

APPLIED ECOLOGY

Declining diversity of wild-caught species puts dietary nutrient supplies at risk

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Although biodiversity loss adversely influences a variety of ecosystem functions, how declining wild food diversity affects nutrient supplies for people is poorly understood. Here, we analyze the impact of declining biodiversity on nutrients supplied by fish using detailed information from the Peruvian Amazon, where inland fisheries provide a critical source of nutrition for many of the region's 800,000 people. We found that the impacts of biodiversity loss on nutrient supplies depended on compensation, trophic dynamics, and functional diversity. When small sedentary species compensated for declines in large migratory species, fatty acid supplies increased, while zinc and iron supplies decreased. In contrast, the probability of failing to maintain supplies or nutrient supply risk increased when species were nutritionally unique. Our results show that trait-based regulations and public health polices need to consider biodiversity's vital role in sustaining nutritional benefits for over 2 billion people dependent on wild foods across the globe.

INTRODUCTION

Biodiversity positively influences the magnitude and stability of ecosystem functions, which motivates utilitarian concerns associated with widespread losses in biodiversity (1, 2). Few studies, however, have actually linked biodiversity loss to services that directly affect human well-being (3). For approximately 2 billion people worldwide, wild-caught or harvested species, such as fish, bushmeat, insects, fruits, and other nonagriculturally produced foods (e.g., wild foods), provide an essential source of nutrition (4, 5). As with changes in biodiversity prevalent in most ecosystems, however, the diversity of wild-caught species is also declining (6). By inference, nutrients supplied by wild foods could be adversely affected when the diversity of harvested or capture species declines. However, trophic dynamics and compensatory growth among harvested species complicate the diversity-function relationship (7), making it difficult to predict how such losses in the biodiversity of wild foods could affect the magnitude and stability of dietary nutrient supplies.

Fish are among the most common and important wild foods, providing people with their primary source of key nutrients, including protein, zinc, iron, calcium, and omega-3 fatty acids (8, 9). However, overfishing, pollution, climate change, and habitat degradation are threatening fish diversity, with large-bodied and migratory species showing substantial declines across many inland and marine ecosystems (10, 11). Despite these biodiversity changes, biomass harvested by fisheries can remain remarkably consistent across time, primarily because small and fast-growing species often compensate for declines in vulnerable species (i.e., large-bodied, migratory, high trophic level) (12–14). Beyond varying in their threat tolerance, fish species also vary substantially in their nutrient content (9, 15). Thus, nonrandom changes in species harvest composition could affect

how fisheries support food security in regions where people rely on fish as a source of nutrition.

Here, we evaluate how declines in wild-caught biodiversity affect the magnitude and stability of nutrient supplies by using detailed trait and landings information for 56 fish taxa (data file S1), representing more than 98% of fish landed in the Department of Loreto in the Peruvian Amazon. As in many other inland and coastal regions, people in Loreto depend heavily on diverse capture fisheries for essential animal-derived nutrients, consuming, on average, 51.6 kg per year or one serving per day (16–18). Wild fish species often provide a nutritionally irreplaceable source of nutrients to approximately 800,000 people in Loreto, both because of their higher nutrient content and accessibility compared with other animal substitutes (19–22). In Loreto, as in other freshwater ecosystems, fish diversity is increasingly threatened by hydropower development and overfishing (23, 24). However, biomass harvests have remained stable across time, largely through compensatory dynamics induced by declines in large and migratory species and their replacement with smaller and more sedentary species (14).

Using trait-based extinction scenario modeling (7, 25), we examined the impact of declining harvest diversity on (i) the magnitude of fish-derived nutrient supplies, estimated as the number of people, scaled to Loreto's population age structure, meeting their annual reference nutrient intakes (RNIs) for seven essential animal-derived nutrients [i.e., protein, iron, zinc, calcium, and omega-3 fatty acids α -linolenic acid (ALA), eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA)], and (ii) the stability of fish-derived nutrient supplies, estimated as the probability of failing to sustain supplies above a set supply threshold with ongoing biodiversity loss or nutrient supply risk (26). Briefly, our trait-based modeling approach simulates empirical patterns of biodiversity change, where biomass harvested remains stable, but community composition changes according to species tolerance to threats (i.e., hydropower development and overexploitation). At each time step, a species is removed from the community with probabilities related to traits associated with local declines, such as body size, migration, and trophic level. Subsequently, the remaining species are allowed to compensate for the extinct species by allocating the extinct species biomass to any

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remaining species (i.e., randomly) or to species in the same trophic guild (i.e., trophically constrained). While no compensation scenarios provide worst-case estimates of biomass loss, random and trophic compensation scenarios model null and conservative estimates of biomass dynamics with ongoing compositional turnover (7). Together, these three scenarios allow us to explore how biodiversity loss can result in changes in the magnitude and stability of nutrient supplies even in the absence of any change in harvested biomass (see Materials and Methods and the Supplementary Materials for additional details on modeling and analytical approaches).

In this study, we quantitatively analyze two central components of food security: availability and stability of fish-derived nutrient supplies (27). Access to and use of fish and other animal substitutes, important social components of food security, are not explicitly addressed but are further considered in light of our findings. By realistically constraining our analysis to a well-studied inland fishery in the Amazon, we highlight the often ignored but invaluable contribution of inland fisheries for human nutrition and, more generally, how declines in wild-caught biodiversity could affect nutrient availability and stability for the millions of people dependent on wild foods for their well-being.

RESULTS AND DISCUSSION

Biodiversity declines and the magnitudes of nutrient supplies

Nonrandom biodiversity loss, where species extinction probabilities are related to hydropower and overharvesting as reflected in larger body size, migration, and higher trophic level, decreased supplies across all nutrients. In the absence of biomass compensation, for each species lost, supplies decreased, on average, by 1.76% across all nutrients ($\pm 0.01\%$; Fig. 1). Compensation by smaller, sedentary, and lower-trophic position species, however, maintained overall harvest biomass and buffered the detrimental consequences of biodiversity loss on the supplies of all nutrients (fig. S2). Despite this overall positive effect of compensation, nutrient supplies exhibited substantial variation with ongoing declines in biodiversity (Fig. 1). Protein and calcium supplies, for example, remained consistent until high numbers of species were lost, whereas ALA, EPA, and DHA supplies increased with moderate levels of biodiversity loss. Iron and zinc slightly declined until high levels of biodiversity loss were reached.

These simulated biodiversity changes largely mirrored ongoing empirical trends exhibited by Amazonian and other tropical inland fish communities (10, 14). Species with the highest extinction probabilities were pimelodid catfish and *Arapaima* sp. By 50% of species loss, both *Brachyplatystoma filamentosum*, the largest pimelodid catfish, and *Arapaima* sp. had a <1% probability of remaining in the community in comparison to 50% in random biodiversity loss scenarios (fig. S1). Following extinction of these large migratory catfish are medium-sized characiforms, such as *Prochilodus nigricans*, which has a 50% chance of remaining in the communities at 50% of species loss. Smaller characiformes, such as *Anodus* spp., have lower extinction probabilities and often compensate for the decline in these larger species, a pattern also observed in analysis of Amazon fisheries time series (14). While the future of fish biodiversity in the Amazon is difficult to predict, with ongoing exploitation and dam development, these trait-based trends in compositional turnover are likely to continue (28, 29).

This variety of responses of nutrient supplies to declining biodiversity reflected several key ecological processes at play. First is the importance of trophic interactions, often absent in biodiversity studies that are monotrophic in design (e.g., plants only), and how they mediate the relationship between biodiversity and ecosystem functions (7). When compensation is limited by trophic structure, such that only species within the same trophic guild can replace extinct species, nutrient supplies are maintained until a threshold of approximately 40 species is reached, after which supplies decline precipitously (Fig. 1). These thresholds, which occur across all nutrients considered, are associated with the extinction of whole trophic guilds, typically meso- and top predators, and biophysical constraints on biomass transfer between species across trophic levels (13). At these high levels of biodiversity loss, compensation fails to maintain biomass production, causing collapsing nutrient supplies, although assumptions about biomass dynamics become uncertain. While fish communities in the Amazon have yet to reach these extinction thresholds, evidence from the region and other systems suggests that overfishing is altering trophic structure (14, 23). Given the vulnerability of species that feed high in the food chain across the world's rivers and oceans (30), similar patterns could play out for other animal-mediated ecosystem functions and services (31).

The second critical factor determining the response of nutrient supplies to biodiversity loss is the variation in nutrient content among species. We found that large-bodied, migrating species typically have lower nutrient content than the smaller, sedentary, and low-trophic position species that replace them, particularly for nutrients such as the three omega-3 fatty acids analyzed (fig. S3). The increase in fatty acid nutrient supplies with moderate biodiversity loss reflects the replacement of low-quality extinction-prone species with more nutritious and less vulnerable species. Conversely, the lack of any changes in protein supplies with ongoing biodiversity loss is associated with the low variability, and hence, high substitutability, of protein content among species. Species variation in other micronutrients, such as iron and zinc, is intermediate, and thus, supplies tend to decline with ongoing biodiversity loss, although only moderately. Furthermore, while we focused on variation among species, variation within species is less well understood, although typically lower than interspecific variation. Nevertheless, changes in food web structure could lead to species dietary shifts and changes in species nutrient content (32, 33). Ultimately, better quantifying intraspecific variation could provide for a more nuanced understanding of the relationship between biodiversity loss and nutrient supplies.

While declining fish catches will undoubtedly have detrimental impacts on human nutrition (34), the degree to which fish biomass is declining, steady, or increasing is a matter of debate (35). Compensation is a central feature of ecological communities and can maintain fish biomass production despite unsustainable fishing practices and other disturbances (12, 13). Beyond maintaining harvested biomass, our results show that compensation can also increase nutrient supplies if species with lower extinction probabilities are also more nutritious. Yet, abrupt declines in nutrient supplies can occur if high levels of disturbance prevent compensatory dynamics, as is projected for many global fisheries with ongoing climate change and overexploitation (36). Recent global analyses show that key nutrients, such as omega-3 fatty acids, are higher in small-bodied species occupying lower trophic levels [e.g., detritivores and grazers; (9, 15, 37)]. Considering the also well-demonstrated relationships among trophic level, body size, and extinction probabilities in fish (10, 11),

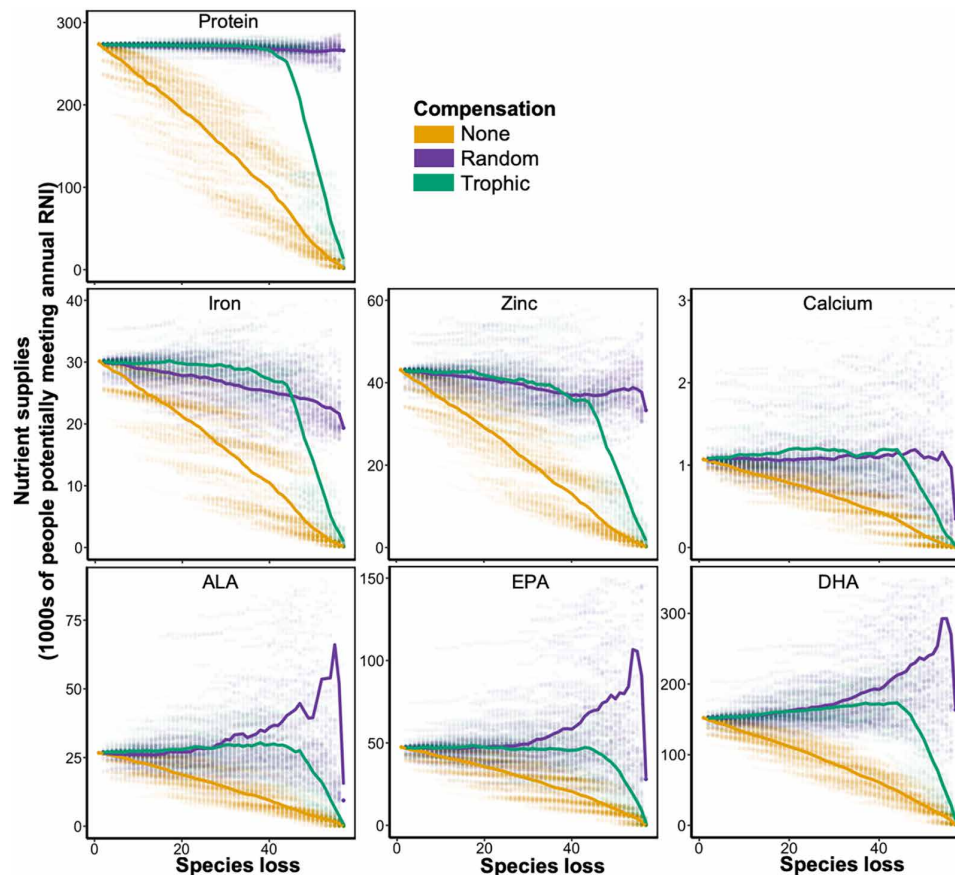


Fig. 1. Nutrient supplies (in 1000s of people potentially meeting their annual RNI with wild harvested fish) vary in their response to nonrandom biodiversity change. Without biomass compensation (orange), nutrient supplies decrease monotonically with species loss, but random (purple) or trophic (green) compensation can maintain or increase nutrient supplies, especially for omega-3 fatty acids (ALA, EPA, and DHA). Points represent individual simulations, whereas lines represent the mean nutrient supplies for each level of species loss.

moderate declines in biodiversity could lead to increasing supplies of some essential nutrients but declines in others. In addition, fish provide multiple nutrients simultaneously, and trade-offs in nutrient content and extinction probabilities could further complicate predictions about the relationship between aggregate nutrient supplies and changing biodiversity.

The risk of ongoing biodiversity loss to nutrient supplies

In contrast to these mixed effects on nutrient supplies, the probability of failing to sustain nutrient supplies or the nutrient supply risk always increased in the face of further biodiversity loss (Fig. 2). As with the magnitude, supply risk, which we equate to a dimension of stability (26), was affected by compensation and trophic structure but varied among nutrients (Fig. 2A; for the full set of nutrients, see fig. S4). For example, the probability of failing to sustain ALA, EPA, and DHA supplies was lower than that for calcium or zinc. The nutrient supply risk of omega-3 fatty acids was the lowest among all nutrients, indicating that a small number of species with low extinction probabilities can collectively sustain both the magnitude and stability of these key nutrients. Varying supply targets did not qualitatively change these results (figs. S5 to S8).

The ecological drivers underlying the variation in nutrient supply risk were largely explained by two opposing facets of functional

diversity and their interaction: tolerance diversity, which is the variety of responses exhibited by species in a community when confronted with a perturbation and is measured as the variation in traits (i.e., trophic level, body size, and migration type) that determine species tolerance to river threats, and nutritional uniqueness, which is the degree to which species in a community contribute similarly to nutrient supplies, measured through the variation in nutrient content among species (38, 39). As expected, communities with low tolerance diversity exhibited high nutrient supply risk (Fig. 2B). In contrast, communities with low uniqueness (also referred to as high redundancy) exhibited low risk because species were more replaceable in terms of their contribution to nutrient supplies (Fig. 2C).

Beyond their independent effects, in fish, the traits that determine tolerance diversity and uniqueness can correlate and link these facets of functional diversity (fig. S3) (9, 15). Regression models, including an interaction term between tolerance diversity and uniqueness, better explained how biodiversity loss affected supply risk ($\Delta AIC = 16$; table S1). Risk was lowest when tolerance diversity was high and uniqueness was low (Fig. 3, quadrant I), intermediate when both tolerance diversity and uniqueness were high (quadrant II), and highest when tolerance diversity was low and uniqueness was high (quadrant IV). In our dataset, communities with low tolerance diversity and low uniqueness were nonexistent, but we expect these to also

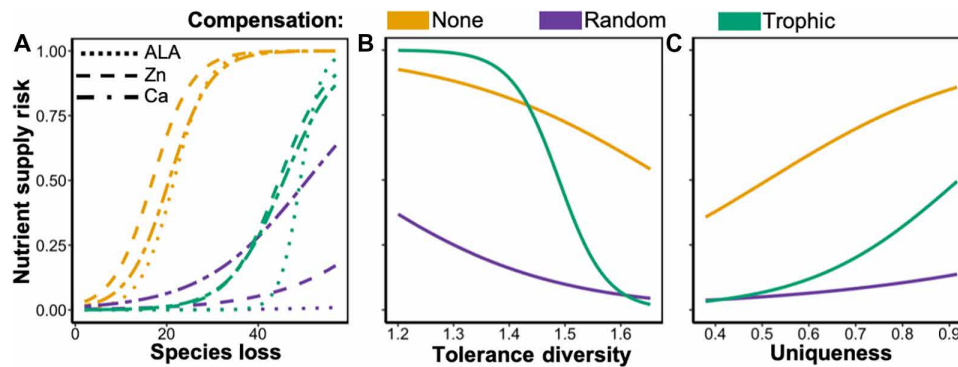


Fig. 2. Nutrient supply risk and its relationship to biodiversity change. Risk is estimated as the probability of failing to meet supply targets (set as 75% of initial nutrient supplies). Nutrient supply risk increases as more species are lost (A) but varies among different nutrients (ALA: linoleic acid; Zn: zinc; and Ca: calcium; for the full set of nutrients, see Supplementary Materials Appendix; fig. S4). Variation in risk is largely explained by biomass compensation (yellow, purple, and green lines), tolerance diversity (B), uniqueness (C), and their interaction (see Fig. 3). Lines represent best-fit models of a generalized linear mixed-effect model (see Materials and Methods).

exhibit intermediate nutrient supply risk given their lower tolerance diversity (quadrant III).

Trait or functional diversity is a fundamental aspect driving ecosystem responses to biodiversity loss, but our results suggest that it does so in more complex ways than previously recognized. Classic studies in ecology show a positive relationship between functional diversity and different aspects of ecosystem stability (40, 41). However, more recently, several investigations have found that biodiversity can have both positive and negative impacts on components of ecosystem stability (7, 42, 43). In fish, as in other taxa, it is common practice to aggregate between different sets of traits, such as those that determine species extinction probabilities and their nutrient content (44, 45). However, when these two facets of functional diversity are nonindependent, trait variation can increase both tolerance diversity and uniqueness, leading to opposing effects on the stability of ecosystem functions. Considering tolerance diversity and uniqueness together provides a more comprehensive understanding of how functional diversity affects the stability of ecosystem functions and services.

Implications of changes in fish-based nutrient supplies for broader food security

Beyond how variation in species traits affects the magnitude and stability of nutrient supplies, food security is multidimensional, and the consequences of biodiversity loss will also depend on access to and utilization of nutritional resources across the food system (27). By interacting with these other dimensions, changes in nutrient supplies are most likely to affect people who heavily depend on wild-caught species, such as fish, and have limited access to alternative dietary nutrient sources. As in other coastal and riverine communities, subgroups in Loreto, particularly poorer and more rural people, derive their animal source food intake nearly exclusively from fish (16–18, 20, 21, 34). Although exact regional estimates are not available, other work suggests that in some communities in Loreto, more than 75% of people consume fish at least once a day (17). This high reliance on fish is primarily driven by their lower prices and higher availability in comparison to other common animal food substitutes, such as chicken and livestock. In addition to price differences between fish and other animal substitutes, price differences among fish species, together with how they are prepared and consumed, could further shape the impacts of biodiversity loss on food

security. Larger fish are often more expensive and filleted, whereas small species are preferentially consumed whole, which increases their nutritional value since organs and bones have higher nutrient density than muscle (37, 46). Thus, differences in access and utilization among species could further expose people to both positive (e.g., ALA, EPA, and DHA) and negative shifts (e.g., Fe) in nutrient supplies, potentially rendering our results as underestimates since we only analyzed nutrients in muscle.

In contrast to subgroups most reliant on fish, people who consume fish less often depend on other foods to meet nutritional needs and, consequently, are less likely to be affected by changing nutrient supplies if nutritionally comparable substitutes are accessible. In Loreto, as in many other regions dependent on small-scale fisheries, chicken is increasingly becoming the main substitute for fish (16, 21, 47). Yet, dietary shifts to chicken, with lower iron and omega-3 fatty acid content, could also reduce nutrients supplied relative to diets based on wild fish (14). In Loreto, this chicken-for-fish substitution might exacerbate existing rates of anemia and malnutrition since fish provide a critical source of iron and omega-3 fatty acids for many of the region's inhabitants (20, 48). In addition, consuming other animal products could compensate for a limited set of nutrients, such as milk and calcium, but are otherwise not similarly used. Yet, other animal foods, such as beef and pork, are more expensive, making them less accessible and less frequently consumed even for wealthier households (20, 21, 48). Thus, shifting to other animal foods will likely remain particularly challenging for the poor who rely heavily on fish (18). Ultimately, while we focused on changes in nutrient supplies induced by fish biodiversity changes, as dietary shifts progress and additional social and economic data become available, their integration into our framework would enrich, but not qualitatively alter, our understanding of how biodiversity loss more broadly affects food security.

We have focused on Loreto's fisheries as an example of a system where wild-caught biodiversity serves as an important source of dietary nutrients, but our findings are likely applicable to other systems where wild foods support food security. Inland fisheries support more than 150 million people, and marine fisheries support more than 1 billion people (34, 49). Similarly, land-based wild foods, including bushmeat, insects, and fruits, are regularly eaten by millions worldwide (50, 51). This dependence on wild foods is particularly strong for indigenous, rural, and low-income urban people

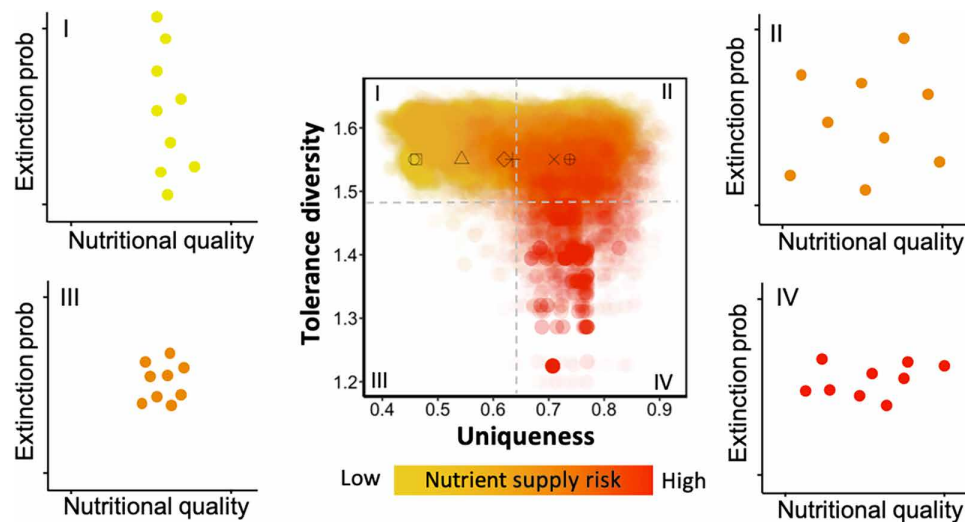


Fig. 3. Trade-offs between tolerance diversity and uniqueness shape nutrient supply risk. The center panel is divided into four quadrants, each represented by a potential relationship between species nutritional qualities, used to estimate community uniqueness, and their extinction probabilities, used to estimate community tolerance diversity. The points in the center panel are simulated communities, whereas the points in the side panels represent species in a hypothesized community. In the center panel, shapes represent the initial communities with uniqueness values varying depending on the specific nutrient (protein: \times , iron: \oplus , zinc: \diamond , calcium: $+$, ALA: \square , EPA: \circ , and DHA: \odot). Quadrant I: Low variation in species nutritional quality and high variation in extinction probabilities result in communities with low uniqueness, high tolerance diversity, and low nutrient supply risk. Quadrant II: High variation in species nutritional qualities and extinction probabilities results in communities with high uniqueness, high tolerance diversity, and moderate nutrient supply risk. Quadrant III: Low variation in species nutritional qualities and extinction probabilities results in communities with low uniqueness, low tolerance diversity, and moderate nutrient supply risk. Quadrant IV: High variation in species nutritional qualities and low variation in extinction probabilities result in communities with high uniqueness, low tolerance diversity, and high nutrient supply risk.

in low-latitude and developing nations, who also face similar challenges associated with accessing other nutritional substitutes (6, 18). Beyond the shared socioeconomic circumstances, these tropical ecosystems tend to be diverse but are also among the most threatened, with declines in wild food biodiversity reflective of broader changes in biodiversity (6, 45). While falling wild food biomass production has raised food security concerns (34), less attention has been paid to how changes in biodiversity will affect nutrient supplies. Our study has shown that compensation, trophic dynamics, and differences in species nutrient content are fundamental ecological attributes affecting the magnitude and stability of nutrients supplied by inland fish in the Amazon. Although the specific outcomes will be context dependent, the same underlying ecological processes are likely to govern how changing biodiversity affects nutrient supplies in regions where people depend on wild foods.

Biodiversity is notably absent from global and regional policies linking wild foods with food security (8). This is particularly true not only for inland fisheries but also for fisheries more broadly. Our results suggest, however, that including biodiversity can maximize the contribution of wild foods to food security and provide for more effective policy for several reasons. First, while compensation can buffer the impact of biodiversity loss on ecosystem services, the potential for compensation depends on high species richness, high tolerance diversity, and low uniqueness. Because these different facets of biodiversity interact, they could become more tightly linked as fewer species remain (39), and efforts to increase food supplies through higher harvest rates could come at the cost of an increased risk of collapses in nutrient supplies. Second, while single-species management approaches prioritize biomass harvest and revenue, management based on multiple species implicitly considers that species vary in their nutrient content and that multiple species are typically

needed to secure nutrient supplies. Aquaculture systems represent an extreme case of single-species management, and increasing farmed species diversity could become a relevant strategy for maximizing aquaculture's nutritional benefits (22). Third, from the public health perspective, gaps in nutrient supplies associated with declines in wild food biodiversity could be alleviated through the promotion of alternative foods, fortification, and supplements. However, the degree to which these strategies will work depends on improving access to animal substitutes and, in particular, increasing their affordability in relation to fish and other wild foods. Both declines in biomass and diversity will most likely affect population segments that are the least capable of responding (34, 47).

Ultimately, mainstreaming biodiversity into the management of wild-caught species, as we have shown here with inland fisheries, requires investing in policy and practices that sustain biodiversity such as protecting key habitats, maintaining habitat connectivity, and enacting temporary moratoriums on capture. Only when biodiversity is valued alongside harvested biomass and revenue will people be able secure and sustain the full set of nutritional benefits provided by wild foods.

MATERIALS AND METHODS

Trait-based approach

For a detailed description of our modeling approach, see (7). Briefly, each simulation started from the same initial community structure dictated by the empirically measured community composition (i.e., taxonomic diversity and abundance). Community composition trajectories then differed on the basis of trait-based extinction scenarios and compensatory dynamics in which the remaining species replace the lost species following three different scenarios: no

compensation, random compensation, and within trophic guild compensation. A total of 100 simulations were run per scenario (i.e., for a total of 300 communities with biodiversity varying from initial diversity to 1 species remaining). We expand upon the modeling approach below.

Study system

To evaluate how declining biodiversity affects nutrients supplied by wild foods, we used data from the Department of Loreto in the Peruvian Amazon. The Amazon is among the world's most productive inland fisheries and has some of the highest rates of fish consumption, ranging from 51.6 to more than 169 kg per year per person in some riverine communities (16, 52). However, fish biodiversity is threatened primarily by overfishing and infrastructure development, although climate change is predicted to poise a large challenge to the river's biodiversity (24, 28, 29). In Loreto, more than 50 species are commonly caught, consumed, and commercialized in urban markets (14, 23). Fishers use a variety of gears, including gill nets, hooks, and cast nets, and species composition in urban markets aggregates across diffuse users using these different techniques.

Demographic information (i.e., age-structured population) was obtained from Peru's Instituto Nacional de Estadística e Informática, which conducted its last census in 2017. Fishery information was obtained from the Dirección Regional de la Producción-Loreto (DIREPRO-Lor), which has the mandate to collect daily landing information, including landed volume and taxonomic information, at ports of the largest urban areas (i.e., Iquitos, Nauta, Requena, Contamana, Caballo Cocha, San Lorenzo, and Yurimaguas). Following landings data resolution available from DIREPRO-Lor, which sometimes aggregates morphologically similar but taxonomically different species into groups, we combined a number of fish taxa into common groups (e.g., piranhas, palometas, and anostomids; data file S1). Species mean annual biomass harvested was estimated from landing data 2000–2016. All of the landed biomass recorded in this database is destined for local consumption.

Traits

Trait values were obtained from a variety of sources and categorized as either affecting species extinction probabilities or their contribution to nutrient production. Extinction-related traits used were maximum body size, trophic level (2 to 4.5 from algae consumers to top predators), which were obtained from FishBase (53), and migration type (nonmigratory; lateral migrants, which migrate into the flooded forest during the high water season; basin migrants, which migrate between 200 and 1500 km; and continental migrants, which migrate more than 1500 km). The link between overexploitation, body size, and trophic level is well known for this and other systems (10, 14), whereas species that migrate a longer distance tend to be more sensitive to disruptions in connectivity associated with dam development (24). Migration type was thus scored in order of vulnerability as 1 (nonmigratory), 2 (lateral migrants), 3 (basin migrants), and 4 (continental migrants). Trait values for each taxon are available in data file S1.

To obtain information on the nutrient content of fish species, we collected between 6 and 20 whole fish specimens for 51 commercially available fish species at the Belén Market in Iquitos, Loreto between February and June 2018. Fresh specimens were transported on ice to the Universidad de la Amazonía Peruana, where each individual was weighed, measured, and photographed. Fish were

then frozen at -20°C and sent whole to the Instituto Tecnológico Pesquero in Lima, Peru, to be analyzed. If the fish was too large (approximately more than 50 cm), only a portion of the fish was shipped for analysis. While some fish are consumed whole, we decided to standardize analysis for all fish species by only using muscle from the left upper portion of an individual's body.

Protein content was obtained by the Kjeldahl method; calcium, iron, and zinc were obtained by atomic absorption spectroscopy (flame atomizer); fats were first extracted using a Soxhelt extractor, and then omega fatty acid content was analyzed by gas chromatography with a flame ionization detector. For taxa that included multiple species, nutrient content was averaged across the representative species. For species for which we were able to obtain six or more individuals, muscle samples were pooled into groups of three, and the average nutrient value was used. While our low sample size does not allow for full accounting of intraspecific variation, the standard error for most species is an order of magnitude lower than the mean value. Accounting for variation within species does not alter the relative ranking of nutrient values among species. For species for which no samples were obtained, values were assigned on the basis of the average value per family or genus since phylogeny is a strong predictor for nutritional content in fish (15). These species, which are rare in landings, are noted in data file S1.

Tolerance diversity was estimated as the community-level dispersion of traits that determine species extinction probabilities (i.e., body size, migration type, and trophic level), which measures the average dissimilarity in trait space in a community (54). Uniqueness was estimated individually for each nutrient as the dispersion in nutrient content among species. Using dispersion to measure functional diversity has the benefit of not being correlated with species richness, which varies in our study. Abundance was not included in the functional diversity estimates since rare species can contribute to both tolerance diversity and uniqueness and species biomass change with ongoing extinctions of conspecifics (see below) (39).

Nutrient supplies

The ecosystem service modeled, nutrient supplies (Y_N), is based on the nutrients derived from fish landings and converted into equivalents of dietary nutritional needs of residents. That is, Y_N is estimated as the total number of people able to obtain 100% of their annual RNI for each nutrient N by dividing the total pool of nutrients available across species by a per-person annual nutritional requirement. Rather than assuming a homogeneous population, RNI values were obtained by stratifying the population into segments: children under 5, children 5 to 10, females 11 to 14, males 11 to 14, women of reproductive age (15 to 49), adult males (15 to 64), menopausal women (50 to 64), elderly females (65+), and elderly males (65+). Thus, Y_N was estimated as

$$Y_N = \sum_{j=1}^P \frac{p_j \sum_{i=1}^S \text{Biomass}_i N}{\text{RNI}_{N,j}}$$

where S is the number of species and p_j is the proportion of the people in population segment j . Initial Biomass_i values for each species were parametrized using the species i mean annual harvest in kilograms from the annual landings data. RNI values for protein and ALA were obtained from the Food and Nutrition Board of the Institute of Medicine, U.S. National Academy of Sciences (55), while RNI

values for Fe, Zn, Ca, EPA, and DHA were obtained from the World Health Organization (56).

Trait-based species extinction scenarios

Biodiversity loss was simulated by removing species from replicate assemblages on the basis of probabilities of local extinction. A species probability of local extinction was determined by a species average dissimilarity from the community's centroid of trait space using body size, trophic level, and migration. There is strong evidence that these traits increase species extinction probabilities in the Amazon and across the world's rivers and oceans (10, 11, 29). At each step, a species was sampled on the basis of the distribution of extinction probabilities, and nutrient supplies were calculated. Subsequently, the remaining species were allowed to compensate for the extinct species, where the biomass of the extinct species was allocated to an extant species on the basis of two replacement scenarios: random replacement (i.e., all the species have the same probability of replacing the extinct species) and trophic replacement (i.e., only species within the same trophic group are able to compensate for the extinct species).

In both replacement scenarios, grazers/detritivores (trophic level 2) needed to be present for predators to remain extant. However, since omnivores (trophic level 3) can consume both basal resources and other fish, lower trophic levels were not necessary for their presence. Once the last species within a trophic group went extinct, the biomass associated with that trophic group was lost. Compensatory responses are common features of ecological communities, exhibited by fisheries in the Amazon and elsewhere (12, 14). While other scenarios beyond those modeled here are possible, these represent the most likely outcomes driven by competition. For a more in-depth discussion of these assumptions, see (7, 57). Each simulation started from the same initial community structure dictated by the 56 initial taxonomic groups and their mean annual harvest biomass, but their trajectories differed on the basis of the probabilistic extinction scenarios. A total of 100 simulations were run per scenario (i.e., no compensation, random compensation, and trophic compensation) for a total of 300 initial communities with 56 taxonomic groups.

Beyond estimating nutrient supplies, at each time step, we calculated tolerance diversity and uniqueness as above and nutrient supply risk, which provides a probabilistic dimension of ecosystem stability. Defined as the probability of an ecosystem's wild-caught species inability to meet nutrient targets, we estimated nutrient supply risk as the proportion of simulated communities that failed to meet a specific target nutrient supply (26). This method of measuring stability entails estimating the risk of a catastrophic or negative outcome in nutrient supplies and was estimated for each level of species richness and for each nutrient individually. Each simulated system was classified as at risk if it supplied less than 1.0, 0.75, or 0.5 of the initial magnitude of nutrient supplies. Results, however, are discussed here for a threshold set at 0.75. Results for other thresholds are presented in the Supplementary Materials.

Statistical analysis

The relationship between species loss and nutrient vulnerability was analyzed using a generalized linear mixed-effect model (GLMM) with nutrient vulnerability as the response variable, species loss as the predictor, and simulation as the random effect, with a binomial distribution, which is considered appropriate for modeling bounded

proportional data such as probabilities (58). To analyze the relationship between nutrient vulnerability, tolerance diversity, and uniqueness, we compared two GLMMs. One model contained a simulation random effect term, with tolerance diversity and uniqueness as main effects. The other model also included the addition of an interaction term between tolerance diversity and uniqueness. Support between the two models was assessed using Akaike's Information Criterion. Data were analyzed in R (59) using the glmer function and the confint function to obtain 95% confidence intervals in the lme4 package (60).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/22/eabf9967/DC1>

REFERENCES AND NOTES

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Declining diversity of wild-caught species puts dietary nutrient supplies at risk

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