nature sustainability

Article

https://doi.org/10.1038/s41893-025-01577-x

Leveraging biodiversity to maximize nutrition and resilience of global fisheries

Received: 27 March 2024

Accepted: 28 April 2025

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Wild fish harvests from freshwaters and oceans per person on Earth have been stagnating for decades due to increased food demand from a burgeoning global human population, raising the stakes for maximizing the nutritional benefits from limited fish stocks. Here we adopt an allocation optimization approach using biogeographic and nutrient data for the world's fishes to identify ideal portfolios of species for consumption in every country. We find that, across nations, biodiversity increases opportunities to fulfil multiple nutritional requirements with less fish biomass. This advantage emerges through complementarity among species; portfolios of complementary species provide >60% more nutrients than the same biomass of the most nutrient-rich species. Moreover, biodiverse fisheries enable harvest allocation towards species with traits enhancing fishery resilience (for example, small size, low trophic position) and offer greater redundancy, whereby a wider range of comparably nutritious species is available. Our analysis underscores that conserving fish biodiversity can improve nutrition and fishery resilience while reducing harvest pressure on already-stressed aquatic ecosystems.

Food systems and biodiversity are interlinked. Food production is among the main drivers of declining biodiversity; hence, sustainably nourishing humanity requires mitigating impacts of food production on biodiversity[1,2]. Biodiversity enhances ecosystem functions underpinning food systems by amplifying niche differentiation among species (complementarity effect) and by increasing the probability of manifesting high-performing species (selection effect)[3,4]. These same mechanisms—complementarity and selection—also apply to nutrition. Foods vary in nutrient content, and a diverse portfolio of species more efficiently provides many essential nutrients simultaneously. Although biodiversity's role in ecosystem functioning and nutrition is well recognized[5], biodiversity mechanisms are underappreciated for their potential to simultaneously enhance nutrient availability and food system sustainability.

Wild fisheries epitomize biodiversity's multifaceted role in food systems (Fig. 1). Capture fisheries nourish billions of people globally[6,7], but as demand increases and stocks stagnate or decline, intensifying harvests may accelerate biodiversity loss[8]. These biodiversity changes could, in turn, undermine how fisheries support food security through nutrition-based ((A)) and resilience-based ((B)) pathways. Species vary in nutrient quality, and diverse fisheries could enhance opportunities for selecting single high-quality species as well as complementary species that combine to provide holistic nutrition. Indeed, drawing from a complementary portfolio of fish species could better meet demands across multiple nutrients simultaneously than any single species ((A))[9]. Resilience-wise, diverse faunas may have nutritionally redundant species within a fishery whereby species can be substituted with minimal nutritional consequences ((B))[10]. In addition, greater trait diversity in

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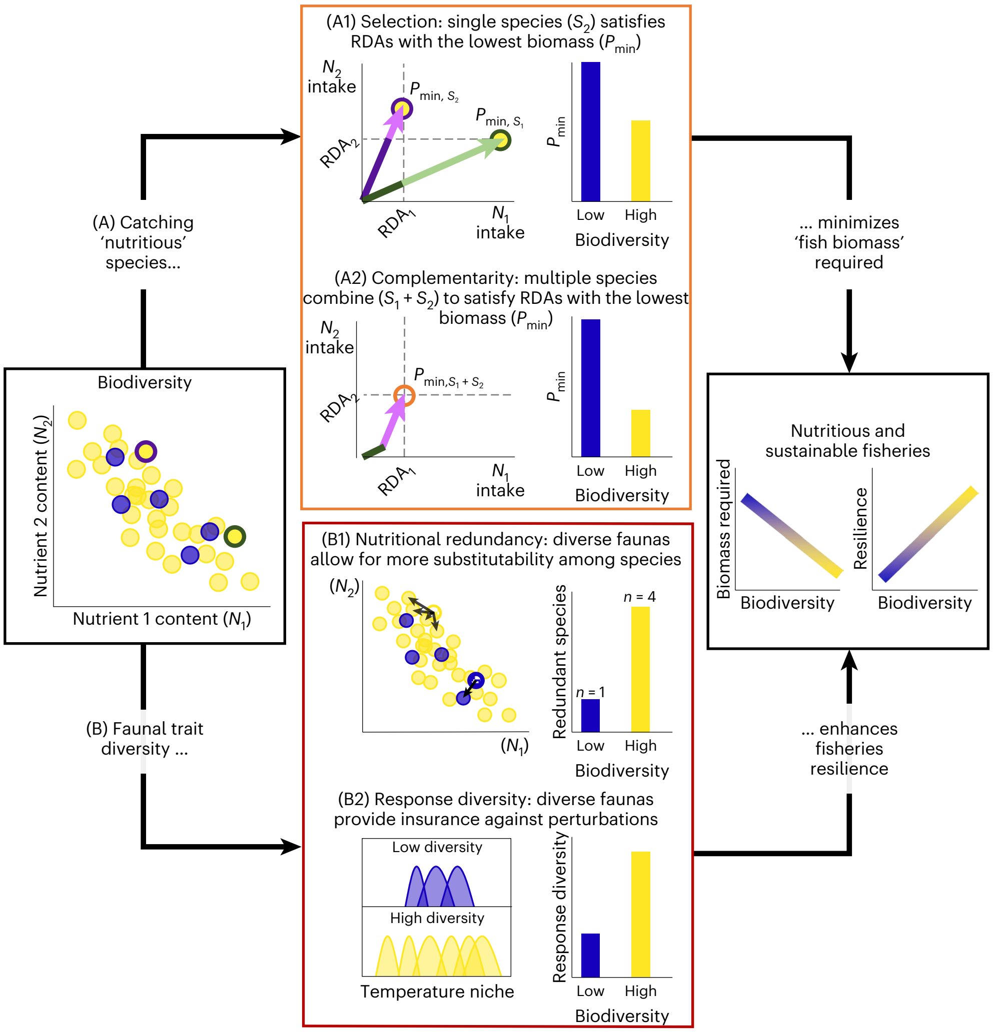

Fig. 1 | The multifaceted role of biodiversity in supporting nutritious and sustainable fisheries. Fisheries are a major driver of aquatic biodiversity change, but biodiversity can also enhance fisheries benefits through nutrition-based ((A)) and resilience-based ((B)) pathways. Pathway (A): species (S_i; depicted as points) vary in their nutrient content for two nutrients (N_1 and N_2) and, consequently, (A1) the minimum fish biomass needed to meet RDAs, depicted as a green vector for S_1 (P_{min,S_1}) and purple vector for S_2 (P_{min,S_2}). Relative to S_1, S_2 has higher N_2 and lower N_1; hence, S_2 meets both RDA_1 and RDA_2 with less biomass (that is, the sum of the dark and light portions of the arrows). Selection refers to the fact that biodiverse fish faunas are more likely to include species that can fulfil multiple RDAs with less biomass (P_{min}). (A2) Biodiverse communities are also more likely to include species with distinct and complementary nutrient content (for example, $S_1 + S_2$) that when consumed together can fulfil multiple RDAs with less biomass than P_{min} of either species alone. By reducing P_{min}, both selection and complementarity mechanisms allow biodiverse fisheries to meet nutritional needs with less fish biomass. Pathway (B): aggregate faunal trait variation also increases with biodiversity. Consequently, (B1) biodiverse fisheries are more likely to include species that are nutritionally redundant, meaning they are substitutable with only minimal increases in P_{min} for multiple RDAs. (B2) Variation in other traits, such as species temperature niches, can also increase response diversity, or how species differ in their responses to environmental perturbations or stressors. By having wider trait variation, biodiversity enhances both redundancy and response diversity, thereby engendering greater resilience and stability of fisheries.

fish faunas can enhance resilience to perturbations (for example, climate shocks), especially when species respond differently to stressors (for example, response diversity[11]; (B)). These benefits are critical in geographies where people rely on capture fisheries[12,13]. Although biodiversity change is often viewed as a consequence of food production, conserving biodiversity may enhance opportunities to harvest species that are both nutritious and resilient, supporting sustainable food systems.

In this Article, we integrate species biogeographic and nutrient content data to assess how fish biodiversity maximizes nutritional and resilience benefits from the world's marine and freshwater fisheries. Using constrained optimization to implement an adaptation of the 'diet problem'[14], we identify native food fish portfolios that minimize biomass required to achieve recommended dietary allowances (RDAs). We used International Union for Conservation of Nature (IUCN) assessments to categorize fish species as food (including sharks and rays) and focused on key nutrients derived from consuming fish (that is, protein, omega-3 fatty acids, vitamin A, iron, zinc and calcium), whose deficiencies have lifelong impacts, especially for children[15,16]. We repeated this analysis for 290 countries and territories, thereby accounting for differences in species richness and nutritional traits characterizing each nation's biodiversity endowment. In addition, we included country-level fish consumption data to contextualize findings with other food sources, trade and consumer preferences. Our integration of ecological theory, fisheries science and nutrition highlights how biodiversity fosters efficient allocation of fisheries for nutritional and conservation goals.

Biodiversity can enhance nutritional outcomes

We find that countries with more fish species can support nutritious diets with less fish biomass (Fig. 2a). For example, with fish portfolios that minimize biomass intake needed to achieve nutrient requirements

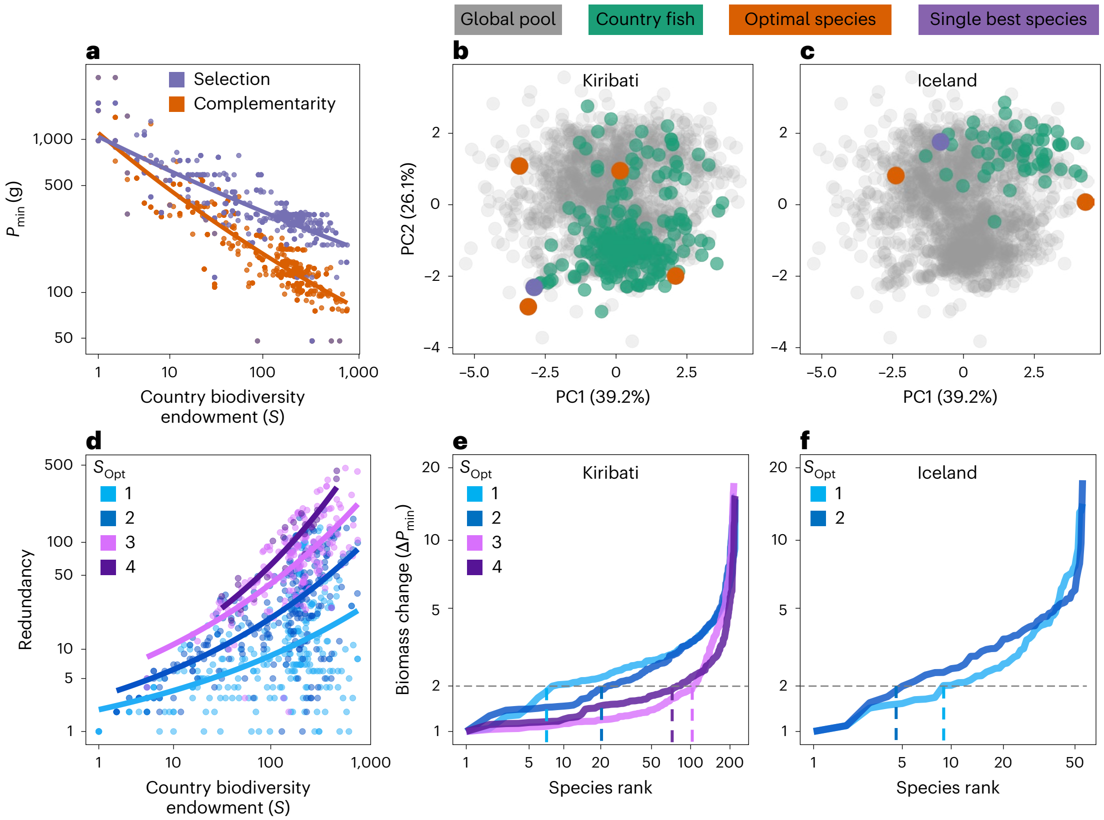

Fig. 2 | Biodiverse countries can fulfil multiple nutritional needs with less fish biomass. a, Both complementarity (multiple species) and selection (single best species) reduced the minimum biomass needed to meet all six RDAs (P_{min}) across countries (depicted by points; $n = 290$) with varying biodiversity (S). **b**,**c**, These effects emerge because of the greater nutritional variation among species in biodiverse countries, such as Kiribati (**b**), compared with countries with fewer species (for example, Iceland (**c**)), as shown by food fish in nutritional space (green) relative to the global pool (grey) using principal component (PC) analysis. Both complementary species in the optimal portfolio and the single best species are typically drawn from the edges of nutritional space (see also Extended Data Figs. 4 and 5). **d**, Nutritional redundancy also increases with biodiversity. **e**,**f**, Between one and four species were identified as the optimal portfolio for each nation (S_{Opt}), and redundancy was estimated as the number of non-optimal species that could replace those in the optimal portfolio and still meet all RDAs with less than a twofold increase in required biomass (illustrated by the grey dashed line). For example, when species were ranked by the increase in biomass (ΔP_{min}) required to replace an optimal species, Kiribati (**e**) had 8 and 21 species that could replace the first and second most abundant optimal species (light blue and dark blue dashed lines), respectively, whereas Iceland (**f**) had 8 and 5 species.

(henceforth, 'P_{min}'), 50% of all RDAs could be achieved in Kiribati (species richness, $S = 221$) with 128 g per day of fish, whereas in Iceland ($S = 56$), up to 423 g would be needed to meet the same nutritional outcome. For every additional species available, P_{min} declined on average by 0.50% (±0.015%, $P < 0.001$, $R^2 = 0.78$). This nonlinear relationship indicates that increased species richness also expands the number of alternative portfolios capable of achieving similar nutritional outcomes

The negative relationship between a country's fish biodiversity and P_{min} stems from complementarity, where multiple species with distinct nutrient profiles combine to satisfy RDAs. Optimal portfolios included up to four species with extremal non-overlapping nutrient profiles, as indicated by principal component analysis across all six nutrients (Fig. 2b,c and Extended Data Fig. 1). The number of species in country-level optimal portfolios is below the theoretical upper bound of n species for n nutrients (Extended Data Fig. 2) due to weak or negative correlations in nutrient content across species[10]. This loose correlation underlies complementarity: although few fishes are rich in all nutrients, a subset of species can be leveraged to meet many RDAs simultaneously. Indeed, biodiverse countries had portfolios with higher nutrient trait diversity (Extended Data Fig. 3), which enhances opportunities to assemble portfolios with nutritionally distinct species and maximizes complementarity.

The selection effect also fostered interdependence between biodiversity and P_{min} (Fig. 2a). For every country, we identified the single species that would minimize biomass to meet RDAs and found that the P_{min} for each nation's single best species was lower in biodiverse countries. As with complementary species, single best species were associated with extremal principal component values (Fig. 2b,c). Thus, biodiverse countries' broader nutritional space was more likely to include distinct species that could singlehandedly meet RDAs with less biomass.

Complementarity, however, is not a guaranteed feature of multi-species portfolios. Comparing optimal portfolios against like-sized sets of species drawn randomly from each country's fish fauna showed that random portfolios from biodiverse countries could meet RDAs with less biomass, but differences with optimal portfolios and single best species were exceptionally large (Extended Data Fig. 4 and Extended Data Table 1). As with complementarity and selection, the negative relationship between biodiversity and P_{min} based on random portfolios emerges from the broader nutrient content variation associated with biodiverse fish faunas. Thus, there is an increased chance of sampling unusually nutrient-rich fishes and complementary species when randomly assembling portfolios from diverse fish faunas, highlighting the benefit of biodiversity for both optimally constructed and randomly chosen portfolios of food fishes.

Biodiversity supports higher nutritional redundancy

These results should not be interpreted as recommending concentrating harvests on few optimal species. Rather, biodiverse countries had more nutritionally redundant species, which could support similar outcomes as optimal species without requiring large increases in fish biomass (<100% increase; Fig. 2d). For example, Kiribati (S = 221) had eight species redundant with the most nutritious species, 22 species with the second, 104 with the third and 78 with the fourth (Fig. 2e). By contrast, Iceland (S = 56) had eight species redundant with the most nutritious species and five with the second (Fig. 2f). Increased redundancy is also evident in the nonlinear relationship between biodiversity and P_{min} (Fig. 2a), underscoring that benefits of complementarity could be achieved with other species beyond those deemed optimal.

These findings emphasize that the sustainability of nutritious fisheries will depend on maintaining faunal diversity. The low species richness in optimal portfolios highlights potential constraints with scaling these benefits of biodiversity for food systems if optimal species diverge from which species are abundant, catchable, economically feasible or culturally preferred. However, safeguarding biodiversity and the nutritional redundancy it supports confers flexibility in the species composition of near-optimal portfolios and reduces the necessity of relying on a few taxa. This redundancy could increase resilience if species need harvest reductions or vary in the face of perturbations. Thus, beyond enhancing complementarity, conserving biodiversity can maintain the benefits of redundancy.

Complementarity scales with the number of RDAs

Considering that non-fish foods may also provide people with focal nutrients, we analysed how the strength of the biodiversity effect on P_{min} varied with RDA thresholds and the number of nutrients considered. At low thresholds, where other foods may satisfy RDAs, P_{min} was low (Extended Data Fig. 5). Increasing RDA thresholds raised the total fish biomass required but did not alter the slope of the relationship between biodiversity and P_{min}. This indicates that the benefits of biodiversity are consistent regardless of reliance on alternative food sources to meet these RDAs.

Considering more RDAs had a pronounced effect by enhancing the strength of complementarity on P_{min} (Fig. 3). While a single species could optimally fulfil one RDA, the loose covariation in nutrient content across species led to multiple species being needed to achieve several RDAs simultaneously (Fig. 3a). Consequently, in biodiverse countries, complementary portfolios would require >60% less fish biomass to meet all six RDAs than would the single most nutritious species (Fig. 3b). Although some countries contained exceptionally nutritious species (for example, Mekong barb in Cambodia), higher biodiversity also increased the likelihood of portfolios being composed of multiple rather than single species (Fig. 3a). This underscores the importance of having diverse species pools when fisheries are the primary source of multiple nutrients.

Beyond enhancing complementarity, additional RDAs also drove species turnover in optimal portfolios (Extended Data Fig. 6). When increasing from one to three RDAs, optimal portfolios contained few, if any, shared species. However, compositional changes between four, five and six RDAs reflected both turnover and compositional overlap (nestedness). These changes were less apparent in low-biodiversity countries, where low diversity required embracing the same small number of species for all RDAs considered. Physiological, ecological and evolutionary constraints determine the covariation among nutrients across species and thus the ability to meet multiple RDAs simultaneously[10]. With larger pools of species available, such constraints can be mitigated by assembling complementary portfolios that overcome the limitations of individual species.

These patterns in turnover highlight how biodiversity can act as a hedge against uncertainty[17] as people's nutritional needs and the dietary contributions of fish and other foods (for example, plants and animals) vary in time and space[6]. Although the composition of optimal portfolios depended on which RDAs were analysed, the benefits of biodiversity applied to all nutrients. Low-biodiversity countries often met multiple RDA combinations with the same species but at the cost of increasing the minimum biomass to compensate for a lack of complementary species. Thus, a wider species pool provides flexibility to tailor portfolios to specific nutritional demands or as environmental or other shocks alter the supply of fishes and other foods[18]. These benefits grow with the number of nutrients considered, implying that biodiversity loss will most impact people reliant on fisheries for nourishment.

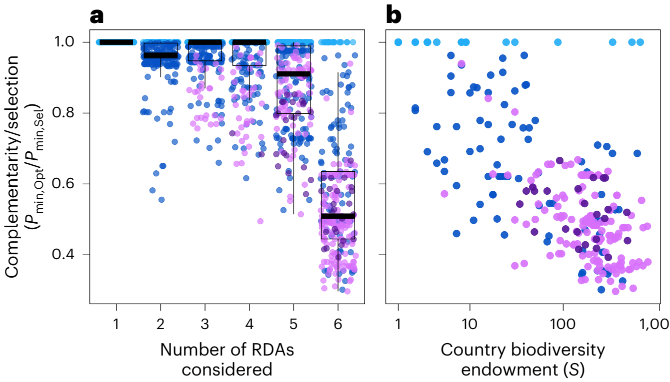

Fig. 3 | Harvesting nutritionally complementary fish species dramatically reduces the fish biomass needed to achieve nutritional targets. a,**b**, The benefits of complementarity increase with both the number of nutrients whose RDAs are considered (**a**) and country biodiversity endowment (**b**). Each point represents a country (n = 290), coloured by the number of species in the optimal portfolio (S_{Opt}; coloured as in Fig. 2). The complementarity/selection ratio is calculated as the biomass needed to meet RDAs using the optimal portfolio of species ($P_{\mathrm{min,Opt}}$, which is driven by complementarity) divided by the biomass needed for the single most nutritious species ($P_{\mathrm{min,Sel}}$, which reflects selection). Box plots in **a** display the median (centre line), interquartile range (box) and whiskers (minimum and maximum values within 1.5 × interquartile range).

Optimal portfolios include inherently resilient species

Optimal portfolios from more diverse countries were more likely than randomly assembled portfolios to exhibit ecological trait signatures associated with resilience to global environmental changes[19–21]. Specifically, optimal portfolios were characterized by smaller species and narrower body size range than like-sized sets of randomly assembled portfolios from each country (Fig. 4a,d and Extended Data Table 2). Species in optimal portfolios also had lower mean trophic levels but were similar in trophic range (Fig. 4b,d). These trait disparities extend recent findings that smaller and lower-trophic-level species tend to be more nutrient-dense[22]. Because smaller and lower-trophic species also tend to have faster growth rates and are more abundant, fishery portfolios including them are also expected to show better-than-average resilience to high exploitation rates and have less destabilizing impacts on food webs[23,24]. In addition, optimal portfolios included species with more flexible temperature requirements (Fig. 4c,f). Faunas with wider temperature preferences tend to exhibit a diversity of responses to climatic shocks (response diversity) and are more likely to persist when perturbed[25,26]. By extension, with their higher response diversity, optimal portfolios could be more resilient to extreme variations in temperature associated with climate change.

Despite these advantages, many species in optimal portfolios are underrepresented in domestic fisheries statistics, indicating that current harvests do not target nutritionally optimal species (Fig. 5). Using the Aquatic Resource Trade in Species (ARTIS) database[27], which derives trade flows from Food and Agricultural Organization national fisheries data, we found only 42% of species in optimal portfolios (50 of 119) are reported, accounting for 7.45% of domestically consumed biomass, although country-level variation is evident (Fig. 5a). At the genus level, where data are better resolved, 80% of optimal genera are reported (72 of 90), accounting for 27.8% of domestic consumption

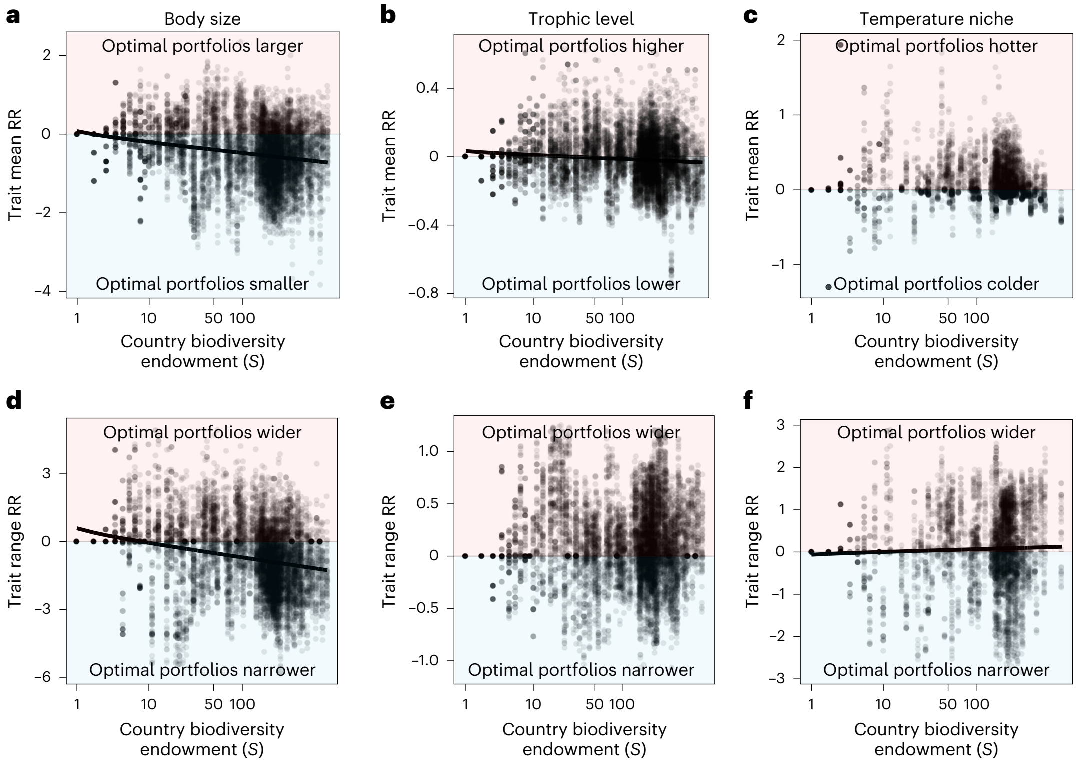

Fig. 4 | Optimal portfolios from biodiverse countries exhibit more resilient trait signatures. a–**f**, We used $\log_{10}$ response ratios (RRs) to compare the nutritionally optimal portfolio of food fishes for each country with randomly assembled portfolios with the same number of species on the basis of means (**a**–**c**) and ranges (**d**–**f**) for three traits that may confer resilience to environmental perturbations. Each point represents a comparison between an optimal and randomly assembled portfolio ($n = 30$ randomizations per country), with the gradient from grey to black depicting point density. Optimal portfolios from biodiverse countries are characterized by smaller species (**a**) and narrower range of body size (**d**), where smaller species are considered to be more resilient. Optimal portfolios also had species occupying lower mean trophic levels (**b**) and wider temperature niche ranges (**f**), where lower trophic levels and wider temperature niches are considered to be more resilient. There were no differences in trophic level range (**e**) or mean temperature niche (**f**) between optimal and randomly assembled portfolios. For full statistical results, see Extended Data Table 1.

(Fig. 5b). These include common genera such as *Decapterus*, *Trachurus* and *Sardinella*. In addition, taxa redundant with optimal species are frequently reported, although their consumption varies across countries. Although optimal and redundant taxa are existing components of fisheries-based food systems for many countries, their rarity in commercial catches may reflect low availability or lack of market opportunities, limiting the ability to fully leverage these fishes for nutrition and resilience.

However, biodiversity in food systems is poorly documented, with many optimal or redundant taxa probably harvested but underreported in fisheries data. For example, in ARTIS, 42% of domestic fish consumption is unresolved at the species level and 24.3% at the genus level. Reported catch data are derived from landings and markets, whose coarse taxonomic resolution and exclusion of non-commercial fisheries can underestimate the true biodiversity consumed, especially in regions with rich fish fauna. These issues are pronounced for freshwater fisheries, contributing to their lack of inclusion in global assessments (for example, Blue Foods Assessment)[6]. Even when monitored, catch biomass is frequently unreported at the species level, or is restricted to select regions or ecosystems (for example, Reef Life Surveys). While our approach integrates biogeography and expert IUCN assessments to address these gaps, the lack of refined taxonomic data across nations limits a full analysis of species biomass in optimal portfolios.

Trait differences between optimal and randomly assembled portfolios probably emerge because the same ecological and evolutionary constraints that shape nutrient content variation also shape ecological trait variation. Covariation between nutrient composition and ecological traits underlies how biodiversity affects nutritional outcomes and fisheries resilience. Other traits linking fish biology to food systems could covary similarly. For example, smaller species are often more abundant, catchable en masse and less expensive[22]. In addition, they are a cornerstone for subsistence, especially in regions with high fishery dependence[22,28], underscoring the importance of small fish biodiversity and the need for their improved monitoring.

Stronger benefits of biodiversity in fish-reliant nations

The nutritional and resilience benefits of biodiversity are pronounced in nations with high consumption of domestic fisheries (Fig. 6a). These include many island countries (for example, Kiribati) as well as those with large river systems (for example, Mekong in Cambodia) where fisheries are integral to culture and livelihoods[29]. Many such countries also face persistent malnutrition, and fisheries are touted for their potential to reduce micronutrient deficiencies, especially because fish are abundant, inexpensive and culturally appropriate[22]. Beyond ensuring availability, our findings emphasize that leveraging domestic fish diversity can foster nutrition and resilience in fisheries-dependent food systems.

Global trade in fishery products complicates these dynamics by altering the availability of species across countries and potentially decoupling local biodiversity from accessible species. By changing available species richness, trade could affect the relationship between biodiversity and nutritional and resilience outcomes. Although we found no direct relationship between country-level foreign fish consumption and biodiversity (Fig. 6b), many biodiverse and fishery-dependent countries are undergoing food system transitions.

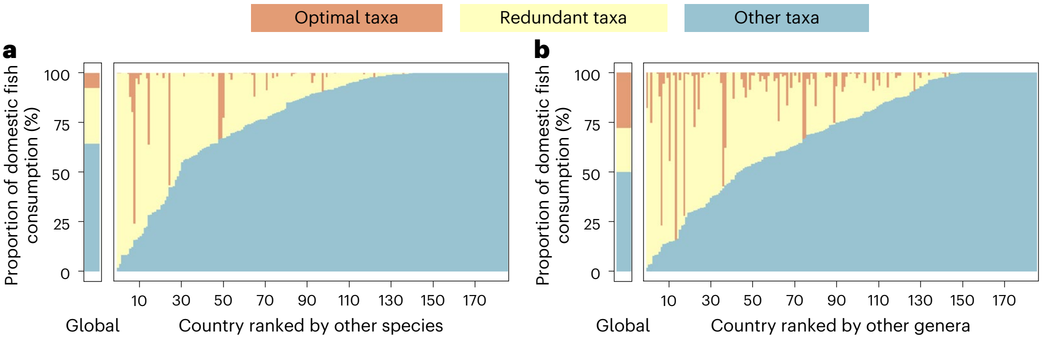

Fig. 5 | Species and genera included in or redundant with optimal fish food portfolios comprise a portion of countries' domestic fish consumption. **a**, Globally, species represented in optimal fish food portfolios accounted for 7.45% of the proportion of domestic fish consumption (orange shading), and nutritionally redundant species an additional 28.2% (yellow shading); but for many countries, most fish consumed are taxa not included in or redundant with species from optimal fish food portfolios ('other taxa', blue shading). **b**, These patterns are similar at the genus level, which is better resolved than species in global fisheries statistics, with genera represented in optimal fish food portfolios comprising 27.8% and redundant genera an additional 22.3% of the global domestic fish consumption.

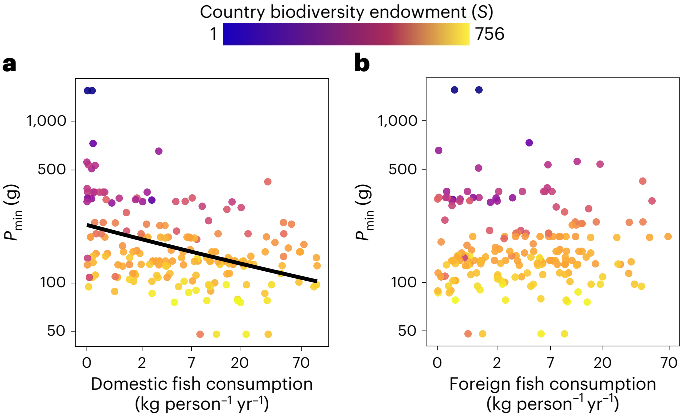

Fig. 6 | The benefits of fisheries biodiversity for nutrition and resilience are most pronounced in countries where people are reliant on domestic fisheries but not on imported fisheries. **a**, The minimum biomass needed to meet RDAs was lowest in countries with high per capita consumption of domestic fish ($R = 0.062$, $P = 0.007$). The line represents a fit from a generalized linear model with a log-link Gaussian distribution. **b**, The relationship between per capita consumption of foreign fish and the minimum biomass needed to meet RDAs was insignificant.

Increased availability and preference for farmed animal-sourced foods (for example, aquaculture, beef, poultry) may ease pressure on wild fisheries but exacerbate malnutrition as farmed options are less nutritious[30]. These trends are expected to continue, underscoring the importance of policies promoting the harvest, consumption and conservation of diverse domestic fisheries.

Finally, we note that fish consumption—and the associated opportunities for leveraging biodiversity—may be greater than reported in many countries. Fish consumption rates estimated from market data often misrepresent true consumption, for example, by missing subsistence harvests[28]. Further, weak fisheries-monitoring infrastructure is commonplace and may further exacerbate underreporting of fish consumption. Improving monitoring of biodiversity in fisheries-based food systems is imperative to adequately tailor decisions that enhance nutrition and ensure the long-term sustainability of fisheries.

Discussion

The benefits of being well endowed with biodiversity are multifaceted and do not imply that only species identified as optimal would lead to the same results. Rather, our study highlights how conserving biodiversity can contribute to better nutrition from and resilience in fisheries. Indeed, greater resilience of biodiverse fisheries food systems springs from the traits of species identified as nutrient-rich, the broader range of redundant species available, greater response diversity and reduced aggregate harvest biomass. Similar biodiversity benefits emerge even when species are drawn randomly from the global pool of food fishes (Extended Data Fig. 7), indicating that these results are a robust feature of biodiversity rather than being specific to the species available in each country. Consequently, biodiversity loss could forgo the nutritional and sustainability opportunities provided by biodiversity.

Beyond availability, realizing the benefits of fish biodiversity will hinge on whether high-nutrition species are palatable to consumers. Consumers exhibit diverse preferences for specific fish, even within the same geographical region or ecosystem, and consumed fish portfolios typically represent only a small subset of available fish biodiversity[28]. Further, preparation methods (for example, eating fish whole or filleted) also vary and can affect nutrient intake. However, consumer preferences are not fixed and have shifted over time, with larger, less nutritious and more vulnerable species becoming more frequently preferred[31]. Market data and choice experiments can help assess consumer willingness to adopt healthier and more resilient diets and provide species-level information for preference-sensitive dietary optimization approaches. Importantly, these would provide the foundation for developing culturally appropriate dietary recommendations[32] that emphasize the nutritional benefits of a portfolio approach for advancing both public health and conservation goals in fisheries.

Proper interpretation of our results must account for additional key realities of current food systems. First, while optimal species are more resilient than average, intensive exploitation of any subset of species may become unsustainable. However, redundancy increases with biodiversity, and species-rich faunas offer opportunities to spread fishing effort across nutritionally similar species. Characterizing the many near-optimal portfolios was beyond the scope of this study but could further guide fisheries towards additional nutritionally substitutable species[33]. In addition, overexploitation is complex, and incorporating ecological traits such as productivity and behaviour (for example, schooling) could provide further insights into the links between biodiversity, nutrition and resilience. Second, we utilized IUCN-based expert assessments to identify food fish species and assumed that they could be consumed throughout their range, which may bias the representation of actual food fish nutrient trait diversity within countries. In addition, we relied on modelled nutritional values, but species vary interspecifically in their nutrient content as well as how they are consumed. Including these factors would add nuance to our findings but not fundamentally alter the relationships between biodiversity, nutrition and resilience. Ultimately, to operationalize fish biodiversity benefits, however, we reiterate calls to improve assessments of catch composition, nutrient content and consumer preferences of wild-caught fishes, especially for inland and subsistence fisheries[6,34]. Third, our analysis was at the country scale, but access to fishes varies depending on factors such as geography, wealth and market proximity[22]. Finer-scale analyses could capture these nuances, but benefits of biodiversity should apply across scales.

Prospects

With the global population expected to surpass 9 billion, decoupling food production from its environmental impacts is a major sustainability challenge[2]. Wild fisheries will remain a central component of global food systems, but overexploitation is transforming aquatic ecosystems[6]. Our analyses show that countries with high fish biodiversity and reliance on fisheries are best positioned to meet nutritional needs with resilient species and underscore four principles for biodiversity's role in sustainable food systems.

First, the benefits of complementarity scale with the size of the available species pool. Fishes represent a subset of the diversity of food species that humanity relies on, including plants and other animals[35]. However, weak correlation among nutrient content is ubiquitous across taxonomic groups, and principles of complementarity apply to other food species[36–38]. Expanding our approach to include other foods could identify when and where the unique nutritional role of fishes[30] can best complement the broader biodiversity represented within food systems.

Second, the benefits of biodiversity for resilience are enabled by greater trait diversity. Reducing the vulnerability of fisheries to global environmental change is paramount for ensuring stable and healthy food supplies. By fostering redundancy and response diversity, conserving biodiversity can enhance fishery resilience to exploitation, climate change and other stressors. Maintaining trait variation in food systems, and leveraging opportunities to increase it, such as with alternative foods or strategic trade, could further advance resilient food systems.

Third, the benefits of biodiversity increase with the number of nutrients considered. Our focus on fish biomass and a set of essential nutrients illustrates how biodiversity reduces the harvest intensity required to achieve multiple dimensions of nutrition simultaneously. Fishes are not merely potential food for people; they mediate many other ecosystem functions and services, from carbon cycling to energy fluxes through food webs[39,40]. Thus, considering other functions and services beyond nutrition will probably amplify the potential to leverage complementarity and redundancy for food system sustainability.

Fourth, fish biodiversity and its benefits for people are not evenly distributed across the globe but reflect deep-rooted biogeographical patterns. The most biodiverse regions are those where people rely heavily on fisheries[41] but where diets are shifting[31]. The overlapping geography of biodiversity, fish dependence and dietary transitions reveals the importance of tailored interventions that both conserve and leverage biodiversity to maximize the contributions fisheries make to people.

Ultimately, our findings underscore how global biodiversity declines are eroding opportunities to harness fish biodiversity for fisheries sustainability. Nearly one-sixth of fishes are threatened with extinction, primarily because of overexploitation[42]. While many of these vulnerable species might not be optimal, the nutritional and resilience opportunities biodiversity provides exist only with rich standing fish faunas. Hence, these interconnections between nutritional and sustainability goals provide ample reasons to redouble efforts to conserve the biodiversity of fishes across Earth.

Methods

Optimization model

We used a constrained optimization approach to account for country-level biodiversity patterns and nutrient content of food fishes. We used species evaluations by the IUCN to categorize each of the world's fish species as either consumed as food or not. For every food species, we then obtained country occurrence and nutrient content information from FishBase[7,43]. For nutrients, we focused on protein, iron, zinc, calcium, omega-3 fatty acids (DHA and EPA) and vitamin A[15,16].

Our optimization algorithm is an adaptation of the diet problem[14], which uses linear programming to consider every country's food fish biodiversity and find which combination of species, and in what proportions, minimizes the biomass required to satisfy the daily nutritional needs of a 5-year-old child across all of the nutrients considered (RDA). Formally, the model minimizes the total biomass of fish (in grams; P_{tot}) on the basis of the nutrient content of the food fishes native to a given country, represented as:

$$P_{\min} = \min P_{\text{tot}} = \min(p_1 + p_2 + p_3 + \ldots + p_i \ldots + p_S) \tag{1}$$

where $P_{\min}$ is the minimum biomass needed to satisfy RDAs, p_i is the optimal biomass contribution of each species i given a country's biodiversity endowment of S species.

The total mass of nutrient k (N_k) in a diet is:

$$N_k = a_{1,k}p_1 + a_{2,k}p_2 + \ldots a_{i,k}p_i + \ldots + a_{S,k}p_S \tag{2}$$

where $a_{i,k}$ is nutrient content per biomass for species i. We bound $p_i \geq 0$ to prevent the consumption of negative biomass.

We add the following nutritional constraints: if an individual consumer receives $(1 - \alpha)$% of their nutrients from non-fish sources, the individual's nutritional requirements are met if and only if,

$$\alpha \mathrm{RDA}_k \leq N_k \tag{3}$$

where RDA_k is the RDA for nutrient k and N_k is the total mass of nutrient k consumed across all species. A diet must satisfy equation (2) for all k nutrients.

To minimize equation (1), we utilized the linear programming solver provided by the lpsolve package in R 4.03 (ref. 44). To improve computational speed, we introduced an additional constraint that P_{tot} must be less than or equal to an upper limit of $P_{\max}$. $P_{\max}$ was set at 10,000 g, but if the optimization process failed to find a feasible solution, we raised $P_{\max}$ for that country. This constraint was important for reducing computing time but had no impact on the reported solutions.

We conducted the optimization analysis for every combination of RDAs (protein, iron, zinc, calcium, vitamin A and omega-3s) and across all thresholds of RDAs ($1 - \alpha$, ranging from 1% to 100%) to determine the sensitivity of P_{Opt} to the number, identity and threshold (α) of RDAs (constraints in the optimization model). We identified the minimum biomass needed for each number of RDAs (1–6).

Comparison of optimal, single-species and random portfolios

To understand the potential benefits of optimal portfolios, we compared the minimum biomass of the optimal portfolio ($P_{\min,\text{Opt}}$) with the minimum biomass needed based on the best performing single species, $P_{\min,\text{Sel}}$, for each country. To do so, first, for each species i in each country, we found the minimum biomass needed that could meet RDAs ($p_{\text{limiting},i}$), which is determined by the most limiting nutrient:

$$p_{\text{limiting},i} = \max{}^{\mathrm{RDA}_k} / \, \mathrm{a}_{i,k} \text{ for } k \,\epsilon\, K \tag{4}$$

Then $P_{\min,\text{Sel}}$ was obtained by identifying the species with the smallest $p_{\text{limiting},i}$.

To understand whether complementarity is a guaranteed feature of multi-species portfolios or if complementarity emerges from the selection of specific species, for every country we generated 30 like-sized sets of randomly selected species from the native food fish species pool. Thus, for every country, the number of species in random portfolios was equal to the number of species in the optimal portfolio. Then we subjected these random portfolios to the same optimization model described in the preceding to identify the minimum biomass needed to meet RDAs, $P_{\mathrm{min,Rand}}$. This model included an additional constraint requiring that the minimum biomass of each species in the random portfolio be no less than the lowest biomass of any species in the optimal portfolio (p_{lowest}). This biomass constraint was added since optimizing over a random set of species could eliminate some of those same species from the portfolio and reduce the species richness represented within that portfolio. In other words, this biomass constraint ensures that all species in each random portfolio were drawn upon to maintain the target number of consumed species.

Biodiversity within optimal portfolios

To understand how a country's biodiversity compares with the biodiversity within an optimal portfolio, we used five complementary approaches. First, we obtained the number of species included within the optimal portfolio, S_{Opt}. Second, we calculated the nutrient trait diversity of the species in the optimal portfolio, $\mathrm{FD}_{\mathrm{Opt}}$, as biomass-weighted multivariate dispersion in nutrient content values for all six nutrients using the fdis function in the FD package in R[45]. Third, we performed principal component analysis on the nutrient content of all food fish species. All nutrients except protein (Fe, Ca, Zn, vitamin A and omega-3s) were $\log_{10}$ transformed and standardized (z transformed) to account for their different scales before analysis. We used Horn's parallel analysis to identify the principal component axes to retain from the paran package for R[46]. Fourth, to quantify whether more biodiverse countries were represented by species occupying a wider nutrient trait space, we compared the nutrient trait richness of every country with that country's species richness as the convex hull volume using the nutrient content values for all species within a country with the dbFD function in the FD package in R. Finally, to quantify how unique a country's optimal species were relative to the country's other species, we estimated the species mean Euclidean distance in nutrient trait values and compared that with the mean Euclidean distance in nutrient trait values of the species within optimal portfolios as well as the single best species.

Type and number of RDAs

To understand how the number and type of RDAs considered shaped the species composition of optimal solutions, we analysed turnover in species composition as successively more RDAs were considered. First, we estimated the pairwise Jaccard dissimilarity index between the species represented in a country's optimal portfolios for each number of RDAs met from one to six using the betapart package in R[47]. We further decomposed Jaccard dissimilarity into turnover and nestedness components for each pairwise comparison[47]. Turnover represents changes in species composition driven by replacement of some species by others. Nestedness represents changes in species composition driven by gains or losses of species.

Ecological trait signatures

Species traits such as temperature niche, body size and trophic level are well known to mediate species responses to global environmental challenges such as climate change, overexploitation and habitat loss[19–21]. Thus, we wanted to understand whether portfolios of species selected to minimize biomass harvest might be expected to be more or less resilient on the basis of their traits when compared with randomly selected portfolios of species (as detailed in the preceding). We used two approaches for these comparisons. First, we estimated the log response ratio in biomass-weighed mean trait values between optimal and randomly assembled portfolios. Differences in mean trait values provide insight into whether portfolios are biased towards certain trait values (for example, larger body sizes). Second, we estimated the log response ratio in the trait range between optimal and randomly assembled portfolios. Trait range is the mean trait distance of each species with respect to other species within the same portfolio; this metric provides insight into whether portfolios are characterized by species that are more dispersed in their trait values than expected at random (for example, occupying a wider range of temperature niches). Trait values were obtained from FishBase[43], and only countries that had data for all species represented within optimal and randomly assembled portfolios were analysed. In total, we were able to analyse 168 countries for temperature niches and 239 countries for body size and trophic level.

We used the ARTIS database[27], which derives trade flows from Food and Agricultural Organization national fisheries data, to identify whether species in optimal portfolios are present in global fishery data, focusing on domestic apparent consumption. Specifically, we estimated which proportion of a country's domestic apparent consumption was composed of optimal, redundant and other taxa. In addition, we repeated this analysis considering genera, which is generally better resolved than species in global fishery data.

Statistical analysis

We analysed the relationship between a country's biodiversity endowment (S) and the minimum biomass needed on the basis of optimal portfolios ($P_{\mathrm{min,Opt}}$), single species ($P_{\mathrm{min,Sel}}$) and random portfolios ($P_{\mathrm{min,Rand}}$) using a generalized linear model with a log-link Gaussian distribution ($n = 290$). To understand how the effect of S on $P_{\mathrm{min,Opt}}$ varies by RDA thresholds and number of nutrients considered, we also extracted the estimates and 95% confidence intervals from regression models for one to all six RDAs across all thresholds. We analysed how a country's biodiversity endowment shapes differences in ecological traits between optimal and random portfolios with our variables of interest ($\mathrm{Trait}_{\mathrm{mean}}$, $\mathrm{Trait}_{\mathrm{Disp}}$) as the response variables and log (S) as the predictor variable using a generalized linear model with a log-link Gaussian distribution. Finally, we analysed the relationship between a country's minimum biomass needed on the basis of optimal portfolios ($P_{\mathrm{min,Opt}}$) and domestic and foreign apparent consumption using a generalized linear model with a log-link Gaussian distribution. For this analysis, we obtained every country's apparent fish consumption from ARTIS[27].

To test whether our results could have been biased by focusing only on species with available nutrient trait information, we re-ran the analysis on random sets of species that ranged across a commensurate biodiversity gradient as represented by the number of species available across all countries. To build this random biodiversity gradient, for every level of species richness as determined by each country's biodiversity endowment, we sampled the global pool of species without replacement. This randomization was performed 30 times for each level of country-level biodiversity. All analysis were conducted in R[48].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data for replicating the analysis and results are available via Figshare at https://doi.org/10.6084/m9.figshare.24615465 (ref. 49). The Aquatic Resource Trade in Species (ARTIS) database is accessible at https://artisdata.weebly.com/ (ref. 27).

Code availability

Code supporting the results is available via Figshare at https://doi.org/10.6084/m9.figshare.24615465 (ref. 49).

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Acknowledgements

We thank C. Bowser, E. Duvall, M. Miranda, F. Pacheco, M. Valdverde and L. Zarri for providing comments that improved the manuscript. We also thank the many researchers that analysed fish nutrient content and developed predictive models for unmeasured species. This project is partially supported by Schmidt Sciences programmes, through an Eric & Wendy Schmidt AI in Science Postdoctoral Fellowship (S.A.H.) and an AI2050 Senior Fellowship (C.G.); a Cornell Presidential Postdoctoral Fellowship (S.A.H.); the National Science Foundation and the National Institute of Food and Agriculture (NSF and USDA/NIFA) no. 2023-67021-39829 (C.G.); the Air Force Office of Scientific Research no. FA9550-23-1-0322 (C.G.) and no. FA9550-23-1-0569 (DURIP; CG); and a David and Lucile Packard Fellowship for Science and Engineering (P.B.M.).

Author contributions

S.A.H. conceived the study with substantial input from F.W.S. and P.B.M; all authors contributed to refining the study design; S.A.H. and F.W.S. developed the methodology and analysis; S.A.H. wrote the first draft with support from P.B.M.; all authors contributed to reviewing and editing.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41893-025-01577-x.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-025-01577-x.

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Peer review information *Nature Sustainability* thanks the anonymous reviewers for their contribution to the peer review of this work.

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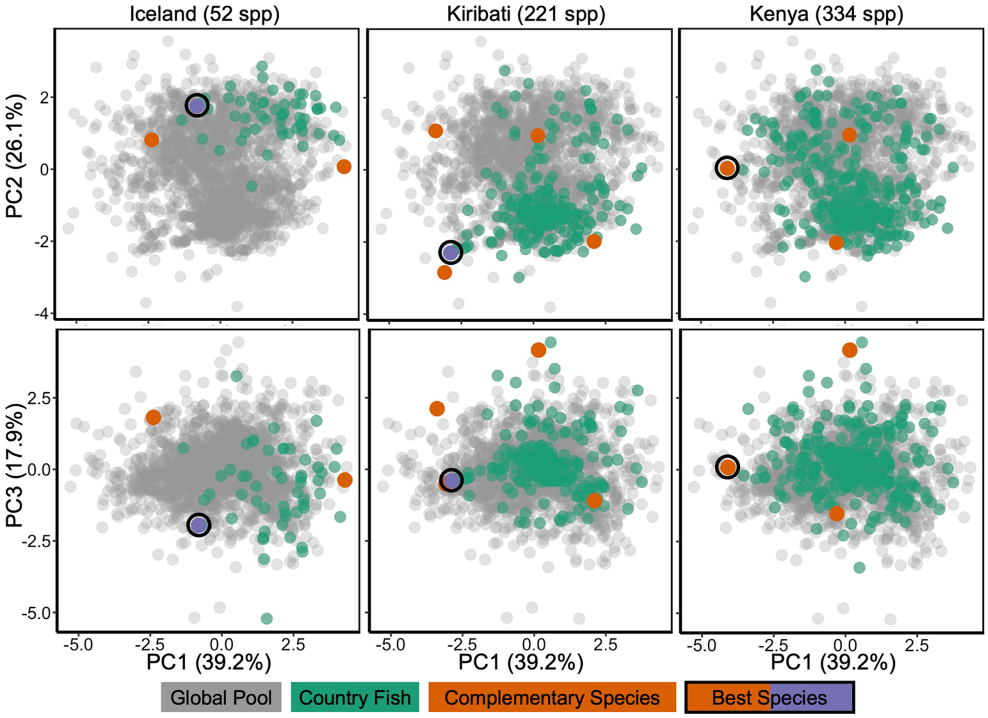
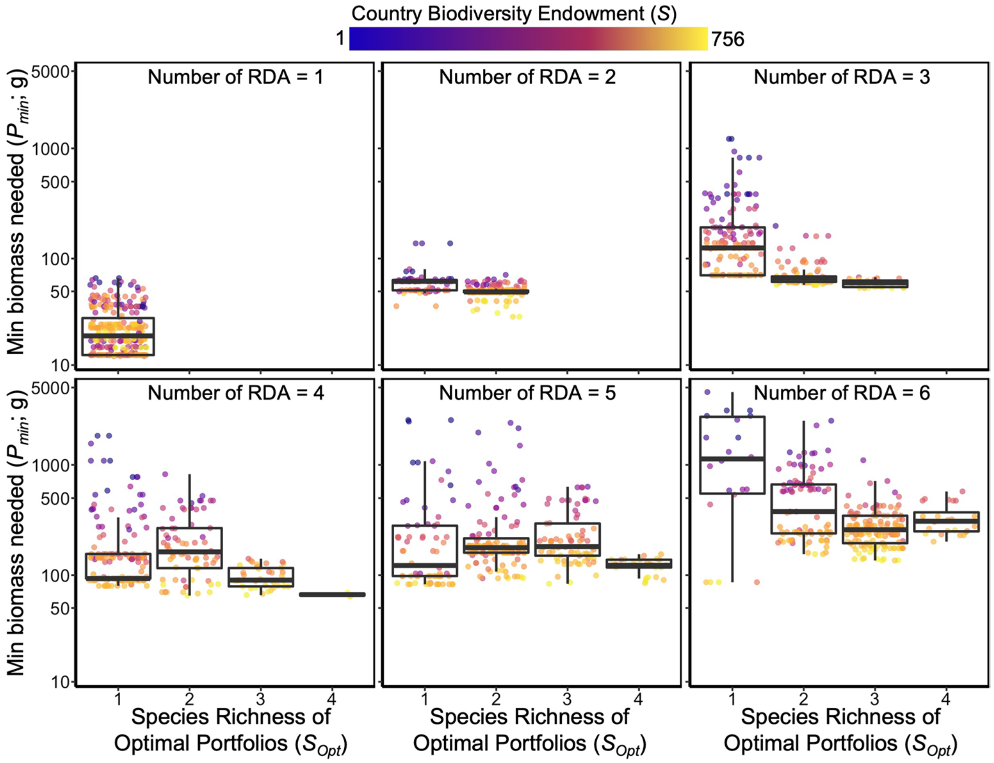


Extended Data Fig. 1 | Variation in nutrient content across all food fish species (grey), and for specific countries (green; first column: Iceland; second column: Kiribati; third column: Kenya), as depicted by the first three principal components using all nutrient content values (for example, protein, iron, zinc, calcium, vitamin A and omega-3s [EPA+DHA]). Complementary species (orange) are the species included within optimal portfolios, while the best species (purple) is the single species that minimizes the biomass needed to support all RDAs. When a single best species is also included in an optimal portfolio, it is orange and outlined in black. More biodiverse countries are typically represented by a wider variation in nutritional trait space. Species included in the optimal portfolio are drawn from the edges of nutritional space, but do not overlap.



Extended Data Fig. 2 | The species richness of an optimal portfolio (S_{Opt}) increases as more RDAs are considered but never exceeds four species. Each point represents a country (n=291) colored by it's biodiversity endowment (*S*). Increasing the number of RDAs considered also leads to an increase in the minimum portion size needed (P_{min}), but more speciose portfolios are associated with lower P_{min}. Box plots display the median (center line), interquartile range (box) and whiskers (minimum and maximum values within 1.5 × IQR).

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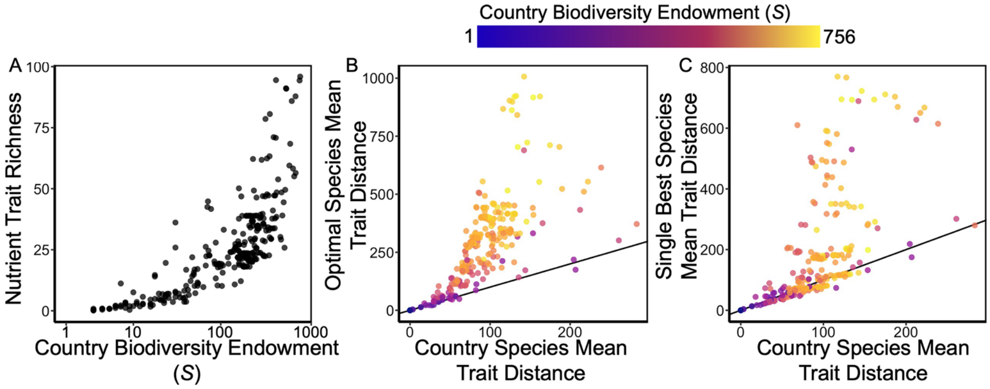
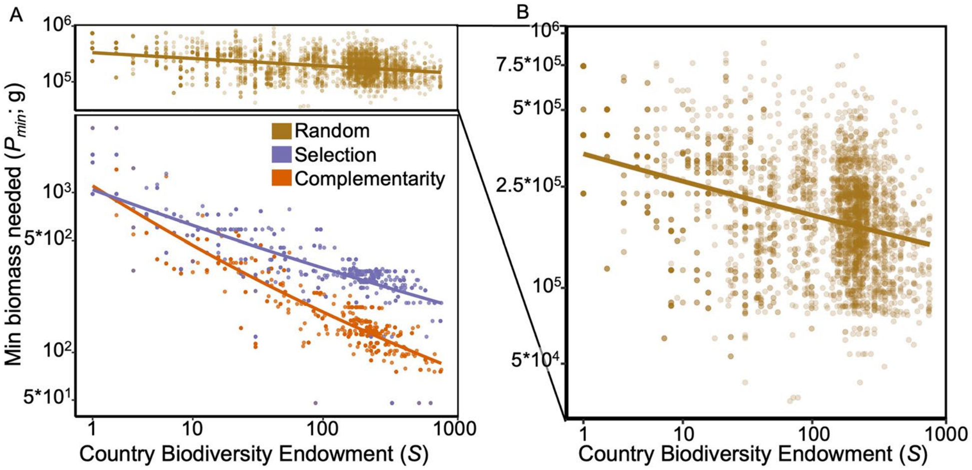
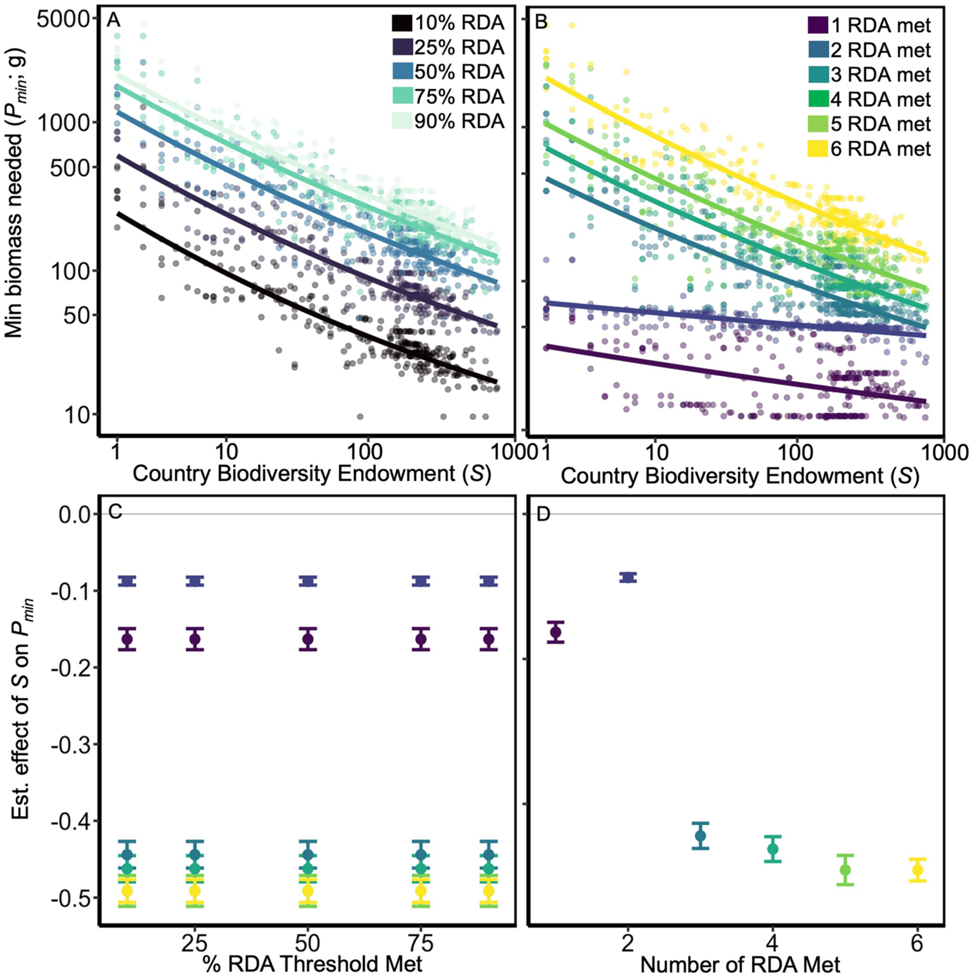


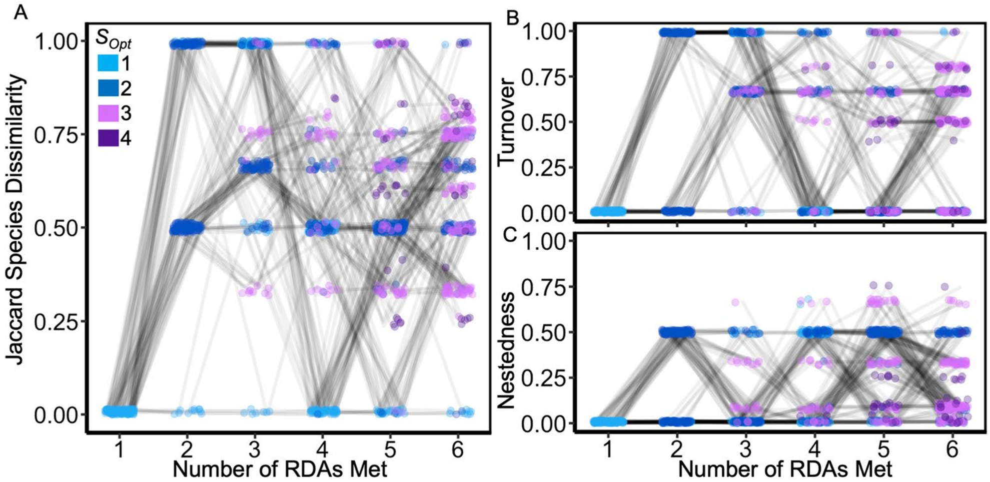
Extended Data Fig. 3 | The wider aggregate nutrient trait content variation in more biodiverse countries increased the potential to assemble optimal species portfolios or select single best species with nutritionally extreme values. (**A**) Species from countries with higher biodiversity exhibit more variation in nutrient content, measured as the convex hull volume considering six key nutrients derived from fish. (**B**) The mean nutrient trait distance of all species within a country tends to be lower than the mean nutrient trait distance of species in optimal portfolios (the black line represents the 1:1 line, with points above representing countries where the mean nutrient trait distance of optimal species is larger than of all species within that respective country). (**C**) The mean nutrient trait distance of all species within a country tends to be lower than the mean nutrient trait distance of single best species (the black line represents the 1:1 line, with points above representing countries where the mean nutrient trait distance of the single best species is larger than of all species within that respective country). Each point corresponds to a country (n=290).



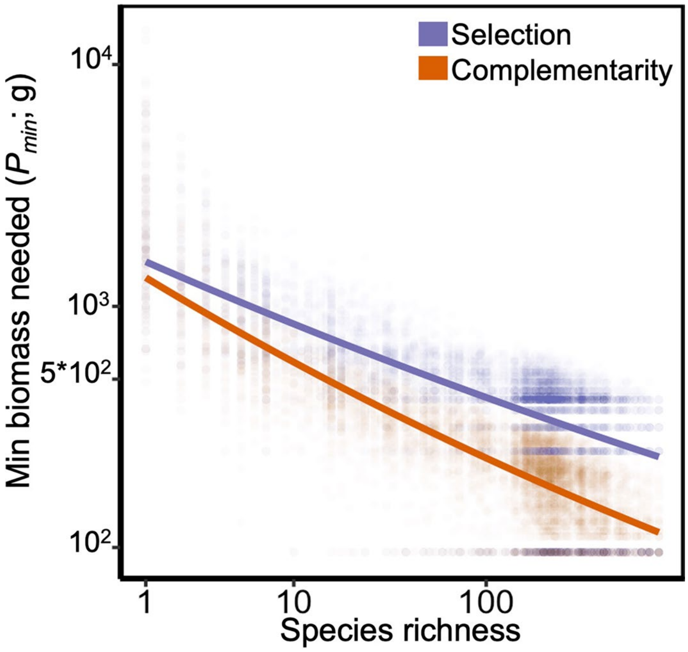
Extended Data Fig. 4 | Randomly assembled portfolios from countries with high biodiversity required less biomass to meet RDAs, but differences with portfolios based on complementarity and selection were exceptionally large (n=290). Random portfolios were assembled by drawing a random sample of the same number of species represented in the optimal portfolio from each country (*see methods*). For full statistical results see Table S1. Panel **B** is a close-up of panel **A**.



Extended Data Fig. 5 | Countries well-endowed with biodiversity sustain nutritionally complete diets with less biomass regardless of (A) %RDA thresholds or (B) number of RDAs considered. The biodiversity effect (that is, estimated effect of *S* on on P_{min}) does not vary based on (**C**) thresholds but (**D**) becomes stronger when more RDAs are considered. The biodiversity effect was obtained by using a generalized linear model and extracting the estimates and 95% confidence intervals.



Extended Data Fig. 6 | The species composition of optimal portfolios depends on the number and type of nutrient RDAs are considered. Each point represents a country (n=290) colored by the number of species within an optimal portfolio as indicated in the legend in (**A**), with lines connecting the same country. Points are jittered for interpretability. Dissimilarity, turnover and nestedness are measured as the pairwise differences between each successive number of RDAs for each country, with 0 indicating that there are no differences in optimal species composition and 1 indicating complete compositional turnover when comparing successive number of RDAs. For example, for the vast majority of countries the species composition of optimal portfolios that meet 2 RDAs is completely different than the species that are optimal to meet one RDA. When increasing from one to three RDAs, compositional changes are primarily driven (**B**) turnover, which represents changes in species composition driven by replacement of some species by others that were not previously included. When increasing from four to six RDAs, compositional changes are represented by a mixture of turnover and (**C**) nestedness, the latter representing changes in species composition driven by gains or losses of species.



Extended Data Fig. 7 | Biodiversity gradient with random species draws from a global pool retains the same relationship between species richness and the minimum amount of fish biomass to meet RDAs based on complementarity and selection. To build this random biodiversity gradient we sampled the global pool of species without replacement from 1 to 756 species, which is the species richness range for the number of food fishes available across nations. For every level of species richness, we performed this randomization 30 times for all 290 countries for a total of 8,700 random assemblages.

Extended Data Table 1 | Results from the generalized linear models with a country's biodiversity endowment as the predictor variable and the minimum amount of fish biomass needed to meet all RDAs considered based on complementarity, selection and randomly assembled portfolios from each country

	Estimate	Std. Error	P-value	McFadden's R^2
Complementarity	-0.49	0.015	<0.001	0.78
Selection	-0.32	0.011	<0.001	0.68
Random	-0.15	0.004	<0.001	0.20

For each country (n=290), 30 randomly assembled portfolios were generated with the same number of species as the country's optimal portfolio (*see methods*).

Extended Data Table 2 | Results from the generalized linear models with a country's biodiversity endowment as the predictor variable and differences in trait mean and trait breadth between optimal and randomly assembled portfolios, estimated as the log response ratio (LRR), as the response variable

Trait	Mean/dst	Estimate	Std Err	P-Value	McFadden's R2
Total length	Mean LRR	-0.121	0.006	<0.001	0.061
	Dst LRR	-0.276	0.013	<0.001	0.074
Trophic Level	Mean LRR	-0.010	0.001	<0.001	0.011
	Dst LRR	0.003	0.003	0.324	0.0001
Temperature Preference	Mean LRR	0.002	0.003	0.562	0.001
	Dst LRR	0.023	0.011	<0.01	0.002

For each country, 30 randomly assembled portfolios were compared against the optimal portfolio (*see methods*).

nature portfolio

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Last updated by author(s): Apr 14, 2025

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We used species evaluations by the IUCN to categorize each or the world's fish species as either consumed as food or not (IUCN, 2023). For every food species, we then obtained country occurrence, nutrient content and ecological trait information from FishBase (Frose and Pauly, 2023). We also obtained information on fish consumption from the Aquatic Resource Trade in Species (ARTIS) (Gephart. et al 2025).
Data analysis	All analysis was conducted in R (R core team) and code supporting the results are available via the Figshare repository with https://figshare.com/s/05676334987da57f7418

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Study description	This study analyzes how biodiversity in fisheries can enable more nutritious and sustainable diets by adopting an allocation optimization approach, where for every country, we identify the species of fish that meet nutritional requirements with the lowest amount of fish biomass.
Research sample	We use information that is publicly available from FishBase and IUCN (as described above). We paired the geographical overlap between fish species ranges and national boundaries for ~2,500 fish species and all nations of the world to obtain country level species lists, which were also paired with each fish species nutrient content information. The nutrient content information is available in FishBase and based upon models developed in Hicks et al. 2019 Nature. In total, we had 183 countries, with fish species richness ranging from 1 to 753.
Sampling strategy	Our unit of analysis was for every of the 290 countries/territories we had fish biodiversity information for.
Data collection	Data was downloaded from FishBase and IUCN.
Timing and spatial scale	The data was downloaded in April of 2023.
Data exclusions	No data was excluded from the analysis.
Reproducibility	Our approach was computational and is available for reproducibility in the code available in Figshare: https://figshare.com/s/05676334987da57f7418
Randomization	This question is not relevant to our study since we used publicly available information, and was not based on treatments. Every country's biodiversity was determined using existing information.
Blinding	This question is not relevant to our study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging