**Food system biodiversity: Pathways from ecosystems to harvest, consumption, and sale**

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**Significance Statement**

**Abstract (251; 250 limit)**

The increasingly rapid decline of global biodiversity makes understanding how biodiversity supports human well-being urgent, especially in geographies where people are strongly reliant on natural resources for their food and income. Yet the extent to which people’s biodiversity use reflects broader patterns of available biodiversity in ecosystems is often assumed but largely unknown. To examine how the biodiversity in ecosystems is used, we analyze how biodiversity filters from ecosystems to household harvest, consumption, and sale. We used a unique, integrated ecological (40 sites, quarterly data collection) and household survey dataset (n=414, every 2 months data collection) over 3 years from rice field fisheries surrounding Cambodia’s Tonlé Sap, one of Earth’s most productive and diverse freshwater systems. We find that household catch and consumption diversity strongly reflected broader ecosystem biodiversity. Forty-three percent of biodiversity present in the ecosystem is consumed by households, with poorer households consuming more biodiversity. In contrast, only 9% of ecosystem biodiversity is sold, with larger, less nutritious and more common species disproportionally represented in portfolios of sold species. The role of ecosystem biodiversity in shaping biodiversity used by households was remarkably consistent, however, despite variation in household demographics and distance to nearest markets. Our results suggest that ongoing biodiversity change could have critical effects on how people use and derive benefits from ecosystems, with particular implications for the poorest households who may be most reliant on current biodiversity.

**Significance Statement (120 word max)**

While most food derives from a limited number of agricultural and livestock species, wild fisheries are have astounding levels of biodiversity. Yet because accounting for biodiversity is difficult, we often track only commercial fish species. Consequently, we have a limited understanding of how people use aquatic biodiversity. In Cambodia’s rice field fisheries, we find that ecosystem biodiversity is a key driver of the biodiversity in people’s catch and what they eat, but not in what is sold. Our findings suggest that tracking only commercial species can greatly underestimate the true biodiversity present in food systems and ultimately the consequences of biodiversity loss on people who rely most strongly on fisheries as a source of nourishment.

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More than 25% of globally assessed plant and animal species are threatened with extinction (1). The rapid degradation of Earth’s forests, plains, reefs, and lakes is primarily driven by food production, from over-exploitation of fisheries to habitat loss for agricultural activities (1, 2). The deterioration of biodiversity and the ecosystem services it provides make understanding the role biodiversity plays in global food systems increasingly urgent. Yet studies that examine the relationship between biodiversity and food often assume that people’s use of biodiversity reflects broader ecosystem-level biodiversity patterns. Integrating ecological and food system data to account for the multiple pathways by which biodiversity filters from ecosystems to people’s uses is requisite to fully understanding how biodiversity loss might affect food systems.

The benefits of biodiversity are of particular concern for poor households who are directly reliant on natural resources for their food and income. These poorer households are also often on the frontlines of natural resource conservation (3, 4). For millions more households, wild foods play a key but poorly quantified role in their broader food environment (5). When natural resource reliance is high or intermittent, whether access to biodiverse natural resources translates to increased household use of that biodiversity to meet food and income needs is unclear. Evidence from agricultural settings suggest that production diversity may have only small effects on consumption diversity (6). Instead, access to markets plays a key role in mediating the relationship between production and consumption diversity (7). However, these dynamics are largely opaque within the wild systems that provide a critical food source, suffer global biodiversity loss, and support much higher numbers of species compared to agricultural settings.

Fish harvested from Earth’s rivers, lakes and oceans are among the most important source of wild food, feeding billions of people worldwide (8). Yet aquatic biodiversity – and particularly biodiversity within freshwater, inland systems – is rapidly changing (1, 9), which could affect the nutritional status of people that rely heavily on capture fisheries (10, 11). Indeed, fish species vary substantially in their nutritional quality (12, 13), and decreases in dietary species richness can affect micronutrient and fatty acid availability (14, 15). Studies examining the relationship between biodiversity change and nutrient availability are often forced by data limitations to assume that changes in ecosystem biodiversty also reflect changes in access and consumption by people. However, appreciating the role of food system biodiversity requires accounting for how biodiversity available in ecosystems is filtered by households’ choices about what species are caught, consumed, and sold. Such filtering may be particularly complex within food systems that are shifting, for example, through expanding aquaculture production (15, 16) or in response to rising temperatures (17).

Limited data availability similarly positions landing data, meaning tabulations of fish caught at commercial sites, as a simplification for both available fish stocks and fish consumed. Fish landings have been well documented to underestimate stocks (18, 19). This is a particular challenge within data poor small-scale fisheries (20), in which an estimated 100 million people catch two thirds of the global fish supply (21). Detailed analyses of household consumption patterns across African fisheries revealed that official reports of harvests underreported the quantity of fish consumed by 65.8% (22). While there is a wide diversity of fish species globally – estimated at more than 31,000 species (23) – a relatively limited number enter markets. Thus, using fish harvest or landing data to represent either the ecosystems where aquatic species originate or the breadth of species consumed on local dinner plates likely introduces substantial biases.

We examine how biodiversity flows from ecosystems to what people use for consumption and sale (Figure 1; Appendix). We first examine how the species richness (i.e., number of fish species) available within the ecosystem (approximated by standardized ecological biomonitoring; see Methods) reflects what households (1a) catch and select for (1b) consumption and (1c) sale (from hereon scales of analysis). Then, we analyze (2) the role of fish ecological characteristics (i.e., body size, nutrient content, commonness) and (3) household characteristics in shaping what households catch, consume, and sell. Together, our analyses illuminate the extent to which natural resource dependent households use and benefit from biodiversity, and how fish ecological and household characteristics shape these biodiversity relationships.



**Figure 1**. Conceptual diagram of our research approach and questions: How does system biodiversity shape (1a) catch, (1b) consumption, and (1c) sale biodiversity? How do (2) ecological traits and (3) household characteristics shape biodiversity utilization?

Our approach integrates ecological and household information within Cambodian rice field fisheries. Fish diversity within this ecosystem is very high, with 135 documented finfish species (24). While engagement in fishing is widespread, livelihoods are relatively diversified and community members around rice field fisheries engage in a suite of activities and often define rice farming as their primary activity (25, 26).

We quantified the overlap between species richness in the ecosystem, household catch, and household sale and consumption using a unique dataset that directly links these features. Ecosystem data were collected quarterly from 2012-2015 from 40 Community Fish Refuges (CFR) surrounding the Tonlé Sap lake in Cambodia by WorldFish (see Materials and Methods and 27). Community Fish Refuges are managed, protected water bodies that are designed to increase fishery productivity in rice fields (27-29). Household level data on fishing effort, catch, consumption, sale and other uses of fish come from a panel of 410 households collected bimonthly from 2012-2015 (see Materials and Methods and 17). We aggregate this panel across time for our analysis to visualize the distribution of species richness at each level (ecosystem, catch, consumption, and sale). Ecosystem biodiversity is defined for each household based on biomonitoring of the nearest Community Fish Refuge. We use pairwise t-tests to determine whether means at each level differ from one another, with Bonferroni corrections for multiple hypotheses.

We analyzed how fish and household characteristics shape relationships between ecosystem and household uses of biodiversity to explain patterns of biodiversity filtering. To examine the role of fish characteristics, for every species we: obtained total length from FishBase (23); used nutrient information from Heilpern et al. (30) to calculate nutrient density based on supply of protein, iron, zinc, calcium, vitamin A, omega-3 fatty acids DHA and EPA;and calculated commonness to provide a metric of abundance within the ecosystem; we repeat the visualizations and analysis across levels described above with each of these characteristics. To examine the role of variation across households in shaping biodiversity use, we a priori selected variables, including socio-demographics, asset index, fishing effort, and market access (Materials and Methods). Using panel fixed effects regressions, we modeled the extent to which the addition of control groups altered the core biodiversity relationships and evaluated these using Wald tests. Using Shapley-Owen decompositions, we also assessed the variance explained by each component of the models. Together these analyses resolved not only the ways biodiversity use varies but identified key patterns within ecological and social spaces of this use.

**Results & Discussion**

***Q1: Biodiversity filters from the ecosystem to human uses***

We find that the biodiversity of households’ catch and consumption increases alongside the biodiversity in the ecosystem (**Figure 2**). On average, 43.1% of biodiversity present in the ecosystem is consumed by households, though only 9% is sold (**Figure 2**, Q1a). While biodiversity is sharply filtered from what is present in the ecosystem to the species caught, of those species that are caught, a large majority (94%) appear on people’s plates (Q1b) while only a fraction of species (18%) are sold by households (Q1c). Further, nearly all species in the ecosystem are caught and then consumed or sold at some point, by at least one household: 93% (123 species) are consumed and 83% (110 species) are sold.

Critically, these findings underscore that relying on representations of fisheries’ value and use through commercial harvests or market data could hugely misestimate the extent of households’ use of biodiversity. For example, UN FAO highlights 20 commercial freshwater species in Cambodia (31), 16 of which appear in our data. These species represent common species caught and consumed by households and comprise a substantial 51% of catch by households in our data by weight. Within this highly biodiverse system, however, these top commercial species represent only small subset of ecosystem-level biodiversity: nearly 8 times more species are routinely consumed by any individual household. Further, 35% of households consume but never sell fish (24), underlining the potential to undercount biodiversity used by households that does not enter markets. Considering that geographies where people rely heavily on freshwater fish are highly diverse (32), misrepresentation of biodiversity use are likely widespread.

***Q2: Filtering of biodiversity for human uses integrates ecological traits***

Fish catch is fundamentally a function of a combination of species availability and the choices of households. Households elect to fish, choose their fishing grounds, and select fishing gears, many of which are highly specialized. Similarly, the choice of which species to consume and sell is dependent on a range of factors, including not only availability but factors such as preferences, prices, and market access. We found that ecological traits – including body size, nutrient profiles, and size – are associated with how biodiversity flows from the ecosystem-level to what households choose to consume and sell.

On average, households sellspecies that are larger and more common, and consume more nutrient dense species (**Figure 3**, Q2). The portfolios of species that households catch *and* those they consume tend to be larger, less nutrient dense, and less common than the portfolio of species found in the ecosystem (Figure 3, column 2). In comparison to the caught and consumed species, species that are sold are more common, larger, and less nutrient dense than the portfolio of species found in the ecosystem (Figure 3, column 4). While our findings are aggregated to show overall patterns, within this highly seasonal flood-pulse system, the sale of fish is most common in seasons when fishing is most productive (24), and availability of common species may thus drive both higher catches and choices of which species to sell.

These findings carry two implications for fisheries sustainability and diets. First, while the full suite of biodiversity available in an ecosystem underpins wider aquatic food web functioning, households do not directly use the entire constellation of species available. Larger species, which are disproportionally represented in sold species portfolios, tend to fetch higher prices but are also more vulnerable to overexploitation. Indeed large species are declining in Tonle Sap Lake, even as small species catches have remained stable or increased (33). Their targeting and continued decline could lead to changes in ecosystems and the sustainability of the same fisheries that most support livelihoods and food security. Second, a potentially incidental outcome of selecting large species for sale, is that portfolios of consumed species tend to be more nutrient dense than those that are sold. Thus, relying on commercial information might not only underestimate the biodiversity within food systems, but also the nutritional contribution fisheries make to people’s diets. However, the nutrient density of consumed portfolios is lower than that available within ecosystems, underscoring that higher quality diets could be achieved if species were used in a way that better reflects ecosystem-level patterns. However, as households do consume species with the same nutrient density as what is represented within their catch portfolio, they are maximizing consumption of the most nutritious species caught while selling larger, less nutrient dense species.

Similar patterns in the multifaceted relationship between smaller fish, higher nutrient density, and lower prices are observed in global settings (34). [ SENTENCE ….] Beyond specific species, the nutritional value and potential of drawing from a diverse portfolio of aquatic species is increasingly recognized as a means to advance food security (10, 13, 35). Thus, within settings like inland Cambodia where people consume many species, it is critical that fisheries, public health and conservation policies broaden focus beyond fish quantity to the biodiversity within fisheries, especially as aquatic ecosystems are transformed by global change.

***Q3: Relationship between ecosystem biodiversity and use of biodiversity is consistent across household characteristics***

Integrating household information into our analysis allows us to examine three key dynamics: whether the addition of household characteristics to our models affects the biodiversity relationships we observe, the relative roles of household characteristics and environmental context in driving biodiversity use by households, and whether specific household characteristics affect biodiversity use by households.

The positive relationship between ecosystem biodiversity and household use of biodiversity remained remarkably consistent, even when accounting for variation in households. After controlling for effort, the core relationships between biodiversity are unchanged by the addition of household characteristics and market access (Q3), highlighting the importance of ecosystem-level biodiversity in influencing use of biodiversity across households. The decomposition of our regression results illustrates nearly 50% of catch and consumption biodiversity are explained by our models (**Figure 4**). Fishing effort is a component of the quantity of fish harvested, and additional sampling of ecosystems is likely to increase biodiversity harvest particularly within fisheries with low selectivity or that are ‘indiscriminate’ as is the case in the Tonlé Sap and other freshwater ecosystems (33, 36). Effort played an expected role in explaining catch biodiversity (26.5%) and consumption biodiversity (25.7%). After accounting for effort and a suite of household characteristics, however, ecosystem biodiversity explained 16.6% of catch biodiversity and 14.6% of consumption biodiversity. Our models explained less than 20% of biodiversity of species sold overall, and ecosystem biodiversity accounted for only 1.9% of variation in the species sold by households. When looking at the predictive value of catch biodiversity, we found much stronger relationships; catch biodiversity predicted 76.8% of consumed biodiversity and 18.3% of sold biodiversity (Supplementary Table).

These findings underscore the role of the ecological food environment in driving household use of biodiversity. The concordance between the biodiversity in catch and diets, and the overwhelming role of catch biodiversity in predicting consumption patterns is a striking recognition of the importance of access to fishery biodiversity to provide a diverse portfolio of fish and nutrients to regional diets. That our models do not explain the diversity of species sold as well, suggests the importance of other factors (e.g., price, preferences) in driving selection of households’ choices about species to sell. This finding underlines the role of ecological traits discussed above. Further, the global focus on quantity of fish harvested and those aquatic species involved in commerce means such statistics may not comprehensively reflect the species *caught, consumed, or present in the ecosystem.*

Although household amenities and livelihood indices explained a limited amount of the aggregate biodiversity at each level, we consistently find that poorer households make more use of regional biodiversity. Holding constant the biodiversity in ecosystems and fishing effort, poorer households both catch and consume more species: for every 1 unit increase in a household amenities index, households catch and consume 1.5 fewer species (Supplementary Table). Natural resources may serve as a ‘safety net’ for vulnerable households (37-39), and this finding suggests that biodiversity could be of particular value for poor households, even if the relationship is driven not by a preference for a biodiverse harvest but that poorer households use more indiscriminate fishing methods. The biodiversity of aquatic foods may thus simultaneously underpin the supply of a nutrient dense portfolio of diverse aquatic species for the poorest households around Cambodia’s rice field fisheries.

Our analyses harnesses a unique and integrated social-ecological dataset to examine how biodiversity filters from ecosystems to household uses, but these analyses have some limitations. First, we use Community Fish Refuges to represent ecological biodiversity, but these are managed protected areas and may not be fully representative of the diverse array of species that households access from a wider range of regional ecosystems. Second, the harvest of aquatic foods could affect biodiversity within regional ecosystems, and we are not able to disentangle these complex feedbacks which likely play a role in this system. Third, our analyses are aggregated across seasons, but the Tonlé Sap exhibits strong seasonality, creating a compelling research need to understand whether patters of biodiversity use will change with ongoing shifts in floodpulse and climate (40, 41). Fourth, fish processing is common in Cambodia (42), but our data does not capture the ultimate fate of these products as consumed or sold, precluding their inclusion in our analysis. Finally, the households sampled within this study owned rice fields; this inclusion criteria limits generalizability about our findings to poorer households within these communities, notably landless households, and more broadly to those reliant directly on the Tonle Sap or Mekong Rivers.

**Conclusion**

Natural resource dependent households rely on surrounding biodiversity for their food and income. Explicating the ways households use biodiversity is critical to appreciating the true value of diverse ecosystems, the myriad roles biodiversity plays for people, and how food systems will shift in the face of the global biodiversity crises. The rich aquatic biodiversity of the Mekong basin faces myriad threats and has a highly dependent population of resource users (43). While our analyses focus on a single setting, the natural resource dependence is mirrored in small-scale fishing communities around the world and paralleled in a range of wild food environments (forest use, wild meat harvest).

Within data-limited systems like Cambodia’s rice field fisheries, market or landing data are often used to stand in for the biodiversity of fish in the system and their use by households. Yet our findings suggest that many consumed species are rarely—if ever—sold by households. Consumed species also tend to be smaller and more nutritious than those that are sold, potentially rendering invisible the extent of biodiversity used and thereby the true contribution fisheries make to households’ food security and nutrition.

As global environmental change is progressing amid broad demands on freshwater for energy production, irrigation, and industrial uses, the values assigned to different resource functions are critically important in balancing these competing demands. Misestimating the value of aquatic biodiversity to people or how they use it could have grave consequences for the households that depend directly on biodiversity.

**Methods**

***Data***

Four sources of data contributed to this analysis (for full details see 17, 27):

1. Natural system data collected at 40 Community Fish Refuges every 3 months over 2 years (13 time points), This data was collected by WorldFish and partner NGOs between November 2012 and November 2015.
2. Household fish catch and consumption data collected from 414 households every 2 months over 3 years (19 time points). This data was collected by WorldFish and partner NGOs between November 2012 and November 2015.
3. Household characteristic data collected from 640 households in 2012 and 2015 (2 time points). This data was collected by WorldFish and partner NGOs. We use only the data from 2012 that overlaps with household fish catch and consumption data (n = 410).
4. Additional species trait information was drawn from FishBase and Heilpern et al (30). We focused on six nutrients that are central to children’s health and development and are often derived from fish: protein, iron, zinc, calcium, vitamin A and omega 3-fatty acids.

***Analysis***

Q1 Biodiversity Filters Through the System – To examine how biodiversity filters, we aggregated data across time and visualized the distribution of biodiversity at each scale, using pairwise t-tests to determine statistical differences in means between the ecosystem, catch, consumed and sold portfolios, with Bonferroni corrections for multiple hypotheses. We repeated this process separately with Shannon and Simpson indices (Supplemental Results).

Q2 Ecological Traits – For each level of biodiversity (i.e., ecosystem, catch, consumption, sold) we computed species richness, and the following ecological characteristics: mean body size, nutrient density score, and mean commonness index. Methods are summarized below; see Supplemental Methods for further details.

*Portfolio mean body size* () was estimated as for each scale *l* (i.e., ecosystem, caught, consumed, sold), associated with each CFR, *j*, using each species total length, *Ls*, as:

*Abundance-weighted mean commonness index* was estimated as:

where is the mean commonness index at scale *l* (i.e., ecosystem, caught, consumed, sold), associated with CFR *j*, and is the relative abundance of species *s* in scale *l* associated with CFR *j.* This mean commonness index sets a baseline at the ecosystem scale (i.e., for the CFR). When values are lower than the baseline, species portfolios are represented by less common species, whereas when higher, portfolios are composed of more common species.

*Portfolio nutrient density,* , was estimated using species-specific nutrient content information () from Heilpern et al (under review), which indicates the amount of each of nutrient (protein, iron, zinc, calcium, vitamin A, omega-3 fatty acids), , in 100g of a given fish species . Using portfolio-specific relative abundance (e.g.), we calculate the nutrient content of 100g of each portfolio as

|  |  |
| --- | --- |
|  | (5) |

We used the USDA Recommended Daily Allowance (RDA) for a child under 5 for each nutrient () as the threshold for adequacy for a given nutrient. We calculated the Nutrient Density Score, , which is the sum of portfolio nutrient content across all nutrients.

Q3 Household Characteristics - Data included: fishing effort (defined as mean number of person-days spent fishing in the prior 7 days), household size, household dependency ratio (defined as the share of household members <16 or >65), maximum educational attainment by any household member, household amenities (e.g., building materials, water access) index, household livelihood asset index, and market access (defined as the distance to the nearest provincial capital: Battambang, Pursat, Siem Reap or Kampong Thom).

To understand the role that household characteristics play in the ways biodiversity filters from ecosystems to household uses (Q3), we examined the role of variation across households using ordinary least squares regression. All regression models cluster standard errors at the CFR level, thus adjusting standard errors to account for correlation between households associated with the same CFR (44). In our models, we added groups of controls in a stepwise fashion and assessed the extent to which the core diversity relationships change with the addition of control groups using Wald tests. We also used Shapley-Owen decompositions to understand the variance explained by each component of the model. Guided by a priori covariate selection, we included the following covariates in our models: effort, effort squared, household size, dependency share, maximum educational attainment, market access, principle component analysis of a household amenities index (45), and principle component analysis of a livelihood asset index (45). See Supplemental Methods for further details.

References

1. IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. ed J. S. E. S. Brondizio, S. Díaz, and H. T. Ngo (IPBES secretariat, Bonn, Germany), p 1148.

2. P. Jaureguiberry *et al.*, The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances* **8**, eabm9982 (2022).

3. N. Myers, R. a. Mittermeier, C. G. Mittermeier, G. a. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858 (2000).

4. M. Herrero *et al.*, Farming and the geography of nutrient production for human use: a transdisciplinary analysis. *The Lancet Planetary Health* **1**, e33-e42 (2017).

5. S. M. Downs, S. Ahmed, J. Fanzo, A. Herforth, Food Environment Typology: Advancing an Expanded Definition, Framework, and Methodological Approach for Improved Characterization of Wild, Cultivated, and Built Food Environments toward Sustainable Diets. *Foods* **9**, 532 (2020).

6. K. T. Sibhatu, M. Qaim, Review: Meta-analysis of the association between production diversity, diets, and nutrition in smallholder farm households. *Food Policy* **77**, 1-18 (2018).

7. D. Tobin, K. Jones, B. C. Thiede, Does crop diversity at the village level influence child nutrition security? Evidence from 11 sub-Saharan African countries. *Popul. Env.* **41**, 74-97 (2019).

8. FAO (2020) State of the World's Fisheries and Aquaculture. (Food and Agriculture Organization of the United Nations, Rome).

9. D. Tickner *et al.*, Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. *Bioscience* **70**, 330-342 (2020).

10. L. O'Meara *et al.*, Inland fisheries critical for the diet quality of young children in sub-Saharan Africa. *Global Food Security* **28**, 100483 (2021).

11. K. J. Fiorella, E. M. Milner, E. Bukusi, L. C. Fernald, Quantity and species of fish consumed shape breast-milk fatty acid concentrations around Lake Victoria, Kenya. *Public Health Nutr.* **31**, 1-8 (2017).

12. S. A. Heilpern *et al.*, Declining diversity of wild-caught species puts dietary nutrient supplies at risk. *Science Advances* **7**, eabf9967 (2021).

13. K. A. Byrd, S. H. Thilsted, K. J. Fiorella, Fish nutrient composition: a review of global data from poorly assessed inland and marine species. *Public Health Nutr.* 10.1017/S1368980020003857, 1-11 (2020).

14. J. R. Bernhardt, M. I. O’Connor, Aquatic biodiversity enhances multiple nutritional benefits to humans. *Proceedings of the National Academy of Sciences* **118**, e1917487118 (2021).

15. S. A. Heilpern *et al.*, Substitution of inland fisheries with aquaculture and chicken undermines human nutrition in the Peruvian Amazon. *Nature Food* **2**, 192-197 (2021).

16. J. R. Bogard, G. C. Marks, S. Wood, S. H. Thilsted, Measuring nutritional quality of agricultural production systems: Application to fish production. *Global Food Security* **16**, 54-64 (2018).

17. K. J. Fiorella, E. R. Bageant, N. B. Schwartz, S. H. Thilsted, C. B. Barrett, Fishers’ response to temperature change reveals the importance of integrating human behavior in climate change analysis. *Science Advances* **7**, eabc7425 (2021).

18. M. N. Maunder *et al.*, Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J. Mar. Sci.* **63**, 1373-1385 (2006).

19. S. J. Harley, R. A. Myers, A. Dunn, Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.* **58**, 1760-1772 (2001).

20. D. Pauly, D. Zeller, Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications* **7** (2016).

21. R. E. Short *et al.*, Harnessing the diversity of small-scale actors is key to the future of aquatic food systems. *Nature Food* **2**, 733-741 (2021).

22. E. Fluet-Chouinard, S. Funge-Smith, P. B. McIntyre, Global hidden harvest of freshwater fish revealed by household surveys. *Proceedings of the National Academy of Sciences* **115** (2018).

23. R. Froese, D. Pauly (2021) FishBase.

24. S. Freed *et al.*, Rice field fisheries: Wild aquatic species diversity, food provision services and contribution to inland fisheries. *Fisheries Research* **229**, 105615 (2020).

25. K. Fiorella, Magnuson, H, Finey-Stable, A, Chork, S, Voleak, P, Fox, E. , Environmental change and resource access in aquatic food systems: A photovoice case study of Cambodian fisheries. *Ecol. Soc.* (in review).

26. Q. Wang *et al.*, Nutrition and Food Safety of a Locally-Processed Fish Product in Cambodia. *Aquatic Ecosystem Health and Management* (In press).

27. K. J. Fiorella *et al.*, Analyzing drivers of fish biomass and biodiversity within community fish refuges in Cambodia. *Ecol. Soc.* **24** (2019).

28. O. Joffre, M. Kosal, Y. Kura, S. Pich, T. Nao (2012) Community fish refuges in Cambodia: Lesson learned. in *Lessons Learned Brief 2012-03* (WorldFish, Phnom Penh, Cambodia).

29. M. Kim, E. Bageant, S. Thilsted, K. Fiorella, "Community Management of Fish Refuges in Cambodian Rice Field Fisheries" in From catastrophe to recovery: stories of fishery management success*,* C. Krueger, W. Taylor, S.-J. Youn, Eds. (American Fisheries Society, Bethesda, Maryland, 2019).

30. S. A. Heilpern, G.A. Herrera-R, K. Fiorella, A.S. Flecker, P. McIntyre. , Functional diversity sustains dietary nutrients supplied by freshwater fisheries. . *In revision at Ecology Letters.* .

31. FAO (2022) Fishery and Aquaculture Country Profiles. Cambodia. in *Country Profile Fact Sheets.* , ed F. a. A. D. [online]. (Rome).

32. P. B. McIntyre, C. A. Reidy Liermann, C. Revenga, Linking freshwater fishery management to global food security and biodiversity conservation. *Proceedings of the National Academy of Sciences* **113**, 12880-12885 (2016).

33. P. B. Ngor *et al.*, Evidence of indiscriminate fishing effects in one of the world’s largest inland fisheries. *Scientific Reports* **8**, 8947 (2018).

34. J. P. W. Robinson *et al.*, Small pelagic fish supply abundant and affordable micronutrients to low- and middle-income countries. *Nature Food* **3**, 1075-1084 (2022).

35. K. A. Byrd, L. Pincus, M. M. Pasqualino, F. Muzofa, S. M. Cole, Dried small fish provide nutrient densities important for the first 1000 days. *Maternal & Child Nutrition* **n/a**, e13192 (2021).

36. S. A. Heilpern *et al.*, Biodiversity underpins fisheries resilience to exploitation in the Amazon river basin. *Proceedings. Biological sciences* **289**, 20220726 (2022).

37. K. J. Fiorella *et al.*, Feedbacks from human health to household reliance on natural resources during the COVID-19 pandemic. *The Lancet Planetary Health* **4**, e441-e442 (2020).

38. C. Shackleton, S. Shackleton, The importance of non-timber forest products in rural livelihood security and as safety nets: a review of evidence from South Africa. *S. Afr. J. Sci.* **100**, 658-664 (2004).

39. J. S. Brashares *et al.*, Wildlife decline and social conflict. *Science* **345**, 376-378 (2014).

40. H. Navy, M. Bhattarai, Economics and livelihoods of small-scale inland fisheries in the Lower Mekong Basin: a survey of three communities in Cambodia. *Water Policy* **11**, 31-51 (2009).

41. S. Brooks, J. Reynolds, E. Allison, Sustained by Snakes? Seasonal Livelihood Strategies and Resource Conservation by Tonle Sap Fishers in Cambodia. *Hum. Ecol.* **36**, 835-851 (2008).

42. W. Qijin *et al.*, Nutrient composition and microbial food safety of a locally-processed fish product in Cambodia. *Aquat. Ecosyst. Health Manage.* **25**, 73-81 (2023).

43. B. Kang, X. Huang, Mekong Fishes: Biogeography, Migration, Resources, Threats, and Conservation. *Reviews in Fisheries Science & Aquaculture* **30**, 170-194 (2022).

44. A. Abadie, S. Athey, G. W. Imbens, J. M. Wooldridge, When Should You Adjust Standard Errors for Clustering?\*. *The Quarterly Journal of Economics* **138**, 1-35 (2022).

45. D. E. Sahn, D. Stifel, Exploring Alternative Measures of Welfare in the Absence of Expenditure Data. *Review of Income and Wealth* **49**, 463-489 (2003).