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Review

Biodiversity integration drives sustainable and restorative aquaculture

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ABSTRACT

We establish an ecological foundation for sustainable aquaculture, highlighting the essential role of ecological mechanisms in achieving biodiversity-positive, resilient aquaculture systems. Restorative aquaculture leverages species with ecosystem benefits – enhancing water quality, expanding habitat and supporting biodiversity - to address conservation challenges within sustainable food production. By combining restorative aquaculture with the concept of biodiversity mainstreaming and specifically with ecological principles dealing with species performances and species coexistence, we show how aquaculture systems can enhance ecosystem functions and economic viability simultaneously. This approach underscores how understanding and incorporating ecological dynamics can fundamentally transform aquaculture into a truly sustainable practice. Restorative aquaculture, when aligned with international biodiversity and sustainability goals, provides a strategic model for integrating biodiversity within food production systems, bridging ecological integrity with human needs in a globally impactful framework.

1. Introduction

Biodiversity, encompassing the variety of all life forms on Earth, is critical for the health and functionality of ecosystems (IPBES, 2019). It underpins essential ecosystem services such as food production, nutrient cycling, water purification, CO_2 absorption and climate regulation, which are vital for human survival and well-being (Pascual et al., 2017). Nevertheless, today biodiversity is under pressure from multiple human-caused factors including, but not limited to, climate change (Bellard et al., 2012; Caro et al., 2021; Jaureguiberry et al., 2022). A new concept, called "the spiral of biodiversity decline", illustrates how various stressors, including pollution, overfishing and habitat fragmentation, interact synergistically to degrade ecosystems (Tomback and Kendall, 2001). This model emphasizes the need to integrate biodiversity into decision making and uses a holistic perspective underpinned by ecosystem-based approaches to manage for the conservation of biodiversity and related ecosystem services. It thus provides a solution that addresses multiple stressors concurrently with the aim of halting or even reversing biodiversity loss (Sarà et al., 2018a, 2018b; Kleespies et al., 2024). Biodiversity mainstreaming represents a paradigm shift in conservation, moving the focus from solely protecting individual species or areas to embedding biodiversity concerns across all levels of economic planning (Penca, 2023). This strategy aims to tackle biodiversity loss by addressing the sectors that impose the most significant pressures on biodiversity, ensuring a comprehensive and effective response to this global challenge.

There is now increasing global recognition of biodiversity's importance, supported by decades of scientific evidence (IPBES, 2019; Brites et al., 2021; Kim et al., 2023), by stakeholders and decision makers on both sides of the so-called science-stakeholders-policy interface, resulting in initial cross-sectorial debates (Whitehorn et al., 2019; Sandström et al., 2023; Runhaar et al., 2024) . This has driven efforts to integrate the role of biodiversity into various economic sectors, including fisheries and aquaculture within the food sector (FAO, 2024; Mangano et al., 2025). This approach, known as "biodiversity integration" or "biodiversity mainstreaming" is rooted in the current ecological principles of Biodiversity-Ecosystem Functioning (BEF) research (see Fig. 1 and below). This approach is now considered essential for reversing the

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trend of biodiversity decline, is a vital tool to aid in the restoration of degraded habitats, and is critical for ensuring the biodiversity goals of the 30 by 30 effort (globally recommended by the Kunming-Montreal Global Biodiversity Framework 2022; adopted at European level by the EU Biodiversity Strategy 2023). Mainstreaming biodiversity involves the progressive incorporation of biodiversity considerations into the policies, strategies and practices of various sectors, including key food production sectors like the fishery and aquaculture industry, which in turn also exert significant pressure on biodiversity. The Convention on Biological Diversity (CBD) and its Aichi Targets, spanning four goals and 23 targets, underscore the importance of integrating biodiversity across all sectors. The latest FAO report (2024) recognizes the critical role of sustainable fisheries and restorative aquaculture as key tools for mainstreaming biodiversity, reflected in their increasing inclusion in United Nations Food Systems Summit dialogues, United Nations Framework Convention on Climate Change negotiations and the Kunming-Montreal Global Biodiversity Framework. Biodiversity mainstreaming across sectoral governance is specifically mentioned in Target 12 of the Kunming-Montreal Global Biodiversity Framework, which specifically calls for a sustainable use of biodiversity, biodiversity-inclusive urban planning, native biodiversity enhancement, ecological connectivity and integrity, and increased human health and well-being through an enhanced connection to nature and the provision of ecosystem functions and services (IPBES, 2019).

Here we focus on aquatic food system production, aimed at providing insights to address biodiversity mainstreaming in this sector, specifically through the concept of *restorative aquaculture* (Alleway et al., 2023). Since mainstreaming biodiversity in aquaculture is essential for sustainable development and environmental health, transformative changes based on scientific evidence are timely and salient. Additionally, considering the role of aquaculture in sustainable development (Subasinghe et al., 2009), the forecasted +12 % increase of global aquaculture production by 2030, and - among others - the framework of the recently defined blue transformation roadmap 2022–2030 (FAO, 2024), restorative aquaculture represents a viable technologically-based farming approach to integrate biodiversity goals into aquaculture

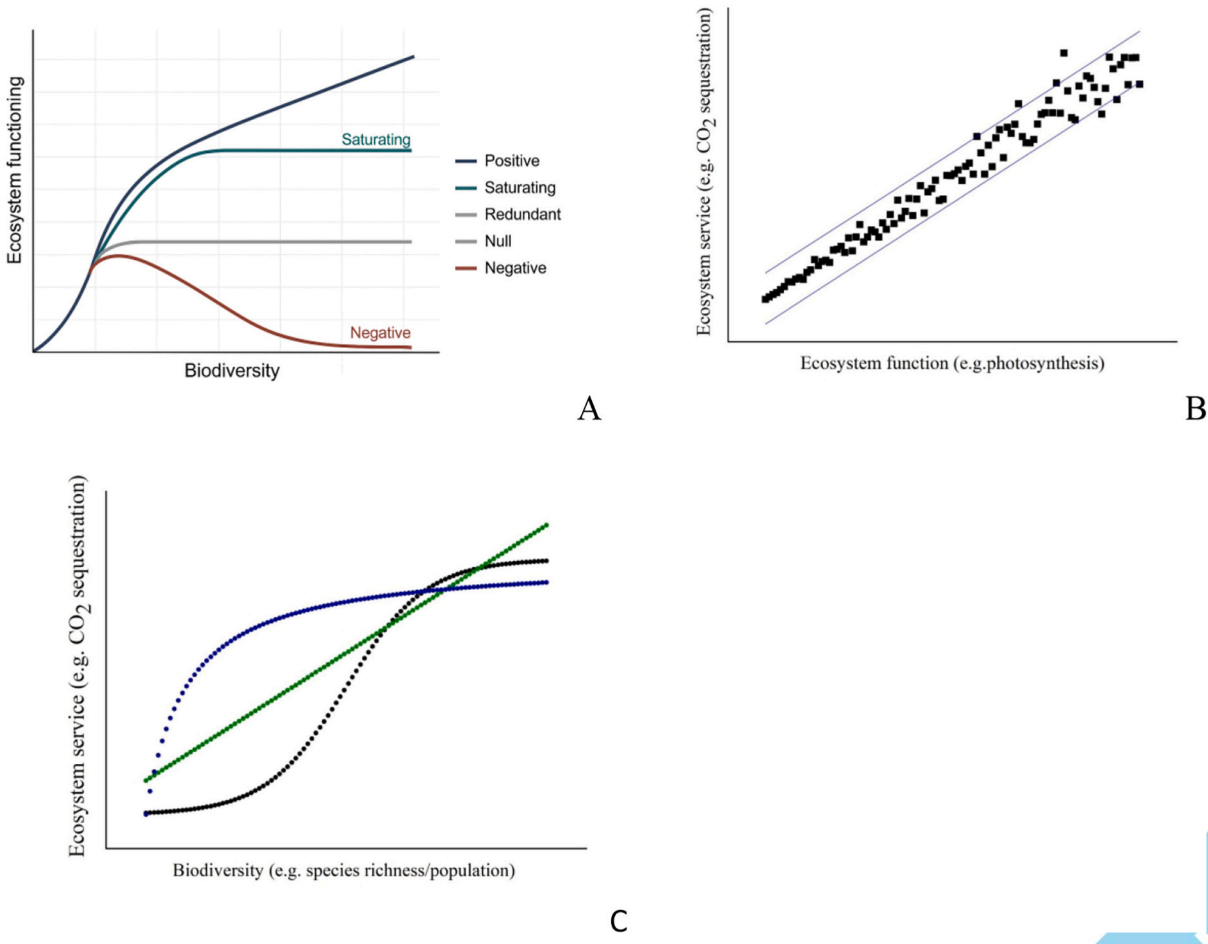

Fig. 1. Conceptual diagrams illustrating the theoretical relationships linking biodiversity to ecosystem functions and services. (A) Conceptual biodiversity–ecosystem functioning (BEF) relationships relevant to aquaculture. Theoretical models illustrate how increasing biodiversity can influence ecosystem functioning in multiple ways. The curves represent: positive linear effects (consistent functional gains), saturating relationships (diminishing returns at high biodiversity), functional redundancy (plateauing effects where additional species do not enhance functioning), null relationships (no effect of biodiversity on functioning), and negative effects (e.g. competition, management inefficiencies, or increased operational costs). While multitrophic biodiversity often supports ecosystem functions, in aquaculture contexts an increase in species richness does not always translate into improved ecosystem services or restorative potential. For instance, combining species with overlapping ecological niches (e.g. adding trout to salmon cages) may increase biodiversity without enhancing productivity or environmental benefits. Adapted from Naeem (2002), Strong et al. (2015) and Daam et al. (2019). (B) A conceptual plot illustrating the generally positive, linear relationship between the level of an ecosystem function (e.g., photosynthesis) and the corresponding ecosystem service (e.g., CO_2 sequestration). The points are illustrative and represent the variability often found in this relationship in natural systems. This principle is supported by extensive literature (e.g., Hooper et al., 2005; Cardinale et al., 2012; Tomimatsu et al. (2013) and Lee and Lautenbach (2016) and the figure is conceptually adapted from the process-based linkage shown in Barbier et al. (2011). (C) A logical extrapolation derived from the principles shown in (A) and (B), illustrating how greater biodiversity is expected to lead to a greater provision of ecosystem services. The different curves represent how the shape of the initial BEF relationship (from A) can propagate through to the final biodiversity-service relationship.

practices, enhancing ecosystem functions while providing economic and social benefits, increasing sustainability of aquaculture practices. Achieving these objectives however requires a comprehensive scientific theoretical framework to build practical guidelines, creating/strengthening collaboration among scientists, policy makers and stakeholders to reduce the potential risk of green-washing (Alleway et al., 2023; Overton et al., 2023). By adopting these principles, aquaculture can significantly contribute to both biodiversity conservation and sustainable resource management.

The implementation of biodiversity mainstreaming in aquaculture is still challenging. We thus synthesize the limited available scientific evidence to draw a road-map facilitating a transition from a purely production-focused economic practice to one that effectively incorporates biodiversity and the ecological and physiological mechanisms that drive biodiversity. Our roadmap moves from a description of the main ecological principles underpinning biodiversity mainstreaming toward the new frontier of restorative ecology, offering insights on the operationalization of ecological trade-off to inform restorative ecology, promoting the use of mechanistic modeling to forecast species performances experiencing environmental change (e.g. climate change), and suggesting the integration of advanced high technologies. Below, we outline key areas that should be highlighted in future scientific research to make restorative aquaculture a common practice worldwide.

2. The role of aquaculture in mainstreaming biodiversity: the new frontier of restorative (ecological) aquaculture

Aquaculture, the farming of aquatic organisms in aquatic habitats, plays a significant role in global food security but exerts considerable pressure on biodiversity at the local level (Naylor et al., 2021). However, when selected species are farmed by following the principles of an Ecosystem Based Approach (Soto et al., 2008; Brugère et al., 2019), aquaculture can become a promising tool for integrating biodiversity into a sector that leads the world in production growth (FAO, 2024). Alleway et al. (2023) recently clarified the concept of restorative aquaculture, distinguishing it from Integrated Multi-Trophic Aquaculture (IMTA) and other related concepts such as conservation aquaculture. They defined restorative aquaculture, in line with Mizuta et al. (2023), as a practice that provides "ecological benefits to the environment, leading to improved environmental sustainability and ecosystem services, in addition to the supply of seafood or other commercial products and livelihood opportunities."

The main difference between restorative aquaculture and other forms of aquaculture is its focus on delivering direct ecological benefits to the environment, with the potential to generate significantly positive environmental outcomes. This approach aims to minimize negative impacts while simultaneously enhancing positive effects on the surrounding ecosystem. In contrast, the primary goal of Integrated Multi-Trophic Aquaculture (IMTA) is to improve the environmental sustainability of an aquaculture system by managing waste and nutrient by-products generated by the operation by simultaneously farming multiple species which coexist in a food web. Although IMTA and restorative aquaculture share certain processes, such as the use of extractive species to absorb nutrients, their core objectives are distinct.

A central tenet of the framework we propose is that restorative aquaculture can best realize its full potential by recognizing that biodiversity underlies ecosystem functioning and the provision and stability of ecosystem services. Using this subtle but distinct differentiation, aquaculture emerges as an ecological practice that can assist conservationists in halting biodiversity loss and achieving conservation objectives by improving aquatic environments, enhancing ecosystem functions and, simultaneously, providing food and livelihood opportunities (Nature Conservancy, 2021). Our proposed framework for restorative aquaculture focuses on farming species across different trophic levels, as multitrophic biodiversity has been shown to enhance key ecosystem functions and services in managed production systems (Buzhdygan and Petermann, 2023). Mainstreaming biodiversity in aquaculture aims to ensure that aquaculture practices not only avoid harming biodiversity but actively contribute to its conservation and sustainable use.

3. Ecological principles of restorative aquaculture

The concept of restorative aquaculture derives from over 30 years of research centered on understanding the differences between observed vs. modeled relationships linking biodiversity and ecosystem functioning (BEF) and is inherently rooted in a well-established framework (Cardinale et al., 2012) that posits: "biodiversity is the main driver of ecosystem functioning", and that it is the main driver of ecosystem stability (Wang et al., 2024). However, this perspective explicitly reverses the dominant paradigm prior to ~2000 when biodiversity was seen as an external commodity, referring to the perception of biodiversity as something existing outside human society and its immediate needs. Biodiversity was primarily viewed either in terms of its utilitarian or economic value (Himes et al., 2024), or for its intrinsic value independent of humans. In that traditional view, biodiversity was often considered an external resource for human exploitation, treating elements of biodiversity - plants, animals and all components of ecosystems - as commodities (Groombridge, 1992) that can be used for human benefits, often emphasizing their monetary or trade value (Fischer et al., 2006). However, contemporary understanding has evolved to see biodiversity as the "independent variable of the system" (on the x-axis), meaning ecosystem functioning, on which the provision of ecosystem services and ultimately human well-being depends (Loreau, 2010; De Bello et al., 2021). BEF relationships are generally explained by positive models (Fig. 1) spanning from concave-down to concave-up models (Mora et al., 2014). Biodiversity–ecosystem functioning (BEF) relationships are conceptually diverse and may be positive, saturating, redundant, neutral, or even negative, depending on the ecological and management context (Naeem, 2002; Strong et al., 2015). This conceptual flexibility is particularly relevant for aquaculture, where increasing species richness does not necessarily imply enhanced ecosystem services or restorative potential.

The consequences of the loss of biodiversity on ecosystem functioning worsen moving from concave-down (saturation) models (Ehrlich and Ehrlich, 1981), in which the magnitude of the effect increases with decreasing biodiversity; to linear models, in which loss is able to cause the same effect; to the concave-up (exponential) model (mechanistically supported by facilitation (Isbell et al., 2017), in which, especially at high levels of biodiversity the loss of even a few species can cause the collapse of ecosystem functioning. The different shapes of the generally positive BEF relationships depend upon many different factors, including the spatial and temporal scales of investigation (Chase and Leibold, 2002; Cardinale et al., 2004) and the experimental strategies used (Emmerson and Raffaelli, 2000); the differential functional role of species (Petchey and Gaston, 2006) and their trophic interactions (Thébault and Loreau, 2003) and also upon the proxies and variables utilized to describe the EF relationship (Bengtsson, 1998). This modern perspective (Naeem et al., 2016) definitively acknowledges that biodiversity contributes to human well-being in complex, indirect and intrinsic ways, encompassing cultural, aesthetic, spiritual and health benefits that transcend mere economic value (Díaz et al., 2018). Such a perspective highlights the interconnectedness of humans and the natural world, advocating that the preservation and health of biodiversity are essential for the overall well-being of human societies.

While our framework builds on the general premise that multitrophic biodiversity can enhance ecosystem functions, it is important to acknowledge that biodiversity–ecosystem functioning (BEF) relationships are not universally positive. Empirical evidence shows that BEF responses can also be saturating, neutral, or even negative, depending on the ecological context and management configuration (Naeem, 2002; Strong et al., 2015). In aquaculture systems, increasing species richness does not necessarily translate into higher restorative value or improved ecosystem services. For instance, combining species with overlapping ecological niches or divergent husbandry requirements (e.g. adding trout to salmon cages) may increase biodiversity without improving water quality, nutrient cycling, or habitat provisioning, and can even compromise growth performance or feed conversion efficiency. Acknowledging these alternative outcomes ensures that our proposed framework remains flexible and applicable across a wide range of aquaculture scenarios.

Nevertheless, most current BEF theory derives from research analyzing the effect of biodiversity on one or few ecosystem functions expressed by biodiversity inside the habitat and community (Eisenhauer et al., 2019). Recent evidence indicates that the biodiversity-ecosystem functioning (BEF) relationship is stronger when multiple functions are considered, a concept known as multifunctionality (Hector and Bagchi, 2007; Gamfeldt et al., 2008; Isbell et al., 2011; Lefcheck et al., 2015). The term "ecosystem multifunctionality" was coined to describe the simultaneous performance of multiple ecosystem functions, for which Byrnes et al. (2014) proposed a comprehensive analytical framework. However, the development of indices to measure multifunctionality is still an active area of research, as the aggregation of contrasting individual functions can obscure the underlying mechanisms, especially when multiple environmental drivers are at play (e.g., Bradford et al., 2015; Manning et al., 2018). Multifunctionality has been extensively studied in terrestrial habitats and has shown, for example, that biodiversity across trophic levels can be a key driver of multifunctionality (Schuldt et al., 2018). However, less research has been conducted in marine ecosystems, which are severely threatened by human-caused biodiversity loss (Betancourtt et al., 2024).

Restorative aquaculture principles align well with the concept of multifunctionality, and this alignment is central to our framework, which involves the artificial assembly of various species from different trophic levels such as autotrophs (e.g., macro-algae), detritivores (e.g., holothurians), suspension feeders (e.g., mussels, oysters), herbivores (finfish) and carnivores (e.g., periwinkles). These species collectively express multiple ecosystem functions (Loayza-Aguilar et al., 2023). Most research is rooted in investigating the effect of species richness (the first component of diversity; Magurran, 2013) on multifunctionality, while restorative aquaculture is more complex as it is based on adding species and removing – across time – species, individuals and biomass (a sort of species push and pull). Within the biodiversity-integrated framework for restorative aquaculture that we propose, the focus is on manipulating the composition of biodiversity to enhance production while maintaining ecosystem multi-service provision. Individuals and biomass of species are removed for commercial production and this practice requires a theoretical framework to predict how to balance biodiversity conservation, multifunctionality benefits and commercial gains effectively. These two benefits often represent contrasting functions that compete from a utilitarian point of view.

4. Optimization in restorative aquaculture

In Fig. 2, we have schematized a possible theoretical relationship between ecosystem multifunctionality and commercial benefits, proposing that a crucial point for effective restorative aquaculture is optimizing these two benefits. A trade-off occurs when these two benefits (i.e., commercial gains versus the number of functions expressed by cultivated species and their services provided) inversely compete, often in a nonlinear manner (Charnov, 1997). The utility function describes the point where both benefits are optimized, highlighting the need for a balanced approach (Sarà et al., 2018a, 2018b). Through this lens, restorative aquaculture effectiveness is deeply rooted in the ecological principles linking biodiversity to ecosystem functioning and ecosystem services (see Fig. 1), and is far from simple green-washing attempts (Whitehorn et al., 2019).

To fully realize the potential of restorative aquaculture, we can refer to a mechanistic-based framework to analyze the causal relationships between biodiversity, ecosystem functions and the benefits provided by cultivated biodiversity. To address related questions, we need to increase our understanding of the factors influencing the trade-offs illustrated in Fig. 2. Such a framework must account for the effects on the abundance of individuals of certain species over time and the impact on biomass, a proxy for ecosystem functioning (Loreau et al., 2022). Since the trade-off point is crucial, we need to increase our understanding on how these functions correlate and vary according to several factors: local environmental conditions, the number of species chosen for cultivation, their functional roles and physiological tolerances to local environmental conditions, the number of trophic levels involved and the initial abundance and density of each cultivated species. The exact nature of this trade-off, however, is dynamic. For example, as highlighted by Alleway et al. (2023), management decisions such as the timing of harvest can alter the curve, potentially reducing ecological benefits and shifting the optimal balance.

Also, further research is needed to understand what happens to the

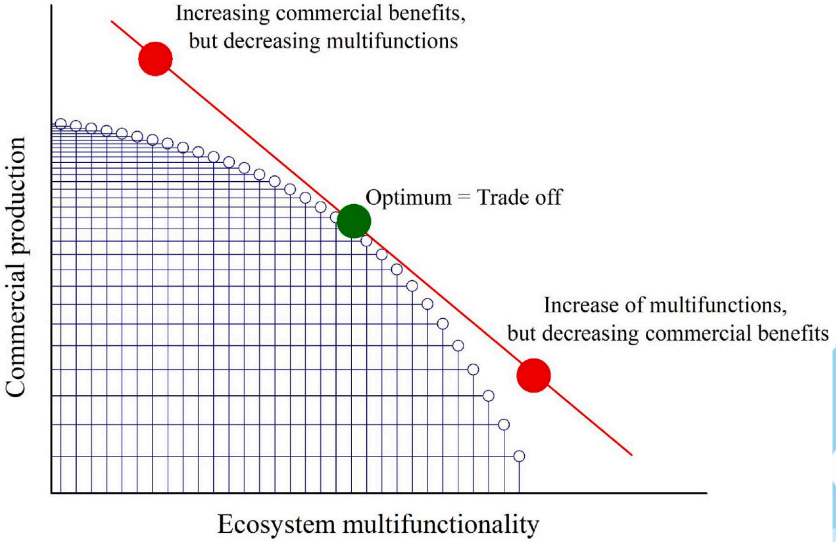

Fig. 2. A possible theoretical relationship between ecosystem multifunctionality and commercial benefits (e.g. biomass), The "optimum" point is the trade-off point optimizing these two benefits and can be suggested as a trade-off measure to operationalize effective restorative aquaculture.

trade-off after any additional species are transplanted following the removal of other species for commercial purposes, which may change the number of species and their relative abundance and biomass. Indeed, transplanting species from different trophic levels together implies choices about the initial abundance of each species, specifically which should be dominant and which less abundant (i.e., the order of transplanting due to phenological aspects). Such an operation involves understanding coexistence mechanisms, such as competition for trophic resources and space, which are characteristic of wild ecological communities and cannot be ignored in the preliminary phase of assembling a restorative aquaculture community.

As an example, most species commonly considered beneficial for restorative aquaculture are sessile in the wild (i.e., fixed to the substrate with minimal or no movement, such as mussels and polychaetes). These species, including macro-algae, mussels and holothurians, act as foundation species with the ability to engineer their own habitats (Troell et al., 2009). Some are dominant species that can contribute disproportionately to ecosystem functions based on their biomass (Isbell et al., 2017). According to the mass-ratio hypothesis, as proposed by Grime (1998), this means that some species contribute to the multifunctionality in proportion to their abundance, thus addressing changes in the system in terms of the abundance/biomass. Nonetheless, rarer species are able to influence ecosystem service provision (Cardinale et al., 2012) by changing species composition and richness. Also, as shown in the wild, species can be subordinates or transient according to their relative abundance and this role usually changes depending on local environmental conditions (i.e. each local condition can favor a species to increase abundance moving from a role of dominant to subordinate and vice versa (Enquist et al., 2015). Under each local condition every species can play a different role and this role can change across time with removal for commercial purposes affecting the trade-off between multifunctionality and commercial gains (Fig. 2).

5. How mechanistic ecological modeling can assist us in predicting the direction of trade-off optimization

Developing effective restorative aquaculture involves mechanistic predictions about how to manage such a complex, multi-faceted operation in the context of which ecological mechanism ensures the balance between biodiversity conservation and commercial benefits. Increasing biodiversity can enhance the provision of multiple ecosystem functions and services, with at least three central mechanisms ensuring the role of biodiversity in addressing effective restorative aquaculture: i) the complementarity effect: different species use resources in ways that enhance overall ecosystem functioning. This resource partitioning or facilitation leads to increased ecosystem productivity and stability (Loreau et al., 2022; Wang et al., 2024); ii) the selection effect (Fox, 2005) when the presence of competitively superior species with stronger functional traits or fitness can dominate ecosystem processes (Loreau et al., 2022). Such a "identity effect" or "selection effect" can be exacerbated by species with large relative abundances (i.e., dominant species; Grime, 1998); iii) the 'Jack-of-all-Trades, Master-of-None' mechanism when in a multispecies mixture, different species promote various functions, ensuring moderate (average) levels of multiple ecosystem services (van der Plas et al., 2016). This latter mechanism implies that while no single species excels in performing all ecosystem functions, the collective presence of multiple species ensures overall ecosystem stability and balanced multifunctionality. Thus, ecosystem functioning may correspond to the biomass-weighted average of the functional levels of the monocultures of its constituent species. As a result, in the absence of other biodiversity effects like complementarity or selection, the functional levels in diverse communities tend to be intermediate, thus avoiding the extremes seen in some monocultures (van der Plas et al., 2016). On this theoretical basis, monitoring programmes in restorative ecology should include, over-time, the measure of ecosystem functioning variables at a local level, around the facilities, following clear and high resolution temporal and spatial sampling designs (Underwood, 1997). The most common variable of ecosystem functioning (mainly adopted in terrestrial ecological research; Loreau et al., 2022) is productivity as measured through proxies such as biomass of species at community or habitat level. Productivity is usually measured as the wet or dry mass of organisms cultivated over time, and then biomass can emerge as an effective proxy of ecosystem functioning. This approach allows for the integration of temporal variability in community biomass (on a weekly, monthly or even seasonal basis), as indicated by wet or preferably dry weights of individual species within the community per unit of surface or volume. This may facilitate the causal explanation of how abiotic environmental factors including extreme events (such as temperature, deoxygenation, desalination, organic enrichment, pollution etc.) influence the trade-off between multifunctionality and commercial gains. Other variables, such as the coverage or numerical density of algae and macro-benthos, can also be valuable and should be even included in aquaculture monitoring programs to inform the management of the trade-off.

These types of variables and sampling methods can generate complex datasets that require different analytical approaches, depending on the type of causal inference we aim to achieve and on the basis of the availability of time and human (and ecological expertise) resources. Indeed, disentangling the causal relationships between biodiversity and ecosystem functioning in the presence of environmental variations is not an easy task. The causal effect of local conditions on the biodiversity and ecosystem functioning relationship can potentially be analyzed correlatively without necessarily disentangling the causal relationships between biodiversity and ecosystem functioning due to environmental variability (Mora et al., 2011). When assessing the causal role of biodiversity on ecosystem functioning to understand the effects of temporal and spatial environmental variations, sophisticated statistical approaches have been employed (Dee et al., 2023). Additionally, Fox (2006) proposed an innovative theoretical framework using Price's eq. (Price, 1970) to decompose the differences in ecosystem function levels or rates between two sites (for example close and far from cages) into additive components attributed to various effects (e.g. pristine vs. aquaculture impacted sites, along a gradient of organic enrichment, or through the time). While this approach is still being evaluated, it has already been applied in various case studies and has proven to be highly versatile, as it can be used for any ecosystem function (e.g. biomass) that arises from the combined contributions of individual species. Such methods have never been applied in aquaculture, but implementing models to automate the data collection in the field and later implementing the analysis of sampling results could enhance farmers' ability to provide data from their farms to decision-makers. This, in turn, could facilitate the analysis of whether the trade-off is optimized over time and space, or if restorative aquaculture objectives are prone to failure (Fig. 2).

6. Species performance under varying local conditions matters

While previous methods have been effective in disentangling the effects of environmental changes at the community level, a significant amount of research over the past three decades has focused on exploring species-level performance. Changes in species performance are crucial for understanding the presence or absence of a species in a given location, as well as thereby its potential for use in restorative aquaculture. More importantly, these changes help clarify the species' ecological role, which is critical in the context of biodiversity and ecosystem functioning relationship in restorative aquaculture. Differential physiological performance of organisms in populations of different species under local conditions influences the abundance of organisms, which in turn can shift the abundance and biomass equilibriums - allowing some species to become dominant under favorable conditions, while others may become subordinate when conditions are less favorable (Enquist et al., 2015). In any given local context, each species can play a different role, and this role may change over time according to local changing conditions impacting, through abundance (density) and biomass, the trade-off between multifunctionality and commercial gains. Harley et al. (2017) reviewed the complex interactions between environmental drivers and physiological performance, highlighting some of the most common physiological responses observed in nature as a function of critical environmental factors, such as light and nitrogen resources for primary producers, as well as temperature and pollutants (Vandenberg et al., 2012). The link between temperature and heterothermic performance, commonly depicted by a thermal performance curve (TPC; Dell et al., 2013; Kingsolver and Woods, 2016; Sinclair et al., 2016), is particularly valuable for examining local performance differences (Fig. 1c in Harley et al., 2017). Thermal Performance Curves (TPCs), which depict how temperature affects various aspects of an organism's performance, generally exhibit a unimodal pattern and are often left-skewed, particularly in temperate species (Angilletta, 2009). This pattern demonstrates a gradual increase in performance as body temperature rises, reaching an optimal point, after which performance declines sharply with further temperature increases, and similarly, declines with decreasing body temperature (Angilletta, 2009; Harley et al., 2017). Therefore, under local conditions of temperature fluctuations - whether due to climate change or extreme local events - aquatic organisms in a restorative aquaculture system, most of which are ectotherms, may be shifted from their optimal temperature range toward either the left or right side of the TPC. This shift can significantly reduce the overall performance of an individual during the period of exposure to these changing conditions, and if this period of stressful conditions is relevantly long, there will be a repercussion at population level with consequent effects on abundance and biomass of cultivated restorative species. Importantly, what constitutes "stressful" environmental changes varies depending on the specific shape and relative position of each species' physiological performance curve, including understanding of what can often be high intraspecific variation in TPCs (Dong et al., 2017). Therefore, it is crucial to evaluate environmental stressors within the specific context of the organisms affected, as these ecophysiological responses are not only species-specific but also exhibit variation within species (Torossian et al., 2016). Despite the well-established theory surrounding performance curves (Kontopoulos et al., 2024), there remains a lack of comprehensive data for many aquatic species that could be utilized in restorative aquaculture, particularly regarding their performance curves. Among these, thermal performance curves are the most extensively documented in the literature (Laurel et al., 2017). However, there is limited information on the effects of other factors, such as light - particularly through studies on turbidity effects on primary production - salinity, dissolved oxygen and pH fluctuations. Current research on pollutants can be of limited usefulness, as it often focuses on dose-response relationships using only a narrow range of concentrations that do not accurately reflect realistic levels in aquatic habitats and are typically conducted in controlled laboratory environments or through in silico models (He et al., 2024). As a result, to better understand the impact of changing local environmental conditions on the trade-off as illustrated in Fig. 2, further research is needed to investigate how multiple human-induced stressors (Crain et al., 2008) can alter local environments over time. This research should also explore the impact of changing performances at species level on subsequent effects on the dominant and subordinate roles of species cultivated in restorative aquaculture.

7. Hi-tech monitoring technologies to assist restorative aquaculture

In the context of restorative aquaculture, the integration of advanced monitoring technologies can significantly enhance our ability to explore and optimize the trade-off between commercial gains and ecosystem multifunctionality. Remote sensing and satellite monitoring provide large-scale environmental data, such as sea surface temperature, chlorophyll concentration and turbidity, which are essential for understanding the broader environmental conditions that influence aquaculture operations (Saitoh et al., 2011; Palmer et al., 2020). These tools allow for real-time monitoring and analysis of how regional and local environmental factors affect the health and productivity of aquaculture systems. However, they must then be extended to conditions experienced by organisms. For example, it is well known that temperature at any depth can be markedly different from surface temperature. Automated environmental monitoring systems, often connected through IoT (Internet of Things) networks, play a crucial role by continuously tracking key abiotic factors, including temperature, salinity, dissolved oxygen, pH and pollutant levels at the level of the organism (Li et al., 2019; Rastegari et al., 2023). The IoT enables sensors to communicate data in real-time, providing a detailed understanding of temporal and spatial variations in environmental conditions experienced by animals (Li et al., 2019). This connectivity allows for rapid responses to changing conditions, helping aquaculture managers anticipate and to both mitigate stressors, or to adapt farming practices to cope with negative effects that could negatively impact both species performance, biodiversity, ecosystem functioning and health, thereby consequently the operational trade-off in restorative aquaculture (Fig. 2). Furthermore, the use of automated image collection systems around aquaculture facilities may enhance these monitoring efforts by capturing high-resolution images of the species on substrates surrounding the aquaculture sites. Advanced image recognition algorithms, integrated within the IoT framework, can automatically identify and catalog species, enabling the study of species' gains and losses within the community. This provides crucial insights into how biodiversity evolves over time in response to environmental fluctuations and aquaculture practices, which is critical information that could be integrated automatically into classical Price's equation or other similar and derived frameworks (e.g. Bannar-Martin et al., 2018; Harrison et al., 2022). The system also should allow for the measurement of organismal body size directly from images, which can then be used to estimate biomass using established length-weight relationships available in many online databases and repositories (e.g. FishBase.org). This automated approach facilitates efficient species monitoring, helping to build a comprehensive understanding of community structure and dynamics (Besson et al., 2022; Wägele et al., 2022). By tracking the number of individuals, their size distribution and changes in species composition, these systems allow aquaculture managers to better assess the ecological impacts of their practices and dynamically make informed decisions that optimize the balance between ecosystem multifunctionality and commercial gains. In addition to monitoring species and environmental conditions, biotelemetry and biologging (Clarke et al., 2021; Jarić et al., 2023; Beltran et al., 2024) technologies enable the tracking of individual organisms' physiological responses to environmental changes, offering valuable insights into species-specific responses. These data may be crucial for depicting thermal performance curves (TPCs) and other species-specific response models. Whether integrated into mechanistic based models such as those based for instance on the Dynamic Energy Budget theory (Kooijman, 2009; Sarà et al., 2013) exploiting environmental monitoring data via IoT platforms and biologging (Li Shing Hiung et al., 2024), the real-time results can form the basis of early warning systems. These systems can detect deviations from optimal conditions that could signal potential threats to the health and productivity of the aquaculture system, allowing for proactive management interventions.

Genomic and metagenomic tools further complement these efforts by assessing biodiversity at a genetic level, revealing the health and functional diversity of both cultivated species and their associated ecological communities. This genetic insight is critical for maintaining ecosystem functionality and resilience. Environmental DNA (eDNA) is a highly efficient and standardized sampling approach using environmental samples (Thomsen and Willerslev, 2015). The widespread application of eDNA technology is largely due to the development of next-generation sequencing technologies, which have significantly enhanced biodiversity monitoring and conservation. For instance, eDNA metabarcoding of benthic bacterial communities has proven to be a sufficiently robust technology to assess the environmental impacts of salmon aquaculture (Dully et al., 2021).

To manage the vast and complex datasets generated by these interconnected technologies, machine learning and AI-based data analysis can be employed (Vinuesa et al., 2020). These tools are capable of identifying patterns and correlations within the data, predicting potential outcomes based on current trends, and guiding the optimization of both commercial and ecological objectives. The integration of AI with IoT systems enhances the capacity for real-time decision-making, further improving the sustainability and efficiency of aquaculture practices. Finally, automated sampling and data logging systems within this IoT-enabled framework enhance the efficiency and accuracy of data collection, reducing human effort and error and providing a more reliable depiction of how the aquaculture environment fluctuations over time. These systems are particularly important for tracking changes in biomass and species diversity, which are key indicators of ecosystem multifunctionality. By integrating these advanced technologies into an innovative monitoring and early warning framework, restorative aquaculture can be managed more effectively, balancing the need for commercial production with the imperative to conserve biodiversity and maintain healthy, functioning ecosystems.

8. Concluding remarks

When it explicitly integrates biodiversity, restorative aquaculture represents a transformative approach to sustainable aquaculture practices that can balance ecological and economic goals. By increasing biodiversity and enhancing the complexity of ecological interactions, this approach not only stabilizes ecosystem functions but also provides resilience against environmental changes. To effectively manage restorative aquaculture, it is crucial to apply sound ecological principles, including species selection, harvesting order and density management, all of which must be informed by a deep understanding of species' functional traits and ecological roles. The development and integration of advanced monitoring technologies, such as IoT-enabled sensors, automated image collection systems, eDNA and AI-driven data analysis, are essential for optimizing the trade-offs between ecosystem multifunctionality and commercial gains. These technologies provide real-time insights into environmental conditions and species performance, enabling proactive management and early warning systems that can mitigate potential risks. As we advance our knowledge of species-specific responses and ecosystem dynamics, we can further refine these practices to ensure they contribute to both biodiversity conservation and sustainable aquaculture production.

In conclusion, the success of biodiversity mainstreamed restorative aquaculture hinges on our ability to continuously innovate and apply interdisciplinary research, meeting the dual goals of ecological sustainability and economic viability in the face of changing global environments. Restorative aquaculture stands at the forefront of innovative practices with the potential to significantly reduce the probability of biodiversity loss. By attracting the attention of producers, this approach not only enhances ecosystem stability and functioning but also aligns with global conservation targets, such as the European Restoration Law (2024) and similar directives worldwide. By explicitly integrating biodiversity into aquaculture frameworks, our approach complements recent perspectives advocating for enhanced environmental performance and socioeconomic sustainability in global aquaculture (Pomeroy et al., 2014; Henriksson et al., 2021). As a powerful tool for safeguarding biodiversity, restorative aquaculture can become a cornerstone in the global effort to ensure sustainable, resilient ecosystems for future generations.

CRediT authorship contribution statement

G. Sarà: Conceptualization, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Funding acquisition, Writing – review & editing. **M.C. Mangano:** Conceptualization, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Funding acquisition, Writing – review & editing. **B. Helmuth:** Conceptualization, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Funding acquisition, Writing – review & editing. **J. Wang:** Writing – original draft, Writing – review & editing. **M. Berlino:** Writing – original draft, Writing – review & editing. **A. Botero:** Writing – original draft, Writing – review & editing. **Y. Dong:** Conceptualization, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

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Data availability

No data was used for the research described in the article.

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