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Nutritional challenges of substituting farmed animals for wild fish in human diets

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E-mail: s.heilpern@cornell.edu**Keywords:** food systems, fisheries, traits, nature's contributions to peopleSupplementary material for this article is available [online](#)**Abstract**

Wild fisheries provide billions of people with a key source of multiple essential nutrients. As fisheries plateau or decline, nourishing more people will partially rely on shifting consumption to farmed animals. The environmental implications of transitions among animal-sourced foods have been scrutinized, but their nutritional substitutability remains unclear. We compared concentrations of six essential dietary nutrients across >5000 species of wild fishes, aquaculture, poultry and livestock species, representing >65% of animals consumed globally. Wild fishes are both more nutrient-dense and variable than farmed animals; achieving recommended intake of all nutrients with farmed species could require consuming almost four times more biomass than with wild fish. The challenge of substituting farmed animals for wild fishes are magnified in fishery-dependent nations with high biodiversity and prevalence of malnutrition. Ultimately, the better ability of wild fishes to meet multiple nutrients simultaneously underscores the importance of drawing upon a diverse portfolio of animal- and plant-based foods as societies seek to offset changes in fisheries while achieving healthy and sustainable diets.

1. Introduction

Over two billion people depend on wild fishes for multiple essential nutrients, but overexploitation, climate change and other factors are affecting harvest amounts and composition (Hicks *et al* 2019). Nourishing a growing human population despite shifting wild fisheries will likely entail substitution with nutritionally similar foods (Golden *et al* 2021b). Farmed species of fish, birds, and mammals represent an alternative class of animal sourced-foods (ASFs) because they are often considered comparably nutritious, widely accessible, and culturally acceptable (Popkin 2014). Farmed ASF, however, comprise few species that have been selected for economic purposes rather than nutritional value. Additionally, farming ASF is a major contributor to global change

(Gephart *et al* 2021). Although there are other options for offsetting fishery declines (e.g. fortification, plant-based diets), growth in availability and demand for ASF features prominently in food system transitions that are underway globally (Popkin 2014). Understanding the nutritional implications of shifts from wild fish to farmed ASF is imperative, especially in geographies that rely heavily on wild fisheries.

Although farmed ASF are often viewed as comparable to wild fishes in nutritional value (Zaharia *et al* 2021), their actual degree of nutritional parity is unclear. Vertebrate animals provide multiple nutrients that are essential for human health, including protein, iron, zinc, calcium, vitamin A and omega-3 s (Hicks *et al* 2019). Although some species are renowned for high concentrations of specific nutrients (e.g. fishes and omega-3 s (Golden *et al* 2021b)),

nutritional value is fundamentally multidimensional: any given food type functions as a source of many nutrients simultaneously. Yet, even within a group of related species in a same geographic region, nutrient content can vary considerably due to ecological (e.g. environment, metabolism, trophic level, feed) and sociocultural factors (e.g. preparation methods, parts consumed, Heilpern *et al* 2021a). Evaluating whether farmed ASF can compensate for the nutritional benefits provided by wild fisheries requires accounting for the multivariate nature of nutrient content, and the heterogeneous distribution of ASF species across the globe.

Here we test the nutritional substitutability among five major groups of vertebrate animals that comprise over two-thirds of global ASF consumption: freshwater capture fisheries, marine capture fisheries, farmed fishes, farmed poultry, and farmed livestock (Food and Agriculture Organization 2014). Pairing a database of estimated nutrient content values for 5485 fish (667 freshwater fish, 4818 marine fish, 19 aquacultured species; (Froese and Pauly 2019)) with measured nutrient content for 20 mammals and 12 birds, we analyze patterns of multivariate variation among ASF groups. To ground these comparisons, we calculate the minimum biomass needed for a child under 5 years old to meet daily recommended dietary allowances (RDAs) for six nutrients simultaneously (i.e. protein, iron, zinc, calcium, omega-3 s and vitamin A) that are essential for human health and development, are derived partly or wholly from consuming ASF and are widely available across all ASF species (Black *et al* 2013, Beal *et al* 2017). Because not all wild species are available across countries, we then pair nutrient content data with species biogeographic information to quantify the potential for farmed ASF to supply comparable nutrition as the wild fishes found in each nation. We focus on these vertebrate groups (i.e. teleosts (bony fishes), elasmobranchs (sharks and rays), poultry and livestock), because of their singular importance in global food systems and availability of relatively complete distribution and nutrient content data. This integration of multivariate statistics on animal nutrient content, dietary needs, and species distributions enables us to test whether shifts in the availability of wild fishes will create nutritional challenges despite replacement with farmed animals. In light of our results, we discuss other options to offset nutrient gaps introduced by shifting wild fish availability (e.g. plant-based diets, fortification, expanding non-vertebrate aquatic food consumption).

2. Methods

2.1. Species nutritional and ecological information

Two nutritional datasets were used in our analysis. First we compiled measured information from three key sources (Hicks *et al* 2019, Byrd *et al* 2021,

FAO 2021), and complemented these by conducting our own search for information between November 2020 and May 2021. Our search specifically targeted countries with neglected freshwater fisheries, such as in the Amazon, sub-Saharan Africa and South East Asia, which were least likely to be included in previous dataset compilations focusing on marine fish (Byrd *et al* 2021). Our search focused on published scientific literature using Web of Science and gray literature using Google for search terms [Country] AND fish* AND nutri* AND (content OR composition OR quality). Inclusion criteria was based on sources being fully traceable and accessible, on analysis conducted on fresh and non-composite samples, measured information (and not estimated; see below), content reported as quantitative (rather than a range or descriptive), and on taxonomy being resolved to the species level. Nutrient composition data and units were extracted for all available macro- and micro-nutrients, including omega-3 s subsidiaries (eicosatetraenoic acid [EPA] and docosahexaenoic acid [DHA]). To avoid duplicated sources when integrating datasets, we only merged species that were not included across all references. Terrestrial animal food nutritional content was obtained from INFOODS (FAO 2021) and the US Department of Agriculture FoodData Central (USDA 2021) using the same criteria as above.

In addition to this dataset with measured values, we obtained nutritional information from FishBase (Froese and Pauly 2019), which includes estimated nutrient content values for over 5000 primarily marine species from a model developed in Hicks *et al* (2019). To merge the datasets with measured and estimated values, we only included species that were not duplicated across datasets. Due to differences in preparation and tissues consumed, we standardized our analysis to raw muscle tissue. In the main text, we report results focusing on the combined estimated and measured dataset whereas the supplement contains results from the measured dataset.

Ecological information on habitat and distribution was downloaded from FishBase using the *rFishBase* package for R (R Core Team 2020, Boettiger *et al* 2021). For habitat, species were categorized as either primarily freshwater or marine. Fish species designated as aquacultured were the 22 species that account for over 75% of global production (Naylor *et al* 2021). Our database was created independently and contemporarily with the Aquatic Food Composition Database (Golden *et al* 2021) and overlaps extensively, but is fully resolved with regards to the taxonomy and across all nutrients, which is required to undertake our multivariate biogeographic analysis.

2.2. Quantifying nutrient variation

We identified the main axis of variation using principal coordinates analysis on all species mean nutrient

values. All nutrients except protein (i.e. Fe, Ca, Zn, vitamin A and ω -3 s) were log-transformed prior to analysis. Then, values were standardized (z-transformed) to account for their different measurement scales. We used Horn's parallel analysis to identify the PC axes with non-redundant information from the *paran* package for R (Dinno 2018). We also computed the nutritional content probabilistic distribution for each ASF group within the first two PC by performing multivariate kernel density estimations using the TPD package for R (Carmona 2019).

2.3. Portion sizes to satisfy recommended daily intakes

For each species, we analyzed the portion size needed to meet RDA for each nutrient, and ranked nutrients in increasing order of portion size. Because each species can theoretically contribute to all nutritional RDAs, standardizing each species' nutritional contribution by a minimum portion size provides a comparable metric of their overall nutritional quality. For this analysis we focused on RDAs for children under five, who have unique nutritional requirements and for whom the lack of adequate nutrition can lead to life-long health problems. RDA values for protein and vitamin A were obtained from FAO/WHO (2004), while RDAs for Fe, Zn, Ca and ω -3 s were obtained from FAO (2010) (table S1). We compared differences in the minimum biomass needed among food groups and number of nutrients considered using a nested analysis of variance with number of RDAs nested within food groups.

2.4. Geography of nutritional substitutions

For each country, we created a list of potentially available fish species using the distribution of each species obtained from FishBase (Froese and Pauly 2019). Farmed ASF species were assumed to be available in every country. To obtain a country-level substitutability estimate for each food group, we first obtained the nutritional substitutability of each species within each country as the change in portion size needed to meet RDA for all nutrients when substituting one species for another species. Then, for each country, we calculated the median change in portion size needed to meet RDA for all nutrients for each food group. To understand how wild fish diversity shapes substitutabilities, we used linear regressions with the change in portion size needed as the dependent variable and number of wild fish species as the independent variable for each food group independently.

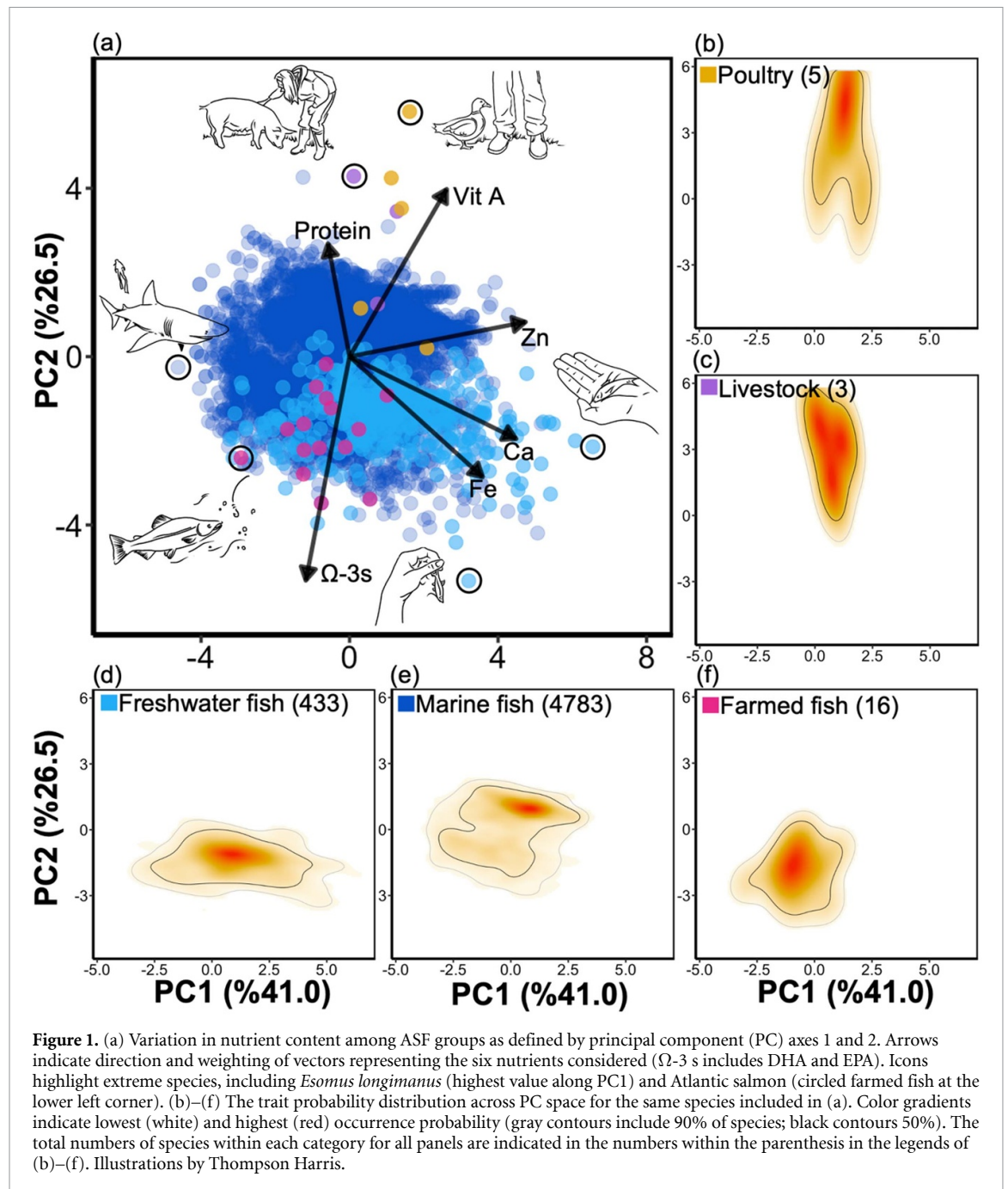
Country-level information on apparent consumption of each food group was obtained from FAOSTAT (Food and Agriculture Organization 2014), and children nutrition data was obtained from the World Bank (2020). All analyses were conducted using R (R Core Team 2020), with the exception of the maps, which were created using Datawrapper (www.datawrapper.de).

3. Results

ASF species exhibit a wide range of nutrient content: differences can be summarized by three principal component (PC) axes accounting for 84.6% of total variation (figure 1(a)). These orthogonal axes feature different loadings of individual nutrients; PC1 (41.8% of variation) is associated with trace mineral content (Fe, Zn and Ca); PC2 (26.5%) primarily reflects omega-3 fatty acids and vitamin A; and PC3 (17.1%) is associated with protein content, and to a lesser degree Fe. The distinct nutrient loadings among the PC axes indicate that covariation among nutrients is generally low. Hence, the distribution of species within this multidimensional space is shaped by disparities among multiple nutrients, rather than any single nutrient.

The five groups of ASF also occupied different positions within multidimensional nutritional space (figures 1(b)–(f)). Terrestrial farmed animals are distinguished from other groups primarily along PC2, reflecting their low omega-3 s and moderate Vitamin A content. Farmed fishes are also differentiated by PC2, primarily because of their higher omega-3 content. Wild fishes, in contrast, are dispersed along all three PC axes, indicating that species span the range of all nutrients considered. Yet differences between wild fishes also emerge: marine fishes are more likely to be found near the center of PC space, whereas freshwater fishes have a high probability of occupying a wide range along PC1 (figures 1(d) and (e)). These multivariate patterns are mirrored by the variation in individual nutrients; wild fishes span an order of magnitude in five of the six nutrients analyzed (figure S1). The exception is protein, which is relatively similar among all ASF. The same patterns were evident when analyzing only species whose nutrient content was measured directly (figures S2 and S3).

ASF groups differed significantly in their minimum portion size needed to meet RDAs ($P < 0.001$; figure S2 and table S2). However, virtually no species offered high content of all nutrients (figure 2). Among 5536 species, only one could meet all six RDAs simultaneously with a portion size of <100 g for a five-year-old child: *Esomus longimanus* (Cypriniformes: Danionidae), a small freshwater fish from the Mekong River (figure 1(a)). For most ASF species, the daily portion size required increased exponentially with the number of nutrients considered, reaching as much as 10 kg for a child to meet all six nutrients ($P < 0.001$; figure 2(a) and table S3). Additionally, considering more nutrients accentuated variation among species potential to meet multiple RDAs simultaneously (figure S2(b) and table S3). Considering the rank order in which nutrients were met, protein was typically first, reflecting its high concentration across all ASF species (figures 2(c)–(h)). Seventy-five percent of farmed fishes, 73% of inland fishes, and 35% of



marine fishes also provide sufficient omega-3 s with less than 100 g, making that the second most frequent RDA met for fishes. In comparison, livestock and poultry met Zn second, but with recommended portion sizes >100 g (figure 2(f)).

Differences in fish faunas among countries created a strong geographical imprint in the nutritional substitutability of ASF groups. In approximately 50% of countries, notably in South America and West Africa, achieving RDAs would require larger portions of marine fish compared to freshwater species (figures 3(a) and (b)). However, larger increases in portion sizes would be required to substitute farmed ASF for wild fishes in all countries (table S4). Achieving all six RDAs simultaneously

with farmed fish would require increasing median daily portion sizes by 155% (1.2 kg; 0.89–3.42 kg, interquartile range) and 230% (1.9 kg; 1.22–3.75 kg, interquartile range) relative to eating wild freshwater and marine fishes, respectively (figures 3(c), (d) and table S3). Substituting poultry for freshwater fishes would require increasing portion sizes by 160% (1.3 kg; 2.02–3.96 kg, interquartile range) and for marine fishes 236% (2 kg; 2.35–4.29 kg, interquartile range; figures 3(e) and (f)). Substituting livestock for freshwater fishes would require increasing portion sizes by 246% (3.2 kg; 4.05–9.16 kg, interquartile range) and for marine fishes 364% (3.9 kg; 4.38–9.49 kg, interquartile range; figures 3(g) and (h)).

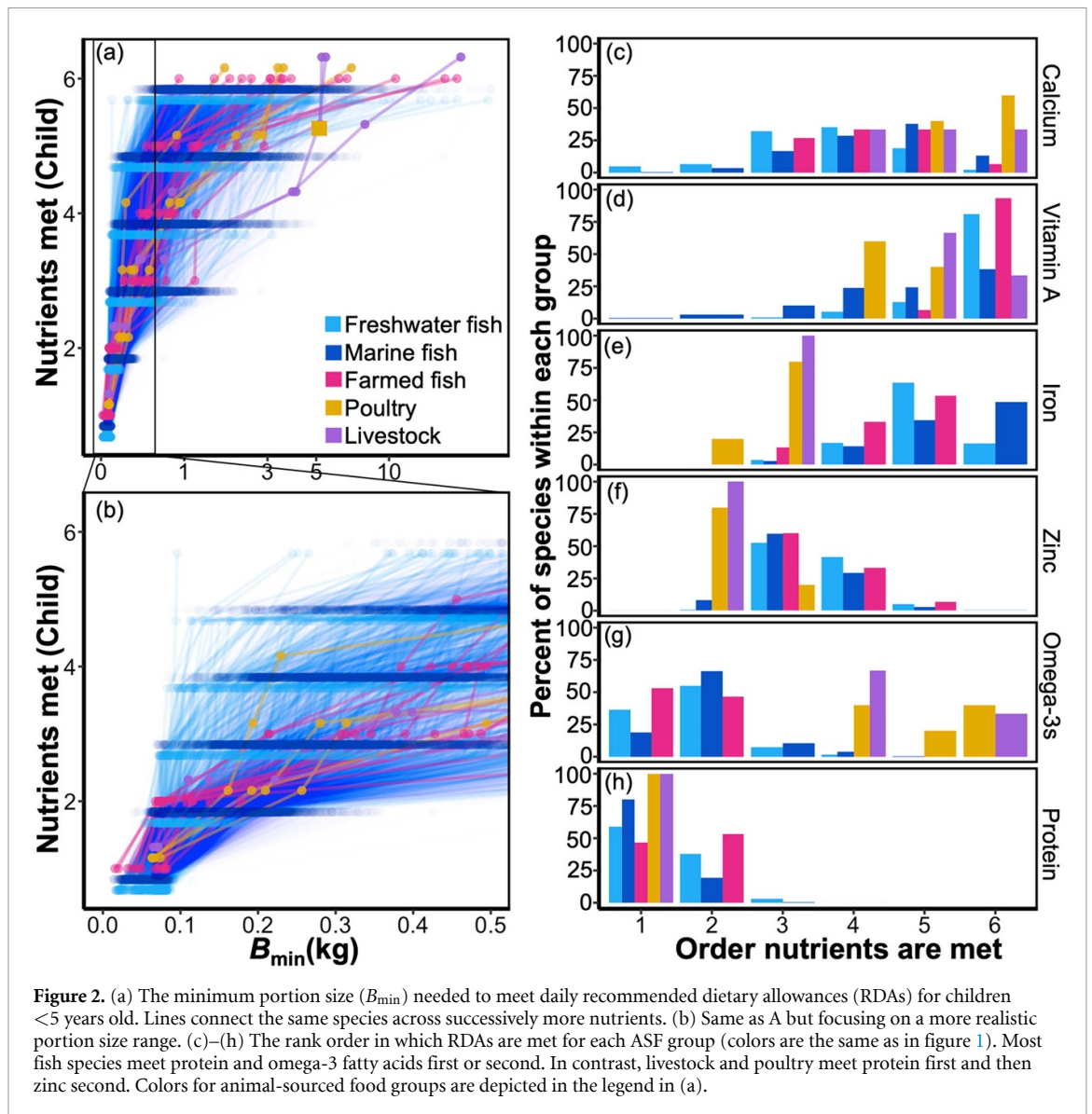


Figure 2. (a) The minimum portion size (B_{\min}) needed to meet daily recommended dietary allowances (RDAs) for children <5 years old. Lines connect the same species across successively more nutrients. (b) Same as A but focusing on a more realistic portion size range. (c)–(h) The rank order in which RDAs are met for each ASF group (colors are the same as in figure 1). Most fish species meet protein and omega-3 fatty acids first or second. In contrast, livestock and poultry meet protein first and then zinc second. Colors for animal-sourced food groups are depicted in the legend in (a).

The challenge of species substitutions was particularly severe in countries with high wild fish biodiversity, and where reliance on fisheries and undernourishment are prevalent (figures 4 and S5). For example, obtaining the same nutrient intake from farmed ASF as freshwater fisheries in Cambodia, which, with 77 freshwater fish species, has both the highest reported consumption of freshwater fishes and a 26% rate of childhood undernourishment, would require increasing portion sizes by approximately 280% (2.02 kg; 0.55–3.64 kg, interquartile range), 288% (2.65 kg; 1.05–6.32 kg, interquartile range) or 444% (4.65 kg; 3.74–7.92 kg, interquartile range) for farmed fishes, poultry or livestock respectively. Similarly, in Sri Lanka (623 marine fish species), which relies heavily on marine fisheries and has 23% of children undernourished, substituting marine fishes with farmed ASF would require 253% (1.92 kg; 0.54–5.21 kg, interquartile range), 260% (2.39 kg; 0.89–6.02 kg, interquartile range) or 401% (4.36 kg;

3.71–16.85 kg, interquartile range) larger portions for farmed fishes, poultry and livestock, respectively.

4. Discussion

Aquatic animals are already acclaimed for having the smallest environmental footprint among ASF (Gephart *et al* 2021, Golden *et al* 2021b), and our findings indicate that wild fishes are also noteworthy for both their high nutrient density and wide multivariate variation in comparison to farmed ASF. Three key patterns emerged from our analyses. First, accounting for multiple nutrients simultaneously reveals that wild fish and farmed animals exhibit fundamentally distinct nutrient profiles (figure 1). Second, virtually no animal species is rich in all nutrients, hence a portfolio approach to dietary recommendations is imperative (figure 2). Third, in most nations, replacing wild fisheries with farmed ASF would require unrealistic changes in portion sizes to

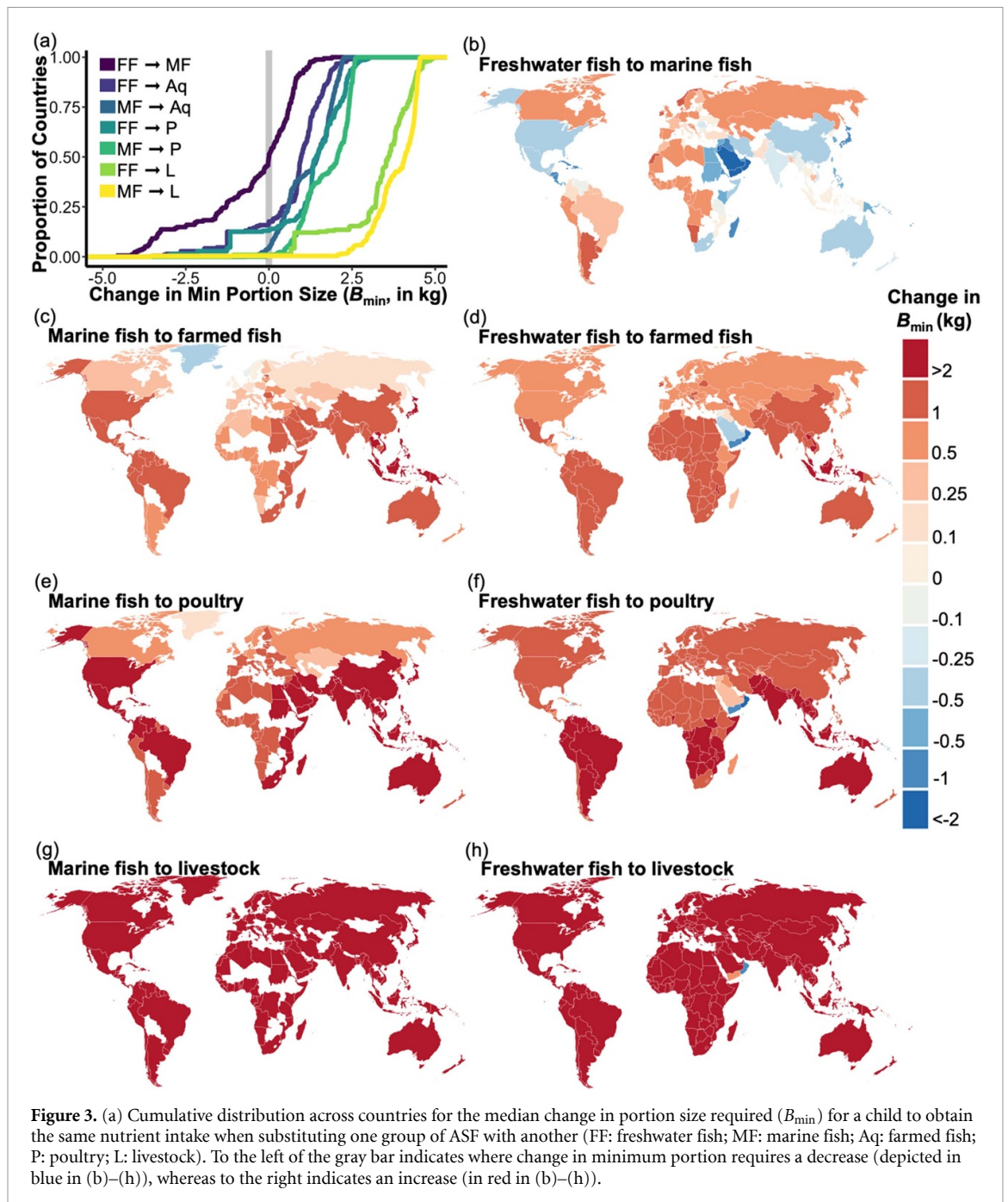
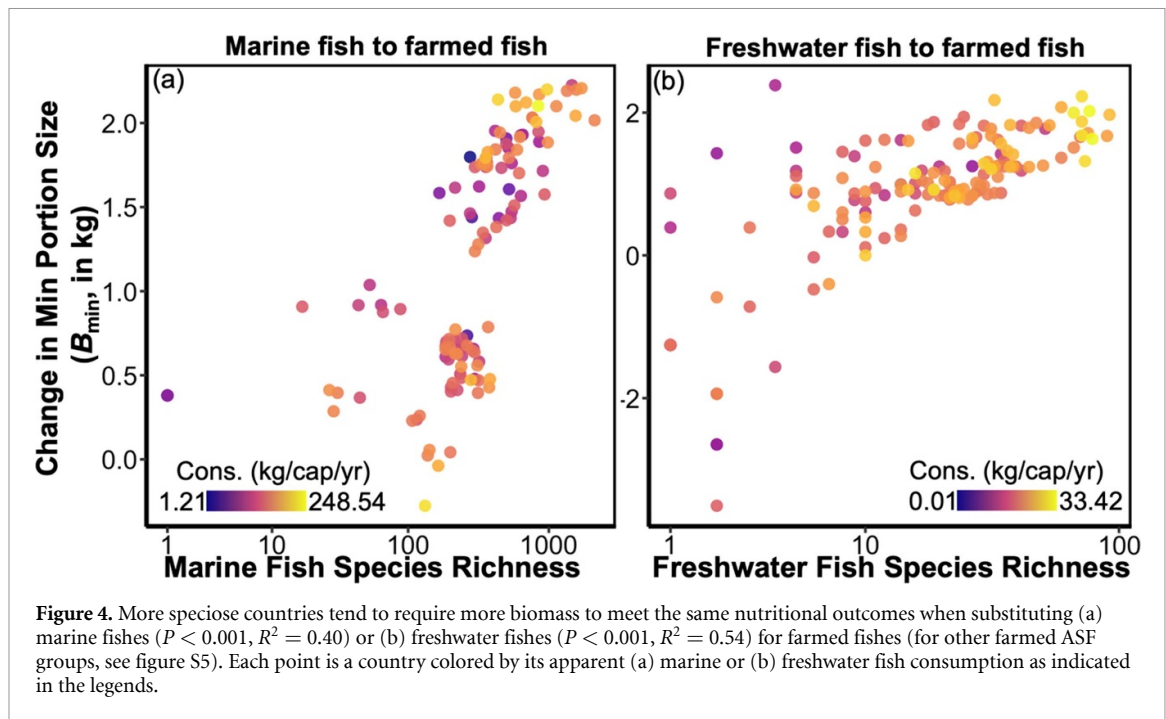


Figure 3. (a) Cumulative distribution across countries for the median change in portion size required (B_{\min}) for a child to obtain the same nutrient intake when substituting one group of ASF with another (FF: freshwater fish; MF: marine fish; Aq: farmed fish; P: poultry; L: livestock). To the left of the gray bar indicates where change in minimum portion requires a decrease (depicted in blue in (b)–(h)), whereas to the right indicates an increase (in red in (b)–(h)).

achieve comparable nutrient intake (figures 3 and 4). All three patterns apply even to farmed fishes, which are often considered central to meet growing demand for ASF as wild fisheries plateau or decline (Fiorella *et al* 2021).

The ability to describe nutritional variation across vertebrate groups with three composite axes (figure 1) suggests that shared biological mechanisms determine nutrient content, presumably as an outcome of both ecological and evolutionary processes (Hicks *et al* 2019). Fisheries harvest the most diverse group of vertebrates, which occupy virtually all of Earth's aquatic habitats and exhibit a vast range of ecological strategies (Rabosky *et al* 2018). In contrast, farmed animals encompass a limited range of phylogenetic

and ecological variation, and are typically fed similar diets designed to maximize growth rates and economic efficiency (Milla *et al* 2018). For example, just 22 fish species account for 75% of global aquaculture production, and most are either salmonids or low-trophic level cyprinoids (Fiorella *et al* 2021). Evolutionary constraints on metabolism and anatomy create contrasts in elemental stoichiometry across vertebrates (Sterner and Elser 2002), and nutrient content is a logical extension of such mechanisms. The differences among groups of ASF suggest limited scope to modify nutrient content of farmed animals without genetic engineering, but use of fortified feeds and selective breeding are well validated for some nutrients (e.g. omega-3 fatty acids; Scollan *et al*



2017). The presence of deep-rooted evolutionary differences in nutrient content also provide opportunities to integrate other conserved traits (e.g. climate vulnerabilities, life history) when seeking to design portfolios of ASF to enhance food system sustainability (Heilpern *et al* 2021a, 2021b).

For most ASF species, the portion size required to meet RDAs increases exponentially with the number of nutrients considered, becoming staggeringly large to meet all six RDAs simultaneously (figure 2(a)). Despite exhibiting a wide variety of nutritional profiles in comparison to farmed ASF (figures 1 and S2), this overall lack of nutritionally-sufficient species contrasts with generalizations about the nutrient-richness of fishes. For instance, only a few fish species provide sufficient Ca and Vitamin A with < 100 g. These two nutrients stand out because they are readily available from sources other than muscle tissue, including both plant (e.g. roots, fortified grains) and animal (internal organs, bones, dairy) materials (Downs *et al* 2020). Thus, our analysis corroborates the widely-held perspective that a nutritionally complete diet must also include a wide portfolio of plant-based foods (Golden *et al* 2021b), because even nutrient-dense ASF can only fill a modest number of RDAs simultaneously.

Further underscoring the value of a portfolio approach are our findings that speciose countries tend to require more biomass to meet the same nutritional outcomes when substituting wild fishes for farmed ASF (figures 4 and S5). Replacement of wild fisheries with farmed ASF manifest as changes in both the nutrient quality represented by any individual species as well as in the nutritional variation represented by each group. These two

factors—species identity and group variation—are well recognized in driving the diversity effect in both ecology and nutrition (Heilpern *et al* 2023), and by extension, are likely associated with the higher substitution costs of replacing the diversity of wild fish with fewer farmed ASF. Many countries with diverse fish faunas also have high apparent wild fish consumption but are transitioning towards western diets (Golden *et al* 2021a). As regional evidence suggests, these dietary transitions from wild fisheries towards farmed ASF could further exacerbate existing micronutrient deficiencies (Heilpern *et al* 2021b). Thus, maintaining access to a wide portfolio of species can increase the potential inclusion of both nutrient rich species as well as a wide variety of complementary species, and better sustain multiple nutritional benefits.

Our multivariate perspective on ASF nutrient content complements other approaches to analyzing the consequences of shifting wild fisheries quantity and diversity in global food systems. ASF provide multiple essential nutrients simultaneously, and estimating the biomass needed to fulfill RDAs reduces this dimensionality to a single-plate level currency that is comparable across nutrients and species. This biomass approach also provides insights into how nutrient content variation scales with the number of dimensions considered. Further, while we focused on ASF, as a species-level metric, our approach could be extended to other food groups and biomass-dependent processes, such as environmental costs or economics. For example, accounting for the greenhouse gas (GHG) emissions of different ASF places wild fishes with the lowest impact (Gephart *et al* 2021). Thus, the more biomass needed to satisfy RDAs when replacing wild fishes with farmed ASF

could result in higher GHG emissions than expected based on single nutrient comparisons (e.g. protein). Biomass production is also related to price, and shifts in production and demand could lead to shifts in accessibility. Ultimately, this biomass approach could be expanded to include linkages between the multivariate nature of nutrition to additional dimensions of sustainability.

We recognize that nutritional outcomes reflect more than just the nutrient content of alternative foods; access to and use of wild and farmed animals are influenced by numerous factors. Trade mediates species prices from local to global scales (Cottrell *et al* 2019). Wild-fishes vary widely in their affordability, although artisanal fisheries for subsistence are widespread, especially for small-bodied and highly nutritious species (Robinson *et al* 2022). At a national scale, import or export of ASF could either dampen or exacerbate nutritional gaps depending on whether trade skews towards nutrient-dense species. For example, aquaculture feeds incorporate small, nutrient-rich fishes that are often exported from food-stressed countries, potentially reducing their local access in exchange for export income (Fiorella *et al* 2021). Cultural traditions also shape how people choose, prepare, and consume ASF. For example, some cultures embrace consuming small fishes whole, including nutrient-dense tissues (e.g. viscera, bones) that are excluded when filleting larger species (Byrd *et al* 2021). Additionally, substitutions are rarely exact; consumers could partially replace, increase, or decrease the amount of biomass consumed depending on factors such as food type, preferences, and price. Accounting for these differences is challenging in a global analysis, but must be included in any full assessment of the multifaceted challenges of substituting farmed ASF for wild fisheries.

Interpretation of our findings, and most other synthetic analyses of nutritional data, rests on several additional assumptions. First, we presume that sampled nutrient content data are representative for each species as a whole, but species can vary intraspecifically in their nutrient content in response to environmental, dietary, or genetic factors (Hixson *et al* 2015). Our findings should be valid as long as the variance among species exceeds that within species. Second, the available data are assumed to represent what people assimilate from consuming ASF, but preparation and cooking practices can strongly mediate nutritional outcomes (Byrd *et al* 2021). Third, we focused on six of the many nutrients that are requisite for health. Data on additional nutrients are generally lacking for most wild fish, but increasing the dimensionality of our analysis would accentuate the nutritional complexity it reveals. This is particularly important considering the multiple pathways associated with the nutritional benefits and costs of ASF consumption, from micronutrients to

omega-3 s to other less healthy constituents (e.g. cholesterol, mercury; Golden *et al* 2021b). Finally, our focus on comparing animal groups does not constitute an endorsement of the centrality of ASF in human diets. Rather, we are responding to the reality that ASF are a major component of the global food system. Ultimately, enhanced nutritional outcomes and reduced environmental footprints will be most achievable by complementing a diversity of ASF with increased reliance on plant-based foods.

5. Conclusions

The multidimensional diversity in nutrient profiles within and among major groups of ASF underscores the importance of ensuring sustainable supplies of wild fishes. However, it is implausible that capture fisheries will meet the needs of a growing human population within planetary boundaries. Hence, sustaining the many nutritional benefits of wild fishes despite stagnating or declining captures fisheries will require addressing at least five issues in parallel. First, because the fisheries that sustain food security are also readily overharvested, improving their management, and halting the ongoing degradation of aquatic ecosystems, is essential (Hilborn *et al* 2020). Second, because nutritionally-complete species are rare, production statistics for ASF must expand beyond biomass by embracing the diversity of wild and farmed animals in the food system (Bernhardt and O'Connor 2021, Heilpern *et al* 2021a). Third, ASF are often viewed as sufficiently nutritionally comparable to be aggregated in surveys, studies and policies (Zaharia *et al* 2021), but our findings emphasize the necessity of accounting for the variation in multiple nutrients simultaneously among and within types of ASF. Indeed, some ASF may contain sufficient content of specific nutrients, but a single-nutrient focus may under or overestimate the nutritional implications of substituting one group with another. Fourth, our results suggest a two-fold challenge around boosting the average nutrient-density of ASF: to expand nutritional variation among farmed animals by expanding their phylogenetic diversity (including non-vertebrates), and to enhance the nutrient-density of the species already used for intensive farming (Fiorella *et al* 2021). Embracing nutritional diversity among ASF may also alleviate the environmental costs of farming animals (Gephart *et al* 2021) by shifting toward polycultures of species with complementary nutrient profiles. Finally, government agencies that manage fisheries and other wild foods are often separate from those overseeing farmed animals and food system policies, which hampers holistic innovations in policy, technology and culture (Moberg *et al* 2021). ASF epitomize the intersection of environmental, cultural, and economical factors, hence integrative policies are necessary to catalyze a

global transition towards healthy, equitable and sustainable food systems.

Data availability statement

Data and code are provided via the following link: <https://figshare.com/s/68286db5506c821b3aed>.

The data that support the findings of this study are openly available at the following URL/DOI: <https://figshare.com/s/68286db5506c821b3aed>. Data will be available from 1 January 2024.

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Author contributions

S A H designed the original research with substantial input from all authors. S A H and D W collated the data. S A H led the analysis and writing of the manuscript with substantial input from P B M. All authors subsequently contributed to research design and writing the manuscript.

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