A global assessment of species diversification in aquaculture

Junning Cai,*[1] Hing Ling Chan,[2] Xue Yan[3] and PingSun Leung[4]

*Corresponding author

1. Fisheries and Aquaculture Division, Food and Agriculture Organization of the United Nations (FAO). Viale delle Terme di Caracalla, 00153 Rome, Italy. junning.cai@fao.org
2. Pacific Islands Fisheries Science Center, NOAA - National Oceanic & Atmospheric Administration. Honolulu, the United States of America. hingling.chan@noaa.gov
3. Chinese Academy of Fishery Sciences (CAFS). Beijing, China. yanx@cafs.ac.cn
4. University of Hawai'i at Manoa. Honolulu, the United States of America. psleung@hawaii.edu

Abstract

Aquaculture is a diverse food production system, and a high species diversity in aquaculture can make the global food system more resilient. Species diversification could facilitate aquaculture growth through multiple mechanisms and increase the sector's resilience and long-term sustainability. Facing increasing challenges from climate change, disease outbreaks, market fluctuations, and other disturbances, species diversification has become a widely recognized and endorsed development strategy in the policy and scientific communities for the growth and resilience of the aquaculture sector. However, many attempts to establish new species have yielded little long-term success, and the private sector often concentrates efforts on the most advantageous species for rapid growth. This paper presents a comprehensive assessment of aquaculture species diversification at the global, regional (more than 30 country groups), and national (nearly 200 countries) levels, covering the period 1950 to 2020 with a focus on 1990 to 2020. The assessment employs the concept of "effective number of species" as a measure of diversity and uses two sub-indicators to assess within-group versus between-group diversity. The indicator system reveals detailed patterns of species diversity and uncovers different driving forces of species diversification. Additionally, the study maps the status and trends of species diversity to offer a refined perspective on species diversity profiles and diversification patterns. The findings reveal that beneath high species diversity in world aquaculture lies generally low diversity at the national level; nearly half of national aquaculture has no within-group or between-group diversity. Furthermore, species diversification has been losing momentum in recent decades, and concentration has become a more prominent development pathway, with a tendency to drive aquaculture towards a low-diversity system similar to terrestrial farming. Public interventions are crucial to promote species diversification in aquaculture for the sector's resilience and long-term sustainability. It is important to not only reduce the cost of species diversification for the private sector but also to dedicate more public efforts towards increasing its benefits and viability. While diverse diversification patterns among national aquaculture indicate no one-style-fits-all species diversification pathway, a country may draw guidance from others' experiences, especially since countries with similar species diversity profiles or diversification patterns tend to cluster geographically. Evidence-based policymaking and sector management regarding species diversification entail collaborative efforts among policymakers, scientists, and the aquaculture community to expand and refine assessment frameworks, improve data availability and quality, and efficiently utilize information, knowledge, and insights generated by these assessments to inform decision making at various levels.

Keyword: aquaculture; diversity; species diversification; effective number of species; within-group diversity; between-group diversity

1. Introduction

As a rapidly expanding sector in the food industry, aquaculture stands out for its diverse range of species compared to terrestrial farming, which could enhance the resilience of the global food system (Troell et al., 2014; FAO, 2019a). Since 1950, more than 600 aquatic species have been farmed in global aquaculture, with more than 400 species still being actively cultivated. Among these, ten species account for approximately half of the total production (FAO, 2019b). In contrast, two thirds of global crop production come from 10 species (out of less than 200 plant species with significant production globally), while only ~40 terrestrial animal species are cultivated for food such as meat, milk, and eggs, and production is concentrated in only a handful, though diversity comes from numerous breeds and varieties (FAO, 2019c).

High species diversity could also be advantageous for the aquaculture sector per se. Technically, species diversification can increase farming efficiency through polyculturing multiple species in the same farming system, cultivating the most suitable species in different farming environments, or rotating different species according to seasonal variations (Ravisankar et al., 2005; Thomas et al., 2021; Newton et al., 2021). Economically, species diversification can help the sector overcome market satiation and broaden its market base (Abellán and Basurco, 1999; Liao, 2000). Finally yet perhaps most importantly, species diversification can enhance aquaculture's resilience against climate change, disease outbreaks, market fluctuations, and other shocks that pose challenges to the sector's long-term sustainability (Wilson and Archer, 2010; Gephart et al., 2017; Metian et al., 2020). Therefore, species diversification is widely endorsed as a prominent strategy for sustainable aquaculture development by both policy and scientific communities (Abellán and Basurco, 1999; CIHEAM, 2000; Naylor and Burke, 2005; Brummett, 2007; Martínez-Cordero, 2007; Megahed and Mesalhy, 2009; Le Francois et al., 2010; FAO, 2011; Schmidt et al., 2011; Guy et al., 2014; Troell et al., 2014; Harvey et al., 2017; Roy, 2019; Boyd et al., 2020; Metian, et al., 2020; García-Márquez et al., 2021; Thomas et al., 2021; Oboh, 2022).

However, although aquaculture is one of the most diverse food production systems at the global level, species diversity is generally low in national aquaculture (Metian et al., 2020; Cai et al., 2022). Many attempts to promote new species have yielded little long-term success (Metian et al., 2020; Harvey et al., 2017; Teletchea and Fontaine, 2014; Muñoz-Lechuga et al., 2018). Failure to establish a novel species could be attributed to various hindrances, such as technical difficulties (Fernández-Polanco and Bjorndal, 2017), limited markets (Basurco and Abellán, 1999), or institutional constraints (Barrington et al., 2009). Yet fundamentally, when aquaculture species that appear promising individually compete for limited resources and markets, market mechanisms, such as economies of scale and maximization of risk-adjusted return, tend to make aquaculture production concentrated towards a few winner species (Cai et al., 2022).

Should a country pursue species diversification or adopt a "concentration" pathway to focus on a few most productive species for high growth and exploit their intra-specific potential for diversity? The answer tends to vary for different countries or for the same country at different stages of aquaculture development, as both pathways have pros and cons (Bilio, 2008; Teletchea and Fontaine, 2014). Information, knowledge, and understanding of past experiences of species diversification is crucial for guiding aquaculture development, especially for countries with a less developed aquaculture sector.

Here we conduct a comprehensive, in-depth assessment of aquaculture species diversification at the global, regional (30+ country groups), and national (~200 countries) levels. Our analysis covers seven decades (1950–2020), with an emphasis on the past three decades (1990–2020). Similar to Cai et al. (2022), we use the "effective number of species" as a measure of "true" diversity (Hill, 1973; Jost, 2006), which is more intuitive than the Shannon (entropy) index used by Metian et al. (2020). While Metian et al. (2020) quantified the diversity of aquaculture species at the national level, we measure it at the national, regional, and global levels. This helps identify inconsistent species diversification patterns at different geographic scales. We further decompose the effective number of species into two sub-indicators: one captures diversity among species groups (i.e. between-group diversity) and the other measures species diversity within species groups (i.e. within-group diversity). The decomposition reveals detailed patterns of species diversity and uncovers different driving forces of species diversification. Similar to Metian et al. (2020), we map species diversity to examine its geographic patterns. Yet the scope of our mapping is broader, including both a comparison of species diversity across countries and a categorization of species diversification trends.

We highlight and discuss key findings in the main text. Some results may be part of conventional wisdom, yet most are less apparent or underappreciated. More comprehensive results are documented in supplementary materials, which can be used to facilitate evidence-based policymaking and sector management in aquaculture at the global, regional, and national levels. We conclude the paper with discussion of lessons learned, future prospects, and way forward, including potential areas for further study.

2. Data and methods

2.1 Data

We use aquaculture production statistics from the Food and Agriculture Organization of the United Nations (FAO) Global Aquaculture Production Statistics 1950–2020 (FAO, 2022). Reporting entities in the database are classified as countries, including non-sovereign territories. In order to facilitate analysis, we combine the statistics of mainland Tanzania and Zanzibar into the United Republic of Tanzania. For all other reporting entities, we use the classifications adopted in the FAO database. In addition to assessments at the country and global levels, we also examine species diversity and diversification patterns in 32 countries groups. For narrative convenience, we refer to aquaculture in these 32 groups as "regional aquaculture" (Table 1).

[Insert Table 1 here]

All ASFIS (Aquatic Sciences and Fisheries Information System) species items recorded in the database are included in our analysis. These species items could refer to individual species, hybrids or "nei" (not elsewhere included) species items that are groups of related species (e.g. genera) when identification to species was not recorded in the database (FAO, 2019b, 2020; Metian et al., 2020). According to the International Standard Statistical Classification of Aquatic Animals and Plants (ISSCAAP), the ASFIS species items fall into eight divisions: (i) marine fishes, (ii) freshwater fishes, (iii) diadromous fishes, (iv) crustaceans, (v) molluscs, (vi) aquatic plants, (vii) miscellaneous aquatic animals, and (viii) miscellaneous aquatic animal products. We group the first three divisions into "finfish" and the last two into "miscellaneous aquatic animals and animal products" (abbreviated as "MAA"), and we rename "aquatic plants" into "algae" to more accurately reflect its species composition. As a result, we have five species groups (finfish, crustaceans, molluscs, MAA, and algae) for the examination of diversity within each group and between them. For narrative convenience, we will refer to the ASFIS species items simply as "species" throughout the rest of this article.

2.2 Measuring species diversity

As a unifying notation of commonly used measures of diversity (Hill, 1973), a general formula for the effective number of species is

$$D_q = \left(\sum_{i=1}^{n} s_i^q\right)^{\frac{1}{1-q}} \tag{1}$$

where *n* represents the total number of species; s_i denotes the share of species *i* in the production of all species; and q indicates the order of diversity. When $q = 0$, $D_0 = n$ is equal to the total number of species, which measures solely richness and gives zero weight to evenness. As q increases, more weight is given to evenness in the measure of diversity. While efforts in biodiversity conservation may focus on species richness, evenness is a crucial dimension of species diversity for sustainable aquaculture development (Harvey et al., 2017).

Like Cai et al. (2022), we measure species diversity in aquaculture using the effective number of species at $q = 1$, i.e.

$$\mathrm{ENS} \equiv D_1 = e^{-\sum_{i=1}^{n} s_i \ln(s_i)}, \tag{2}$$

where the summation term is the Shannon index：

$$\mathrm{H} \equiv -\sum_{i=1}^{n} s_i \ln(s_i) = \ln(\mathrm{ENS}). \tag{3}$$

The Shannon index is a well-known diversity index, and it was used by Metian et al. (2020) to map species diversity in global aquaculture. ENS is less widely used, but it is considered a more intuitive measure of true diversity (Hill, 1973; Jost, 2006). The scale of ENS ranges from 1 to the total number of species (n). When production is evenly distributed among all species, the ENS value is equal to n. The more uneven the distribution of production is, the closer the ENS value will be to 1.

ENS in equation (2) can be partitioned into two components:

$$\mathrm{ENS} = \mathrm{WGENS} \times \mathrm{ENSG}. \quad (4)$$

The first component (WGENS), which is a measure of within-group diversity, is calculated as a weighted geometric mean of ENS within different species groups (denoted as ENS_j). As discussed in section 2.1, here we consider five species groups (finfish, crustaceans, molluscs, MAA, and algae). The weight assigned to each group is based on its share of total production (denoted as s_j), i.e.

$$\mathrm{WGENS} = \prod_j (\mathrm{ENS}_j)^{s_j}. \quad (5)$$

The second component (ENSG) represents the effective number of species groups, i.e.

$$\mathrm{ENSG} = e^{\sum_j -s_j \ln(s_j)}, \quad (6)$$

which measures the evenness of production distribution among the five species groups (i.e. between-group diversity). WGENS, ENSG, and ENS are equivalent to three diversity measures (alpha, beta, and gamma diversity, respectively) that have been used to assess biological diversity in an ecosystem (Jost, 2007; Tuomisto, 2010). While ENS has been used in Cai et al. (2022) to facilitate benchmarking species diversification in aquaculture, this is the first study, to the best of our knowledge, to apply within-group diversity (WGENS) and between-group diversity (ENSG) as sub-indicators of species diversity in aquaculture.

According to equations (3)–(6), the Shannon index can also be partitioned into

$$\mathrm{H} = \mathrm{H}_{\mathrm{within}} + \mathrm{H}_{\mathrm{between}}, \quad (7)$$

where $\mathrm{H}_{\mathrm{within}} = \sum_j s_j \mathrm{H}_j$ and $\mathrm{H}_{\mathrm{between}} = \sum_j -s_j \ln(s_j)$ are alternative measures of within-group and between-group diversity.

While ENS and its two components (WGENS and ENSG) are more intuitive diversity measures – see numerical examples at the beginning of section 3.1, the multiplicative partition of ENS in equation (4) makes it inconvenient to calculate the shares of WGENS and ENSG in ENS. Therefore, we used the partition of the Shannon index defined in equation (7) to calculate the shares of within-group diversity and between-group diversity in overall species diversity: $\mathrm{H_{within}}/\mathrm{H}$ measures the within-group share; $\mathrm{H_{between}}/\mathrm{H}$ measures the between-group share; and the two shares sum up to 100%. The within-group share can be further decomposed into the share of each species group in overall diversity (i.e. $s_j\mathrm{H}_j/\mathrm{H}$).

2.3 Categorizing changes in species diversity

Table 2 presents six scenarios of ENS changes and six patterns of ENS trends. The six scenarios links a change in ENS to changes in its within-group and between-group components, while the six patterns categorize the trends of species diversification during three decades (1990–2020) or two decades (2000 – 2020).

[Insert Table 2 here]

While originally used to measure biological diversity, the concept of "effective number" has been applied to measure diversity in other areas, such as the effective number of parties in a political system (Laakso and Taagepera, 1979) and the effective number of firms in an economy (Ordover et al., 1982). Similarly, we use the "effective number of diversification patterns" (ENDP) to measure the diversity of the six patterns among countries (i.e. the evenness of the distribution of these six patterns among all countries worldwide or in the country group). The formula is

$$\mathrm{ENDP} = e^{-\sum_{i=1}^{6} p_i \ln(p_i)}, \tag{8}$$

where $p_i = n_i / \sum n_i$ measures the prevalence of diversification pattern *i* among countries, as n_i is the number of countries with pattern *i*. Similarly, equation (8) can be used to calculate the ENDP among regional aquaculture.

3. Results

3.1 Species diversification in world aquaculture

In 2020, a total of 448 species contributed the world aquaculture production of 123 million tonnes. Yet the production was concentrated on a much lower number of species – 46 species contributed 90% of the production. The diversity of the species composition can be measured by the effective number of species (ENS) of 47.5 (Figure 1a).

While the 123 million tonnes of world aquaculture production spread across five species groups, finfish (46.9%), algae (28.6%), and molluscs (14.5%) contributed 90% of the production. The rest primarily came from crustaceans (9.2%), with a small amount of miscellaneous aquatic animals and animal products (MAA; 0.9%). As a measure of between-group diversity, the 3.5 effective number of species groups (ENSG) reflects this imbalanced taxonomic composition (Figure 1b).

In 2020, finfish accounted for nearly half of world aquaculture production, its species diversity (30.5 ENS) was also much higher than the other four species groups (Figure 1c–1g). The production of algae was nearly twice of molluscs, yet its species diversity (6.1 ENS) was lower than that of molluscs (9.4 ENS). The species diversity in crustaceans (4.9 ENS) was the lowest, whereas the 6.3 ENS of MAA, the smallest species group notwithstanding, was higher than algae and crustaceans. As a measure of within-group diversity, the 13.56 within-group ENS (WGENS) measures the average species diversity within these five species groups (Figure 1b).

In summary, world aquaculture production in 2020 (123 million tonnes) comprised 448 species, with a species diversity of 47.5 ENS. Between-group diversity (3.5 ENSG) accounted for 32% of the overall species diversity, whereas the rest 68% came from within-group diversity (13.56 WGENS), including 41.5% from (species diversity within) finfish, 13.4% from algae, 8.4% from molluscs, 3.8% from crustaceans, and 0.4% from MAA.

[Insert Figure 1 (colored) here]

Historically, species diversity in world aquaculture more than doubled in four decades between 1950 and 1990 through a "straight-up" diversification trend, with increased ENS in all eight mid-term (5-year) intervals during the period (Figure 1a). Species diversity increased further during the recent three decades (1990–2020), yet the diversification trend was less monotonic. Two ENS declines have resulted in an "inverted N-shape (И)" ENS trend that declined in the first decade (1990–2000) and the last decade

(2010–2020), whereas increased in the middle decade (2000–2010). The first decline occurred in the first half of the 1990s, with a partial recovery in the second half. A similar pattern occurred in the 2010s (Figure 1a).

The future will tell whether the second decline (during 2010–2020) was a temporary dip similar to the first one (during 1990–2000); or it may be the beginning of a longer term downward ENS trend in world aquaculture similar to the pattern for the rest of the world, excluding China (i.e. the ROW aquaculture) since 2000 (Supplementary Figure 1a). However, the downward ENS trend in world aquaculture in the third decade (2010–2020) differed from the downward trend in the first decade (1990–2000) in that the former was consistent with regional and national situations, whereas the latter was not.

3.2 Inconsistent species diversification at different geographic scales

In the first decade (1990–2000), species diversity declined in world aquaculture yet increased in most (22 out of 32) regional aquaculture (Table 1; column X) as well as nearly two thirds of national aquaculture that accounted for nearly 90% of world production (Figure 2b). The inconsistency could seemingly be explained by the fact that species diversification in world aquaculture mimicked that of Asia, the largest aquaculture region that contributed more than 90% of world production (Table 1, column III). A deeper look, however, reveals another inconsistency: declined species diversity in Asia versus increased diversity in all five Asian sub-regions (Table 1; column X). A similar inconsistency occurred between 1990 and 2020 when species diversity declined in Africa (as well as sub-Saharan Africa) while increased in all five African sub-regions (Table 1; column IX).

[Insert Figure 2 (colored) here]

Inconsistencies could occur not only on diversification trends but also on the status of species diversity. As China has been the largest national aquaculture with the most diverse species composition, one may expect that species diversity in world aquaculture should always be higher than diversity in the ROW aquaculture. The opposite occurred, nevertheless, in 1990 and 2000 (Table 1; columns IV and V). Such inconsistencies indicate that species diversification in world or regional aquaculture may not necessarily reflect situations in national aquaculture. After all, if every country cultivated a unique species at the same amount, world aquaculture would have a high species diversity even with no species diversity at the national level.

3.3 Decelerating species diversification

During the three decades between 1990 and 2020, species diversity increased in most (22 out of 32) regional aquaculture. This, however, reflects the situation in the first and second decades (Table 1; Supplementary Table 1a), whereas species diversity declined in most (19) regional aquaculture in the third decade (Table 1; Supplementary Table 1b). Such decelerating diversification process also occurred in national aquaculture.

Between 1990 and 2020, species diversity increased in nearly three quarters of national aquaculture that accounted for more than 80% of world production (Figure 2a). The situations in the first decade (Figure 2b) and the second decade (Figure 2c) were consistent with the overall trend. Yet species diversity declined in a higher proportion of national aquaculture in the second decade compared with the first one (37% versus 34.6%), and the production share of countries with a declined species diversity in the second decade (23.7%; Figure 2c) nearly doubled the level in the first decade (11.9%; Figure 2b). Indeed, the 23.7% would be higher than the remaining 11.1% when China's production share (65%) is excluded from the 76.1% production share of national aquaculture with an increased diversity in the second decade (Figure 2c).

The diversification trend appeared to reach a turning point in the third decade when the prevalence of national aquaculture with an increased diversity declined to exactly 50%, and they contributed less than 20% of world production (Figure 2d). The large decline in the production share of more diversified aquaculture was primarily due to the shift of China's aquaculture from diversification trends in the first and second decades to a concentration trend in the third decade. However, even when China' production share (58%) is excluded from the 81% production share of national aquaculture with a declined diversity in the third decade, the remaining 23% would still be higher than the 18.9% production share of those with an increased diversity (Figure 2d).

3.4 Diverse species diversification patterns

Among 196 national aquaculture in 2020, we identify six patterns of ENS trends (Table 2) for 161 countries (Figure 2e). Most of the 161 ENS trends were 30-year trends between 1990 and 2020, with a few 20-year trends between 2000 and 2020 in case of no aquaculture production in 1990 (Figure 2e). Thirty-five relatively young national aquaculture, which accounted for less than 0.1% of world production in 2020, had no such 30- or 20-year trends, resulting in their exclusion from the six diversification patterns.

As species diversity increased in 89 countries (nearly two thirds of national aquaculture) in the first decade (Figure 2b) while declined in 91 countries (exactly half) in the third decade (Figure 2d), an inverted U-shape trend emerged as the prevailing pattern in national aquaculture during 1990–2020 (Figure 2e). This most common pattern nevertheless occurred in only 59 countries (around one third). These 59 countries spread across Africa (17), Asia (17), Europe (12), the Americas (10), and Oceania (3), and they contributed nearly 80% of world production in 2020, including six of the top 10 largest national aquaculture (Figure 2e; Supplementary Table 2a).

The inverted N-shape pattern is similar to the inverted U-shape pattern in that both are associated with a decline in diversity in the third decade. While characterizing the ENS trend in world aquaculture, the inverted N-shape pattern occurred in only 18 countries that contributed to just half a percent of world production (Figure 2e; Supplementary Table 2b). This further exemplifies the inconsistency discussed in section 3.2. Straight-down, which is another pattern with a declined diversity in the third decade, was the least common pattern that occurred in only eight national aquaculture (0.2% of world production) (Figure 2e; Supplementary Table 2c). In contrast, straight-up ENS trends occurred in 31 countries that accounted for 6.7% of world production; most of which are in Europe (14) or Asia (10) (Figure 2e; Supplementary Table 2d). U-shape and N-shape are another two patterns with increased diversity in the third decade, which occurred in 28 countries (4.8% of world production; Supplementary Table 2e) and 17 countries (8.5%; Supplementary Table 2f), respectively.

Based on equation (8), we calculate the effective number of diversification patterns (ENDP) to measure the diversity of diversification patterns, i.e. the evenness of the distribution of the six patterns among countries. The results indicate diverse diversification patterns among national aquaculture: 5.06 ENDP for the 161 national aquaculture worldwide, ~4–5 ENDP for national aquaculture in each of the five regions (from 4.34 ENDP for national aquaculture in Oceania to 5.03 ENDP for national aquaculture in the Americas), 5.21 ENDP for landlocked national aquaculture, and 4.51 ENDP for island national aquaculture (Supplementary Figure 2).

However, there were clusters of national aquaculture with the same or similar patterns (Figure 2e), such as (i) a cluster of (national aquaculture with) straight-up ENS trends in East-Central Europe; (ii) two clusters of U-shape or N-shape trends: one in South-Central Asia; the other stretching from the United States of America southward through Central America (except Nicaragua) to three of the four members of the Andean Community (Bolivia, Colombia and Peru, except Ecuador) as well as two associated members (Paraguay and Uruguay); and (iii) several clusters of inverted U-shape or inverted N-shape trends in (a) the Mediterranean Basin, (b) Western and Southern Africa, (c) the south and east parts of South America, and (d) three countries in Maritime Southeast Asia (Indonesia, Malaysia and Brunei Darussalam) plus Australia and New Zealand plus four nearby Pacific SIDS (Papua New Guinea, New Caledonia, Guam, and Palau).

The distribution of the six diversification patterns among the 32 regional aquaculture was similar to the situation in the 161 national aquaculture, i.e. inverted U-shape being the most common pattern (occurred in 14 regional aquaculture), followed by straight-up (6), U-shape (5), inverted N-shape (4), N-shape (2), and straight-down in only one regional aquaculture (Supplementary Table 3). The diversity of the six patterns among the 32 regional aquaculture was 4.5 ENDP.

3.5 Within-group versus between-group diversity

Within-group diversity contributed approximately 60 to 70% of species diversity in world aquaculture during 1950–2020. This share was generally on an upward trend, increasing from 63.1% in 1960 to 67.5% in 2020 (Supplementary Figure 3). For the 32 regional aquaculture, the average within-group share in species diversity during 1990–2020 varied from 23% in Pacific Islands to 100% in Central Asia, yet the share was above 50% for most regional aquaculture with a few exceptions (Supplementary Table 4).

The pattern of within-group share in national aquaculture has remained relatively unchanged over 1990, 2000, 2010 and 2020 (Supplementary Figure 4). In 2020, the within-group share in national aquaculture varied from zero to 100%, yet it was more than 50% in 126 of all 196 national aquaculture (Supplementary Figure 4d). These 126 countries (illustrated with different shades of blue in Figure 3d) accounted for more than 90% of world production.

[Insert Figure 3 (colored) here]

As highlighted in section 3.1, finfish diversity was the primary source that contributed more than 40% of species diversity in world aquaculture in 2020. For national aquaculture, finfish was the primary source of species diversity in 114 countries. Among all finfish farming countries, the median finfish share in species diversity was nearly 80% (Supplementary Figure 5b).

Apparently from Figure 1a and 1b, species diversification in world aquaculture mimicked the trend of within-group diversity. Similarly, within-group diversity has been the main driving force of species diversification in regional aquaculture (Table 1; Supplementary Tables 1a and 1b) and national aquaculture (Figure 2; Supplementary Figure 6). During 1990–2020, ENS increased in 109 national aquaculture; 93 of which had a higher WGENS (Figure 2a: U1 and U2), whereas 33 of 40 countries with a declined ENS had a lower WGENS (Figure 2a: D1 and D2). Similarly, within-group diversity was the primary driving force of species diversification in all three sub-decades (Figure 2b–2d).

In 2020, within-group diversity was the sole source of species diversity (ENSG =1; the within-group share = 100%) in 67 national aquaculture; nearly all (65) of them farmed only finfish (Supplementary Table 5). Representing more than one third of all 196 national aquaculture notwithstanding, these 67 countries contributed only half a percent of world production. They were mostly clustered in Africa, Central Asia, and Eastern and Central Europe (Figure 3d, highlighted in dark blue). Nearly half (29) of them are landlocked countries, including 24 Landlocked Developing Countries (LLDCs). Among 37 landlocked countries (Supplementary Table 6), the within-group share in 2020 was equal to 100% in 29 countries, above 90% in 34 countries, and above 60% in nearly all of them (except one country with no species diversity, i.e. ENS = 1).

As highlighted in section 3.1, between-group diversity accounted for around one third of species diversity in world aquaculture in 2020, which was lower than the contribution of finfish yet higher than each of the other four species groups. In 2020, between-group diversity was the primary source (compared with each of the five species groups) of species diversity in 61 countries (~30% of all 196 national aquaculture). Among them, between-group diversity was greater than within-group diversity (ENSG > WGENS; the within-group share < 50%) in 55 countries that contributed 7.8% of world production (Supplementary Table 7). Most of these 55 countries, highlighted in warm colors in Figure 3d, were located in the Americas (24 countries; 57% of national aquaculture in the region) and Oceania (10 countries; 53%). The remaining 21 countries were spread across the other three regions, with eight in Asia, seven in Europe, and six in Africa. More than half (28) of the 55 countries were island economies, including 22 Small Island Developing States (SIDS). These 28 island economies represented nearly half of 60 island aquaculture in 2020 (Supplementary Table 8).

During 1990–2020 and the three sub-decades, between-group diversity remained unchanged in ~30–40% of national aquaculture where only one species group was farmed, whereas it increased in most of the other countries (Supplementary Figure 7). During 1990–2020, between-group and within-group diversity moved in different directions in nearly 100 national aquaculture that accounted for nearly 20% of world production (Figure 2a: U2, U3, D2, and D3). Among them, ENSG dictated the direction of ENS trends in only 23 countries (7.7% of world production; Figure 2a: U3 and D3), including (i) 16 countries where increased between-group diversity drove up the overall species diversity in spite of declined or unchanged within-group diversity (6%; Figure 2a: U3; Supplementary Table 9a) and (ii) seven countries where overall species diversity declined because of between-group diversity despite increased or unchanged within-group diversity (1.7%; Figure 2a: D3; Supplementary Table 9b). The pattern of between-group diversity dictating the direction of species diversification in a small portion of national aquaculture occurred in all three sub-decades (Figure 2b–2d).

3.6 Generally low (often no) diversity in national aquaculture

In 2020, ENS varied from 1 to 28 among 196 national aquaculture, yet half of them were less than 2.5 and three fourths less than 4 (Figure 3a; Supplementary Figure 8). The median WGENS was below 2 (Figure 3b), whereas the median ENSG was slightly above 1 (Figure 3c). Nearly half (94) of the 196 countries had no within-group or between-group diversity, including 82 countries (42% of all 196 national aquaculture) with no between-group diversity (ENSG = 1), 27 countries (14%) with no within-group diversity (WGENS = 1), and among them, 15 countries (8%) with neither (i.e. no species diversity; WGENS = ENSG = ENS = 1). No species diversity was a more common phenomenon within the five species groups (Supplementary Table 10). In 2020, finfish was the only species group with median ENS (among all countries that farmed finfish) above 2; molluscs was another species group (besides finfish) with median ENS greater than 1; and median ENS was equal to 1 for all the other three species groups (Supplementary Figure 9).

In 2020, countries with relatively low (below-median) ENS contributed less than 5% of world production, whereas a quarter of countries with the highest ENS contributed more than 90% (Figure 3a). Thirty-three countries had extraordinarily high diversity in terms of at least one of the eight diversity measures (ENS, WGENS, ENSG and ENS in each of the five species groups). Most (21) of these countries belonged to the top 50 national aquaculture (Supplementary Table 11), and China (the largest national aquaculture with extraordinarily high diversity in terms of all eight measures) contributed nearly 60% of world production.

There were large national aquaculture with low species diversity, such as export-oriented aquaculture in Norway (1.5 million tonnes of production with 1.31 ENS) and Ecuador (0.8 million tonnes with 1.11 ENS). A small national aquaculture could nevertheless have a high species diversity. For instance, Singapore, a high-income city state with strong consumer preferences for a variety of aquatic foods, had a small aquaculture sector (less than 5 000 tonnes of production in 2020) with the third highest species diversity among all national aquaculture (Supplementary Table 11).

3.7 Correlations between production and diversity

It has been recognized that larger aquaculture production tend to be associated with higher species diversity (Metian et al., 2020). Cai et al. (2022) found a positive correlation (r = ~0.6) between aquaculture production and species diversity based on data from over 200 countries for three decades (over 5000 observations). They used this relationship to set benchmarks for species diversification.

The positive correlation between aquaculture production and species diversity raises the question of whether species composition would tend to become more diverse as aquaculture production grows bigger (i.e. species diversification as a natural course of aquaculture expansion). A closer examination that distinguishes between cross-sectional correlation (i.e., correlation between production and diversity for a number of countries in a specific time) and temporal correlation (i.e., correlation between production and diversity for a specific country over time) will shed light on this question.

In 2020, a strong, positive correlation between aquaculture production and ENS was found among all 196 countries ($r = 0.65$). This positive cross-sectional correlation was consistent across the years 1990–2020, with a median value of $r = 0.64$ (Supplementary Table 12). In addition to the positive correlation between aquaculture production and overall species diversity, cross-sectional correlations between production and the two components of ENS (WGENS and ENSG) were also found to be positive, albeit weaker (median $r = 0.24$ and 0.34, respectively). So were the correlations between production and ENS in each of the five species groups, with median r varied from 0.38 for finfish to 0.84 for MAA (Supplementary Table 12). These positive cross-sectional correlations indicate that countries with a relatively large aquaculture production generally have a higher species diversity than those with a relatively small production.

Temporal correlation between a country's production and diversity over time is less straightforward. During 1990–2020, temporal correlation between production and ENS varied between –1 and 0.99 in all countries, and it was positive in 55% of the countries (108 out of 196) yet negative in 45% (88 out of 196), with the median $r = 0.1$. In 73 countries (37%), the temporal correlation was significantly positive (p-value < 0.05), which indicates that these countries' aquaculture production and ENS generally moved in the same direction during the period. The temporal correlation was significantly negative in 49 countries (25%) where aquaculture production and ENS generally moved in different directions. In the rest 74 countries (38%), the temporal correlation was not statistically significant (Supplementary Table 13). While these findings may be deemed evidence of generally positive, albeit weak, temporal correlation between production and ENS in national aquaculture during 1990–2020, such a generally positive relationship was less obvious in the first two decades (median r around –0.03 in both periods) and became non-existent in the last decade (Supplementary Table 13). During the third decade (2010–2020), the temporal correlation between production and ENS was negative in more than half (101) of all 189 national aquaculture with median $r = -0.08$. The correlation was significantly positive in 46 countries (less than 5% of world production) while significantly negative in 49 countries (over 20%) (Supplementary Figure 10; Supplementary Table 14). Similarly, there was a lack of generally positive temporal correlations between production and the other seven diversity measures (Supplementary Table 13). These findings indicate that while countries with a larger aquaculture production tend to have a higher species diversity than those with a lower production, there is no obvious tendency that a country's species diversity would move in the same direction with its production. In other words, species diversification has no tendency to be a natural course of aquaculture expansion.

3.8 Geo-clustering of countries with similar species diversity

National aquaculture within close geographic proximity tend to have similar species diversity profiles. We have highlighted clusters of countries with similar diversification patterns in section 3.4 and those with similar diversity profiles in section 3.5. Here we systematically examine geo-clustering patterns by grouping countries into four categories according to their within-group and between-group diversity (Figure 3e).

In 2020, 48 countries (illustrated in blue in Figure 3e) had a relatively high (above-median) within-group diversity as well as a relatively high between-group diversity; all of them also had relatively high overall diversity (Supplementary Table 15a). This "both > median" category primarily includes 19 countries in Asia (primarily Eastern and South-eastern Asia) and 11 countries in Europe (primarily

Western and Southern Europe). The rest spread in Africa (8 countries), the Americas (7), and Oceania (3). Representing less than a quarter of all 196 national aquaculture notwithstanding, “both > median” appears to be the most prominent pattern in the map (Figure 3e) because it includes nine of the top 10 countries with the largest land area, except Kazakhstan (Supplementary Table 16). This may reflect that abundant, diverse natural resources, such as indigenous species and suitable farm sites, tend to be conducive to high species diversity. Indeed, while Kazakhstan, like most landlocked countries, farmed only finfish hence had no between-group diversity, its overall species diversity was higher than three quarter of ~200 national aquaculture because of its extraordinarily high species diversity in finfish aquaculture (Supplementary Table 11). The “both > median” category accounted for more than 90% of world production, including six of the top 10 national aquaculture, 20 of the top 30, and 25 of the top 50 (Supplementary Table 15a).

In contrast, another 48 countries (illustrated in red in Figure 3e) in the category of “both < median” contributed only 1.5% of world production (Supplementary Table 15b). The contribution primarily came from Norway, which was the only top 10 largest national aquaculture with relatively low within-group diversity and between-group diversity; and Ghana was the only other top-50 national aquaculture in this category. A large proportion of the countries in the “both < median” category are located in Africa (21 countries), and the rest spread across the other four regions: six in Asia (primarily Western Asia) and seven each in the Americas (primarily the Caribbean), Europe (primarily Northern Europe) and Oceania (entirely Pacific SIDS).

Fifty countries (illustrated in green in Figure 3e) had a relatively high within-group diversity yet a relatively low between-group diversity; most (36) of them had a relatively high overall diversity (Supplementary Table 15c). This category of “WGENS > median; ENSG ≤ median” primarily includes 16 countries in Asia (mostly landlocked countries in Central, Southern, or Western Asia), 15 countries in Europe (mostly East-Central Europe), and 13 countries in Africa (nearly half of them clustered in Western Africa). Only five countries in the Americas belonged to this category, which nevertheless included the only two landlocked countries in the region (Figure 3e). Indeed, most (24) of the 37 landlocked national aquaculture worldwide, including 19 of the 31 LLDCs, belonged to this category. Landlocked aquaculture's relatively low between-group diversity may primarily reflect their lack of coastal resources (needed for the farming of most algae and molluscs species) as well as their relatively low preferences for aquatic foods (Cai and Leung, 2022). The "WGENS > median; ENSG ≤ median" category accounted for 2.2% of world production, including one top-10 national aquaculture (Egypt), two top-30, and nine top-50 (Supplementary Table 15c).

Another 50 countries (illustrated in purple in Figure 3e) had a relatively high between-group diversity yet a relatively low within-group diversity, with a relatively low overall diversity in most (36) of them (Supplementary Table 15d). This is the exact opposite of the previous category. Nearly half (23) of the 50 countries in this category of "WGENS ≤ median; ENSG > median" are in the Americas. This is nevertheless not obvious in Figure 3e, because these 23 countries include a cluster of 13 Caribbean SIDS indiscernible in the map. Indeed, more than half (28) of the 50 countries in this category are island economies, including 22 SIDS. While island states tend to have a relatively high between-group diversity thanks to long coastlines – algae and molluscs are primarily cultivated in marine areas, a small island aquaculture usually has a low within-group diversity because of small market (constrained by its small population and high transportation costs) and low production scale. Other clusters in the "WGENS ≤ median; ENSG > median" category include (i) 10 countries in Central America, and the east and north coasts of South America; (ii) seven Pacific SIDS in Oceania, (iii) five countries in Northern Europe and (iv) five countries in South and South-eastern Africa (Supplementary 16d; Figure 3e). This category accounted for 5.5% of world production, including two top-10 national aquaculture (the Philippines and Chile), seven top-30, and 13 top-50 (Supplementary Table 15d).

4. Discussion

4.1 Lessons learned

Species diversification may not be consistent at different geographic scales (section 3.2). Hypothetically, if there were 200 countries each cultivating a unique species in equal amounts, the species composition of global aquaculture would be highly diverse (ENS = 200), even with no species diversity (ENS = 1) at the national level. In reality, beneath high species diversity in world aquaculture lies low species diversity in most national aquaculture (section 3.6). Therefore, species diversification should be assessed at various levels (world, regional, sub-regional, national, and sub-national) for evidence-based policymaking and sector management in aquaculture.

Policy and planning for species diversification should take a holistic approach recognizing that species diversity in aquaculture is shaped by many factors, such as resource endowments, climate conditions, farming systems and technologies, consumer preferences, market structure, and institutional arrangements, among others (Guy et al., 2014; Metian et al., 2020; Cai et al., 2022). Species diversification in aquaculture tends to be a long-term, fluctuating process with diverse diversification patterns varying across countries (section 3.4).

A young aquaculture sector may start with a relatively high species diversity when farmers attempt to cultivate a variety of species in the exploratory stage (Brummett, 2007). Yet technical, market, or other breakthroughs would tend to first occur in the most promising species and result in production concentrated towards a few major species. The development of minor species, together with diminishing growth potential in major species because of various constraints, such as depletion of suitable farm sites, productivity limit, and market satiation, could turn the concentration process into a diversification trend with production expansion primarily driven by more advantageous minor species. These minor species may eventually become major species; then their further expansion could turn the diversification trend back into a concentration process.

Technical, economic, or institutional constraints may hinder the establishment of minor species, whereas the advantages of major species could be sustained or amplified by constant innovations, economies of scales, insatiable global market, or other facilitating factors. Under this situation, a concentration trend may go on for a long period. On the other hand, certain factors, such as high consumer preferences for new varieties of aquatic foods or aquaculture entrepreneurs' passion and perseverance in cultivating new species, may constantly bring about breakthroughs in new species to sustain a straight-up species diversification trend. Therefore, there is no one-style-fits-all species diversification pathway, and species diversification may not be a suitable development strategy for all countries, or for a particular country at different stages of aquaculture development.

Species diversification could stimulate aquaculture growth under certain situations, such as (i) increasing market demand in places where consumers have high preferences over a variety of aquatic foods, (ii) improving farming efficiency through polyculture, or (iii) utilizing diverse farming environments and resources. However, instead of spreading efforts across a range of species, concentrating on the most advantageous ones tends to be a more effective way to promote aquaculture growth, especially in a young aquaculture sector that lacks capacities (e.g. entrepreneurship, technical expertise, and supply chain) to expand aquaculture through species diversification. For an aquaculture sector at its infancy, focusing on the most promising species would tend to result in production concentration towards a few major species. Not only can such species concentration facilitate rapid growth, it could also be a process of building capacities for the development of novel or minor species through spillover effects to lay a foundation for potential species diversification in the future.

Species diversification is often considered a panacea to addressing challenges faced by existing species, such as market satiation (Abellán and Basurco, 1999), low productivity (Carrera-Quintana et al., 2022), or disease outbreaks (Guy et al., 2014). Yet focusing on improving existing species could sometimes be a more effective way to address such challenges. For instance, after a shrimp disease outbreak in 1999 devastated Ecuador's aquaculture sector that was dominated by whiteleg shrimp (*Litopenaeus vannamei*), the recovery was not via species diversification but through improving shrimp farming regulations and management (Marcillo, 2017). As a result, the share of whiteleg shrimp in the country's aquaculture production increased from 82% in 2000 to 98% in 2020, and the country experienced rapid aquaculture growth at a rate of 13.5% a year, compared to 7.7% in South America, 5.7% in the Americas, and 5.4% in world aquaculture.

In contrast with enthusiasm in the public sector, the private sector is often more cautious about species diversification because establishing novel species tends to be a technically challenging, financially demanding, time-consuming, and risky process that may deter even an advanced aquaculture sector

(Harvey et al., 2017). For instance, Norway's attempt to diversify its salmon-dominated aquaculture industry through the farming of Atlantic cod (*Gadus morhua*) was hindered by technical difficulties (e.g. knowledge gaps in intensive cod juvenile production, inadequate broodstock development, and high mortality) and foiled by competition from increased wild cod production (Fernández-Polanco and Bjorndal, 2017; Puvanendran et al., 2021).

Institutional arrangements may be a subtle yet important factor affecting species diversification. While measures for biodiversity conservation may constrain diversification via non-native species, regulations that force farmers to internalize the impacts of their operations on the ecosystem could motivate them to adopt a more diversified farming system, such as Integrated Multi-trophic Aquaculture (IMTA) of finfish, bivalves, and seaweeds (Cai et al., 2021). An aquaculture sector comprised by numerous small or medium-scale farmers could be more conducive to species diversification than one dominated by a few large operators. Small or medium entrepreneurs tend to have more incentives to pursue species diversification as a means to gain competitive advantages because it is easier for them reap the full benefit of a successful diversification by shifting their entire operations to the new species. In contrast, large operators usually lack such flexibilities, and new species may encroach the market of their existing species. Conversely, large operators tend to be better rewarded by concentrating efforts on strengthening their dominance in established species to benefit from economies of scale along the supply chain.

4.2 Future prospects

Accumulated efforts (e.g. domesticated seed, tailor-made feed, and dedicated marketing) in improving the performance of established species, which are usually the most advantageous species in the first place, would tend to further strengthen their dominance and make aquaculture production concentrated towards a few winner species. Indeed, species concentration has become an increasingly prominent aquaculture development pathway in recent decades (section 3.3 and 3.7).

The characteristics of modern aquaculture (e.g. monoculture, formulated feed, specialized seed production, global markets, and industrialized operations), which tend to facilitate the accumulation of economies of scale along the supply chain, are conducive to fostering winner species (Cai et al., 2022).

Increasingly stringent restrictions over the use of non-native species in aquaculture for biodiversity conservation could facilitate initial species diversification among indigenous species, such as the case of tilapia farming in Malawi (Cai et al., 2022). In the long run, however, the production may have a tendency to concentrate towards a few local winner species, which could result in high species diversity in world aquaculture cum low diversity in national aquaculture.

On the demand side, consumers' willingness to pay for novelty and variety is a crucial factor to motivate and sustain species diversification, yet such willingness tends to be weak in countries with low consumer preferences for aquatic foods. Unfortunately, most countries have relatively low preferences for aquatic foods, and these countries are expected to be the primary contributors to world population growth (Cai and Leung, 2022).

In light of these supply- and demand-side factors that are unfavourable to species diversification, we envision that the decelerating trend of species diversification in recent decades (section 3.3) would tend to continue and eventually drive aquaculture towards a low-diversity system similar to terrestrial farming, unless there are effective public interventions to turn the tide.

4.3 Way forward

Diversity is one of the 10 elements of agroecology that have been synthesized to guide the transition to sustainable food and agricultural systems (FAO, 2018). Public interventions to facilitate species diversification in aquaculture are beneficial for the sector's resilience and long-term sustainability. Public support has largely focused on reducing the cost of species diversification for the private sector. This includes research in areas such as species selection methods and criteria (Abellán and Basurco, 1999; Leung et al., 2007; Le Francois, 2010; Alvarez-Lajonchère and Ibarra-Castro, 2013) as well as development projects such as breeding programmes (Harvey et al., 2017). There has also been a strong emphasis on building close partnership between research and the industry (Metian et al., 2020).

More public efforts should be dedicated to increasing the benefits and viability of species diversification, such as (i) promoting farming systems and technologies that are conducive to species diversification (e.g. polyculture); (ii) market development to increase consumer preferences for aquatic foods and foster diverse dietary habits and culinary cultures; and (iii) creating policy and business environments that encourage long-term investments and award entrepreneurship.

While funding and other supports to develop potential species for aquaculture would always be worthwhile in the long run, limited capacities (e.g. natural resources, human resources, and markets) do not allow all promising species to establish at the same time. Therefore, prioritization is necessary for efficient allocation of limited public resources, and a country may seek guidance from species diversification pathways in other countries, especially with geo-clustering of countries with similar species diversity profiles or diversification patterns (section 3.4 and section 3.8).

For instance, while efforts in promoting species diversification have been mostly focused on finfish diversity (Le Francois et al., 2010), between-group diversity deserves more attention in light of the finding of no between-group diversity in more than 40% of national aquaculture (section 3.6). Nearly all landlocked national aquaculture had virtually no between-group diversity, and the experiences of two exceptions (i.e. a relatively high between-group diversity in Central African Republic and Chad because of the farming of spirulina) may not offer much guidance because of their low production scale (Supplementary Table 6). China's experiences in inland aquaculture could provide useful guidance in this regard (Newton et al., 2021). Better yet, landlocked countries may learn from the global experiences of relatively high between-group diversity in inland aquaculture of different scales. For example, in 2020, Singapore had a nearly 700-tonne inland aquaculture production, with a between-group diversity of 2.04 ENSG. Other inland aquaculture sectors with a relatively high between-group diversity include Chile (nearly 2 000 tonnes with 1.86 ENSG), Spain (nearly 20 000 tonnes with 1.54 ENSG), and Taiwan Province of China (over 100 000 tonnes with 1.72 ENSG), among others (Supplementary Table 17).

Based on ENS as an intuitive diversity measure, Cai et al. (2022) established a benchmarking system to synthesize global experiences to guide policy and planning for species diversification in national aquaculture. The in-depth assessment conducted here could expand the benchmarking system to incorporate the measures of within-group diversity (WGENS) and between-group diversity (ENSG) (section 2.2). The two measures provide important insights about the sources of species diversity in aquaculture (section 3.5), such as relatively low between-group diversity in landlocked countries versus relatively low within-group diversity in small island states (section 3.8). It has been recognized that the impact of biological diversity on the resilience of a dynamic ecosystem depends on the diversity of functional groups and the species diversity within these groups (Elmqvist et al., 2003). Similarly, different sources of species diversity in aquaculture would tend to influence its contribution to the sector's growth and resilience. Further study in this area is worthwhile.

ENS and its within- and between-group components, which correspond to gamma, alpha and beta diversity in ecology, should become a standard indicator system widely used in the study of species diversity in aquaculture and mainstreamed in policy dialogues. The within- and between-group partition here is based on the categorization of five customary taxonomic groups; other partitions can be adopted according to different planning or research purposes.

4.4 Concluding remarks

The results of our systematic assessment have uncovered a wealth of information that sheds light on species diversification in aquaculture. We document the comprehensive results in the supplementary materials (including a summary in Supplementary Table 18) to facilitate further analysis. Policymakers and practitioners can use this information to inform their decision-making at the national, regional, and global levels. However, the usefulness of these results depends on the quality of the underlying data. The existence of nei species items in the FAO statistics, i.e. inadequate data disaggregation at the species level (section 2.1) affects accuracies in the measure of species diversity (FAO, 2020; Metian et al., 2020). Cai et al. (2022) used an example to demonstrate that this thorny issue tends to have a less impact on ENS as a diversity measure that captures both richness and evenness, because nei species items are usually associated with relatively small production. However, the data imperfection tends to hinder more in-depth analyses, such as examining species richness and evenness separately. Joint efforts from all stakeholders (governments, international organizations, research communities, the private sector, and others) are needed to narrow the data gap.

References

Abellán, E., Basurco, B. (Eds), 1999. Marine finfish species diversification: current situation and prospects in Mediterranean aquaculture. Zaragoza: CIHEAM.

Alvarez-Lajonchère, L., Ibarra-Castro, L., 2013. Aquaculture species selection method applied to marine fish in the Caribbean. Aquaculture. 408–409, 20–29. doi: 10.1016/j. aquaculture.2013.05.020

Barrington, K., Chopin, T., Robinson, S., 2009. Integrated multi-trophic aquaculture (IMTA) in marine temperate waters, in: Soto, D. (Ed), Integrated Mariculture: A Global Review. FAO Fisheries and Aquaculture Technical Paper No. 529, Rome, pp. 7–46.

Basurco, B., Abellán, E., 1999. Finfish species diversification in the context of Mediterranean marine fish farming development, in: Abellán, E., Basurco, B. (Eds), Marine Finfish Species Diversification: Current Situation and Prospects in Mediterranean Aquaculture. Zaragoza: CIHEAM, pp. 9–25.

Bilio, M., 2008. Controlled reproduction and domestication in aquaculture – the current state of the art. Part IV. Aquaculture Europe. 33 (2), 12–24.

Boyd, C.E., D'Abramo, L.R., Glencross, B.D., et al., 2020. Achieving sustainable aquaculture: historical and current perspectives and future needs and challenges. J World Aquac Soc. 51, 578-633.

Brummett, R.E., 2007. Indigenous species for African aquaculture development, in: Bert, T.M. (Ed), Ecological and Genetic Implications of Aquaculture Activities. Methods and Technologies in Fish Biology and Fisheries, vol 6. Springer, Dordrecht, 229–245. https://doi.org/10.1007/978-1-4020-6148-6_13

Cai, J., Leung, P.S., 2022. Unlocking the potential of aquatic foods in global food security and nutrition: A missing piece under the lens of seafood liking index. Global Food Security. 33, 100641. https://doi.org/10.1016/j.gfs.2022.100641

Cai, J., Lovatelli, A., Aguilar-Manjarrez, J., Cornish, L., Dabbadie, L., Desrochers, A., Diffey, S., Garrido Gamarro, E., Geehan, J., Hurtado, A., Lucente, D., Mair, G., Miao, W., Potin, P., Przybyla, C., Reantaso, M., Roubach, R., Tauati, M., Yuan, X., 2021. Seaweeds and microalgae: an overview for unlocking their potential in global aquaculture development. FAO Fisheries and Aquaculture Circular No. 1229. Rome. https://doi.org/10.4060/cb5670en

Cai, J., Yan, X., Leung, P.S., 2022. Benchmarking species diversification in global aquaculture. FAO Fisheries and Aquaculture Technical Paper No. 605. Rome. https://doi.org/10.4060/cb8335en

Carrera-Quintana, S.C., Gentile, P., Girón-Hernández, J., 2022. An overview on the aquaculture development in Colombia: current status, opportunities and challenges. Aquaculture. 561, 738583. https://doi.org/10.1016/j.aquaculture.2022.738583.

CIHEAM, 1999. Recent advances in Mediterranean aquaculture finfish species diversification. Zaragoza: CIHEAM. (Cahiers Options Méditerranéennes; n. 47). Seminar of the CIHEAM Network on Technology of Aquaculture in the Mediterranean on "Recent advances in Mediterranean aquaculture finfish species diversification", 1999/05/24-28, Zaragoza (Spain). https://om.ciheam.org/option.php?IDOM=760#prettyPhoto

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. et al., 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment. 1, 488–494.

FAO (Food and Agriculture Organization of the United Nations), 2011. World aquaculture 2010. FAO Fisheries and Aquaculture Department. Technical Paper. No. 500/1. Rome.

FAO (Food and Agriculture Organization of the United Nations), 2018. The 10 elements of agroecology. Guiding the transition to sustainable food and agricultural systems. Rome.

FAO (Food and Agriculture Organization of the United Nations), 2019a. The State of the World's Aquatic Genetic Resources for Food and Agriculture. FAO Commission on Genetic Resources for Food and Agriculture assessments. Rome.

FAO (Food and Agriculture Organization of the United Nations), 2019b. Top 10 species groups in global aquaculture 2017. World Aquaculture Performance Indicators (WAPI) factsheet. Rome. www.fao.org/3/ca5224en/ca5224en.pdf

FAO (Food and Agriculture Organization of the United Nations), 2019c. The State of the World's Biodiversity for Food and Agriculture, J. Bélanger & D. Pilling (Eds.). FAO Commission on Genetic Resources for Food and Agriculture Assessments. Rome. http://www.fao.org/3/CA3129EN/CA3129EN.pdf

FAO (Food and Agriculture Organization of the United Nations), 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action. Rome. https://doi.org/10.4060/ca9229en

FAO (Food and Agriculture Organization of the United Nations), 2022. Fishery and Aquaculture Statistics. Global production by production source 1950–2020 (FishStatJ). Rome. www.fao.org/fishery/en/statistics/software/fishstatj

Fernández-Polanco, J., Bjorndal, T., 2017. Aquaculture diversification in Europe: the Kingdom of Spain and the Kingdom of Norway, in: Harvey, B., Soto, D., Carolsfeld, J., Beveridge, M., Bartley, D.M. (Eds), Planning for aquaculture diversification: the importance of climate change and other drivers. FAO Technical Workshop, 23–25 June 2016, FAO, Rome. FAO Fisheries and Aquaculture Proceedings No. 47. Rome, pp. 37–49.

García-Márquez, J., Galafat, A., Alarcón, F.J., Figueroa, F.L., Martínez-Manzanares, E., Arijo, S., Abdala-Díaz, R.T., 2021. Cultivated and wild juvenile thick-lipped grey mullet, *Chelon labrosus*: a comparison from a nutritional point of view. Animals (Basel). 11 (7), 2112. doi: 10.3390/ani11072112. PMID: 34359240; PMCID: PMC8300304.

Gephart, J.A., Deutsch, L., Pace, M.L., Troell, M., Seekell, D.A., 2017. Shocks to fish production: identification, trends, and consequences. Glob. Environ. Change. 42, 24–32. https://doi.org/10.1016/J.GLOENVCHA.2016.11.003.

Guy, J.A., McIlgorm, A., Waterman, P., 2014. Aquaculture in Regional Australia: responding to trade externalities. A Northern NSW case study. Journal of Economic & Social Policy. 16 (1), 1–29.

Harvey, B., Soto, D., Carolsfeld, J., Beveridge, M., Bartley, D.M. (Eds), 2017. Planning for aquaculture diversification: the importance of climate change and other drivers. FAO Technical Workshop, 23–25 June 2016, FAO, Rome. FAO Fisheries and Aquaculture Proceedings No. 47. Rome.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology. 54 (2), 427–432.

Jost, L., 2006. Entropy and diversity. Oikos. 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology. 88 (10), 2427–39. doi: 10.1890/06-1736.1. Erratum in: Ecology. 2009. 90 (12), 3593. PMID: 18027744.

Laakso, M., Taagepera, R., 1979. ""Effective" number of parties: a measure with application to West Europe". Comparative Political Studies. 12 (1): 3–27. doi:10.1177/001041407901200101

Le Francois, N.R., Jobling, M., Carter, C., Blier, P.U., Savoie, A. (Eds.), 2010. Finfish aquaculture diversification. CAB International, Oxford.

Leung, P.S., Lee, C.S., O'Bryen, P.J. (Eds.), 2007. Species and system selection for sustainable aquaculture. Blackwell Publishing, Ames.

Liao, I.C., 2000. The state of finfish diversification in Asian aquaculture. Recent advances in Mediterranean aquaculture finfish species diversification. Zaragoza: CIHEAM, pp. 109–125. (Cahiers Options Méditerranéennes, No. 47.) Seminar of the CIHEAM Network on Technology of Aquaculture in the Mediterranean on "Recent advances in Mediterranean aquaculture finfish species diversification", 1999/05/24–28, Zaragoza (Spain) http://om.ciheam.org/om/pdf/c47/00600610.pdf

Marcillo, F., 2017. Shrimp farming and the environment in Ecuador: past and present. World Aquaculture. 48 (3), 39–42.

Martínez-Cordero, F.J., 2007. Socioeconomic aspects of species and system selection for sustainable aquaculture development in Mexico: historic overview and current general trends, in: Leung, P.S., Lee, C.S., O'Bryen, P.J. (Eds), Species and System Selection for Sustainable Aquaculture. Blackwell Publishing, Ames, pp. 225–239.

Megahed, M.E., Aly, S.M., 2009. Domestication and species diversification to improve marine aquaculture in Egypt (a prospective view). Abbassa International Journal for Aquaculture. Special issue for Global Fisheries and Aquaculture Research Conference, Cairo International Convention Center, 24–26 October 2009, pp. 529–546.

Metian, M., Troell, M., Christensen, V., Steenbeek, J., Pouil, S., 2020. Mapping diversity of species in global aquaculture. Reviews in Aquaculture. 12, 1090–1100. doi:10.1111/raq.12374.

Muñoz-Lechuga, R., Sanz-Fernández, V., Cabrera-Castro, R., 2018. An overview of freshwater and marine finfish aquaculture in Spain: emphasis on regions. Reviews in Fisheries Science & Aquaculture. 26 (2), 195–213. DOI: 10.1080/23308249.2017.1381832

Naylor, R.L., Burke, M., 2005. Aquaculture and ocean resources: raising tigers of the sea. Annual Review Environmental Resources. 30, 185–218.

Newton, R., Zhang, W., Xian, Z., McAdam, B., Little, D.C., 2021. Intensification, regulation and diversification: the changing face of inland aquaculture in China. Ambio. 65, 1–18.

Oboh, A., 2022. Diversification of farmed fish species: a means to increase aquaculture production in Nigeria. Review in Aquaculture. 14 (4), 2089–2098. doi:10.1111/raq.12690

Ordover, J. A., Sykes, A.O., Willig, R.D., 1982. Herfindahl concentration, rivalry, and mergers. Harvard Law Review. 95 (8), 1857–1874. https://doi.org/10.2307/1340652

Puvanendran, V, Mortensen, A, Johansen, L-H, et al. 2021. Development of cod farming in Norway: Past and current biological and market status and future prospects and directions. Review in Aquaculture. 14 (1): 308- 342. https://doi.org/10.1111/raq.12599

Ravisankar, T., Sarada, C., Krishnan, M., 2005. Diversification of fish culture and exports among major shrimp-producing countries of Asia: a spatial and temporal analysis. Agricult. Econ. Res. Rev. 18, 187–195.

Roy, K., 2019. Technicalities to be considered for culture fisheries development in Indian inland waters: seed and feed policy review. Environ Dev Sustain. 21, 281–302. https://doi.org/10.1007/s10668-017-0037-3

Schmidt, G., Espinos, F., Ruiz, F., Segarrax, M., Mañanos, E., Muñoz, J.L. et al., 2011. Diversification in Aquaculture: A Tool for Sustainability. Spanish Ministry of Environmental, Rural and Marine Affairs, Publications Centre, Madrid.

Teletcheac, F., Fontaine, P., 2014. Levels of domestication in fish: implications for the sustainable future of aquaculture. Fish and Fisheries. 15, 181–195.

Thomas, M., Pasquet, A., Aubin, J., Nahon, S., Lecocq, T., 2021. When more is more: taking advantage of species diversity to move towards sustainable aquaculture. Biol Rev. 96, 767–784. https://doi.org/10.1111/brv.12677

Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C. et al., 2014. Does aquaculture add resilience to the global food system? Proceedings of the National Academy of Sciences of the United States of America. 111, 13257–13263.

Tuomisto, H., 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography. 33 (1), 2–22. http://www.jstor.org/stable/20696326

Wilson, J.R., Archer, B., 2010. Diversification pays: economic perspectives on investment in diversified aquaculture: in Le Francois, N.R., Jobling, M., Carter, C., Blier, P.U., Savoie, A. (Eds), Finfish Aquaculture Diversification. CAB International, Oxford, pp.514–530.