

1 **Aquatic biodiversity enhances multiple nutritional benefits to humans**

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17 and visualized the data with input from MIO. JRB wrote the original draft of the manuscript,  
18 JRB and MIO contributed to writing and editing. MIO supervised the study.

19

20 **This PDF file includes:**

21 Main Text

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24

## 25 **Abstract**

26 Global food security relies on protein and essential micronutrients provided by seafood (Latham  
27 1997, Golden et al. 2016). The importance of seafood-derived micronutrients to human health  
28 suggests that consuming diverse aquatic species could enhance human well-being (Penafiel et al.  
29 2011). Biodiversity provides important ecosystem benefits to humanity (Cardinale et al. 2012),  
30 causing concern that declining biodiversity may affect human health (Myers et al. 2013). A key  
31 scientific question remains unanswered - does increasing species diversity in seafood diets  
32 improve their ability to meet nutritional needs? Here we used biodiversity-ecosystem functioning  
33 theory to test whether increasing species diversity allows seafood diets to fulfill multiple  
34 nutritional requirements simultaneously, a condition necessary for human health. We found that  
35 aquatic species with different ecological traits have distinct and complementary micronutrient  
36 profiles. The same complementarity mechanisms that generate positive biodiversity effects on  
37 ecosystem functioning in terrestrial ecosystems also operate in seafood assemblages, allowing  
38 for more diverse diets to yield increased nutritional benefits. Notably, nutritional metrics that  
39 capture multiple micronutrients essential for human well-being depend more strongly on  
40 biodiversity than ecological measures of function such as productivity. In contrast to the  
41 micronutrients, we found that increasing species diversity did not increase the amount of protein  
42 in seafood diets. We unify biodiversity-ecosystem functioning theory and human nutrition,  
43 demonstrating a direct link between multiple nutritional benefits of biodiversity and an  
44 ecosystem service underpinning human wellbeing. Our findings demonstrate that minimizing  
45 biodiversity loss at local and global scales will benefit global food and nutrition security.  
46

47 **Significance statement:**

48 Food security is not simply about maintaining yields, it is also the need for a stable supply of  
49 nutritionally diverse foods. Obtaining nutritious food is a major challenge facing humanity, and  
50 aquatic ecosystems can help meet this goal. From the perspective of human nutrition, how much  
51 biodiversity is enough biodiversity? How ecological processes influence the capacity of aquatic  
52 ecosystems to provide nutritionally diverse diets is largely unknown. We found that aquatic  
53 biodiversity enhanced nutritional benefits, because edible species showed distinct and  
54 complementary multi-nutrient profiles. Protein supply was independent of biodiversity, but the  
55 supply of micronutrients increased with biodiversity. Extending the multifunctional benefits of  
56 biodiversity to human nutrition underscores the need to minimize biodiversity loss for the  
57 benefits of humanity.

58

59

## 60 **Introduction**

61 Species losses and range shifts due to climate change, harvesting and other human activities alter  
62 aquatic biodiversity locally and globally (6, 7), affecting ecosystem functions and services to  
63 humans (8, 9). Seafood, consisting of wild-caught marine and freshwater finfish and  
64 invertebrates, not only provides an important source of protein and calories to human consumers,  
65 but also provides essential micronutrients, such as vitamins and minerals (1, 2, 10, 11). Though it  
66 is appreciated that biodiversity (variety and composition of species) in diets can lead to a more  
67 nutritious or beneficial diet overall (3, 12–18), aquatic biodiversity *per se* is only nutritionally  
68 valuable if consuming a more diverse seafood diet is more beneficial than simply consuming  
69 more seafood biomass. Understanding the value of biodiversity - distinct from total biomass - is  
70 a critical challenge as patterns of biodiversity continue to change in the Anthropocene.

71  
72 Ecological theory predicts that biodiversity can be ecologically and economically important,  
73 apart from the importance of total biomass or the presence of particular species (4, 19).  
74 Experiments and theory have shown that for a given species pool and ecological context (e.g.,  
75 prairie grasses, crops or intertidal seaweeds) diversity in ecological communities and agricultural  
76 systems enhances ecosystem functioning by two mechanisms: (i) more diverse assemblages may  
77 outperform less diverse assemblages of the same biomass because more diverse assemblages are  
78 more likely to include high performing species (a *selection effect*), or (ii) more diverse  
79 assemblages contain species with complementary functional traits that are not correlated or are  
80 correlated negatively among species, allowing them to function more efficiently (a  
81 *complementarity effect*) (20, 21). For aquatic animals, increased diversity enhances productivity  
82 of fish biomass (22) and also enhances temporal stability of biomass production and total yields

83 (22–24), providing economic and nutritional benefits to humans related to increased stability of  
84 harvests and production of biomass for consumption (23). When considering aquatic species  
85 from the perspective of human consumers however, functions other than biomass production  
86 become relevant. In addition to providing an important source of calories and protein in the  
87 human diet, seafood is increasingly recognized for its value in providing micronutrients, which  
88 are often scarce in the human diet (25, 26) but critical for human health. Total seafood biomass  
89 yields are not predictive of micronutrient benefits, suggesting that micronutrient content does not  
90 increase proportionally with community biomass or total seafood intake (26).

91  
92 Relationships between biodiversity (broadly defined to include abundance and biomass of  
93 species) and ecosystem function have been extended to ecosystem services, which include the  
94 cultural, economic or health benefits people derive from nature (5, 8, 27). Though there is clear  
95 evidence that certain species, such as salmon, provide important ecosystem services to humans  
96 (28), here we are interested in whether aquatic biodiversity *per se* (distinct from the identities  
97 and abundance of species) provides ecosystem services in the form of human nutrition, beyond  
98 total yields. For biodiversity *per se* (as opposed to increasing total seafood consumption) to  
99 enhance nutritional benefits as predicted by biodiversity-ecosystem functioning theory,  
100 micronutrient profiles must differ across species and their concentrations must be either  
101 uncorrelated or negatively correlated (21). Specifically, a ‘biodiversity effect’ (sensu (21)) of  
102 nutritional benefits requires that some seafood species contain high concentrations of some  
103 micronutrients while other species contain high concentrations of different micronutrients (i.e.  
104 nutrient concentrations are negatively correlated or uncorrelated across species), creating a  
105 complementary distribution of micronutrients across species. In contrast, if key micronutrients

106 are positively correlated across species such that, for example, a species containing high amounts  
107 of iron also has a calcium concentration, diversity in the diet would not be important. In the case  
108 of positive correlations among micronutrients, the ecosystem service of nutritional benefits  
109 would be enhanced by consuming more fish biomass or by selecting a few highly nutritious  
110 species, rather than by biodiversity *per se*.

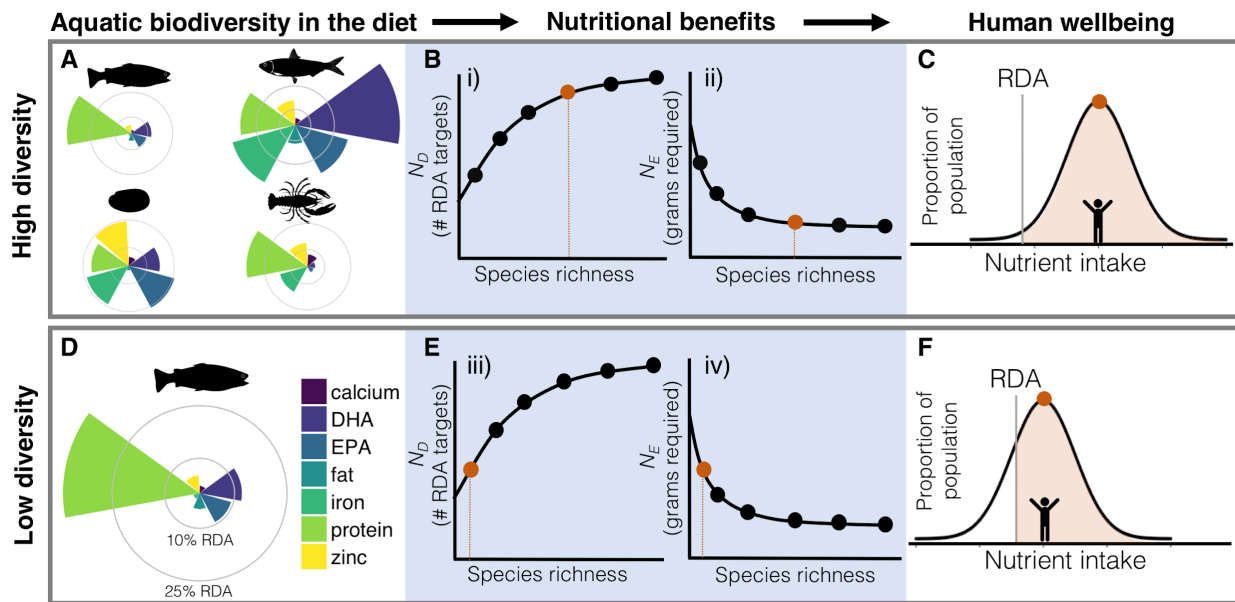
111  
112 Differences in species' micronutrient content (29), if complementary and not positively  
113 correlated across species, could lead to positive effects of seafood diversity for human nutritional  
114 well-being. Furthermore, because micronutrient content does not appear to be correlated with  
115 protein or calorie content (26), there is no reason to expect that a positive effect of diversity on  
116 biomass or protein would imply a similar relationship between diversity and nutritional benefits.  
117 We hypothesized that aquatic biodiversity leads to nutritional complementarity in human diets of  
118 seafood, conferring potential benefits for humans via complementarity or selection effects, as  
119 predicted by biodiversity-ecosystem functioning theory. We quantified these benefits using  
120 recommended dietary allowance (RDA) indices, which are nutrient-based reference values that  
121 indicate the average daily dietary intake level that is sufficient to meet the nutrient requirement  
122 of nearly all (97 to 98 percent) healthy individuals in a particular life stage and gender group  
123 (30). Here we used the RDA for females aged 19-50 (SI Appendix Table S1). We consider  
124 nutritional benefits provided by seafood as how much nutrition is provided in a single standard  
125 amount of seafood (such as a 100g portion of seafood). We ask whether consuming a more  
126 diverse set of species actually increases the nutritional content of a potential seafood diet.  
127 Though it is possible to consider alternative ways to increase seafood derived nutrition in a diet,  
128 such as increasing total seafood biomass consumed or increasing consumption of certain species,

129 these approaches do not necessarily implicate biodiversity as an important element of the  
130 ecosystem service. Furthermore, from an economic or cultural perspective, increasing total  
131 seafood consumption is also not always feasible or desirable, especially if seafood is costly or  
132 only forms a small part of meals.

133  
134 We tested the hypothesis that aquatic biodiversity confers nutritional benefits through  
135 complementarity in nutrient concentrations among species. We quantified nutritional benefits in  
136 two ways: 1) the number of distinct nutritional needs met in a single 100g portion (referred to as  
137 ‘nutritional diversity’,  $N_D$ ) and 2) the amount of seafood tissue required to meet a given  
138 nutritional threshold (referred to as ‘nutritional efficiency’,  $N_E$ ). We tested whether 1) aquatic  
139 biodiversity enhances nutritional diversity ( $N_D$ ) in potential seafood diets and 2) biodiversity  
140 increases the nutritional content of an edible portion of seafood, thereby improving the efficiency  
141 ( $N_E$ ) with which seafood consumers reach nutritional targets (Fig 1). We predicted that increased  
142 species richness (one measure of biodiversity) in potential seafood diets yields increased  
143 nutritional benefits, and that variation in nutrient concentrations among species is related to  
144 species’ ecological traits. In a global analysis of 430 aquatic species, we considered provision of  
145 nutritional benefits to human consumers accessing worldwide seafood markets. To assess the  
146 extent to which the relationships between biodiversity and human nutrition benefits depend on  
147 spatial scale (8), we tested whether seafood biodiversity is associated with higher nutritional  
148 benefits at local scales in fourteen traditional indigenous seafood diets in North America. Fish is  
149 critical for indigenous groups, who on average consume fish at a rate of 15 times higher than the  
150 global average (31). We quantified variation in nutrient concentrations in edible tissues of 430  
151 commonly consumed aquatic species in the global species pool, and 25 – 57 species in fourteen

152 local dietary species pools. We extend biodiversity-ecosystem functioning theory to a  
 153 multivariate ecosystem service (32) that is defined from the perspective of the human beneficiary  
 154 and is directly relevant to human health.

155



156

157 **Fig 1.** Aquatic biodiversity increases human well-being because edible species have distinct and  
 158 complementary multi-nutrient profiles (A) and differ in mean micro- and macronutrient content  
 159 (shown here relative to 10% and 25% thresholds of recommended dietary allowance (RDA)  
 160 guidelines for representative finfish (*Abramis brama*, *Mullus surmuletus*), mollusc (*Mytilus*  
 161 *galloprovincialis*) and crustacean species (*Nephrops norvegicus*). Biodiversity – ecosystem  
 162 functioning theory predicts that nutritional benefits, including nutritional diversity ( $N_D$ ; i, iii) and  
 163 nutritional efficiency ( $N_E$ ; ii, iv) (B, E), are enhanced with increasing dietary species richness.  
 164 Seafood consumers with limited access to seafood each day may not reach RDA targets if diets  
 165 are low in diversity (F vs C; orange shading indicates proportion of population that meets  
 166 nutrient requirements). DHA: docosahexaenoic acid, EPA: eicosapentaenoic acid.

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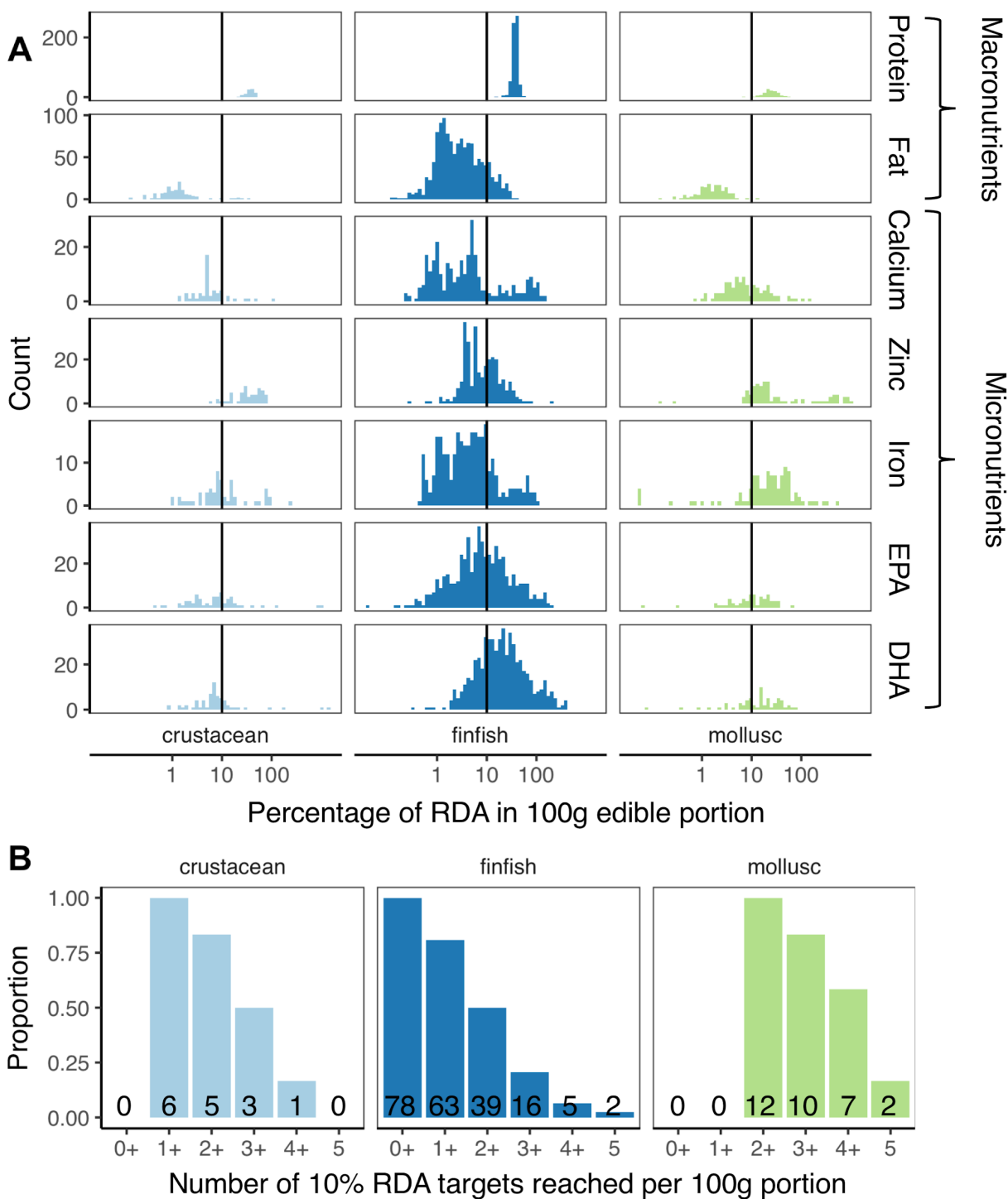
## 168 Results and Discussion

169

### 170 Biodiversity and nutritional benefits of edible aquatic species



171 We found that for a given amount of seafood, biodiversity not only enhances nutritional benefits  
172 for consumers selecting seafood from our global species dataset, but that biodiversity *per se* is  
173 essential to meeting nutritional targets. To assess the contribution of species diversity and traits  
174 to the ecosystem service of promoting human well-being, we assessed species' protein, fat, and  
175 micronutrient concentrations in edible tissues of a standard amount - 100g - relative to a measure  
176 of requirements for these nutritional elements set by public health organizations - the  
177 recommended dietary allowance (RDA) targets ((30); Methods). The global species pool was  
178 highly diverse with regard to concentrations of the micronutrients iron, zinc, calcium, and two  
179 fatty acids DHA and EPA in edible fish tissue relative to RDA targets for those micronutrients  
180 (Fig 2; micronutrient geometric CVs:  $\ln(\text{iron}) = 3.97$ ,  $\ln(\text{calcium}) = 3.25$ ,  $\ln(\text{EPA}) = 2.52$ ,  
181  $\ln(\text{zinc}) = 2.10$ ,  $\ln(\text{DHA}) = 1.70$ ). There was very little diversity in species' protein  
182 concentrations relative to RDA targets (Fig 2;  $\ln(\text{protein})$  geometric coefficient of variation  
183 (geometric CV) = 0.03). Most species did not meet a single micronutrient RDA threshold: when  
184 we considered each micronutrient separately we found that fewer than half of the 430 species  
185 reached a single-nutrient threshold of 10% of the daily RDA target (30) for calcium, iron and the  
186 essential fatty acid EPA in a standard 100g portion of a single species (Table S2).  
187



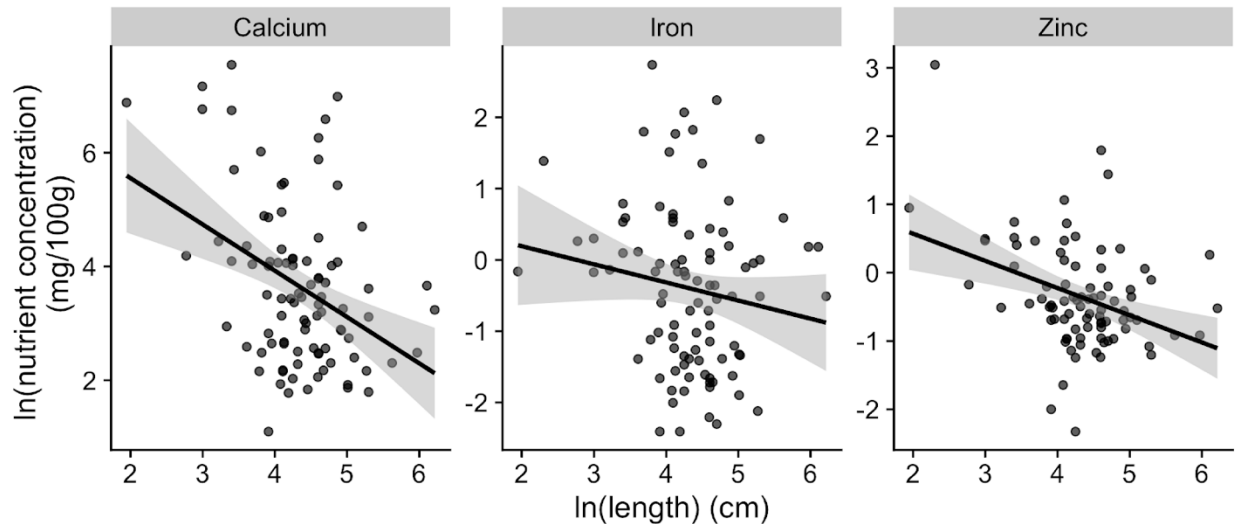
188

189 **Fig 2.** Variation in nutrient concentrations differs among taxonomic groups. (A) Frequency of  
 190 reported protein, fat and micronutrient (including eicosapentaenoic acid (EPA), docosahexaenoic  
 191 acid (DHA)) content in 100 g of the edible portion of 430 seafood species (references in Dataset  
 192 S1). (B) Proportion of species, and number shown on each bar, with available data that reach  
 193 10% of RDI targets for any one, two or up to five of the micronutrients examined here.  
 194

195 ***Nutritional traits covary with ecological traits***

196 Substantial variation in nutrient concentrations in edible portions among species can be  
197 explained partly by major ecological attributes and traits: taxonomic group, latitude, body size,  
198 diet breadth and feeding habits (Tables S3-S7). Finfish, crustaceans and molluscs differed  
199 significantly in their multi-nutrient profiles (PERMANOVA,  $F_{2,103} = 3.429$ ,  $p = 0.006$ ). Among  
200 finfish, concentrations of calcium, iron and zinc in edible tissue decreased with increasing body  
201 size (Fig 3, negative slopes,  $p < 0.05$ ). Variation in protein and fat was poorly explained by  
202 species' ecological traits ( $R^2 = 0.023$ ,  $0.09$ , for protein and fat). In addition to ecological traits,  
203 finfish species that are eaten whole, or whose edible portions include organs such as skin, liver or  
204 bones, have higher nutrient concentrations in the edible portion than those whose edible portions  
205 are restricted to muscle tissue ( $R^2 = 0.60$ ,  $F_{5,251} = 76.24$ ,  $p < 0.01$ ; Fig S3). Nutrient  
206 concentrations were typically weakly negatively correlated or uncorrelated with each other  
207 among species (Fig S4), allowing complementarity among species to increase nutritional  
208 benefits.  
209

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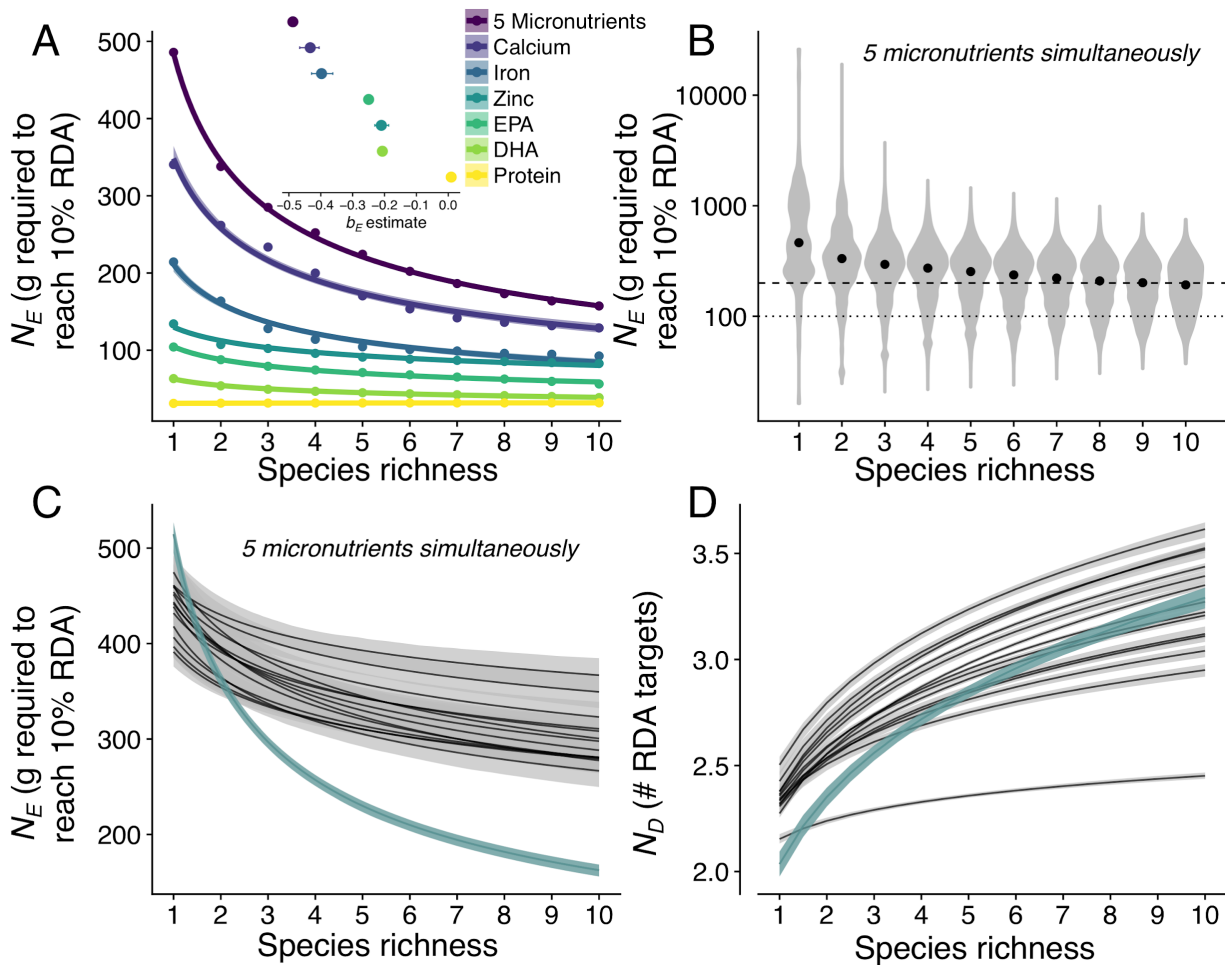


211  
212 **Fig 3.** Micronutrient concentrations are significantly negatively related to body size (length, cm)  
213 in finfish. Negative slopes from phylogenetic least squares: calcium: -0.63 (95% CI -0.94, -0.33,  
214  $n = 89$ ), iron: -0.31 (95% CI -0.61, -0.0075,  $n = 92$ ), zinc: -0.33 (95% CI -0.52, -0.13,  $n = 86$ ).  
215

### 216 *Aquatic biodiversity effects on nutritional benefits to humans*

217 To quantify the effect of biodiversity on nutritional benefits, we first quantified the amount of  
218 seafood, in grams, that would be required to reach a given nutrient intake target (10% of RDA,  
219 Table S1) at each of ten levels of species richness (nutritional efficiency,  $N_E$ , for which lower  
220 values signify higher nutrition benefits to consumers). We then estimated the biodiversity effect  
221 using Equation 1, in which  $b_E$  is the scaling coefficient that describes how function (i.e.  $N_E$ )  
222 varies with species richness. As species richness increased in potential diets, 10% RDA for any  
223 micronutrient was achieved with less total seafood intake (Fig 4A,  $b_E < 0$  for every  
224 micronutrient: calcium -0.43 (95% CI -0.47, -0.40), iron -0.40 (95% CI -0.43, -0.36), zinc -0.21  
225 (95% CI -0.21, -0.23), EPA -0.25 (95% CI -0.26, -0.24) and DHA -0.21 (95% CI -0.21, -0.20)).  
226 This indicates that increasing species richness enhanced nutritional efficiency ( $N_E$ ) in our sample  
227 diets, independent of any changes in the identity of species included, since the diets were  
228 assembled using a random sample of the species pool. All species reached the 10% protein RDA

229 target, so that there was no benefit of seafood diversity for protein (Fig 4A,  $b_E = 0.0092$  95% CI  
 230 0.0086, 0.010). In other words, the ecosystem service of protein provision to diets is adequately  
 231 provided by seafood edible biomass, and not by diversity or even species identity.  
 232



233

234 **Fig 4.** Aquatic biodiversity enhances nutritional benefits at global and local scales. A) Seafood  
 235 species richness improves the efficiency with which human diets can meet 10% of RDA by  
 236 reducing the grams of seafood required to meet nutritional thresholds. Nutritional efficiency ( $N_E$ )  
 237 is shown for five micronutrients and protein separately (points are median values for calcium,  
 238 iron, zinc, EPA, DHA and protein, lines show the fit of Equation 1 to the data and shading refers  
 239 to 95% CI) as well as for five micronutrients simultaneously (purple line labeled ‘5  
 240 Micronutrients’); estimates for the  $b_E$  parameter ( $\pm$  standard error, inset) describe the strength of  
 241 the biodiversity effect. B) Increasing dietary species richness sourced from global seafood  
 242 markets increases the efficiency with which five micronutrient nutritional targets are reached;  
 243 solid circles are median values, as plotted in the purple line in A. C) Increasing species richness

244 increases the efficiency with which five micronutrient nutritional targets are reached at local and  
245 global scales; shaded areas are 95% confidence intervals about the mean; black lines are the fit of  
246 Equation 1 for each of fourteen traditional indigenous diets in North America, green line is for a  
247 diet sourced from the global seafood market. D) Species richness increases the number of  
248 distinct RDA targets met in a 100g seafood portion (nutritional diversity,  $N_D$ ) in local and global  
249 seafood diets; lines are the fit of Equation 2, color coding as in C.

250

### 251 ***Multi-functional biodiversity benefits of aquatic species***

252 We then considered the effects of seafood species richness on the provisioning of multiple  
253 nutrients simultaneously. This is referred to as a multifunctional benefit of biodiversity (32–34),  
254 and takes into account possible trade-offs or correlations among functions, in this case,  
255 concentrations of micronutrients. For some ecosystem services (e.g. water quality or  
256 ecotourism), benefits of biodiversity accumulate when multiple ecosystem functions are  
257 considered simultaneously (32, 35, 36). We treated each micronutrient concentration (relative to  
258 10% RDA for that micronutrient, Table S1) as one ecosystem function. Consistent with  
259 biodiversity-ecosystem functioning theory (37), we found that in the case of a multifunctional  
260 metric of an ecosystem service defined from the human perspective (i.e. multiple micronutrient  
261 targets reached simultaneously), biodiversity benefits for the multifunctional service are greater  
262 than for individual functions ( $b_E$  for all five micronutrients simultaneously = -0.49 (95% CI -  
263 0.50, -0.48) vs. single nutrients  $b_E$  range from -0.43 (95% CI -0.47, -0.40) for calcium to -0.21  
264 for EPA (95% CI -0.21, -0.20)) that comprise the ecosystem service (Fig 4A). Increasing species  
265 diversity from one to five species in 1000 simulated, resampled hypothetical diets drawing from  
266 our global species pool allowed consumers to meet 10% of RDA for five essential microelements  
267 and fatty acids simultaneously more than twice as efficiently (i.e. a median of 485.83g of tissue  
268 required with one species vs. median of 216.96g of tissue required with five species) (Fig 4B, C).  
269 Then, we assessed the effects of biodiversity when the total seafood biomass is held constant, at

270 100g, by counting the number of distinct RDA thresholds in a 100g portion ( $N_D$ ). We also found  
271 positive effects of biodiversity on the number of distinct nutritional functions (10% of RDA  
272 reached) in a single 100g portion (Fig 4D): more diverse diets reached more nutritional targets  
273 (higher  $N_D$ ) per 100g serving than diets of the same fish biomass comprising fewer species ( $b_D =$   
274 0.21 (95% CI: 0.18-0.24) Fig 4D). These results demonstrate a benefit of biodiversity for human  
275 nutritional well-being, over and above the benefits of consuming a particular amount (biomass)  
276 or identity of aquatic species.

277  
278 Our analysis provides new and robust evidence that biodiversity is critical to multifunctionality  
279 of ecosystem services when function thresholds are grounded *a priori* in multivariate metrics  
280 meaningful for human well-being such as RDA. Our approach overcomes the critique that  
281 multifunctionality is not enhanced by biodiversity (37), but rather a statistical artifact of how  
282 multifunctionality was commonly estimated. Our findings are robust to multiple RDA threshold  
283 levels (Fig S1), and the biodiversity effect is strongest at a threshold of approximately 28% of  
284 RDA (Fig S1). In this case, the positive effects of biodiversity are greatest at levels of nutritional  
285 benefit that are significant for human nutrition, highlighting the importance of species diversity  
286 in seafood diets. More generally, ecosystem service benefits, as defined in metrics of human  
287 wellbeing rather than the traits of the species pool under consideration (e.g., biomass or stability  
288 of the food web), typically are produced by several underlying ecosystem functions (32). The  
289 strong effects of diversity on multifunctional benefits observed here may also apply to  
290 relationships between diversity and other services e.g., desired filtration rates of pollutants in  
291 wetlands (38), or desired pest consumption rates in agricultural systems (39).

292

293 ***Biodiversity benefits are consistent from local to global scales***

294 Consistent with the positive biodiversity effects we observed when assuming consumers have  
295 access to global seafood markets, we also found benefits of seafood diversity in a local context.  
296 We analyzed the effects of biodiversity in fourteen traditional indigenous North American diets  
297 of seafood harvested locally, and found a consistent, positive effect of biodiversity on  $N_D$  and  $N_E$ ,  
298 although the magnitude of the biodiversity effect was generally lower at the local scale than the  
299 global scale (Fig 4C-D, Fig S2, S5) (global  $b_D = 0.21$  (95% CI 0.18, 0.24) vs mean local  $b_D =$   
300  $0.14 \pm 0.0083$  S.E. and global  $b_E = -0.50$  (95% CI -0.52, -0.47) vs mean local  $b_E = -0.16 \pm 0.0091$   
301 S.E.). This finding is consistent with lower nutritional functional diversity (mean local  $FD = 2.77$   
302  $\pm 0.17$  S.E. vs. global  $FD = 3.87 \pm 0.0096$  S.E.) and higher nutritional functional evenness in  
303 local diets (mean local  $FEve = 0.76 \pm 0.01$  S.E. vs. global  $FEve = 0.71 \pm 0.0018$  S.E.) (Fig S2,  
304 S5), suggesting that functional consequences of changes to diversity in local seafood diets may  
305 be buffered by higher redundancy among species. Given increasing trends towards  
306 homogenization of the global food supply (40) including aquaculture (41, 42), this local-scale  
307 finding highlights the importance of local species diversity in the diets of vulnerable populations  
308 (26).

309

310 ***Potential benefits of aquatic biodiversity for human well being***

311 The problem of ‘hidden hunger’, in which people have access to sufficient calories but  
312 insufficient essential micronutrients, is becoming increasingly recognized as a major contributor  
313 to the burden of disease in developing countries (43, 44). Indeed, more than two billion people  
314 suffer from micronutrient deficiencies, and it is the aim of the United Nations Sustainable  
315 Development Goals (SDGs) to end all forms of malnutrition (44). Micronutrients in fish lead to a



316 variety of health benefits, including lowered risk of cardiovascular disease, improved maternal  
317 health and pregnancy outcomes, increased early childhood physical and cognitive development.  
318 Polyunsaturated fatty acids such as EPA and DHA are important for cardiovascular and brain  
319 health. The amount of seafood in the human diet is often limited, either by costs or because  
320 traditionally harvested species are being replaced by other ‘junk foods’ (45). In light of this, we  
321 have focused here on the nutritional benefits potentially provided by seafood biodiversity over  
322 and above the services provided by consuming seafood in general, and by consuming particular  
323 highly nutritious species. Seafood consumption is influenced by many factors including cultural  
324 preferences, social status, and economic pressures, none of which are considered here. Still, our  
325 study adds to our knowledge of seafood and nutrition by quantifying the contribution of  
326 biodiversity *per se* to meeting nutritional needs, and this biodiversity effect occurs in addition to  
327 how diversity enhances and stabilizes total yields (22). This finding bridges the growing  
328 understanding of hidden hunger and food security with the large theoretical and empirical  
329 understanding of relationships between biodiversity, ecosystem function and benefits to people.

330

### 331 ***Aquatic biodiversity and food security in a changing world***

332 Maintaining the diversity of global fisheries is important for ensuring food and nutrition security.  
333 A diverse seafood species pool feeds not only local communities but also seafood markets  
334 worldwide, and aquatic species contain micronutrients not found in other foods. Many of the  
335 most nutritionally vulnerable populations – those that are deficient in essential micronutrients  
336 during particularly sensitive stages of life (i.e. pregnancy, breastfeeding and childhood) may rely  
337 on local ecosystems to meet their nutritional demands (2, 25, 29). These populations may have  
338 access to a limited amount of locally available fish tissue each day or to fish from a subset of

339 habitat types, suggesting that for these populations nutritional efficiency may be particularly  
340 important. In tropical regions, fish diversity in coastal regions has plummeted in recent decades  
341 (46) characterized by two-fold declines in body sizes of fish (47, 48). These regions are also  
342 regions of high nutritional vulnerability and reliance on locally harvested seafood (49). However,  
343 as the seafood trade becomes increasingly global (50, 51), seafood-derived nutrition available to  
344 consumers participating in the global market may be related to globally harvested seafood  
345 biodiversity. As a result, changes to local biodiversity and resultant impacts on human nutrition  
346 may be buffered by access to global seafood markets. Together, our results suggest that in the  
347 context of global change, understanding and protecting the potential for nature to support diverse  
348 and productive aquatic ecosystems has direct and immediate benefits to humanity.

349

## 350 **Conclusions**

351 Nutritional diversity appears to be derived from ecological diversity, suggesting links between  
352 the complexity of aquatic ecosystems and their capacity to produce nutritional benefits. While  
353 the role of seafood is well recognized as an important source of protein in the human diet, the  
354 role of seafood as a source of essential micronutrients is often overlooked. This study provides  
355 the first global assessment of patterns in the macro- and micronutrient content of aquatic species.  
356 Our results reveal that not all fish species are equally nutritionally valuable to humans and that  
357 aspects of ecological structure, including species and trait diversity enhance nutritional diversity,  
358 thereby linking the processes that structure ecosystems with the benefits they provide.

## 359 **Methods**

### 360 *Quantifying nutritional value in terms of human health benefits*

361 We characterized an aquatic species' nutritional profile by drawing on two well-established  
362 nutritional metrics: nutrient concentration (nutrient content/100g edible portion) and  
363 Recommended Dietary Allowances (RDA). RDAs are developed following health guidelines,  
364 and quantify the recommended amount of a particular nutrient required to maintain health (30).  
365 The RDAs used here were established by the Food and Nutrition Board of the United States  
366 Institute of Medicine, and quantify the daily intake level of a nutrient needed to meet the  
367 requirements of 97–98% of healthy adults (females aged 19-50) (30). We defined the nutritional  
368 value of a fish species for each nutrient in terms of the nutrient content in an edible portion  
369 relative to the RDA for that nutrient. For some aquatic species, micronutrients are in such high  
370 concentrations in edible tissues that a single 100g portion contains the entire RDA for that  
371 nutrient, while edible tissues from other species provide only small fractions of the RDA. We  
372 considered thresholds of nutritional benefit (function) between 1% and 100% of the RDA,  
373 although we focus on 10% of RDA since it is a minimum threshold for a food to be considered  
374 of nutritional benefit (30). We defined an RDA target as 10% of RDA for a given nutrient. We  
375 characterized nutritional profiles in two ways: first, in terms of concentrations of each nutrient  
376 (single nutrient profile), and secondly, in terms of multiple nutrients simultaneously (i.e. multi-  
377 nutrient profile).

378

379

380 *Defining nutritional benefits*

381 We quantified the effect of biodiversity on nutritional benefits in two ways (Fig 1): 1) nutritional  
382 efficiency,  $N_E$ , which quantifies the amount of tissue, in grams, required to reach a given number  
383 of RDA targets for different nutrients simultaneously and 2) nutritional diversity,  $N_D$ , which  
384 quantifies the number of distinct RDA thresholds for different nutrients met in a standard 100g  
385 edible portion. Nutritional benefit increases with decreasing values of  $N_E$ , since  $N_E$  quantifies the  
386 grams required to reach RDA targets, and fewer grams required is better from the perspective of  
387 human nutrition. We quantified  $N_D$  in an arbitrary daily diet, assuming that the seafood diet  
388 contains 100g of seafood per day.

389

390 *Literature search and data collection*

391 We assembled a dataset of published nutrient concentrations in edible portions of 430 aquatic  
392 species. We analyzed tissue concentrations of nutrients for which RDA standards exist and that  
393 are implicated in a range of biologically important processes that affect organismal growth and  
394 reproduction, and therefore may potentially relate ecological function with human nutritional  
395 wellbeing. We examined macronutrients including protein and fat, as well as five micronutrients:  
396 metals beneficial at low concentrations but toxic at high concentrations (zinc and iron), one  
397 beneficial mineral (calcium) and the polyunsaturated fatty acids eicosapentaenoic acid (EPA)  
398 and docosahexaenoic acid (DHA). We aimed to include as many marine and freshwater species  
399 as possible covering a wide geographic extent. We searched peer-reviewed literature for  
400 analytical food composition values as well as the Food and Agriculture Organization's Global  
401 Food Composition Database for Fish and Shellfish (52). For finfish, we restricted our analysis to  
402 include only edible portions of wild, raw fish (excluding prepared or farmed seafood items). We

403 included both farmed and wild mollusc species because mollusc farming does not typically  
404 involve additional food inputs, which could influence tissue nutrient composition. For each  
405 species, we noted which body parts are included in the edible portion and season of collection.  
406 For each sample, we noted the location of origin (e.g. latitude and longitude). To address  
407 inconsistencies in fatty acid data reporting, we standardized fatty acid measurements using the  
408 fatty acid conversion factors proposed by Nowak et al. 2014 (53). When there were multiple  
409 observations available for a single species, we averaged nutrient concentrations across the  
410 observations. We did not include data from national food composition tables because these data  
411 usually report seafood data with a generic food description, which does not allow for a clear  
412 description of which fish tissues are included in the edible portion. For each species with  
413 nutritional data, we collected ecological trait information from FishBase (54) and SeaLifeBase  
414 (55). We included body size (maximum length), fractional trophic position, temperature  
415 preference (using latitude as a proxy), diet breadth and feeding mode.

416

#### 417 Statistical analyses and hypothesis testing

#### 418 **Hypothesis 1: Biodiversity enhances nutritional benefits**

419 We tested the effect of species diversity (quantified as the number of species, or species richness,  
420  $S$ ), on nutritional diversity and efficiency by randomly assembling diets from the global seafood  
421 species pool, keeping the portion size constant (100 grams) across all levels of diversity. In  
422 analyses using the global dataset (430 species), we assumed that human populations have access  
423 to the entire global species pool and choose species at random. Though this assumption certainly  
424 ignores economic, social and cultural factors that affect which species people consume, in the  
425 absence of detailed diet information for the majority of the world's populations this is a

426 necessary assumption. To assess potential effects of biodiversity on nutritional benefits for  
427 populations that consume seafood locally and not as part of the global seafood market, we  
428 sampled diets from species contained within traditional diets in fourteen indigenous cultures in  
429 North America. We used species lists for local diets that were obtained from an ethnographic  
430 database of traditional animal foods of indigenous peoples of northern North America, and only  
431 included species that were harvested wild and whose nutrient compositions were analyzed when  
432 raw (Table S7, (56)). To avoid confounding differences in biodiversity effects at global and local  
433 scales with the sizes of the species pools at each of these scales, we matched the size of the  
434 global species pool to the average size of the local species pools (40 species).

435

436 We calculated two metrics of nutritional benefits for hypothetical diets comprising species drawn  
437 randomly from either the global dataset (global diet) or local datasets (local diets):

438

439 1) Nutritional efficiency ( $N_E$ ). We tested the hypothesis that complementarity in nutrient  
440 concentrations among species enhances  $N_E$  by estimating the effect of species richness on  $N_E$  (the  
441 ‘biodiversity effect’). To estimate the ‘biodiversity effect’ on  $N_E$ , we took an approach to  
442 modeling dietary species composition that is analogous to a biodiversity-ecosystem function  
443 experiment with a replacement design, where species abundances decline proportionally as  
444 species richness increases. From the global species pool, we sampled ten species at random and  
445 then assembled seafood diets from all possible combinations of these ten randomly chosen  
446 species at 10 levels of species richness (1-10). We repeated this process of sampling ten species  
447 from the global species pool and then assembling all possible diets 1000 times. For each  
448 combination of species in each dietary diversity level (1-10 species), we calculated the number

449 of grams required to reach a given RDA target (either: one of six possible nutrient targets  
450 individually, or five micronutrient (calcium, iron, zinc, EPA and DHA) targets simultaneously).  
451 We quantified the effect of species richness in a diet on nutritional efficiency,  $N_E$ , by fitting a  
452 power function to these bootstrapped nutritional efficiency estimates:

$$453 \quad \quad \quad 454 \quad \quad \quad N_E = aS^{b_E} \quad \quad \quad (1)$$

455 where the parameter  $b_E$  describes the relationship between a change in species richness,  $S$ , and a  
456 change in  $N_E$ , and  $a$  is a constant (in units of grams). Since  $N_E$  is measured in grams required to  
457 reach a given RDA target, and fewer grams required is better from the perspective of human  
458 nutrition, then a benefit of biodiversity would be reflected in a negative  $b_E$  (i.e.  $N_E$ , measured in  
459 grams of tissue required, decreases with species richness). For each nutrient individually, and for  
460 all five micronutrients together, we estimated the exponent parameter,  $b_E$ , using non-linear  
461 regression using the *nls.LM* function in the *minpack.lm* package in R (57). To quantify  
462 uncertainty in parameter estimates associated with sampling from the pool of observed nutrient  
463 content values, we calculated bootstrapped confidence intervals using non-parametric  
464 bootstrapping of mean centered-residuals using the *nlsBoot* function in the R package *nlstools*  
465 (58).

466  
467 2) Nutritional diversity ( $N_D$ ). To test the hypothesis that complementarity in nutrient  
468 concentrations among species increases nutritional benefits by increasing the number of distinct  
469 RDA targets in a 100g portion, we constructed recommended dietary allowance (RDA) target  
470 accumulation curves. These are analogous to species accumulation curves used in ecological  
471 studies to assess patterns of beta-diversity, or species turnover, in ecological community

472 composition data. We assessed turnover of nutrients content in edible tissues among fish species.  
473 Each fish species is associated with a set of 0s and 1s corresponding to whether or not it achieves  
474 10% of RDA for each of five micronutrients (equivalent to a species presence-absence matrix in  
475 community composition data), sampled with replacement 1000 times. This approach allowed us  
476 to explore how likely it would be for human diets containing different numbers of fish species to  
477 reach a given number of micronutrient RDA targets ( $N_D$  ranges between 0 and 5), assuming that  
478 fish species were included in the human diet at random. We quantified the effect of biodiversity  
479 on nutritional diversity,  $N_D$ , by fitting a power function,

480

$$481 \quad N_D = aS^{b_D} \quad (2)$$

482 where the parameter  $b_D$  describes the relationship between a change in species richness,  $S$ , and a  
483 change in  $N_D$  (i.e. the number of RDA targets reached per average 100g portion), and  $a$  is a  
484 constant.

485

486 For both  $N_E$  and  $N_D$ , we tested the hypothesis that biodiversity enhances nutritional benefits by  
487 assessing whether the estimate of the scaling exponent,  $b$ , had confidence intervals not  
488 overlapping zero. We concluded that biodiversity enhanced nutritional benefits if  $b_E$  was  
489 negative and  $b_D$  was positive.

490

491 We tested the hypothesis that nutritional functional diversity drives positive biodiversity effects  
492 by testing for a positive association between nutritional functional diversity and the biodiversity  
493 scaling exponent,  $b$ . We hypothesized that nutritional functional diversity would be higher at the



494 global scale than the local scale, because the global species pool contains more ecological and  
495 biogeographic diversity. To assess levels of nutritional functional diversity among species, we  
496 calculated functional diversity (*FD*) (59). *FD* is based on an assessment of the entire functional  
497 diversity of a group represented as a functional dendrogram, and *FD* allows estimation of  
498 complementarity among species' nutrient concentrations (i.e. nutritional functional traits) using  
499 the dendrogram. We treated the concentration of each micronutrient (calcium, iron, zinc, EPA  
500 and DHA) as a functional trait. We also quantified functional evenness metric (*FEve*) using the  
501 *FD* package in R, which normally quantifies the evenness of abundance in a functional trait  
502 space. Here, we used *FEve* to quantify the evenness in concentration of nutrients across species  
503 (60). To compare *FD* and *FEve* at the global and local scales, we first subsampled 40 species  
504 (the average species pool at the local scale) from the global pool, then calculated the functional  
505 diversity metrics on the subsample, and repeated this process 1000 times. Using this same  
506 approach, we calculated levels of 'expected' *FD* and *FEve* for each local diet by choosing  
507 random subsets of the global pool with sample size equal to the species pool in each local diet,  
508 and repeated this process 1000 times (Fig S5).

509

510 **Hypothesis 2: Diversity in nutrient concentrations of the edible portion is related to**  
511 **ecological diversity estimated as species' ecological traits.**

512

513 We tested the hypothesis that nutrient concentrations are related to species' ecological traits in  
514 two ways: 1) testing whether multi-nutrient profiles (i.e. concentrations of all five  
515 micronutrients) differ among major phylogenetic groups and 2) whether differences in single  
516 nutrient concentrations differ with species ecological traits. We examined variation in multi-

517 nutrient profiles among seafood species using the *vegan* package in R (61). We ln transformed  
518 nutrient concentration data to achieve normality. Differences in multi-nutrient profiles were  
519 visualized through non-metric dimensional scaling (NMDS) using the *metaMDS* function. The  
520 ordination ran for 1000 iterations, and the stress score of 0.032 for the final solution was  
521 sufficiently low to enable reliable interpretation in the two dimensions (62). First, we tested the  
522 hypothesis that major phylogenetic groups correlated with functional differences in life history,  
523 resource use and ecology (i.e. finfish, mollusc, and crustacean) differ in their multi-nutrient  
524 profiles via permutational multivariate ANOVA (PERMANOVA) using the *adonis* function (999  
525 permutations) based on Bray-Curtis dissimilarity matrices. We used an overall (three-way)  
526 PERMANOVA first to investigate phylogenetic group effects on nutrient profile of a species'  
527 edible tissue.

528

529 To test for associations between species' ecological functional traits and their nutrient  
530 concentrations, we modeled the relationship between traits and ln(nutrient concentration) with  
531 phylogenetic least squares regression (PGLS). The full model included the entire set of trait  
532 predictors as fixed effects:

533

$$534 \ln(\text{nutrient}) = \beta_0 + \beta_1 \times \ln(\text{body size}) + \beta_2 \times \text{latitude} + \beta_3 \times \text{trophic position} + \beta_4 \times \text{feeding mode} + \\ 535 \beta_5 \times \text{diet breadth} + \varepsilon$$

536

537 Unlike in ordinary least squares (OLS), which assumes there is no covariance structure in the  
538 error term,  $\varepsilon$ , (all species are independent from one another, and residuals from closely related  
539 species are not more similar on average than residuals from distantly related species), PGLS

540 assumes that the residuals are non-independent, and that the expected covariance is related to the  
541 shared evolutionary history between the species. To assess whether the relationships between  
542 species' traits and their nutritional profiles were associated, we fit multiple regression models  
543 using PGLS using the *gls* function in the *nlme* package in R using the Brownian motion model of  
544 evolution. This approach allowed us to account for phylogenetic non-independence by using  
545 shared ancestry as weights on the elements of the residual variance-covariance matrix used in the  
546 model. We created a supertree by combining phylogenies that included the species of finfish,  
547 molluscs and crustaceans in our nutrient dataset using the *rotl* package in R (63), which is an  
548 interface to the Open Tree of Life (64). We computed branch lengths according to taxonomic  
549 depth (65) using the *compute.brlen* function in the *ape* package in R (66).

550

551 We created models from subsets of the full model that represented hypotheses based on the  
552 known physiological roles of micronutrients and their relationships to our set of predictors  
553 (Tables S3-S7, S10). To avoid issues associated with multicollinearity of predictor variables, we  
554 excluded other possible variables if they were highly correlated (i.e. correlation coefficient >  
555 0.6). We identified the best subset of models using the Akaike Information Criterion, adjusted  
556 for small sample sizes (AICc). We used AICc,  $\delta_{aic}$  and Akaike weights ( $w$ ) to compare models.  
557 We ranked models based on  $w$ , and selected the set of models that produced a cumulative  $w >$   
558 0.95, meaning that we are 95% confident that the chosen set includes the best model (67). In  
559 cases where we could not obtain measurements of all traits for all species, we performed model  
560 selection on reduced datasets without missing values.

561

562 To account for model uncertainty in the ecological trait correlation analyses, we performed  
563 model averaging of coefficients in all models that produced a cumulative  $w > 0.95$ , and included  
564 zeros as coefficients when variables did not enter a given model (67). We conducted our model  
565 selection and averaging analyses with the *MuMIn* package (68) and all other analyses in R  
566 version 3.3.2 (69).

567

568 Uncertainties:

569 There are several sources of uncertainty in our analyses. First, there are substantial sources of  
570 uncertainty in food composition estimates. The data in our dataset meet international standards  
571 for data quality and standardization, meaning that we followed guidelines for checking food  
572 composition data and converting units, denominators and expressions (70). Still, tissue  
573 concentrations may vary depending on analytical techniques, labs, season, diet of the animal, life  
574 stage etc. Some of these sources of uncertainty (e.g. differences in analytical techniques) are  
575 unavoidable consequences of synthesizing previously published data collected across many labs.  
576 We assumed that these uncertainties in the data were randomly distributed over our  
577 geographically and taxonomically diverse dataset. Further uncertainty is associated with how  
578 well our set of 430 species represents the global pool of seafood consumed. We do not know  
579 whether our sample is random or biased, though we can say that our dataset includes 41 of the 67  
580 most consumed species worldwide (as determined by FAO production volumes (71), species  
581 with capture production of 150 000 tonnes or more, after removing species for which the  
582 majority of production volume is diverted to fish meal and oil (72), Table S9). A remaining  
583 source of variation among samples is likely due to natural sources of variation associated with

584 seasonal and other sources of temporal variability, which we consider to be an important  
585 component of biodiversity.

586

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593  
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## 596 **References**

- 597 1. M. C. Latham, *Human nutrition in the developing world* (Food & Agriculture Org., 1997).
- 598 2. C. D. Golden, *et al.*, Fall in fish catch threatens human health. *Nature* **534**, 317–320 (2016).
- 599 3. D. Penafiel, C. Lachat, R. Espinel, P. Van Damme, P. Kolsteren, A systematic review on  
600 the contributions of edible plant and animal biodiversity to human diets. *EcoHealth* **8**, 381–  
601 399 (2011).
- 602 4. B. J. Cardinale, *et al.*, Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67  
603 (2012).
- 604 5. S. S. Myers, *et al.*, Human health impacts of ecosystem alteration. *Proc. Natl. Acad. Sci. U.*  
605 *S. A.* **110**, 18753–18760 (2013).
- 606 6. R. Elahi, *et al.*, Recent trends in local-scale marine biodiversity reflect community structure  
607 and human impacts. *Curr. Biol.* **25**, 1938–1943 (2015).
- 608 7. M. L. Pinsky, B. Worm, M. J. Fogarty, J. L. Sarmiento, S. A. Levin, Marine taxa track local  
609 climate velocities. *Science* **341**, 1239–1242 (2013).
- 610 8. F. Isbell, *et al.*, Linking the influence and dependence of people on biodiversity across  
611 scales. *Nature* **546**, 65–72 (2017).
- 612 9. M. I. O’Connor, *et al.*, A general biodiversity--function relationship is mediated by trophic  
613 level. *Oikos* **126**, 18–31 (2017).
- 614 10. B. Belton, S. H. Thilsted, Fisheries in transition: Food and nutrition security implications  
615 for the global South. *Global Food Security* **3**, 59–66 (2014).
- 616 11. FAO, *The State of World Fisheries and Aquaculture 2018 - Meeting the sustainable*  
617 *development goals* (2018).
- 618 12. A. D. Jones, Critical review of the emerging research evidence on agricultural biodiversity,  
619 diet diversity, and nutritional status in low- and middle-income countries. *Nutr. Rev.* **75**,  
620 769–782 (2017).
- 621 13. C. Lachat, *et al.*, Dietary species richness as a measure of food biodiversity and nutritional  
622 quality of diets. *Proc. Natl. Acad. Sci. U. S. A.* **115**, 127–132 (2018).
- 623 14. R. Remans, *et al.*, Assessing nutritional diversity of cropping systems in African villages.  
624 *PLoS One* **6** (2011).
- 625 15. F. A. J. DeClerck, J. Fanzo, C. Palm, R. Remans, Ecological approaches to human nutrition.  
626 *Food Nutr. Bull.* **32**, S41–50 (2011).
- 627 16. M. T. Ruel, Operationalizing dietary diversity: a review of measurement issues and research

- 628 priorities. *J. Nutr.* **133**, 3911S–3926S (2003).
- 629 17. FAO, Compendium of Indicators for Nutrition-Sensitive Agriculture (2013).
- 630 18. J. Fanzo, D. Hunter, T. Borelli, F. Mattei, *Diversifying Food and Diets: Using Agricultural*  
631 *Biodiversity to Improve Nutrition and Health* (Routledge, 2013).
- 632 19. M. Loreau, N. Mouquet, A. Gonzalez, Biodiversity as spatial insurance in heterogeneous  
633 landscapes. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 12765–12770 (2003).
- 634 20. M. Loreau, A. Hector, Partitioning selection and complementarity in biodiversity  
635 experiments. *Nature* **412**, 72–76 (2001).
- 636 21. M. Loreau, Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**,  
637 3–17 (2000).
- 638 22. J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, Biodiversity  
639 enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci. U. S. A.*  
640 **113**, 6230–6235 (2016).
- 641 23. R. Hilborn, T. P. Quinn, D. E. Schindler, D. E. Rogers, Biocomplexity and fisheries  
642 sustainability. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 6564–6568 (2003).
- 643 24. S. Wang, M. Loreau, Biodiversity and ecosystem stability across scales in  
644 metacommunities. *Ecol. Lett.* **19**, 510–518 (2016).
- 645 25. N. Kawarazuka, C. Béné, Linking small-scale fisheries and aquaculture to household  
646 nutritional security: an overview. *Food Security* **2**, 343–357 (2010).
- 647 26. J. R. Bogard, *et al.*, Higher fish but lower micronutrient intakes: Temporal changes in fish  
648 consumption from capture fisheries and aquaculture in Bangladesh. *PLoS One* **12** (2017).
- 649 27. P. Balvanera, *et al.*, Linking Biodiversity and Ecosystem Services: Current Uncertainties  
650 and the Necessary Next Steps. *Bioscience* **64**, 49–57 (2014).
- 651 28. D. E. Schindler, *et al.*, Pacific salmon and the ecology of coastal ecosystems. *Front. Ecol.*  
652 *Environ.* **1**, 31–37 (2003).
- 653 29. J. R. Bogard, *et al.*, Nutrient composition of important fish species in Bangladesh and  
654 potential contribution to recommended nutrient intakes. *J. Food Compos. Anal.* **42**, 120–  
655 133 (2015).
- 656 30. Institute of Medicine, *Dietary Reference Intakes for Calcium and Vitamin D* (National  
657 Academies Press, 2012; <http://nationalacademies.org/hmd/~media/Files/Activity>  
658 [Files/Nutrition/DRI-Tables/2\\_RDA and AI Values\\_Vitamin and Elements.pdf?la=en](http://nationalacademies.org/hmd/~media/Files/Activity)), vol.  
659 130.
- 660 31. A. M. Cisneros-Montemayor, D. Pauly, L. V. Weatherdon, Y. Ota, A Global Estimate of



- 661 Seafood Consumption by Coastal Indigenous Peoples. *PLoS One* **11**, e0166681 (2016).
- 662 32. P. Manning, *et al.*, Redefining ecosystem multifunctionality. *Nature Ecology & Evolution* **2**,  
663 427–436 (2018).
- 664 33. J. E. K. Byrnes, *et al.*, Investigating the relationship between biodiversity and ecosystem  
665 multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution* **5**, 111–124  
666 (2014).
- 667 34. M. E. Mastrangelo, *et al.*, Concepts and methods for landscape multifunctionality and a  
668 unifying framework based on ecosystem services. *Landsc. Ecol.* **29**, 345–358 (2014).
- 669 35. A. Hector, R. Bagchi, Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188–190  
670 (2007).
- 671 36. L. Gamfeldt, H. Hillebrand, P. R. Jonsson, Multiple functions increase the importance of  
672 biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223–1231 (2008).
- 673 37. L. Gamfeldt, F. Roger, Revisiting the biodiversity--ecosystem multifunctionality  
674 relationship. *Nature Ecology & Evolution* **1**, s41559–017 (2017).
- 675 38. T. Boyer, S. Polasky, Valuing urban wetlands: A review of non-market valuation studies.  
676 *Wetlands* **24**, 744–755 (2004).
- 677 39. D. S. Karp, *et al.*, Forest bolsters bird abundance, pest control and coffee yield. *Ecol. Lett.*  
678 **16**, 1339–1347 (2013).
- 679 40. C. K. Khoury, *et al.*, Increasing homogeneity in global food supplies and the implications  
680 for food security. *Proceedings of the National Academy of Sciences* **111**, 4001–4006 (2014).
- 681 41. J. Bostock, *et al.*, Aquaculture: global status and trends. *Philos. Trans. R. Soc. Lond. B Biol.*  
682 *Sci.* **365**, 2897–2912 (2010).
- 683 42. C. M. Duarte, *et al.*, Will the oceans help feed humanity? *Bioscience* **59**, 967–976 (2009).
- 684 43. G. Kennedy, G. Nantel, P. Shetty, The scourge of “hidden hunger”: global dimensions of  
685 micronutrient deficiencies. *Food Nutrition and Agriculture* **32**, 8–16 (2003).
- 686 44. K. von Grebmer A. Saltzman E. Birol D. Wiesmann N. Prasai S. Yin Y. Yohannes P.  
687 Menon J. Thompson A. Sonntag, 2014 Global hunger index: The challenge of hidden  
688 hunger (2014) (September 2, 2019).
- 689 45. H. V. Kuhnlein, O. Receveur, Local Cultural Animal Food Contributes High Levels of  
690 Nutrients for Arctic Canadian Indigenous Adults and Children. *J. Nutr.* **137**, 1110–1114  
691 (2007).
- 692 46. G. P. Jones, M. I. McCormick, M. Srinivasan, J. V. Eagle, Coral decline threatens fish  
693 biodiversity in marine reserves. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 8251–8253 (2004).

- 694 47. J. G. Molinos, *et al.*, Climate velocity and the future global redistribution of marine  
695 biodiversity. *Nat. Clim. Chang.* **6**, 83–88 (2016).
- 696 48. W. W. L. Cheung, *et al.*, Shrinking of fishes exacerbates impacts of global ocean changes  
697 on marine ecosystems. *Nat. Clim. Chang.* **3**, 254–258 (2013).
- 698 49. E. H. Allison, *et al.*, Vulnerability of national economies to the impacts of climate change  
699 on fisheries. *Fish Fish* **10**, 173–196 (2009).
- 700 50. J. A. Gephart, M. L. Pace, Structure and evolution of the global seafood trade network.  
701 *Environ. Res. Lett.* **10**, 125014 (2015).
- 702 51. R. A. Watson, B. S. Green, S. R. Tracey, A. Farmery, T. J. Pitcher, Provenance of global  
703 seafood. *Fish Fish* **17**, 585–595 (2016).
- 704 52. Food and Agriculture Organization of the United Nations, “FAO/INFOODS Global Food  
705 Composition Database for Fish and Shellfish Version 1.0- uFiSh1.0” (2016).
- 706 53. V. Nowak, D. Rittenschober, J. Exler, U. R. Charrondiere, Proposal on the usage of  
707 conversion factors for fatty acids in fish and shellfish. *Food Chem.* **153**, 457–463 (2014).
- 708 54. R. A. D. P. Froese, “Fishbase version (06/2017).”
- 709 55. M. L. D. A. D. P. Palomares, “SeaLifeBase version (06/2017).”
- 710 56. H. V. Kuhnlein, M. M. Humphries, Traditional Animal Foods of Indigenous Peoples of  
711 Northern North America (2017).
- 712 57. T. V. Elzhov, K. M. Mullen, A.-N. Spiess, B. Bolker, *minpack.lm: R interface to the*  
713 *Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support*  
714 *for bounds* (2013).
- 715 58. F. Baty, *et al.*, A Toolbox for Nonlinear Regression in R : The Package nlstools. *J. Stat.*  
716 *Softw.* **66**, 1–21 (2015).
- 717 59. O. L. Petchey, K. J. Gaston, Functional diversity (FD), species richness and community  
718 composition. *Ecol. Lett.* **5**, 402–411 (2002).
- 719 60. S. Villéger, N. W. H. Mason, D. Mouillot, New multidimensional functional diversity  
720 indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301 (2008).
- 721 61. J. Oksanen, *et al.*, Package “vegan.” *Community ecology package, version 2* (2013).
- 722 62. P. Legendre, L. Legendre, *Numerical Ecology* (1998).
- 723 63. F. Michonneau, J. W. Brown, D. J. Winter, rotl : an R package to interact with the Open  
724 Tree of Life data. *Methods Ecol. Evol.* **7**, 1476–1481 (2016).
- 725 64. C. E. Hinchliff, *et al.*, Synthesis of phylogeny and taxonomy into a comprehensive tree of

- 726 life. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 12764–12769 (2015).
- 727 65. A. Grafen, The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **326**, 119–  
728 157 (1989).
- 729 66. E. Paradis, J. Claude, K. Strimmer, APE: Analyses of Phylogenetics and Evolution in R  
730 language. *Bioinformatics* **20**, 289–290 (2004).
- 731 67. K. P. Burnham, D. R. Anderson, *Information and likelihood theory: a basis for model*  
732 *selection and inference* (2002).
- 733 68. K. Barton, MuMIn: Multi-model inference. R package version 1.9. 13. *The Comprehensive*  
734 *R Archive Network (CRAN), Vienna, Austria* (2013).
- 735 69. R Core Team, R: A Language and Environment for Statistical Computing (2017).
- 736 70. Food and Agriculture Organization/ International Network of Food Data Systems  
737 (INFOODS), “FAO / INFOODS Guidelines for Checking Food Composition Data prior to  
738 the publication of a User Table / Database - Version 1 . 0” (2012).
- 739 71. Food and Agriculture Organization of the United Nations, “FAOSTAT. Calculated from  
740 food balance sheets” (2016).
- 741 72. T. Cashion, F. Le Manach, D. Zeller, D. Pauly, Most fish destined for fishmeal production  
742 are food-grade fish. *Fish Fish* **18**, 837–844 (2017).
- 743
- 744

745 **Figure legends**

746 **Fig 1.** Aquatic biodiversity increases human well-being because edible species have distinct and  
747 complementary multi-nutrient profiles (A) and differ in mean micro- and macronutrient content  
748 (shown here relative to 10% and 25% thresholds of recommended dietary allowance (RDA)  
749 guidelines for representative finfish (*Abramis brama*, *Mullus surmuletus*), mollusc (*Mytilus*  
750 *galloprovincialis*) and crustacean species (*Nephrops norvegicus*). Biodiversity – ecosystem  
751 functioning theory predicts that nutritional benefits, including nutritional diversity ( $N_D$ ; i, iii) and  
752 nutritional efficiency ( $N_E$ ; ii, iv) (B, E), are enhanced with increasing dietary species richness.  
753 Seafood consumers with limited access to seafood each day may not reach RDA targets if diets  
754 are low in diversity (F vs C; orange shading indicates proportion of population that meets  
755 nutrient requirements). DHA: docosahexaenoic acid, EPA: eicosapentaenoic acid.

756  
757 **Fig 2.** Variation in nutrient concentrations differs among taxonomic groups. (A) Frequency of  
758 reported protein, fat and micronutrient (including eicosapentaenoic acid (EPA), docosahexaenoic  
759 acid (DHA)) content in 100 g of the edible portion of 430 seafood species (references in Dataset  
760 S1). (B) Proportion of species, and number shown on each bar, with available data that reach  
761 10% of RDI targets for any one, two or up to five of the micronutrients examined here.

762  
763 **Fig 3.** Micronutrient concentrations are significantly negatively related to body size (length, cm)  
764 in finfish. Negative slopes from phylogenetic least squares: calcium: -0.63 (95% CI -0.94, -0.33,  
765  $n = 89$ ), iron: -0.31 (95% CI -0.61, -0.0075,  $n = 92$ ), zinc: -0.33 (95% CI -0.52, -0.13,  $n = 86$ ).

766

767 **Fig 4.** Aquatic biodiversity enhances nutritional benefits at global and local scales. A) Seafood  
768 species richness improves the efficiency with which human diets can meet 10% of RDA by  
769 reducing the grams of seafood required to meet nutritional thresholds. Nutritional efficiency ( $N_E$ )  
770 is shown for five micronutrients and protein separately (points are median values for calcium,  
771 iron, zinc, EPA, DHA and protein, lines show the fit of Equation 1 to the data and shading refers  
772 to 95% CI) as well as for five micronutrients simultaneously (purple line labeled ‘5  
773 Micronutrients’); estimates for the  $b_E$  parameter ( $\pm$  standard error, inset) describe the strength of  
774 the biodiversity effect. B) Increasing dietary species richness sourced from global seafood  
775 markets increases the efficiency with which five micronutrient nutritional targets are reached;  
776 solid circles are median values, as plotted in the purple line in A. C) Increasing species richness  
777 increases the efficiency with which five micronutrient nutritional targets are reached at local and  
778 global scales; shaded areas are 95% confidence intervals about the mean; black lines are the fit of  
779 Equation 1 for each of fourteen traditional indigenous diets in North America, green line is for a  
780 diet sourced from the global seafood market. D) Species richness increases the number of  
781 distinct RDA targets met in a 100g seafood portion (nutritional diversity,  $N_D$ ) in local and global  
782 seafood diets; lines are the fit of Equation 2, color coding as in C.  
783  
784