such as Chile (18.1 million tonnes) and France (8.8 million tonnes) that ranked 6th and 9th, respectively, also emerged with substantial non-native production (see Figure S6 for details across taxonomic groups). Among the 186 countries that have ever produced non-native species, those with the highest number of farmed non-native species were Singapore ($n = 25$), Spain ($n = 22$), and Italy ($n = 21$), with nine countries having farmed 15 or more non-native species (Table S3). In contrast, 21 species have been farmed in 10 or more countries outside their natural distribution range (Figure S7).

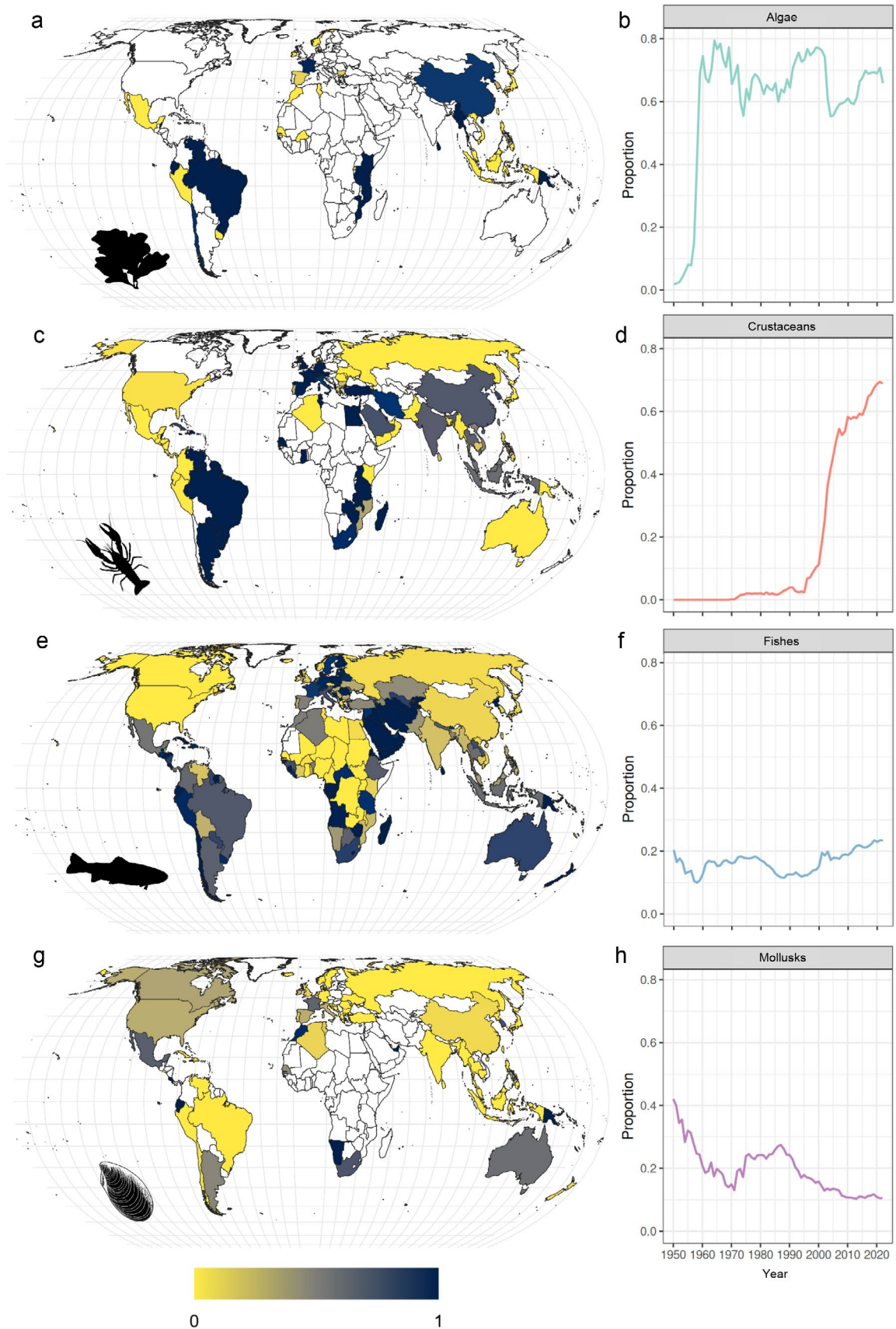
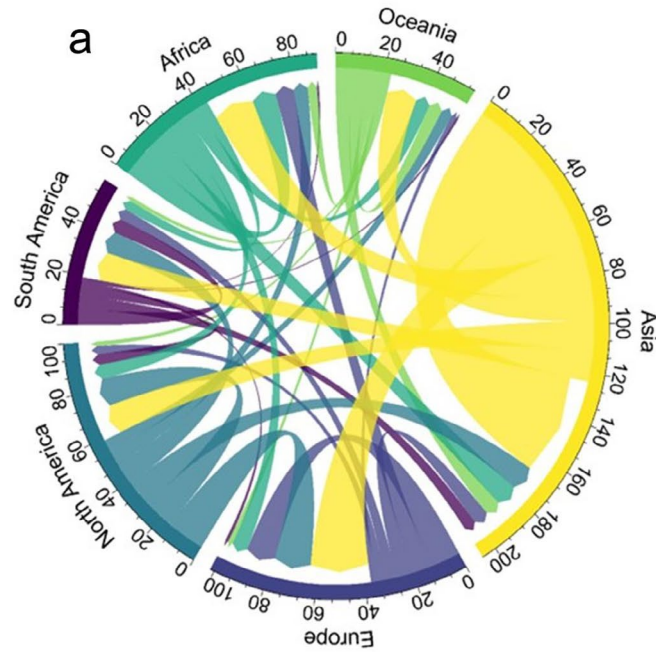
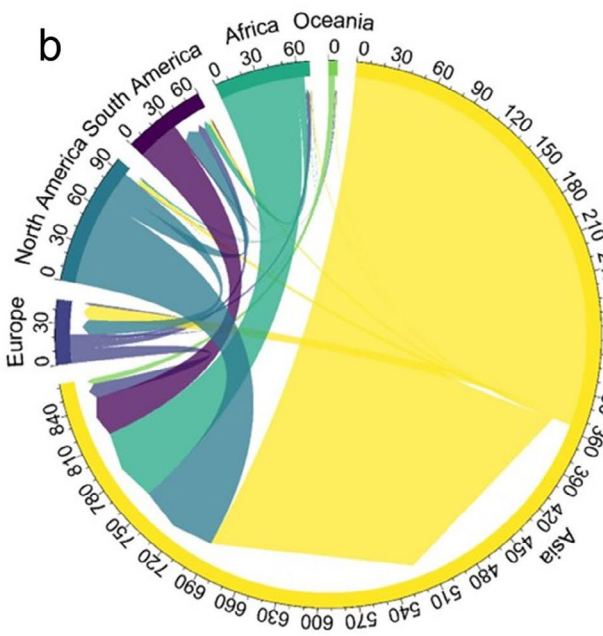


FIGURE 4 | Proportion of non-native production relative to total aquaculture production (1950–2022) for each country (left panels) and annual variation in global non-native production over the entire period (right panels), for the four most representative taxonomic groups in terms of production volume: Algae (a, b), crustaceans (c, d), fishes (e, f), and mollusks (g, h). Source: FishStatJ database—<https://www.fao.org/fishery/en/statistics/software/fishstatj>. Maps were projected by using Sphere Equal Earth Greenwich (ESRI:53035) in QGIS 3.32.1-Lima.

Number of species



Volume of production



Economic value

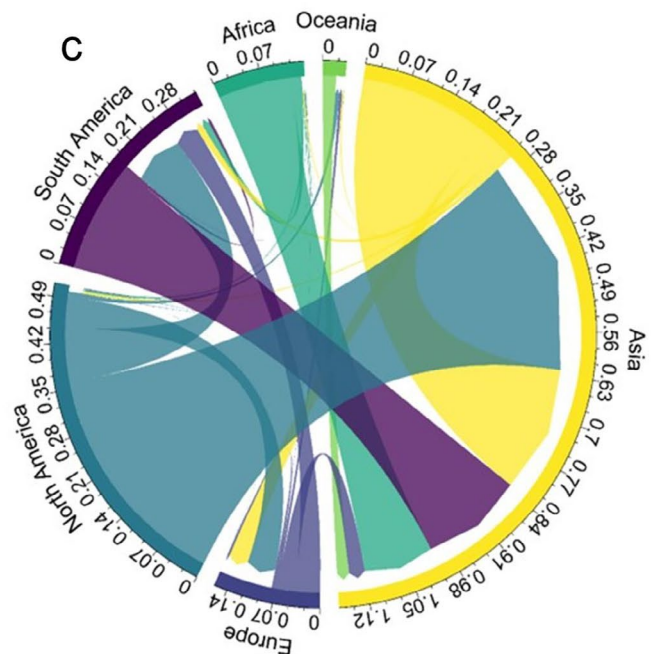


FIGURE 5 | Flows of the number of non-native species used in aquaculture (a), the volume of aquaculture production (in million tonnes) (b) and their economic value (in 2017 USD billion) (c) originating from non-native species between the continents of species origin and the continents producing non-native aquaculture. While arrow thickness represents the number of species or production quantity farmed in receiving continents, arrows indicate known native ranges and final recipient regions of reported aquaculture production (colored according to the continent of origin). Note that intracontinental flows represent introductions between countries within the same continent.

The number of non-native species translocated, and their associated volume of production and economic values, varied depending on their native continent and farmed species (Figure 5). Species have been both translocated abroad to other continents but also moved within the boundaries of their native continents where they are equally regarded as non-native species.

According to the proportion of species donated and received, Asia and North America were the primary donors of non-native species, while Europe and South America acted as sinks, receiving a large number of species. In particular, Asian species have been extensively translocated both inter- and intra-continently for aquaculture (Figure 5a).

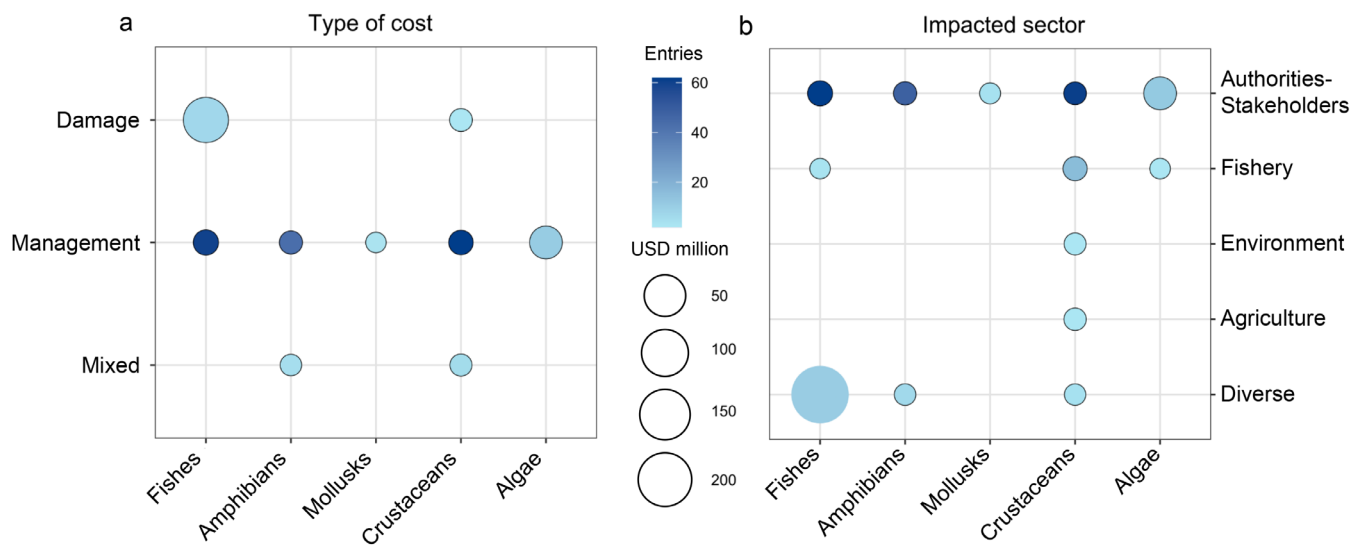


FIGURE 6 | Monetary costs associated with major aquaculture farmed non-native species between 1960 and 2020, as reported in InvaCost. Highly reliable and observed costs (in 2017 USD million) for farmed non-native species by type of costs (a) and by impacted sector (b). Node sizes are proportional to total costs (in 2017 USD million), and color shading corresponds to the number of cost entries. Note that before 1980 a single entry of 70,099.5 USD attributed to the common carp *C. carpio* was documented (see Figure S8).

While numerous species have been translocated both between and within continents, the volume of non-native production estimated primarily relied on Asian (336 million tonnes), American (97 million tonnes), and African (58 million tonnes) species introduced in Asia (Figure 5b). Non-native production in other continents, while significant, was relatively lower by comparison. For instance, it is estimated that Europe farmed 23 million tonnes of Asian and North American species (11.6 and 11.8 million tonnes, respectively), while South America produced approximately 13 million tonnes of North American species (Figure 5b). The economic value of the species produced, however, follows a different pattern (Figure 5c) depending primarily on the species being farmed. For instance, Asia produced North American species with an economic value exceeding USD 360 billion. Similarly, it also produced non-native Asian species worth USD 170 billion, South American species valued at USD 170 billion, and African species at USD 107 billion (Figure 5c). A significant portion of the economic value of non-native species farmed in Asia was mainly attributed to the farming of the American crustaceans *Procambarus clarkii* and *Penaeus vannamei*, the Asian brown seaweed *Laminaria japonica*, and, to a lesser extent, Nile tilapia *O. niloticus* from Africa. Also, the production of Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss* in Chile has generated an estimated economic value of approximately 60 billion USD for this South American country.

3.4 | Monetary Costs From Non-Native Species Used in Aquaculture

Of the 560 species farmed in aquaculture, we identified 27 species with documented monetary costs in the InvaCost database, amounting to a total of USD 19.2 billion across all continents except Antarctica (see list of species and costs in Table S2). Particularly, for the species with the highest volume of production (Table 2), total costs amounted to USD 6.4 billion from 1960 to 2020. After filtering highly reliable observed costs of those

species, eight aquaculture species including four fishes (*Carassius auratus*, *Cyprinus carpio*, *Micropterus salmoides*, and *O. mykiss*), a mollusk (*M. gigas*), a crustacean (*P. clarkii*), an alga (*Undaria pinnatifida*) and an amphibian (*Lithobates catesbeianus*) had documented monetary costs accounting for USD 287.2 million from 1960 to 2020 (Figure 6). This amounted to an average annual cost of USD 4.8 million over the entire period, or USD 7.2 million per year from 1980 to 2020 when excluding one entry with fewer costs documented in 1962 (Figure S8). Annual estimates of average monetary costs have shown a tendency to plateau or even decrease in recent years, possibly due to the effects of time lags in cost reporting. According to the type of cost, 75.2% were associated with damage costs (USD 216.0 million), while management costs constituted 24.3% of the total (USD 69.7 million) (Figure 6a). The majority of costs related to impacted sectors were classified under “Diverse” sectors such as fisheries or public and social welfare (USD 215.5 million; 75.1%), followed by impacts to “Authorities-Stakeholders” (USD 64.9 million; 22.6%). Other impacted sectors, such as fisheries, agriculture, and the environment, were less represented, with USD 6.7 million in total (Figure 6b). Globally, the costliest non-native species was the common carp *C. carpio* (USD 216.8 million) linked to damage to native commercial and recreational fisheries in Australia, as well as expenditures resulting from management actions in Australia and Spain (Table S2). Other documented damage costs include those caused by *P. clarkii* to the agricultural sector in Portugal and the health status of Spanish lakes. Regarding management costs, expenditures by authorities and stakeholders on control actions for the invasive alga *U. pinnatifida* in New Zealand, and the largemouth bass *Micropterus salmoides* in Japan illustrate how non-native species outside their native range can also generate monetary costs (Table S2).

4 | Discussion

Since 1950, non-native species have accounted for approximately one-third of global annual aquaculture production, with this

proportion exceeding 35% over the past 5 years. While offering economic opportunities and sustaining livelihoods in certain regions, these increasing patterns in non-native production also pose significant risks to environmental, social, and economic sustainability. This study highlights both an increase in the diversity of non-native species and in the volume of non-native production across taxa and geographic regions. The non-native aquaculture production has grown enormously since 1950, reaching a peak annual growth rate of 7.5% for quantity during the 1980s and 1990s, and 13% for economic value in the late 2000s. Subsequently, the growth rates have gradually declined but have consistently remained higher than the growth rate of native species. Non-native production is largely dominated by algae (mainly *L. japonica*) totaling 275.5 million tonnes (151.7 million tonnes between 2000 and 2019) and fishes, which account for 181.8 million tonnes in total (123.3 million tonnes between 2000 and 2019). However, non-native crustacean production experienced the fastest growth, with an astonishing increase of over 11,000% between 2000 and 2019 compared to the last two decades of the 20th century. Global production of non-native crustaceans increased from just over half a million tonnes between 1980 and 1999 to nearly 58 million tonnes between 2000 and 2019. While numerous non-native species have been farmed globally (up to 160), Asia leads in both the number of non-native species translocated to other continents and in non-native production, particularly concerning non-native algae, fishes, and crustaceans. We further illustrate how some of the major aquaculture species have documented ecological (e.g., decrease in species population size, changes in food web structure, changes in nutrient pool and fluxes) and socio-economic (e.g., loss of traditional fisheries) impacts (see Table 2, and below in Section 4.2). When these species are established and spread over non-native areas, they can pose a risk to biodiversity and ecosystems as well as economic sectors, ultimately leading to monetary costs. Approximately 40% ($n = 62$ out of 160) of farmed species have been classified as harmful invaders on regional or global lists of invasive species. This underscores the potential risk that could arise if they escape from aquaculture facilities into the environment.

4.1 | Rising Non-Native Species Production

Despite the intensification in the production of native species and the emergence of new farmed species in recent decades, the demand for protein and economic interests may have spurred the proliferation in the use of non-native species, further triggering the increase in global aquaculture production [12, 28, 100, 101]. Overall, we found that 33% of species (160 out of 560) produced in aquaculture have ever been farmed outside their native range. Although the number of species has increased over time, the identity of the non-native species produced has varied, especially in recent years. While several of the major aquaculture species have been farmed annually outside their native range since 1950 (e.g., silver grass, bighead, and common carps as well as Nile tilapia), there have been attempts to farm new species in non-native ranges. For example, aquaculture of African catfish *Clarias gariepinus* was highly promoted in Brazil in the 1980s, but its lower acceptance and escapes to the wild caused a rapid decline in production later [64]. In many cases, efforts to farm new species have remained limited to small-scale production trials, without establishing a lasting farming activity. Nevertheless, since 2017, over a hundred non-native species have been

produced annually in countries outside their native range, many of them also found in the wild. In China, for example, a quarter of introduced aquaculture fish species are already established in the wild, and 15% are identified as invasive [18].

Crustaceans particularly demonstrate how total production outside their native ranges (over 82 million tonnes since 1950) can, within a few decades, surpass production within their native ranges (over 66 million tonnes). This increase in non-native production is likely a consequence of the substantial contribution that crustacean aquaculture makes to economic development associated with their trade and empowerment, particularly in low-income countries [102]. Global prices of crustaceans (e.g., shrimps) are traditionally higher than those of finfish [103, 104]. This price disparity suggests that the motivation to farm crustaceans in aquaculture may already be greater than that for finfish, as the former can be closely tied to economic security, while the latter is more linked to food security. Similarly, non-native algae production has exceeded native production since the early 1950s, mainly due to the farming of the brown seaweed *L. japonica* in China. It is likely that the numerous ecosystem services and versatile applications that seaweeds offer, including direct human consumption or processed into food additives, biofuels, fertilizers, among others [105] can increase the impetus for farming them elsewhere in the non-native range. Both crustaceans and algae exhibit short production life cycles to reach marketable sizes and experience high demand in the seafood consumerism sector. Additionally, while crustaceans usually command premium prices, algae can be a high-volume, low-price product. Most non-native aquaculture species contribute significantly to local and regional economies, either as high-value cash crops [such as non-native penaeid shrimps (*Penaeus* spp.) in southeastern Asia and Latin America or Atlantic salmon (*S. salar*) in Chile] or as more efficient alternatives to native species with slower growth rates or more specific nutritional requirements. In Europe, for example, the non-native rainbow trout *O. mykiss* and African catfish *C. gariepinus* are widely preferred over native brown trout *Salmo trutta* and the European catfish *Silurus glanis* due to their faster growth rates, higher feed conversion efficiency, and tolerance to intensive farming conditions. Our analysis identified that, since the 1990s—when the growth of native species production began to decline—the economic value growth rate of non-native species has surpassed that of native species. This observed pattern may be driven by several factors, including the high yield and market value of non-native crustaceans, the greater productivity and economic margins of non-native fish species compared to native ones, and the diversification of new, higher-value markets, where the price and added value of non-native species have increased more rapidly due to greater demand.

4.2 | Ecological, Social, and Economic Impacts

Aquaculture is one of the main introduction pathways for aquatic non-native species, especially in inland waters [22]. Although recent reports such as *The State of the World's Aquatic Genetic Resources for Food and Agriculture* [106] have acknowledged the impact that some aquaculture species can have when established in the wild (see Box 13; Sections 2.6 and 3.2.5 in FAO [106]), these impacts have received relatively little attention in

sustainability goals, with the focus mainly remained on genetic introgression and the adverse effects of farmed species on wild stocks, such as Atlantic salmon [107]. Nonetheless, out of the 160 species farmed in non-native areas, approximately 40% ($n=62$) are included in at least one list of non-native species of global or regional concern (e.g., Union list—the list of invasive alien species of Union concern, and European Alien Species Information Network—EASIN, at European Union level; species currently listed as injurious wildlife under in the United States—USFWS [108]; or the [more than] “100 of the worst” globally in Lowe et al. [109] and Nentwig et al. [110]). Their inclusion serves as a warning of the potential damage that these species can cause to recipient ecosystems outside their native range, posing a risk to the environment and biodiversity if they establish in the wild.

When the major aquaculture species globally (including groups) were explored, approximately 40% (at least 24 out of 58 species/groups) were found to cause some ecological, social, and/or economic impacts (Table 2). However, the magnitude of impacts caused by invasive species is often context-dependent [111]; hence, the absence of observed impacts in a given case does not necessarily imply that the species is harmless, but rather that it currently has a low likelihood of causing damage. For instance, although the introduction of non-native Nile tilapia and carps (e.g., mrigal *Cirrhinus cirrhosus*, rohu and bighead carp) showed mild–moderate impacts on native fish communities in southeastern Asian freshwater wetlands [112], there is evidence that the same species can cause damage in other regions (e.g., *Tilapia* spp. in Brazil, [66, 113]). This complexity regarding the context dependency of impacts is further compounded by the risk associated with unnoticed introduction of organisms alongside aquaculture species, such as invertebrates, algae, and pathogens [29]. For example, the first report of the invasive macroalga *Rugolopteria okamurae* in the Mediterranean Sea, where it is causing detrimental impacts on coasts [114], was associated with oyster mariculture activities of the Pacific oyster in France [115]. Similarly, several zooplankton species, including the North American copepod *Skistodiaptomus pallidus*, an efficient omnivorous predator, have been detected in freshwater fish farms in New Zealand [116]. The development and advancement of new methodologies for prompt identification and surveillance programs in aquaculture practices are crucial to reducing the risk of hitchhiker taxa translocations in the context of current globalized trade.

Positive social and economic impacts have predominantly centered on how aquaculture can alleviate poverty and enhance protein enrichment in human nutrition [15]. It is also important to acknowledge that some non-native aquaculture species have saved collapsing aquaculture enterprise(s) and re-stabilized aquatic food production and supply chains from disruption [117]. For example, the non-native Pacific whiteleg shrimp *P. vannamei* replaced both the tiger shrimp *P. monodon* and the giant river prawn *Macrobrachium rosenbergii* when the white spot syndrome wreaked havoc on native shrimp farming. This disease nearly compromised regional crustacean aquaculture (e.g., Southeastern Asia); however, the crisis was averted through farming a wild non-native alternative, which had resistance to the pathogen [118]. While aquaculture contributes significantly to food security and economic development, its rapid expansion (both intensively and extensively) has often involved trade-offs

between profitability and sustainability [119]. Efforts to promote sustainable practices must navigate the complex challenge of maintaining profitability while minimizing ecological impacts. Nevertheless, non-native aquaculture, both in number of species and production quantity, continues to rise, with nearly 40% of global production in recent years attributed to non-native species. For instance, the farming of non-native species such as the red swamp or the redclaw crayfish *Cherax quadricarinatus* is mainly produced in non-native regions rather than in their native ranges, despite well-documented ecological risks [120, 121]. The vast majority of global non-native production takes place in low-income countries [122], where addressing hunger, livelihood opportunities, or economic development often shape policy priorities and can take precedence over biodiversity conservation [123, 124]. While these priorities are legitimate, they may coexist with limited institutional capacity and preparedness to counter biological invasions [125].

The deliberate introduction of non-native species often serves economic interests within particular sectors. The challenge of using non-native species is a classic example of externality, wherein entities who benefit from the presence of these species are not the ones bearing the main environmental or monetary costs—other private companies benefit, but costs are usually borne by society at large [35]. For instance, aquaculture companies generate profits from the main species farmed outside their native range. However, the escape of these species can incur monetary costs, which are mainly attributed to damages associated with fisheries, as well as costs borne by authorities for management (i.e., government agencies and/or official organizations responsible for managing biological invasions). Such monetary costs are likely underestimated or not yet identified [126], as many of the 160 species farmed with production outside their native range, including major aquaculture species, have documented impacts in the literature. For example, in India, major aquaculture species, including carps (silver, bighead, black, and grass carp), tilapias (Nile and Mozambique tilapia), and African catfish, are recognized invasive species with naturalized populations, expanded distributions, and adverse impacts according to a risk assessment [57] but monetary costs have not been reported. Other non-native species such as the Amazonian pacu *Piaractus brachipomus*, which incurs costs associated with their introduction (e.g., competition with native aquaculture carps), have newfound “production services” (benefits) in the invaded aquaculture landscape; thereby replacing traditional aquaculture for increased profitability [117]. Approximately 100,000 t of pacu are produced annually in India, with an average yield of no less than 7000 kg/ha and a current sale price ranging from €1 to €1.34 per kg. This translates into a mean annual business of €100 million for pacu farming (only food production) outside its native range in India alone, excluding the economy activity generated at the hatchery level [117, 127, 128]. Furthermore, pacu has established naturally breeding populations in the wetlands and rivers of the farmed areas too (reviewed in Singh [129]). In this study, we analyzed only eight species used in aquaculture with monetary costs, but this low number is partly due to the conservative approach employed (i.e., only major aquaculture species with highly reliable observed costs). This highlights the importance of assessing the monetary costs of these non-native species to better understand their potential to generate costs in specific contexts.

Our aim in presenting the monetary costs of non-native species used in aquaculture was to highlight a potential socio-economic imbalance where the losses—often underestimated—are challenging to quantify and compare directly with reported revenues. Although this is not a formal cost-benefit analysis, the underlying tension between economic benefits and environmental costs reflects a broader trade-off that warrants attention. It could take longer for costs (both damage and management) to outweigh the benefits, though these are difficult to compare [130]. While the benefits of non-native species production may either be transient or accumulate over time (e.g., in terms of economic development, job creation, or increased protein production), the associated costs to the environment could be irreversible and difficult to express in monetary terms (e.g., loss of native populations, extinction of native species or long-term ecosystem degradation; [131]). Even if benefits accumulate over time, they may not always outweigh long-term costs, particularly given the complexities involved in valuing environmental change. While *InvaCost* provides the most comprehensive and standardized global repository of monetary costs associated with invasive species, it is not exhaustive and may underrepresent costs for underreported taxa, regions, or sectors such as aquaculture [47]. Nonetheless, it offers a critical and transparent foundation for identifying and comparing cost patterns across species and contexts. However, it is not without limitations—for instance, issues of precision and consistency across estimates have been noted [132], highlighting the need for cautious interpretation in sector-specific applications such as aquaculture.

4.3 | Management Implications, Policy and Legislative Challenges

The sustainable use of non-native species in aquaculture is a long-standing issue [24, 100, 133], which is being addressed by international organizations [39, 134]. Recommendations, guidelines, and contingency measures for mitigating aquaculture escapees have been conducted in the past [135], with firmer biosecurity protocols and assessments being crucial to prevent the establishment of introduced populations [17]. For instance, early guidelines from organizations such as the International Council for the Exploration of the Sea addressed the environmental issues associated with escapes of non-native marine species from farming facilities [136]. Similarly, the FAO developed a *Precautionary Approach to Fisheries and Species Introductions* [137] and *Guidelines on assessing and minimizing the possible impacts from the use of non-indigenous species in aquaculture* [135] in which the introduction of non-native species is addressed. Promising protocols, such as the *European Non-native Species in Aquaculture Risk Analysis Scheme (ENSARS)*, have been successfully implemented for the proposed introduction of non-native aquatic species to new areas for aquaculture purposes by assessing the risks of escape and species' life-history traits [16]. An example of ENSARS application is the assessment of the striped catfish (*Pangasianodon hypophthalmus*) in Türkiye, where its farming was recently approved despite previous reports of escapees. The risk assessment identified potential ecological concerns, particularly related to disease transmission and escape risk, leading to recommendations for enhanced biosecurity and monitoring [138]. Similarly, ENSARS was applied in China to evaluate the invasion risk of largemouth bass (*Micropterus*

nigricans), a widely introduced species for sport fishing and aquaculture. The assessment classified the species as a medium-risk invader, highlighting concerns over its expansion into natural water bodies and its potential ecological impacts [139]. They are particularly vital in low- and middle-income countries, where food security is an issue and the risks of escapes can be more pronounced with often a lack of conservation policies [140]. More recently, Manfrini et al. [82] proposed a pre-risk assessment framework based on two key criteria: (1) whether the species is considered invasive (has an invasion history), and (2) whether the species is farmed outside its native range. This classification system categorizes species into four risk levels ranging from the lowest risk (species farmed within their native range with no invasion history) to the highest risk (species farmed outside their native range with a documented invasion history), providing broad management recommendations for each group. Examples of aquaculture species included in the FAO database could be the Chinese razor clam *Sinonovacula constricta* or the Japanese amberjack *Seriola quinqueradiata* in the former category (low risk), whereas the rainbow trout *O. mykiss* or the red swamp crayfish *P. clarkii* fall into the latter (high risk).

Biosecurity policies and specific targeted management strategies that seek to tackle non-native species in the early-stages of an invasion (e.g., interception, limits to and secure keeping; *sensu* Robertson et al. 2020) necessitate careful consideration. Different stakeholders and communities near these facilities often have conflicting interests and varying levels of influence. Thus, negotiation and strong governance are necessary to manage ecological risks with economic and social priorities, ensuring that management actions are both effective and equitable in their implementation. Conversely, policies and legislation have even shifted toward the “protection” of non-native species in aquaculture because they were introduced a long time ago and are economically important, whereby prohibition could now result in a considerable economic impact [141]. Brazil's recent fish farming Federal Decree (10,576/2020) [142], the 2016 Executive Order 13751 in the United States, and the Regulation (EU) No 708/2007 in the European Union are examples. The latter lists a range of recognized invasive, yet economically viable, species such as the rainbow trout, the grass carp, and the Pacific oyster, which can be farmed within the European Union upon the submission of a risk assessment. In fact, these non-native species included in the Annex IV of the Regulation No 708/2007 when used in aquaculture fall outside of the scope of the Regulation (EU) No 1143/2014 on the prevention and management of the introduction and spread of invasive species. This is unsurprising, given the industry's imperative to maintain competitiveness, leading to a diversification strategy that involves the utilization of both native and non-native species.

Potential solutions are not easily attained as conflicts can arise from non-consensual decisions [143]. A “One Health” framework, involving a wide variety of stakeholders, has been recently proposed as a more inclusive solution to the issue of non-native species with negative and positive effects on animal, ecosystem, and human health [144]. While the negative impact mechanisms—such as pathogen transmission (including those affecting humans), competition for food and space, hybridization, habitat alteration, disruption of ecosystem functioning, and

impacts on functional diversity—have already been outlined (cf. Table 2), it is also necessary to acknowledge the positive aspects. These include pathogen dilution in polyculture systems and, most importantly, the role played by non-native species aquaculture in supporting human well-being, livelihoods, food security, and economic sustainability (see references in [144]). This duality underscores the need to move beyond disciplinary linearity and adopt a multidisciplinary approach, which is essential for addressing the complex challenges situated at the interface of biodiversity conservation, sustainable development, and human welfare [144].

In addition, aquaculture farmers can also be incentivized to invest into biosecurity measures that minimize the chances of species escaping to the wild [145]. Public and private incentives could also facilitate a smooth transition from the use of non-native species to their native farmed counterparts in the region if available. Although the domestication of new species is a lengthy and endless process [146], farming native species—particularly those already domesticated—is generally the most environmentally-friendly option, though it is not inherently risk-free. In some cases, it can pose environmental challenges comparable to those of non-native alternatives, such as habitat degradation, genetic homogenization of wild populations, or increased disease transmission, highlighting the need for case-specific assessments when considering such transitions (see translocations of native species [147]). Farmers and policymakers may need time and careful planning to shift toward farming native species, but this approach offers a pathway to greater environmental sustainability. For example, in Asian aquaculture, replacing *P. brachypomus* with the analogous already farmed—but native—Asian fish species *Wallago attu*, could require thorough research and monitoring to ensure both ecological and economic sustainability. The feasibility of such a transition would depend on investment in domestication efforts, market acceptance, and the costs associated with adapting farming practices. Fernández de Alaiza García Madrigal et al. [148] acknowledged the advantages of farming non-native shrimps such as *P. vannamei* but suggested that a transition to native penaeid shrimps would be feasible. Also, environmentally related taxes are a common economic mechanism for internalizing the external costs of environmentally harmful activities (see list of environmental tax bases for European Commission in Table 1 of Eurostat [149]). These environmental taxes are commonly imposed to promote more sustainable practices regarding the overexploitation of wild biological resources (e.g., fished species) [149]. In this context, while not without controversy, policies aligned with the “polluter pays” principle could be explored for aquaculture enterprises farming high-risk non-native species, particularly in cases where escapes or environmental degradation pose significant risks [150]. This approach has been recently considered for other environmental externalities (e.g., emissions) in efforts to enhance the sustainability of aquaculture [151, 152]. Although this remains a debated issue, it may present a potential approach to promoting more environmentally responsible practices.

Certainly, nations have the sovereign right to determine how to balance economic growth and conservation within their territories—often viewing sustainable use of resources as a conservation

mechanism, as supported by organizations such as the Nature Conservancy and the International Union for Conservation of Nature. The trade-off between economic development and unintended consequences across borders (e.g., escapees of non-native species) is a pressing in sustainability agendas, though it often presents a context-dependent challenge [153].

4.4 | Concluding Remarks

While the growth of aquaculture relies on the farming of native species, this study shows how the volume of production (and economic value) of non-native species has gained increasing relevance, with a higher annual growth rate in recent years. For example, in 2022, non-native species accounted for nearly 40% of total global aquaculture production, with over 100 species being farmed outside their native ranges. In crustaceans and algae, non-native production has even exceeded that of native ones. The increasing number and volume of non-native species in global aquaculture has been recognized by international organizations such as FAO and ICES. However, in past decades, risk assessments focused mostly on disease transmission and the alteration of genetic resources [136, 137], while the broader ecological impacts of non-native species themselves have received comparatively less attention [106, 154]. Our study highlights the risks and impacts—also for the most widely farmed aquaculture species—associated with the translocation and escape of non-native aquaculture species, acknowledging their non-negligible socio-economic impacts.

Aquaculture can boost local economies, especially in low- and middle-income countries where most of the production occurs, but the introduction of non-native species entails considerable risks that must be addressed through biosecurity policies to safeguard biodiversity, minimizing damage to ecosystems and local livelihoods. Key measures include the effective confinement of species through improved technology, incentives for farmers to avoid escapes, or more environmentally protective policies. A major challenge for the future lies in the domestication of new native species, as well as in the promotion of native species already farmed where viable market alternatives exist [155]. However, these objectives face significant practical challenges in a globalized market for a rapidly expanding industry, which demands cross-disciplinary collaboration and consensus-driven decision-making among stakeholders [144]. These measures would contribute to reducing environmental risks and long-term economic costs associated with non-native species, while also recognizing their positive contributions to aquaculture production, ecosystem services, and socio-economic development.

Author Contributions

Francisco J. Oficialdegui, Ross N. Cuthbert, Phillip J. Haubrock, Antonín Kouba, Melina Kourantidou: conceptualization. **Francisco J. Oficialdegui, Ismael Soto, Ali Serhan Tarkan:** data curation. **Francisco J. Oficialdegui, Ismael Soto, Melina Kourantidou:** formal analysis. **Francisco J. Oficialdegui, Ismael Soto:** visualization. **Francisco J. Oficialdegui:** writing – original draft. **Francisco J. Oficialdegui, Ross N. Cuthbert, Antonín Kouba, Ali Serhan Tarkan, Paride Balzani, Phillip J. Haubrock, Melina Kourantidou, Eléna Manfrini, Irmak Kurtul, Rafael L. Macêdo, Camille L. Musseau, Koushik Roy, Ismael Soto:** writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GitHub at <https://github.com/IsmaSA/Aquaculture>.

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Supporting Information

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