

Article

# Managing nutrition-biodiversity trade-offs on coral reefs

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## SUMMARY

Coral reefs support an incredible abundance and diversity of fish species, with reef-associated fisheries providing important sources of income, food, and dietary micronutrients to millions of people across the tropics. However, the rapid degradation of the world's coral reefs and the decline in their biodiversity may limit their capacity to supply nutritious and affordable seafood while meeting conservation goals for sustainability. Here, we conduct a global-scale analysis of how the nutritional quality of reef fish assemblages (nutritional contribution to the recommended daily intake of calcium, iron, and zinc contained in an average 100 g fish on the reef) relates to key environmental, socioeconomic, and ecological conditions, including two key metrics of fish biodiversity. Our global analysis of more than 1,600 tropical reefs reveals that fish trophic composition is a more important driver of micronutrient concentrations than socioeconomic and environmental conditions. Specifically, micronutrient density increases as the relative biomass of herbivores and detritivores increases at lower overall biomass or under high human pressure. This suggests that the provision of essential micronutrients can be maintained or even increase where fish biomass decreases, reinforcing the need for policies that ensure sustainable fishing, and that these micronutrients are retained locally for nutrition. Furthermore, we found a negative association between micronutrient density and two metrics of fish biodiversity, revealing an important nutrition-biodiversity trade-off. Protecting reefs with high levels of biodiversity maintains key ecosystem functions, whereas sustainable fisheries management in locations with high micronutrient density could sustain the essential supply of micronutrients to coastal human communities.

## INTRODUCTION

Coral reefs support a high abundance and diversity of fish species,<sup>1,2</sup> and reef-associated fisheries provide an important source of income and food security to millions of people across the tropics.<sup>3,4</sup> However, maintaining both biodiversity and food security benefits is challenging,<sup>5</sup> particularly under rising anthropogenic pressures.<sup>6</sup> Reef-fish catches are rich in bioavailable micronutrients, including minerals and vitamins important to human health, that play essential roles in immunity and health, cognition, growth, and development, particularly for women and children.<sup>4,7</sup> Fish are also generally more affordable and accessible than other animal source foods, suggesting reef

fishes could help reduce nutrient deficiencies, which are particularly prevalent across the tropics.<sup>8–11</sup> Yet coral reefs are among the most vulnerable ecosystems to human-induced pressures,<sup>12,13</sup> highlighting the need to understand whether reefs can be managed to support human nutrition while also meeting conservation goals.

A key aim of marine conservation is to protect, or restore, the amount (i.e., standing biomass) and diversity of fish on a reef (SDG 14).<sup>14</sup> Biomass and diversity are closely related as biodiversity supports ecosystem functioning that increases with fish biomass.<sup>15,16</sup> However, social, environmental, and governance characteristics also influence fish diversity and biomass.<sup>15–17</sup> For example, human pressure in the form of



markets and overfishing depletes fish biomass, but effective management can slow or reverse this effect.<sup>13,18,19</sup> Recent research has highlighted how as fishing intensity increases, standing reef fish biomass and biomass turnover can be decoupled,<sup>20</sup> resulting in compositional changes that favor fast-growing species.<sup>21</sup> Although these compositional changes may mitigate fisheries collapse under coral reef degradation,<sup>22</sup> it is unclear how they affect the nutrient quality of local fisheries. Indeed, fish nutrient content varies considerably among fish species<sup>23,24</sup> such that the nutrient quality of a fishery is largely determined by the composition of what can be caught.<sup>25</sup> Therefore, a key gap in establishing whether reef fisheries can sustainably support human nutrition is determining how nutritional quality changes with fish biomass and diversity.

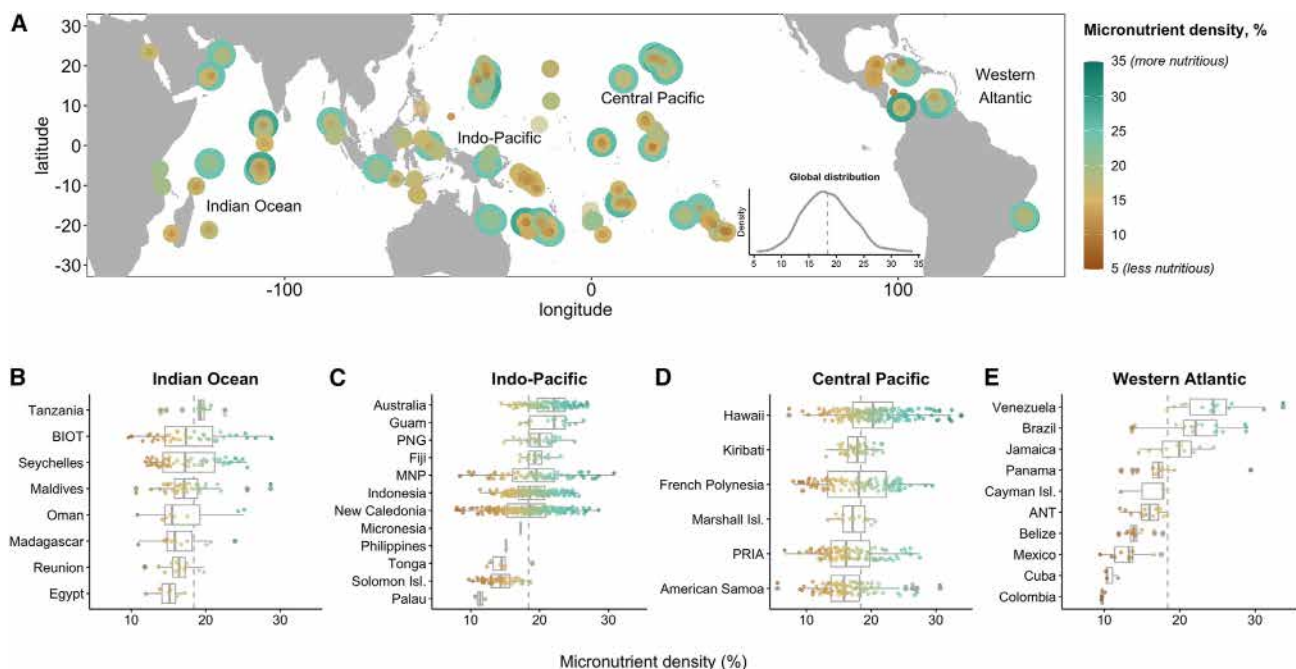
Here, using fisheries-independent underwater survey data from more than 1,600 tropical coral reef sites worldwide and focusing on calcium, zinc, and iron, for which inadequate intakes are particularly prevalent across the tropics,<sup>10,11,23</sup> we (1) develop a structural causal model (SCM) framework to establish how micronutrient concentrations of reef fish communities are influenced by key environmental, socioeconomic, and

ecological conditions and (2) explore how micronutrient concentrations of reef fish communities are related to fish biodiversity. In doing so, we explore the feasibility and opportunities to sustain the essential supply of nutrients from reef-associated fisheries to coastal communities without compromising efforts to reverse biodiversity loss.

## RESULTS

### Micronutrient variability among tropical coral reefs

Using species-specific micronutrient concentration estimates of calcium, iron, and zinc, we adapted the concept of micronutrient density,<sup>25,26</sup> which refers to the percent contribution a fixed weight (here 100 g) of fish (wet muscle weight) would make to a recommended daily intake. We averaged the estimates across the 3 micronutrients to create a standardized metric from 0% to 100% (STAR Methods). Higher micronutrient density indicates that a higher proportion of recommended daily calcium, iron, and zinc intake is covered by an average 100 g of fish on the reef, and 100% means that daily needs would be fulfilled for all 3 micronutrients. We then computed this metric as the biomass-weighted average value based on species composition

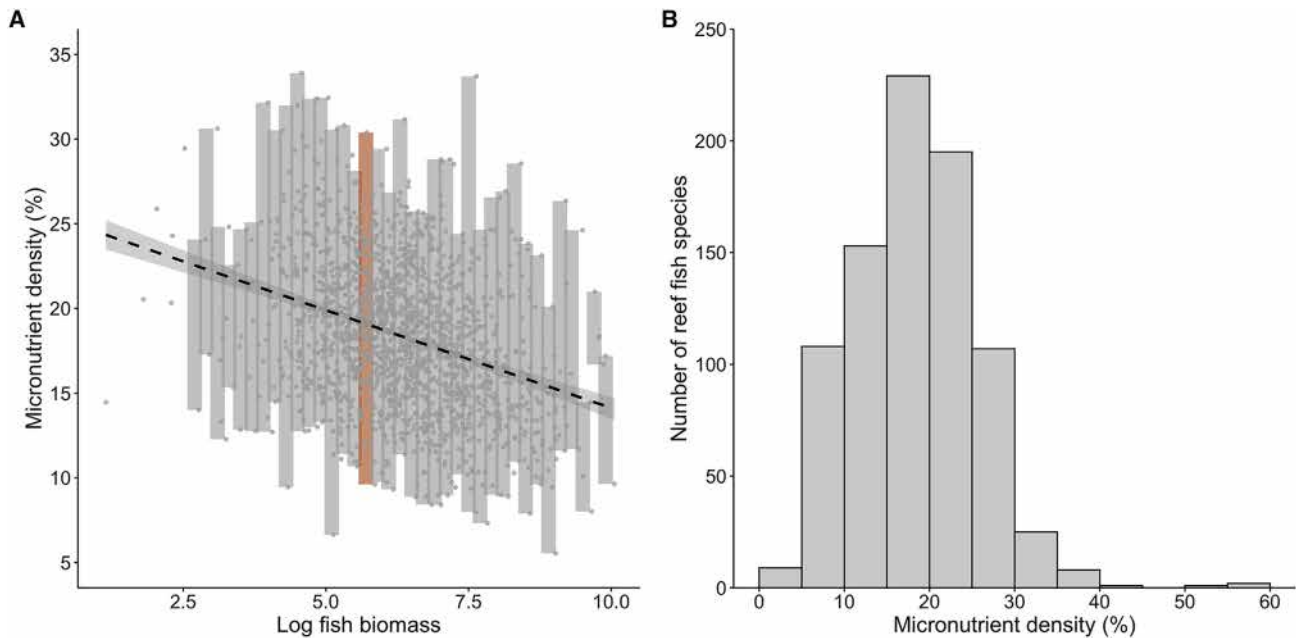


**Figure 1. Variation in micronutrient density among tropical coral reefs**

Global variation in the micronutrient density of an average 100 g of fish on the reef based on biomass-weighted values for (A) 1,661 reef sites globally and (B)–(E) split by region: Indian Ocean, Indo-Pacific, Central-Pacific, and Western Atlantic. Micronutrient density represents contribution of an average 100 g of fish to recommended daily intake summed across calcium, iron, and zinc and standardized by the number of focus micronutrients (three) so that our metric indicated the contribution (from 0% to 100%) to the recommended daily intake of three nutrients contained in an average 100 g of fish on the reef. Points vary in color from lower (less nutritious, brown) to higher (more nutritious, green) density score and in size such that bottom (<13%) and top (>24%) 10% values are smaller and bigger, respectively (global range: 5%–34%) (A). The boxplots represent nation-level values of micronutrient density. Each colored dot represents one reef site, gray solid vertical bars correspond to the median, and the upper and lower hinges are the 25% and 75% quantiles. Upper whisker is the largest observation less than or equal to upper hinge + 1.5 × inter-quartile range (IQR), and lower whisker is the smallest observation greater than or equal to lower hinge – 1.5 × IQR. Dashed vertical lines represent the global average.

BIOT, British Indian Ocean Territory; PNG, Papua New Guinea; MNP, Commonwealth of the Northern Mariana Islands; PRIA, US Pacific Remote Island Area; ANT, Netherlands Antilles (B)–(E).

Recommended daily intakes are for children between 6 months and 5 years of age.<sup>27</sup>



**Figure 2. Relationships between micronutrient density and reef fish communities' characteristics**

Relationship between micronutrient density and standing fish biomass (log) at 1,661 reef sites (A), based on micronutrient density of 838 coral reef fish species (B). A small range of fish biomass (a moving window of 0.2 log unit, gray polygons) may correspond to a wide range of micronutrient density values. Dashed line represents fitted linear regression with a negative slope =  $-1.2 \pm 0.08$ , 95% CI) (A). Micronutrient density of 838 individual fish species, representing the accumulated contribution of a single 100 g of individual reef fish species to recommended daily intakes summed across calcium, iron, and zinc and standardized by the number of focus micronutrients (B).

Recommended daily intakes are for children between 6 months and 5 years of age.<sup>27</sup>

at each reef site, reflecting the nutritional contribution to recommended daily intake contained in an average 100 g of fish from a given reef (Figure 1).

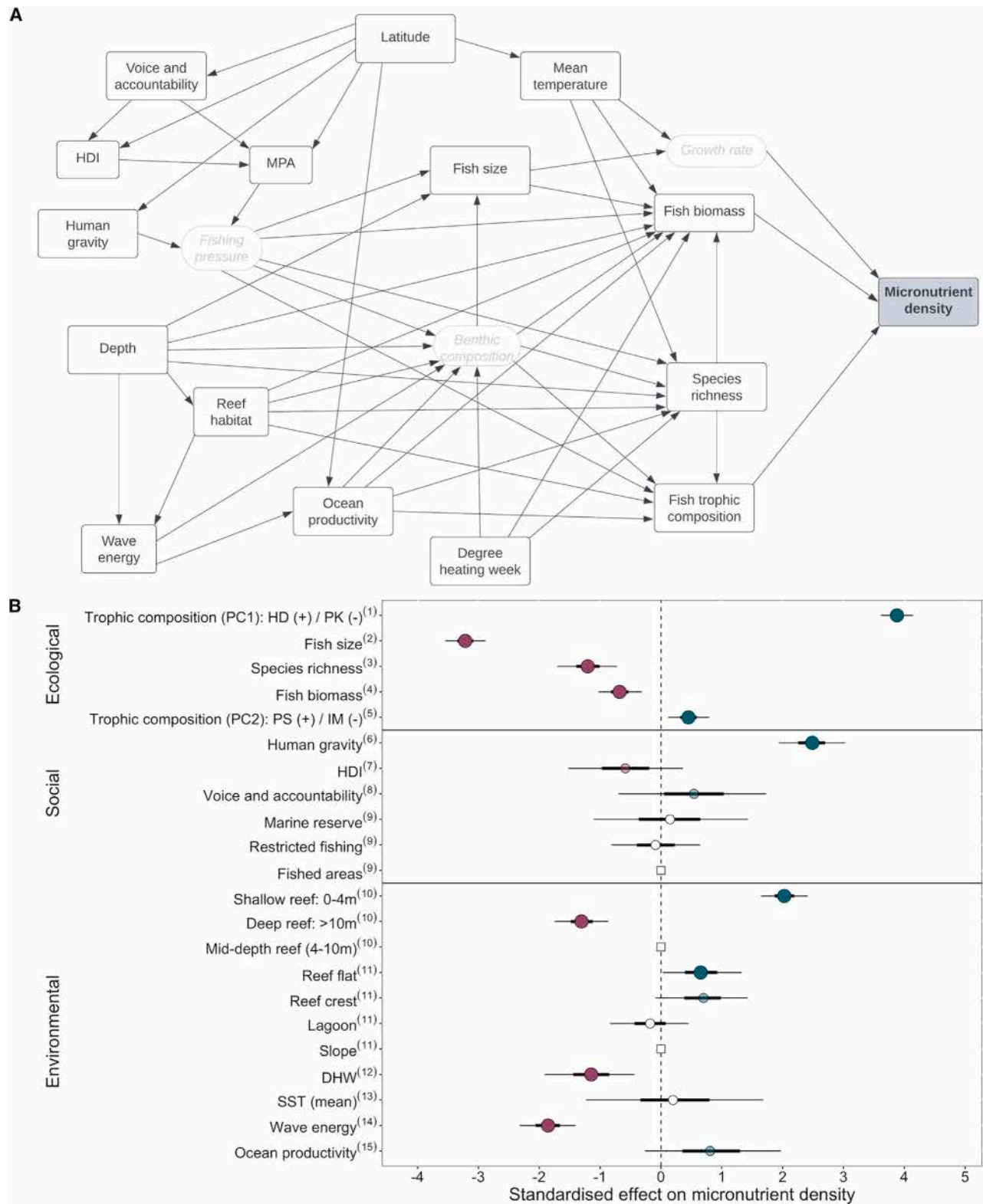
We find substantial spatial variability in micronutrient density, both within and across tropical regions. More importantly, many nations exhibit great variability in micronutrient density, encompassing both less and more nutritious sites (Figures 1B–1E). Because micronutrient density is given for an average 100 g of fish on the reef, fish communities of similar total biomass can have a higher or lower micronutrient density depending on species composition. For example, fish communities with a standing biomass of approximately 300 kg/ha (298–365 kg/ha) span nearly (9%–30%) the entire range of micronutrient density values (5%–34%, Figure 2A). Reef-level differences in micronutrient density arise from species-level variation in nutrient concentrations of fish muscle tissue,<sup>23</sup> meaning that the composition of fish communities strongly influences nutrient availability. Indeed, the accumulated contribution to the recommended daily intake of calcium, iron, and zinc that a single 100 g of individual reef fish species would make varies from 4% for the least nutritious species to 60% for the most nutritious species (Figure 2B). Despite high variability, micronutrient density at the reef site level is negatively associated with fish biomass (Figure 2A), suggesting that an average 100 g of fish on the reef tends to be more nutrient-dense when taken on reefs with lower total biomass.

### Causal drivers of micronutrient density

As nutrient content varies with fish traits,<sup>23,28</sup> micronutrient density at the site level is determined by community composition

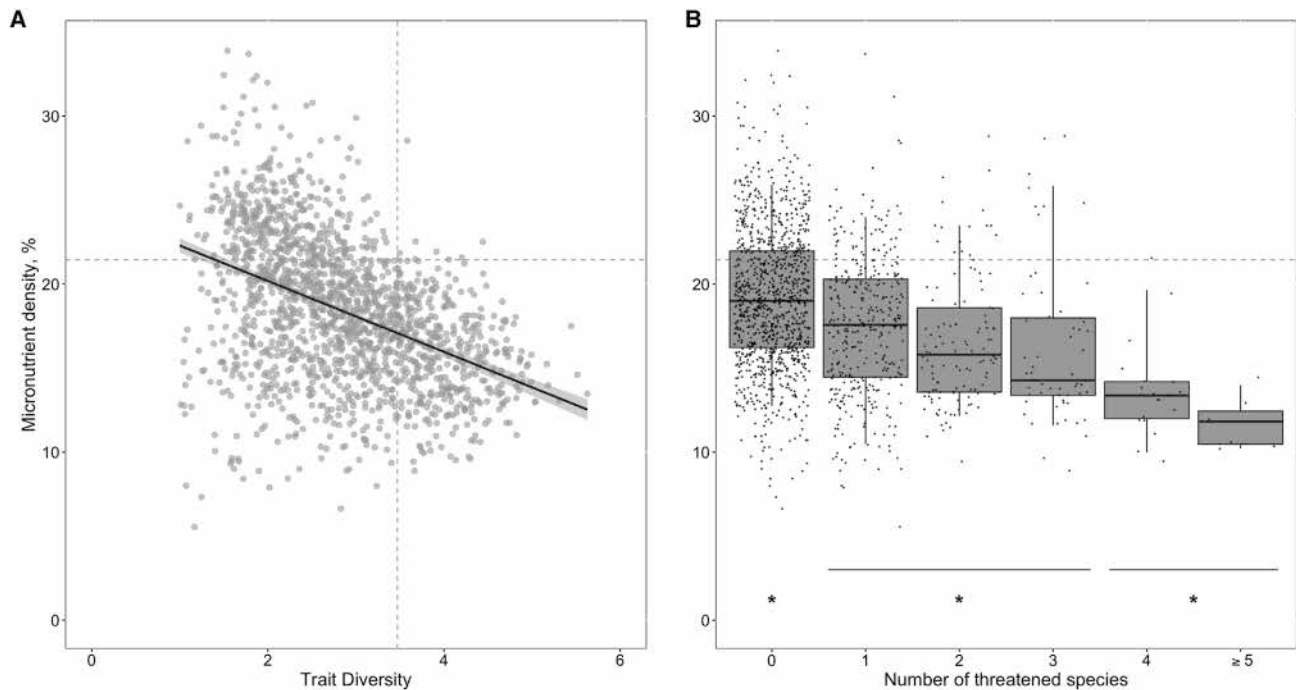
and species' relative biomass and is also influenced by environmental and socioeconomic conditions that shape reef fish communities.<sup>13,18,29</sup> To explore these relationships, we implemented a recently emerging causal inference framework, the SCM framework, which relies on a directed acyclic graph (DAG) to formalize the hypothesized causal structure of a system under study and subsequently applies a graphical rule known as the backdoor criterion to determine adjustment sets required to address specific causal queries.<sup>30,31</sup> Based on our DAG (Figure 3A), representing how different factors (e.g., ecological, social, and environmental conditions) are expected to influence micronutrient density, and the application of the backdoor criterion, we developed a series of Bayesian linear mixed models, one for each causal variable of interest (where the response variable was micronutrient density score), and extracted the standardized effect size of each predictor from its associated model (STAR Methods).

We demonstrate that fish trophic composition, represented by the two first axes of a principal-component analysis (PCA, STAR Methods) of site-level relative biomass values, has a strong relationship with micronutrient density (Figure 3B). Specifically, we show that micronutrient density increases as the relative biomass of herbivores and detritivores increases and the relative biomass of planktivores decreases (PC1). To a lesser extent, micronutrient density also increases with a smaller proportion of invertivores compared with piscivores (PC2). Micronutrient density is also higher when fish communities have fewer species and are dominated by smaller individuals (biomass-weighted average size of fish communities decreased) and decreases as standing



**Figure 3. Causal effects of ecological, social, and environmental conditions on micronutrient density in fish communities on coral reefs**  
(A) Directed acyclic graph (DAG) illustrating the causal relationships (directed arrows pointing from cause to effect) to investigate how micronutrient density is affected by ecological, social, and environmental conditions experienced by coral reefs. Square boxes represent predictor variables of micronutrient density (response variable, gray box) that are specifically quantified, while round boxes (fishing pressure, benthic composition, and fish growth rate) represent predictor

(legend continued on next page)



**Figure 4. Relationships between micronutrient density and two metrics of fish biodiversity**

Relationships between micronutrient density of an average 100 g of fish on the reef and (A) trait diversity and (B) the total number of threatened species according to the IUCN for the 1,661 reef sites. (A) Micronutrient density that represents the accumulated contribution of an average 100 g of fish on the reef to the recommended daily intake of calcium, iron, and zinc, was negatively associated with trait diversity (trait diversity was computed using the Chao's  $FDq = 1$ , see STAR Methods), suggesting that reef sites with the highest trait diversity had lower micronutrient density. Black line represents fitted linear regression with a negative slope =  $-2.1 \pm 0.21$ , 95% CI). (B) The accumulation of threatened species co-occurring on coral reefs was negatively related to micronutrient density. Reefs with the highest number of co-occurring threatened species (4 or more species) exhibited lower micronutrient density (p value < 0.05 from Tukey's multiple comparison test). Dashed vertical and horizontal lines represent top quartile values of micronutrient density and trait diversity. See also Figure S6.

fish biomass increases. Micronutrient density increases in places with higher human gravity, a proxy for human pressures including fishing, expressed as a function of human population size and travel time to a reef,<sup>32</sup> and, to a lesser extent, in places with lower levels of human development and greater levels of voice and accountability (i.e., democratic processes and freedom of expression). Both marine reserves and restricted fishing areas are found to have no causal effect on the micronutrient density compared with fished reefs (Figure 3B). We find that micronutrient density is higher on shallow reefs, with reef flats and reef crests having the highest values (Figure 3B). Reefs with more extreme past climate disturbances (as assessed by the maximum degree heating week [DHW] between 2005 and

2011) or higher wave energy have lower micronutrient density (Figure 3B).

#### Relationships between micronutrient density and biodiversity

To assess potential trade-offs between nutrient content of reef fish communities and biodiversity, we explored the link between micronutrient density and biodiversity across reef sites by focusing on two metrics: (1) the diversity of species traits and (2) the number of species classified as threatened by extinction, based on the IUCN Red List of Threatened Species (STAR Methods). Trait diversity (i.e., body size, diet, diurnal activity, home range, schooling behavior, and position in the water

variables that do affect our system but that are not specifically measured due to technical or methodological limitations. All causal links are supported by past research and literature (STAR Methods; Table S2).

(B) Standardized effect sizes of drivers influencing micronutrient density estimated from separate models representing the total causal effect of each driver (superscripts refer to individual models, STAR Methods). Parameter estimates are Bayesian posterior median values, 90% highest posterior density credible intervals (thin lines), and 50% credible intervals (thick lines). Dark larger circles indicate 90% credible intervals do not overlap 0 and that the estimate was either positive (green) or negative (red). Light smaller circles indicate 50% of credible intervals do not overlap zero and that the estimate was either positive (green) or negative (red). White circles indicate 50% credible interval overlaps zero. Fish trophic composition was reduced as the two first components of the PCA performed with site-level relative biomass values: PC1 was associated with more (+) herbivores and detritivores (HD) and less (–) planktivores (PK), whereas PC2 was associated with less (–) invertivores (mobile [IM]) and more (+) piscivores (PS) (STAR Methods; Figure S2). White squares indicate the baseline category in the statistical models used to compare the effect sizes of other categories.

See also Figures S3–S5 and Table S3.

column) underpins key aspects of community processes such as ecosystem productivity and stability,<sup>16,33</sup> and the number of threatened species identifies species of high societal value according to the Convention on Biological Diversity (CBD 2010–2020). These two metrics represent complementary metrics of fish biodiversity for which conservation is imperative and distinct from the importance of fish for nutrition. We find that micronutrient density is negatively associated with both metrics. Micronutrient density is negatively associated with trait diversity (slope =  $-2.1 \pm 0.21$ , 95% confidence interval [CI]), suggesting that reef sites with the highest trait diversity have the lowest micronutrient density (Figure 4A). Similarly, sites with more threatened species have lower micronutrient density (Figure 4B). These threatened species, mostly piscivores or mixed-diet feeders such as groupers, carangids, snappers, and barracudas (but also iconic species such as bumphead parrotfish, *Bolbometopon muricatum*, and humphead wrasse, *Cheilinus undulatus*), tend to co-occur more often on reefs that have reduced micronutrient density (Figure 4B).

## DISCUSSION

Substantial spatial variability exists in micronutrient density, both within and between tropical nations (Figure 1). Differences in micronutrient density at the reef level arise from species-level variation in nutrient concentrations, suggesting that the composition of reef fish communities strongly influences nutrient availability. Overall, an average 100 g of fish on the reef tends to be more nutrient-dense on reefs with lower total biomass (Figure 2). Fish trophic composition, with a dominance of herbivores and detritivores, is a more important driver of micronutrient density than socioeconomic and environmental conditions (Figure 3). Finally, micronutrient density is negatively associated with two metrics of fish biodiversity, revealing an important nutrition-biodiversity trade-off on coral reefs (Figure 4). Overall, our key findings suggest that opportunities may exist to sustain the essential supply of nutrients from reef-associated fisheries. Here we explore (1) the causal insights from our analysis, (2) a new target for reef fisheries management that balances nutritional harvest and conservation efforts to protect biodiversity, and (3) how the nutritional contribution of coral reef fisheries is likely to change in the near future.

### Causal insights and implications for micronutrient density

Our causal models reveal several factors that affect micronutrient density in coral reef fish communities. In particular, we find that increased relative biomass of herbivores and detritivores results in greater micronutrient density. Although herbivores and detritivores have comparable calcium and iron concentrations to those of other functional groups, they are particularly rich in zinc (Figure S3). Our findings also suggest that the nutrient content of reef fish communities may vary according to depth, habitat type, and fisheries (Figure 3B). For example, shallow reef environments such as reef flats and crests generally support high biomass of grazing surgeonfishes, parrotfishes, and rabbitfishes<sup>34</sup> that are particularly rich in zinc (Figure S4), meaning that catches from these environments will

tend to have higher micronutrient density. By contrast, hook and line gears deployed in deeper waters typically target higher trophic level species and mixed-diet feeders that have lower concentrations of calcium, iron, and zinc (Figures S3 and S4) and may ultimately result in lower micronutrient densities. These results identify links between fish community composition and micronutrient densities, highlighting that a diversity of gears and fisheries deployed in different reef habitats may vary micronutrient density in catches, potentially providing complementary sources of nutrients from different fish species.

Reefs that experienced more extreme past climate disturbances are associated with lower micronutrient density (Figure 3B), which aligns with alterations to reef fish community structure following heat stress.<sup>35</sup> Reefs with more extreme past climate disturbances (higher maximum DHW) tend to have fewer competitive and generalist corals, such as branching and plating corals, while massive stress-tolerant and weedy corals tend to persist through severe thermal disturbances.<sup>36</sup> This affects reef structural complexity and ultimately the associated abundance, biomass, and trophic structure of reef fish communities.<sup>37</sup> Although it is recognized that changes in reef habitat can affect the nutrient content of individual fish species,<sup>28</sup> there is limited understanding of how climate-driven habitat shifts alter nutrient flows through food webs, making these effects difficult to quantify at large scale. Moreover, coral reefs can follow different ecological regimes in terms of both fish and benthic communities as a response to climatic disturbances<sup>38</sup>; however, consequences for the associated micronutrient availability from reef fisheries are still unclear.<sup>39</sup>

We show that micronutrient density increases in places with high human gravity owing to changes in fish community composition along a human gravity gradient. Reefs with higher gravity values, which have lower fish biomass, tend to be dominated by low trophic level species like herbivores, detritivores, and mobile invertivores (Figure S5). These are more concentrated in calcium, iron, and zinc compared with planktivores and piscivores (Figure S3) that are nearly absent when standing fish biomass decreases, for example, under high human pressure (Figure S5). Conversely, fish biomass is expected to decline along a human gravity gradient,<sup>32</sup> suggesting that a trade-off between fish biomass and micronutrient density occurs when human gravity increases. More specifically, this suggests that even where fish biomass decreases, the nutrient quality of fish, reflected by our micronutrient density metric, can be maintained or even increase. Similarly, compensatory buffering production has been demonstrated on exploited reefs, where high fish community productivity can be maintained despite increased fishing pressure, contributing to persistent biomass yields.<sup>40</sup> Such buffering may result in nutritional benefits if policies ensure fisheries retain these micronutrients (calcium, iron, and zinc specifically) locally for vulnerable human populations.<sup>4</sup> Of course, the positive relationship between total fish biomass and total nutrient availability (Figure S1) suggests the nutritional needs of more people can be met when biomass is greater. However, increases in fish biomass productivity and micronutrient density at intermediate biomass levels also points to important food security services from reef fisheries in areas where human populations, and thus needs, are greater.

### Conservation versus fisheries targets

We show that micronutrient density is negatively associated with both standing biomass and species richness (with a stronger negative effect for species richness; Figure 3B), suggesting that an average 100 g of fish on the reef tends to be less nutrient-dense on reefs with high total biomass and high species richness. Although higher fish biomass typically results in greater total fishable quantity of micronutrients (Figure S1), micronutrient density of a standardized amount of fish varies depending on species composition.<sup>25</sup> Herbivores and detritivores are zinc-dense species (Figure S4) that are particularly dominant at low and intermediate levels of biomass (100–600 kg/ha), while piscivores and planktivores, which are less concentrated in calcium, iron, and zinc, become more abundant at higher levels of biomass (>600 kg/ha, Figure S5). Species richness at a given reef does not necessarily result in higher diversity in individual people's diets, which typically results in greater nutritional benefits.<sup>41</sup> In the same vein, we find a negative association between micronutrient density and trait diversity. Reef sites with higher total number of species or trait diversity do not have higher micronutrient density (Figures 3 and 4) because rare species or species with the most distinct traits, such as piscivores, tend to be less concentrated in calcium, iron, and zinc (Figures S4–S6). More importantly, threatened species—which are mostly piscivores or mixed-diet feeders such as groupers, carangids, snappers, and barracudas, but also iconic species such as bumphead parrotfish (*Bolbometopon muricatum*) and humphead wrasse (*Cheilinus undulatus*) of high societal value—tend to be less nutritious (Figure S6) and to co-occur more often on reefs that have reduced micronutrient density (Figure 4).

Although marine protected areas (MPAs) have been strongly advocated as beneficial instruments for fisheries management,<sup>42–44</sup> they have no direct effect on micronutrient density, probably because the effect of protection favors specific targeted groups<sup>43,45</sup> and does not affect species communities in ways that change the overall micronutrient density. This suggests that species composition and the associated micronutrient value greatly vary among different levels of protection and non-regulated areas.<sup>46</sup> Conversely, MPAs—especially no-take marine reserves—are recognized tools to protect different facets of biodiversity, and a wide range of beneficial responses have been documented over the last 30 years.<sup>42,43</sup> Despite trade-offs between micronutrient density (fish quality) and biodiversity, protecting biodiversity does not jeopardize micronutrient quality of fish from coral reefs. Opportunities may exist to strategically prioritize management approaches to both: (1) protect reefs with high levels of biodiversity and (2) regulate fishing on reefs with high nutrition quality potential (high micronutrient density) so that they can support sustainable nutrient-dense food supplies to local populations.<sup>4</sup>

Protecting coral reefs with high levels of biodiversity is widely thought to help safeguard healthy reefs, as the multi-functionality of coral reefs (i.e., the ability of fish communities to simultaneously provide multiple functions and services) relies strongly on biodiversity<sup>33,47–49</sup> and because some species play unique and thus irreplaceable roles in ecosystems.<sup>50,51</sup> Therefore, prioritizing no-take marine reserves on reefs where biodiversity levels are particularly high and facing low to intermediate human pressure can substantially increase fish biomass along with a range

of ecosystem states and processes,<sup>1,13</sup> but they can also result in spillover of adults and larvae to surrounding areas, which can benefit fishers.<sup>52–54</sup> Conversely, coral reefs with higher micronutrient density may help sustain the supply of nutritious fish from coral reef fisheries. Indeed, these reefs are generally dominated by herbivores and detritivores (Figure 3B) and smaller individuals with high biomass turnover<sup>20</sup> following the removal of higher trophic level species.<sup>55</sup> Herbivores and detritivores have been shown to dominate nutrient production<sup>56</sup> and are associated with local high productivity even if fish biomass levels are low,<sup>21</sup> suggesting that some heavily fished reefs may still supply nutrient-dense seafood (dense in calcium, iron, and zinc specifically). However, even if this compensatory ecological mechanism may sustain small-scale fisheries, intensifying fishing pressure may eventually lead to biomass collapse, with important ecological consequences. This suggests that monitoring reef fish biomass and implementing strategic management restrictions that avoid extreme biomass depletion below the 300–600 kg/ha that is recommended to avoid fishery collapse<sup>57</sup> remains critical to sustaining food security.<sup>56</sup> Maintaining reef fish biomass levels above such biomass-based targets is also expected to sustain critical ecosystem functions and can be achieved with the use of culturally and socially appropriate management forms that permits fishing.<sup>56–58</sup>

Contrary to previous findings in terrestrial systems,<sup>5</sup> our results show that nutrition-biodiversity trade-offs can exist on coral reefs. Coral reefs host a high diversity of fish species,<sup>2</sup> but those that are particularly dense in micronutrients and are important fishery targets in many tropical countries<sup>59–61</sup> also tend to be more functionally redundant<sup>62,63</sup> and less vulnerable to anthropogenic threats.<sup>64</sup> Nature-for-nature protection scenarios (e.g., the preservation of nature's diversity and functions being of primary importance<sup>65</sup>) would, in coral reef ecosystems, help sustain the multi-functionality of coral reefs in some locations, whereas sustainable fisheries management in locations with high micronutrient density would help sustain the essential supply of calcium, iron, and zinc from reef-associated fisheries to coastal human communities (nature-for-people scenario<sup>65</sup>).

### The nutritional contribution of coral reef fisheries in a changing world

Our results highlight the critical role that low trophic level species—especially herbivores—could play in local food systems. At the reef level, the most important contributors (top 5 species) to total calcium, iron, and zinc availability are from a range of feeding groups, and non-herbivore species tend to contribute substantially. This contrasts with the global effect of herbivores and detritivores, which account for 48%, 50%, and 57% of total calcium, iron, and zinc availability across all reef sites (Figure S7) due to biomass dominance of the entire functional group, and increases in their relative biomass result in greater micronutrient density on reefs (Figure 3B). Moreover, these groups are generally less vulnerable to climate-change associated habitat degradation<sup>64</sup> and fishing.<sup>66</sup> Consequently, supply of calcium, iron, and zinc from fished reefs may also withstand short-term climate impacts, as loss of coral cover is typically followed by increases in algal productivity and enhanced biomass of low trophic level fishes that feed on algal resources.<sup>28,67</sup> Such stressors are therefore likely to change the nutrient concentration of small-scale

fisheries catches and can result in greater iron and zinc supply for fisheries after macroalgal regime shifts.<sup>28</sup> Reefs dominated by low trophic level fishes may therefore still provide continued supply of nutrient-dense seafood (dense in calcium, iron, and zinc specifically) and could contribute substantially to dietary requirements in places with high reef fish consumption.

Herbivorous reef fish deliver key ecosystem functions and support coral reef resilience by preventing coral-algal phase shifts.<sup>68</sup> These species, such as parrotfishes and rabbitfishes, are also targeted by fishers on many reefs globally, consumed locally, and they also tend to grow faster in response to algal growth, leading to higher fish biomass and productivity.<sup>21,61,69</sup> We therefore caution that sustainable management remains essential to ensure these fisheries continue to contribute to the nutritional security of the most vulnerable and food-insecure populations globally,<sup>4</sup> while ecosystem functions are maintained on coral reefs. Adaptation of both the fishery to respond to the change in composition and abundance of the fish species targeted locally and national policies to retain and promote consumption of nutritious fish sourced locally will be necessary to ensure that coral reefs can continue to nourish people.<sup>4,28,70</sup>

#### RESOURCE AVAILABILITY

##### Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Eva Maire ([eva.maire@ird.fr](mailto:eva.maire@ird.fr)).

##### Materials availability

This study did not generate new, unique reagents.

##### Data and code availability

Data and R code used for running the analyses and figures supporting the manuscript can be found at <https://github.com/EvaMaire/ReefFishNutrients>.

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#### AUTHOR CONTRIBUTIONS

E.M. conceived the study with J.P.W.R., C.C.H., and N.A.J.G.; E.M., J.P.W.R., M.M., and S.A. developed and implemented the analyses. E.M. led the manuscript with input from all authors.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

#### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- Standing reef fish biomass
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#### SUPPLEMENTAL INFORMATION

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<b>Deposited data</b>		
Reef fish biomass estimates, socioeconomic and environmental drivers	Cinner et al. <sup>18</sup>	<a href="https://doi.org/10.1038/nature18607">https://doi.org/10.1038/nature18607</a>
Estimated micronutrient concentrations of reef fish species	Froese and Pauly <sup>24</sup>	<a href="https://www.fishbase.org/">https://www.fishbase.org/</a>
Trait database on tropical reef fishes	Mouillot et al. <sup>62</sup>	<a href="https://doi.org/10.1073/pnas.1317625111">https://doi.org/10.1073/pnas.1317625111</a>
Conservation global status of reef fish species based on the IUCN Red List of Threatened Species	Borgelt et al. <sup>71</sup>	<a href="https://doi.org/10.1038/s42003-022-03638-9">https://doi.org/10.1038/s42003-022-03638-9</a>
Dataset and R code for running the analyses and figures	This paper; GitHub repository	<a href="https://github.com/EvaMaire/ReefFishNutrients">github.com/EvaMaire/ReefFishNutrients</a>
<b>Software and algorithms</b>		
R 4.3.2 binary for macOS 11 (Big Sur) and higher	The R Project for Statistical Computing	<a href="https://cran.r-project.org">https://cran.r-project.org</a>

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### Scales of data

Our data were organized at three spatial scales: reef site (n=1,662), reef cluster (n=649), and nation/state (n=36).

- (i) Reef site, the smallest scale, which had an average of 2.5 surveys/transects (range: 1-10) hereafter ‘reef’.
- (ii) Reef cluster which had an average of 2.4 reef sites (range: 1-22). Reefs within 4km of each other were clustered, and we used the centroid to estimate reef cluster-level socio-economic variables as described by Cinner et al.<sup>18</sup>
- (iii) Nation/state (nation, state, or territory), which had an average of 18 reef clusters (range: 1-118). The larger scale in our analysis which is jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions), within which reef sites and reef clusters were nested for analysis.

#### Standing reef fish biomass

Reef fish biomass estimates were based on instantaneous visual counts from 4,164 surveys collected from 1,662 reef sites. Surveys were carried out using three census methods (stationary point count, belt transect, or distance sampling) and were conducted between 2004 and 2013. Within each surveyed area, reef associated fishes were identified to species level, abundance was counted, and total length (TL) estimated. To make estimates of biomass from these transect-level data comparable among studies, we retained families that were consistently included in surveys and were above a minimum size cut-off. Thus, we only retained counts of non-cryptic reef fish species >10cm in total length, that are reef-associated (32 families, 838 species) (Table S1). We did not include sharks as they were often excluded from visual surveys. We further distinguished the surveys to include both fishery-target biomass estimates, and all (including non-target) biomass (Table S1). We removed 1 site which had only non-target biomass. Therefore, we considered 1,661 reef sites in our analyses. We calculated total biomass of fishes on each reef using published species-level length-weight relationship parameters or those available on FishBase.<sup>24</sup> When length-weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus. Total biomass values were calculated at the reef scale and showed a high variability (mean=1,072 kg.ha<sup>-1</sup>; range: 2-23,274 kg.ha<sup>-1</sup>). All reported log values are the natural log.

#### Fish communities’ characteristics

##### Species richness

We extracted the total number of fish species recorded at each reef site, including both targeted and non-targeted species. Because surveys were carried out using different census methods and sampling areas, species richness was standardised by dividing the total number of fish species by the total area sampled.

##### Fish composition

We assigned each fish species a functional feeding group (herbivores-detritivore, planktivore, piscivore, and species feeding on mobile and sessile invertebrates).<sup>62</sup> We then computed for each site the relative biomass of each functional feeding group and

performed a Principal Component Analysis (PCA) to describe similarities between fish communities among reef sites. The two first components (PC1 and PC2) explained 70% of the variation observed between reef sites. PC1 was mostly associated with more herbivore-detritivore, while PC2 was associated with more piscivore, and less invertivores feeding on mobile invertebrates (Figure S2).

### Size of fish communities

We used the total length of each individual fish recorded during visual counts and then computed the biomass-weighted average size of fish at each reef site.

### Micronutrient densities of reef fish communities

We focused on three essential micronutrients (calcium, iron, and zinc) for which inadequate intakes are particularly prevalent across the tropics and for which sufficient data are available.<sup>10,11,23</sup> Micronutrient concentrations for each species were sourced from FishBase,<sup>24</sup> which uses Bayesian hierarchical models to integrate information on both species traits and phylogenetic relatedness. Specifically, the models estimate how diet (feeding pathway, trophic level, and the position in the water column), energetic demand (maximum length, age at maturity, the fish growth parameter K, and body shape) and thermal regime (maximum depth and geographical zone) predict nutrient content of finfish species, whilst including phylogenetic relatedness<sup>72</sup> within the correlation structure of the models (see the 'model' folder at <https://github.com/mamacneil/NutrientFishbase>). This is based on an updated database and model that was first developed in Hicks et al.<sup>23</sup> The updated database includes > 3,500 measurements of 610 fish species. Note that this dataset is expanded (66 %) from that used in Hicks et al.<sup>23</sup> (367 species) and includes new nutrient analyses of tropical coral reef species.<sup>28</sup> Model diagnostics (no evidence for lack of convergence and posterior predictive checks), suggest this updated model was well calibrated and could readily generate out of sample estimates of the kind observed in our nutrients database. All data, and original sources, are freely available through FishBase.<sup>24</sup> For this study, we specifically used estimated micronutrient concentrations of 838 tropical marine fish species in 32 families recorded during visual counts (Table S1).

We then applied the concept of micronutrient density which refers to the percent contribution of a fixed weight (here 100-g) of fish (wet muscle weight) to a recommended daily intake (e.g., recommended dietary allowance) summed across three key micronutrients (calcium, iron, and zinc)<sup>25,26</sup> and standardised by the number of focus micronutrients (three). We used recommended dietary allowance (RDA) for children between 6 months and 5 years of age.<sup>27</sup> Therefore, our metric indicates the contribution (from 0 to 100%) to recommended daily intake of three nutrients that an average 100g of fish from the reef could make and thus is driven by species composition. It defers from nutrient availability which was obtained by converting standing biomass estimates into total nutrient amounts (Figure S1). Contribution of each functional group to total nutrient availability at the reef level was also computed (Figure S7).

Reef fishes are particularly rich in selenium (averaged contributions > 99% of RDA).<sup>25</sup> Including selenium would have increased the micronutrient density score but would not have allowed to distinguish reefs with high *versus* low micronutrient density. It is also recognised that reef fishes, as tropical species, have relatively lower concentrations of omega-3 and vitamin A than their cold-water and temperate counterparts.<sup>23</sup> Selenium, omega-3, and vitamin A were therefore not included in the analysis. The lack of available data precluded inclusion of other essential micronutrients in our analysis, such as amino acids and vitamin B.<sup>73,74</sup>

### Socioeconomic drivers

- Human gravity: We used the human gravity index which is a proxy for human pressures including fishing, expressed as a function of human population size and travel time to a reef and examines the amount of human pressure within the surrounding 500km of a reef.<sup>32</sup>
- Management: For each reef, we determined if it was: i) marine reserve- whether it fell within the borders of a no-take marine reserve and we asked data providers to further classify whether the reserve had high or low levels of compliance; ii) restricted - whether there were active restrictions on gears (e.g. bans on the use of nets, spearguns, or traps) or fishing effort (which could have included areas inside marine protected areas that were not necessarily no take); or iii) fished - regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and validated this with a global database of marine reserve boundaries.<sup>75</sup>
- Human Development Index (HDI): HDI is a summary measure of human development encompassing: a long and healthy life, being knowledgeable, and having a decent standard of living. To account for regional variability in HDI values, we used the sub-national HDI database which provides HDI estimates for 1625 regions within 161 countries for the year 2010<sup>76</sup> and calculated the average HDI value of the nearest three regions for each reef site.
- Voice and accountability: the voice and accountability index from the World Bank survey on governance<sup>77</sup> reflects the perceptions of the extent to which a country's citizens are able to participate in selecting their government, as well as freedom of expression, freedom of association, and a free media (the complete list of individuals variables can be found at <https://www.worldbank.org/content/dam/sites/govindicators/doc/va.pdf>). Estimate gives the country's score on the aggregate indicator, in units of a standard normal distribution, i.e. ranging from approximately -2.5 to 2.5.

### Environmental variables

- Depth: The depth of reef surveys was grouped into the following categories: <4m, 4-10m, >10m to account for broad differences in reef fish community structure attributable to a number of inter-linked depth-related factors. Categories were necessary to

- standardize methods used by data providers and were determined by pre-existing categories used by several data providers.
- **Habitat:** We included the following habitat categories: i) Slope: The reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water; ii) Crest: The reef crest habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e. where the waves break) and a change in the angle of the reef from an inclined slope to a horizontal reef flat; iii) Flat: The reef flat habitat is typically horizontal and extends back from the reef crest for 10's to 100's of meters; iv) Lagoon / back reef: Lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind barrier / fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous 'lagoon style' reef habitat. For this analysis, we excluded other less prevalent habitat types (channels and banks) and we verified the sites' habitat information using Google Earth, and site depth information.
  - **Productivity:** We extracted primary productivity from Yeager et al.<sup>78</sup> which provides net primary productivity (NPP) values corrected for shallow-water reflectance following the procedure described by Gove et al.<sup>79</sup> to filter out grid cells with minimum depth <30 m. This dataset draws on NPP values from 8-day composite layers of chlorophyll-a concentration (proxy for phytoplankton biomass) using data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging Spectro-radiometer) for years 2003 to 2013. For each reef site, we extracted the overall mean chlorophyll-a concentration for the period 2003-2013 using a 100-km buffer around each site.
  - **Temperature data:** we used the NOAA Coral Reef Watch Daily Global 5-km Satellite Coral Bleaching Monitoring ([https://coralreefwatch.noaa.gov/product/5km/index\\_5km\\_composite.php](https://coralreefwatch.noaa.gov/product/5km/index_5km_composite.php)) which provided daily sea surface temperature (SST) values and degree heating week (DHW) at a 5km-resolution. To reflect past temperature conditions and heat stress experienced by each reef site, we calculated the average of daily SST and the maximum DHW for the past 5 years of each reef site using a 100-km buffer around each reef site.
  - **Wave energy:** We used wave energy from the Marine Socio-Environmental Covariates dataset for the global oceans<sup>78</sup> and extracted the overall mean of wave energy flux for each reef.

## METHOD DETAILS

### Causal models

We implemented the structural causal model (SCM) framework, an emerging causal inference technique that can be used to answer causal queries from observational data.<sup>30,31</sup> The SCM framework relies on directed acyclic graphs (DAGs), which are used to visualize the hypothesized causal structure of a system under study, with directed arrows pointing from cause to effect. We created our DAG to answer how species composition or social and environmental conditions experienced by coral reefs affect micronutrient density (Figure 3A). Our DAG was created during a weeklong workshop, with expert input from several reef researchers (EM, JPWR, MM, SA, JEC, NAJG, MAM & CCH), included all relevant measured and unmeasured variables, and was further supported by past research and literature (see [supplemental information](#) for rationale). We used the R package 'dagitty'<sup>80</sup> to test DAG-data consistency between our observational data and specified DAG. Dagitty uses a formal test of zero (partial) correlation for each identified independence based on d-separation rules. There were 80 conditional independencies implied by our DAG (Table S3) and each was tested against our observational data. For example, we verified that average sea surface temperature was independent of wave energy and species richness was independent of micronutrient density when fish biomass, fish size, fish trophic composition, and average sea surface temperature are adjusted for (Table S3). Specifically, we checked that all independencies had an absolute partial correlation coefficient smaller than 0.4 (see Table S3), providing additional support for the overall structure of our DAG.<sup>31,81</sup> We then applied a graphical rule known as the backdoor criterion to determine the adjustment set (i.e., controls) required to answer specific causal queries; this in turn eliminates common statistical biases that can otherwise plague observational correlative studies, including confounding, overcontrol, and collider bias.<sup>31</sup> We identified the minimum adjustment set necessary to obtain the total causal effect of each predictor variable which represents the list of additional covariates that must be included in a regression model to satisfy the backdoor criterion and account for the potential statistical biases outlined above, and finally a separate causal model for each predictor variable of interest was created (see models' equations below for adjustment sets). Relationships between micronutrient density and all predictor variables can be found in [Figures S8 and S9](#).

### Relationships between micronutrient density and biodiversity

To assess potential trade-offs between nutrient content of reef fish communities and biodiversity, we explored the relationships between:

- micronutrient density, that was computed by considering only fish species that are commonly targeted in artisanal fisheries (Table S1) to reflect the potential micronutrient concentrations available for local human populations and,
- two complementary metrics of biodiversity: (1) the diversity of species traits and (2) the number of species classified as threatened by extinction, based on the IUCN Red List of Threatened Species (see below for further details). Indeed, trait diversity underpins key aspects of community processes such as ecosystem productivity and stability<sup>16,33</sup> and the number of threatened

species identifies species of high societal value according to the Convention on Biological Diversity (CBD 2010-2020). Both metrics were computed using the entire fish community.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Causal models

After validating our DAG, the final step is to choose a statistical model, to estimate effect sizes of each covariate. Directed acyclic graphs are used to guide covariate selection (i.e., which variables to adjust for) and are non-parametric, meaning that they make no assumptions about the distribution of variables (e.g. normally distributed) or the functional form of causal effects (e.g. linear). We developed a series of Bayesian linear mixed effects models, one for each of our causal models, using a normal error distribution, where the response variable was our micronutrient density metric and which explicitly recognize the nested structure of reefs within reef clusters (j) within nations/states (k) in our data. The effect size of each predictor variable of interest, representing the total causal effect, was interpreted for its associated model, with additional variables acting as required controls based on the backdoor criterion. We specifically accounted for any potential bias among census methods by controlling for sampling method and area in the fish biomass model. Geography plays an important role in shaping biophysical ocean conditions and the distribution of the world population, income, economic growth, we thus used latitude (absolute value for linearity) as a proxy for these conditions affecting HDI, voice and accountability, MPAs, human gravity, sea surface temperature and ocean productivity (see [Table S2](#) for rationale).

Based on the backdoor criterion, our initial Bayesian linear mixed models (one for each predictor variable) were as follows:

$$Y_i = \text{Normal}(\mu, \sigma)$$

- (1) Trophic composition (PC1):  $\mu = \beta_{0jk} + \beta_1 TC_{PC1} + \beta_2 Biomass + \beta_3 FishSize + \beta_4 SST_{mean}$
- (2) Biomass-weighted average size of fish assemblages' model:  $\mu = \beta_{0jk} + \beta_1 FishSize + \beta_2 Depth + \beta_3 Benthic\ Composition + \beta_4 FishingPressure$
- (3) Species richness model:  $\mu = \beta_{0jk} + \beta_1 SpeciesRichness + \beta_2 Depth + \beta_3 Productivity + \beta_4 SST_{mean} + \beta_5 ReefHabitat + \beta_6 DHW + \beta_7 Benthic\ Composition + \beta_8 FishingPressure$
- (4) Fish biomass model:  $\mu = \beta_{0jk} + \beta_1 Biomass + \beta_2 TC_{PC1} + \beta_3 TC_{PC2} + \beta_4 SST_{mean} + \beta_5 FishSize + \beta_6 CensusMethod + \beta_7 SamplingArea$
- (5) Trophic composition (PC2):  $\mu = \beta_{0jk} + \beta_1 TC_{PC2} + \beta_2 Biomass + \beta_3 FishSize + \beta_4 SST_{mean}$
- (6) Human gravity model:  $\mu = \beta_{0jk} + \beta_1 Gravity + \beta_2 Latitude$
- (7) HDI model:  $\mu = \beta_{0jk} + \beta_1 HDI + \beta_2 VoiceAcc + \beta_3 Latitude$
- (8) Voice and accountability model:  $\mu = \beta_{0jk} + \beta_1 VoiceAcc + \beta_2 Latitude$
- (9) MPA model:  $\mu = \beta_{0jk} + \beta_1 MPA + \beta_2 Latitude$
- (10) Depth model:  $\mu = \beta_{0jk} + \beta_1 Depth$
- (11) Reef habitat model:  $\mu = \beta_{0jk} + \beta_1 ReefHabitat + \beta_2 Depth$
- (12) Degree Heating Week model:  $\mu = \beta_{0jk} + \beta_1 DHW$
- (13) Average sea surface temperature:  $\mu = \beta_{0jk} + \beta_1 SST_{mean} + \beta_2 Latitude$
- (14) Wave energy model  $\mu = \beta_{0jk} + \beta_1 WaveEnergy + \beta_2 Depth + \beta_3 ReefHabitat$
- (15) Ocean productivity model:  $\mu = \beta_{0jk} + \beta_1 Productivity + \beta_2 WaveEnergy + \beta_3 Latitude$

$$\text{Priors : } \beta_{0...7} = \text{Normal}(0, 3)$$

$$\sigma = \text{half-t}(\nu, \eta)$$

We were not able to control for two predictor variables, fishing pressure and benthic composition, because of technical or methodological limitations. We used MPA status (marine reserve, restricted areas, or fished areas) as a proxy for fishing pressure. We used a subset of reef sites (n = 594) for which hard coral cover was available to quantify the importance of this predictor. Using this subset data, we ran two similar models, one with hard coral cover and one without hard coral cover and found no difference in the standardised effect sizes of species richness and fish size on micronutrient density ([Table S4](#)). This lent support to run the final models without benthic composition for the entire dataset. The final models for species richness and fish size were as follows:

$$\begin{aligned} \text{Species richness model: } \mu = & \beta_{0jk} + \beta_1 SpeciesRichness + \beta_2 Depth + \beta_3 Productivity \\ & + \beta_4 SST_{mean} + \beta_5 ReefHabitat + \beta_6 DHW + \beta_7 MPA \end{aligned}$$

Biomass-weighted average size of fish assemblages' model:  $\mu = \beta_{0jk} + \beta_1 \text{FishSize} + \beta_2 \text{Depth} + \beta_3 \text{MPA}$

All predictor variables were standardized by subtracting the mean of each variable and dividing by two standard deviations in order to assess their relative effect sizes.<sup>62</sup> Human gravity and ocean productivity were log-transformed prior to standardisation. We ran our models using the 'brms' package on R, using weakly informative priors. Standard deviations ( $\sigma$ ) of group-level ('random') effects have a half student-t prior with 3 degrees of freedom and a scale parameter that depends on the standard deviation of the response after applying the link function.

### Relationships between micronutrient density and biodiversity

To assess potential trade-offs between nutrient content of reef fish communities and biodiversity, we computed two complementary metrics of biodiversity: (1) the diversity of species traits and (2) the number of species classified as threatened by extinction, based on the IUCN Red List of Threatened Species.

### Trait diversity

Trait diversity of the fish assemblage (target and non-target) was computed for each reef site, and we used the trait database on tropical reef fishes from Mouillot et al.<sup>62</sup> The six traits considered were: (1) size (observed length of each individual fish) coded using 5 ordered categories: 10-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm, >80 cm; (2) mobility coded using 3 ordered categories: sedentary, mobile within a reef, and mobile between reefs; (3) period of activity coded using 3 ordered categories: diurnal, both diurnal and nocturnal, and nocturnal; (4) schooling coded using 5 ordered categories: solitary, paired, or living in small (3-20 individuals), medium (20-50 individuals), or large groups (>50 groups); (5) vertical position in the water column coded using 3 ordered categories: benthic, benthic-pelagic, and pelagic; (6) diet coded using 7 trophic categories: herbivorous-detritivorous, macro-algal herbivorous, invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrates, planktivorous, piscivorous, and omnivorous, (i.e. fishes that feed on both vegetal and animal material). Since all traits were categorical, species with identical traits were grouped into entities. We then computed the Gower distance between all pairs of entities. Finally, for each fish community we computed trait-diversity using the Chao's  $FD_{q=1}$  index<sup>83</sup> implemented in the mFD package<sup>84</sup> as follows:

$$FD_{q=1} = \exp\left(-\sum_{i=q}^s p_i \cdot \log\left(1 - \sum_{i \neq j} \frac{1 - \min(d_{ij}, mD)}{mD} \cdot p_j\right)\right)$$

where  $p_i$  and  $p_j$  are the respective relative biomasses of the two entities  $i$  and  $j$  in the community,  $d_{ij}$  is the Gower distance between entities  $i$  and  $j$ ,  $mD$  is the average of all Gower distances between the entities present in the global pool of species. This index is expressed as an equivalent number of species.<sup>83</sup> Hence, it is minimal and equals 1 when all biomass is supported by the same entity (i.e. when one species is ultra-dominant or when all species have the same trait values) and it is maximal and equals the number of species when all species pairs have dissimilarities higher than the average dissimilarity in the global species pool and equal biomasses.

### IUCN status

We assigned each reef fish species a conservation global status which described how likely a species is threatened with extinction, based on the IUCN Red List of Threatened Species and recent advances to retrieve status for data-deficient species from machine learning-derived technics using species taxonomy and occurrence, range extent, and environmental and human stressors within species range maps.<sup>71</sup> In total, 808 of the species in our surveyed were included (target and non-target); we reclassified these fish species into 3 groups and found that 25 species were classified as Threatened (TH: Critically Endangered, Endangered, or Vulnerable), 783 species were classified as not threatened (LC: Least Concern or Near Threatened), and 30 species had no status or were absent from both sources. We then determined for each site, the number of species which were classified as threatened (range: 0-7 species).