

Waldock, Conor ORCID: <https://orcid.org/0000-0002-2818-9859> , Maire, Eva, Albouy, Camille, Andreoli, Vania ORCID: <https://orcid.org/0000-0001-9163-011X> , Beger, Maria, Claverie, Thomas, Cramer, Katie ORCID: <https://orcid.org/0000-0001-8760-180X> , Feary, David, Ferse, Sebastian, Hoey, Andrew ORCID: <https://orcid.org/0000-0002-4261-5594> , Loiseau, Nicolas ORCID: <https://orcid.org/0000-0002-2469-1980> , MacNeil, M. Aaron ORCID: <https://orcid.org/0000-0001-8406-325X> , McLean, Matthew ORCID: <https://orcid.org/0000-0001-6518-6043> , Mellin, Camille ORCID: <https://orcid.org/0000-0002-7369-2349> , Ahouansou Montcho, Simon, Palomares, Maria Lourdes, de la Puente, Santiago ORCID: <https://orcid.org/0000-0002-6189-9596> , Tupper, Mark ORCID: <https://orcid.org/0000-0002-6157-7714> , Wilson, Shaun, Velez, Laure, Zamborain-Mason, Jessica, Zeller, Dirk ORCID: <https://orcid.org/0000-0001-7304-4125> , Mouillot, David and Pellissier, Loïc ORCID: <https://orcid.org/0000-0002-2289-8259> (2024) Micronutrient levels of global tropical reef fish communities differ from fisheries capture. *People and Nature* .

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# Micronutrient levels of global tropical reef fish communities differ from fisheries capture

Conor Waldock<sup>1,2,3,4</sup>  | Eva Maire<sup>5,6</sup> | Camille Albouy<sup>1,2</sup> | Vania Andreoli<sup>7</sup>  | Maria Beger<sup>8,9</sup> | Thomas Claverie<sup>10</sup> | Katie L. Cramer<sup>11</sup>  | David A. Feary<sup>12</sup> | Sebastian C. A. Ferse<sup>13,14,15</sup> | Andrew Hoey<sup>16</sup>  | Nicolas Loiseau<sup>6</sup>  | M. Aaron MacNeil<sup>17</sup>  | Matthew McLean<sup>17</sup>  | Camille Mellin<sup>18</sup>  | Simon Ahouansou Montcho<sup>19</sup> | Maria Lourdes Palomares<sup>20</sup> | Santiago de la Puente<sup>21,22</sup>  | Mark Tupper<sup>23,24</sup> | Shaun Wilson<sup>25,26</sup> | Laure Velez<sup>6</sup> | Jessica Zamborain-Mason<sup>27</sup> | Dirk Zeller<sup>7</sup>  | David Mouillot<sup>6</sup> | Loïc Pellissier<sup>1,2</sup> 

## Correspondence

Conor Waldock

Email: [conorwaldock@gmail.com](mailto:conorwaldock@gmail.com); [conor.waldock@unibe.ch](mailto:conor.waldock@unibe.ch)

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## Abstract

1. The exceptional diversity of shallow-water marine fishes contributes to the nutrition of millions of people worldwide through coastal wild-capture fisheries, with different species having diverse nutritional profiles. Fishes in ecosystems are reservoirs of micronutrients with benefits to human health. Yet, the amount of micronutrients contained in fish species on coral reefs and in shallow tropical waters is challenging to estimate, and the micronutrients caught by fisheries remain uncertain.
2. To assess whether micronutrient deficiencies could be addressed through specific fisheries management actions, we first require a quantification of the potentially available micronutrients contained in biodiverse reef fish assemblages. Here, we therefore undertake a broad heuristic assessment of available micronutrients on tropical reefs using ensemble species distribution modelling and identify potential mismatches with micronutrients derived from summarising coastal fisheries landings data.
3. We find a mismatch between modelled estimates of micronutrients available in the ecosystem on the one hand and the micronutrients in small-scale fisheries landings data. Fisheries had lower micronutrients than expected from fishes in the modelled assemblage. Further, fisheries were selective for vitamin A, thus resulting in a trade-off with other micronutrients. Our results remained unchanged after accounting for the under-sampling of fish communities and under-reporting of small-scale fisheries catches—two major sources of uncertainty.

For affiliations refer to page 14.

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4. This reported mismatch indicates that current estimates of fished micronutrients are not adequate to fully assess micronutrient inventories. However, small-scale fisheries in some countries were already selective towards micronutrient mass, indicating policies that target improved access, distribution and consumption of fish could leverage this existing high micronutrient mass.
5. Enhanced taxonomic resolution of catches and biodiversity inventories using localised species consumption surveys could improve understanding of nature–people linkages. Improving fisheries reporting and monitoring of reef fish assemblages will advance the understanding of micronutrient mismatches, which overall indicate a weak uptake of nutritional goals in fisheries practices.
6. The decoupling between micronutrients in ecosystems and in fisheries catches indicates that social, economic, and biodiversity management goals are not shaped around nutritional targets—but this is key to achieve a sustainable and healthy planet for both people and nature.

**KEYWORDS**

biodiversity modelling, catch reconstructions, fisheries catch, nutrition, reef fish, reef fisheries, seafood

## 1 | INTRODUCTION

More than 100 million people globally live within 5 km of coral reefs (Sing Wong et al., 2022). Reef systems support the livelihoods of at least 5–6 million people in low-to-middle income countries (Teh et al., 2013). Aquatic foods such as fish are an important source of micronutrients such as omega-3, calcium, iron, vitamin A and zinc (Hicks et al., 2019), and access to fish-sourced micronutrients is associated with multiple improved health outcomes (e.g., Angkasa et al., 2017). Yet, one in three people are without access to adequate food in 2020 and most countries are off-track to achieve food security by 2030 (SDG 2, Sustainable Development Goal 2: Zero Hunger)—which raises the question of how biodiverse wild aquatic food sources could help alleviate malnutrition (FAO et al., 2023).

Fisheries on reefs tend to be in the small-scale sector, which plays a prominent role in achieving food security but is particularly affected by knowledge gaps and catch under-reporting (FAO et al., 2023). A better understanding of where and when small-scale fishing practices capture available micronutrients could help improve policies targeted at reducing micronutrient deficiencies (FAO et al., 2023; Kawarazuka & Béné, 2011; Vianna et al., 2020). The economic dominance in human–nature relationships, as typified by fisheries focused on maximising biomass captured, leads to little attention being paid to the nutritional composition of the catch that could benefit human health. Local wild-capture fisheries provide relatively cheap and accessible micronutrient sources, yet they are also threatened by human pressures and climate change (Cheung et al., 2023; Maire et al., 2021; Mellin et al., 2022; Robinson, Mills, et al., 2022). The continued decline in global fisheries catches may put millions of people at risk of furthering micronutrient deficiencies

(Golden et al., 2016; Pauly & Zeller, 2016). However, to evaluate if micronutrient deficiencies could be addressed through specific fisheries management actions, we first require a quantification of the potentially available micronutrients contained in biodiverse reef fish assemblages. This will help understand whether the micronutrients contained in current catches from small-scale fisheries on reefs align with the micronutrients expected to be available locally. This can be achieved through modelling reef fish distributions and biomass in combination with their micronutrient content.

Micronutrient guidelines to increase fish consumption have benefited human health (Bogard et al., 2015), but micronutrient targets are rarely integrated into fisheries policies. The benefits of deliberately shifting catch compositions (Robinson, Nash, et al., 2022), rebuilding micronutrient-rich stocks, or domestically retaining species that would otherwise be discarded or exported are emerging as options to improve the composition of locally consumed micronutrients (Koehn et al., 2022). This topic needs to be further investigated to enable “blue food” systems to shift beyond measuring fisheries benefits as purely an economic commodity of tonnes of fish caught or money earned (Farmery et al., 2021; Robinson, Nash, et al., 2022). At present, we do not know the extent that available micronutrients from reef fish communities are captured. It remains uncertain whether micronutrients in the ecosystem are well-represented in catches, indicated by a good match between micronutrients available in the ecosystems and those extracted through fishing. Two measures that could help identify the extent micronutrients are captured based on current fishing practices include: (i) the proportion of an ecosystem's micronutrients reported as caught (i.e., the micronutrient ‘optimality’ of a fishery); and (ii) the selection of species with higher micronutrient potential relative to all available species in an ecosystem (i.e., the micronutrient ‘selectivity’ of a fishery). However, the ‘optimality’



and 'selectivity' of reef fisheries for micronutrients currently remain unquantified. Given the ongoing global biodiversity decline and high prevalence of nutritional deficiencies in many regions, it is critical to better assess which species are available to be consumed and to do so without further exacerbating biodiversity loss or preventing biomass recovery on reefs (Cinner et al., 2018).

The micronutrients content of fishes varies considerably among species (Robinson et al., 2023; Vaitla et al., 2018), and seafood derived micronutrients vary among countries due to spatial variation in both fisheries targeting or gear used, as well as species geographic ranges, abundance, and biomass (Hicks et al., 2019; Kulbicki et al., 2013; Waldock et al., 2019). For example, the generally smaller-bodied fishes that predominate on tropical reefs contain high concentrations of calcium, iron, and zinc, whereas pelagic fishes contain higher levels of omega-3 fatty acids (Hicks et al., 2021). As such, the multi-species reef fisheries likely vary in potential micronutrients available because the composition of fished species will largely reflect local fisheries practice as well as local biodiversity and how total biomass is distributed among species. In addition, local socio-economic factors influence the subset of species caught, consumed, sold, and reported (FAO et al., 2023). These variations drive differences in micronutrients available from local biodiversity that offer opportunities for countries to design fisheries management and monitoring policies that can be more focused on addressing malnutrition. At present, it remains unassessed how spatial variation in naturally available micronutrients intersects with countries' reef fisheries capture of micronutrients. Furthermore, because micronutrient content varies among species, better quantifying trade-offs between micronutrients is important to consider when evaluating differences between natural micronutrient supply and capture.

Here we used species-specific spatial biomass models to define a natural ecosystem's potential micronutrient available from reef fish, and asked four questions:

1. Do micronutrients derived from captured seafood match the micronutrients potentially available from the biodiversity of fishes within natural ecosystems?
2. Are reef fisheries optimised and selective towards species that contain higher amounts of micronutrients?
3. When comparing micronutrients available in biodiversity source pools and those reported in fisheries, how do countries differ in their optimisation and selectivity of micronutrients?
4. Are there trade-offs between different micronutrients in their selectivity? i.e., if you select one micronutrient for capture, does it come at the cost of others?

We focus on 87 tropical low-to-middle income countries and on calcium, iron, vitamin A and zinc as the focal vitamins and minerals. These micronutrients have a high prevalence of inadequate intake (PII) in human populations, which creates a burden of non-communicable diet-related diseases (Zamborain-Mason et al., 2023). Specifically, for these four micronutrients people have high levels of inadequate intake across 126 countries (calcium=43%, iron=20%,

vitamin A=31% and zinc=19% Beal et al., 2017), and these figures are higher (68%, 25%, 43% and 19%) in our focal countries with available data ( $n=36$ ) leading to substantial negative health effects (Afshin et al., 2019). We estimate micronutrient concentrations as average micronutrient mass per 100g raw portion of fish muscle using micronutrient data from FishBase (FishNutrient database 2022; <https://fishbase.de/Nutrients/NutrientSearch.php>) and total micronutrient mass available in situ from reef-associated fish using species distribution and biomass models for more than 1000 tropical shallow-water fish species that are targets of fishing. We compare estimates of expected in-water fish biomass and micronutrient availability to the reconstructed small-scale catch data for the 87 countries from the *Sea Around Us* project (Pauly & Zeller, 2016; Zeller, Palomares, et al., 2023). We utilise these data to quantify the micronutrient optimality and micronutrient selectivity of domestic small-scale catches to identify potential mismatches between modelled in situ availability of micronutrients compared to the micronutrient content of actual reef fisheries catches.

## 2 | METHODS

### 2.1 | Identification of fished and consumed species in focal countries

We had 2320 species available for analysis with fitted species distribution and biomass models from which we could define micronutrient source pools (see below). From this set, we identified 1081 fish species that are also expected to be caught and eaten globally (see Figure S1 for an overview of this filtering procedure) and were defined as being 'reef-associated' in FishBase habitat association table. We define species as 'fished' using two large databases containing information on global fisheries: (i) the *Sea Around Us* reconstructed catch database (Pauly & Zeller, 2016) and (ii) FishBase (Froese & Pauly, 2024). We used the *Sea Around Us* reconstructed catch data rather than the international fisheries statistics as reported by the Food and Agriculture Organisation (FAO) on behalf of member countries for two reasons. First, the *Sea Around Us* data has better taxonomic resolution, fisheries sectoral disaggregation, and detailed spatial allocation of catch data (Pauly & Zeller, 2016; Zeller et al., 2016; Zeller, Ansell, et al., 2023; Zeller, Palomares, et al., 2023). Second, the *Sea Around Us* data are more comprehensive than reported data due to the addition of unreported catch estimates, especially for small-scale fisheries in low-to-middle income countries (Pauly & Charles, 2015; Pauly & Zeller, 2016; Zeller et al., 2015, 2016; Zeller, Ansell, et al., 2023; Zeller, Palomares, et al., 2023). Furthermore, we obtained fisheries-related information from the *importance* field of the *species* table in FishBase, using the *species* function in the R package 'rfishbase' (package version 3.1.9; data version 21.04; Boettiger et al., 2012). We considered species as potentially caught if the *importance* field was reported as 'subsistence fisheries', 'minor commercial', 'commercial' and 'highly commercial'.

Finally, to avoid conflicts between biodiversity conservation and food provision, we excluded all Elasmobranchii (i.e., sharks and rays) and all species classified by the IUCN as globally Critically Endangered, Endangered, Near Threatened or Vulnerable (using R package 'redlist' version 0.7.0; Gearty & Chamberlain, 2022) from further consideration, giving a final set of 1081 species either known to be 'caught' or 'potentially caught' globally. Note, however, that sharks and rays can form important food sources and fisheries but were not included here.

In addition to categorising species as potentially caught, we obtained quantitative country-level catch tonnage data from the *Sea Around Us* database. We extracted data for the small-scale fisheries sectors only (i.e., artisanal, subsistence and recreational) from the *Sea Around Us* reconstructed catch database for the exclusive economic zones of all 144 countries with small-scale catches in the *Sea Around Us* catch data for the years 2000–2018 (*Sea Around Us* catch data version v48.0, accessed 20.09.2021). We summed landed tonnes of fish caught in each country's exclusive economic zones per year (2000–2018). We separated the data for landings destined for direct human consumption from other end use categories, such as discards or fishmeal (Cashion et al., 2017). We took the mean of these summed values across all years, resulting in average tonnes per year landed by small-scale fisheries per taxonomic entity, country, and consumption (end use) category. Therefore, for each country, we identified the tonnage of species caught by their small-scale fisheries for direct human consumption.

To focus our analysis on countries expected to consume reef fishes in diets, we used several approximate indicators of reef-food dependency. We aimed to restrict our analysis to countries with small-scale fisheries that supply reef fishes for local nutrition. Thus, we excluded high-income countries, where consumption is underpinned and influenced mostly by fish imports. Our final country list contained 87 countries which: (i) have small-scale landings data in the *Sea Around Us* reconstructed catch data, (ii) are located between 30° N and 30° S, (iii) have a human development index of less than 0.8 in 2019 (United Nations Development Program Human Development Report: <https://hdr.undp.org/en/indicators/137506>), (iv) have more than 50% of their population living within 10 km of the coast in the year 2000 (Gao, 2017; Jones & O'Neill, 2016), and/or (v) have more than 20% of animal protein obtained from seafood (Micha et al., 2015). Countries were excluded from the analysis set only if they lacked all criteria *iii* to *v*, while a match for one criterion of *iii* to *v* was sufficient for inclusion.

## 2.2 | Species distribution modelling to define micronutrient source pools

We built species distribution models and species biomass models (Waldock et al., 2022) for 2320 reef fish species (see Appendix S2; Data Sources; Auber et al., 2022), including the final subset of 1081 species either known to be 'caught' or 'potentially caught' at

a global scale, and thus with a high likelihood of being caught and eaten. We separately modelled species-level presence and biomass when present in response to large-scale gradients in shallow-water environments. We predicted habitat suitability, presence, and biomass on a consistent 0.25° global grid, which provides a global species-by-site matrix for coastal and reef systems.

We integrated over 12 million records of species presence from open access databases (GBIF, OBIS) and local SCUBA transects using the Reef Life Survey (Edgar et al., 2020; Edgar & Stuart-Smith, 2014), SERF project datasets (Cinner et al., 2018), and GASPARG project dataset (Barneche et al., 2019; Kulbicki et al., 2013). Additionally, we compiled transect (500 m<sup>2</sup>) scale biomass estimates of reef fishes from the above local SCUBA surveys providing more than 850,000 biomass observations. We built presence-only species distribution models using 350,000 records with an average of 250 records per species, and most species (75%) having more than 100 presence records. We also built models describing spatial variation in species-level biomass using 50,000 records with 140 biomass records per species on average and most species (75%) having more than 70 biomass records. Thus, species had sufficient records above the recommended threshold for robust species distribution modelling (Wisz et al., 2008).

As covariates in our species distribution and biomass models, we extracted the environmental conditions measured for all fish observations for six environmental variables: averaged yearly minimum and maximum sea surface temperature from daily records (SST), minimum annual pH, minimum annual sea surface salinity (SSS), mean annual net primary productivity (NPP), mean annual degree heating weeks to indicate past heatwave events (DHW; Liu et al., 2014), and the integrative 'human gravity' index which represents anthropogenic effects, expressed as a function of human population size and travel time to a reef (Maire et al., 2016). The 'human gravity' index examines the amount of human pressure within 500 km of a reef (Cinner et al., 2018). These 6 variables were selected as they have potentially important effects that ultimately determine or influence the spatial distribution and spatial variation in biomass of reef fishes at large spatial scales (SST, SSS, pH), determine bottom-up ecosystem processes (NPP), or represent anthropogenic effects through proximity to human populations (human gravity) and the influence of past heatwaves (DHW). This analysis aimed to help define regional species pools and make spatial predictions in non-surveyed locations. Therefore, we could not include more local variables such as coral cover that have poor global data coverage and are often unknown in non-surveyed locations.

We built ensemble species distribution and biomass models including three algorithms (generalised linear models, generalised additive models, and random forests) that cover a range of complexity relating the response variable to covariates. These models explained the relationships among species presence, species biomass, and environmental conditions. For each model, we checked that the Pearson correlation between pairs of variables was less than 0.7, and if not, retained the variable with the highest deviance explained (generalised linear models and generalised additive models) and lowest error rate (random forests). We iterated this

process until we obtained a set of variables correlated with Pearson correlation  $<0.7$  which also maximised explanatory power. For the presence-only models, we used a target-group pseudo-absence approach (Phillips et al., 2009). We generated 5-folds of background data to reduce uncertainty occurring in modelling presence-only data. For the biomass-based models, we modelled log-transformed 'biomass-when-present' as our response variable (removing '0' biomass values), to avoid conflating species presence with biomass. We performed model evaluations using spatially blocked 5-fold out-of-sample predictions retaining only models with a true-skill statistic of more than 0.35 for species distribution models (Righetti et al., 2019), and Spearman's rank correlations between predicted and observed biomass of more than 0.2 for species biomass models (Waldock et al., 2022). Note that only 139 of 1081 species had well-performing species biomass models based on these criteria. For the remaining species without well-performing species biomass models, we transposed the habitat suitability estimates (ranging from 0 to 1) to the natural range of observed biomass for a given species (ranging from the lowest observed biomass to the highest for a given species). As such, we assume that local biomass is positively correlated with habitat suitability (as supported by VanDerWal et al., (2009) and Weber et al., (2017); but see Dallas & Santini, (2020) for potential deviations from such relationships). We perform this necessary simplification to ensure we include major gradients in biomass in estimates of ecosystem services (i.e., differences between species and spatial biomass variation within species).

We used our models to predict the habitat suitability and biomass of species in present-day environmental conditions. To improve the accuracy of model predictions, we mean-averaged across sources of uncertainty in the form of model algorithms and background data iterations (Dormann et al., 2018). For each species, we removed grid cells that had habitat suitability predictions below the threshold value that maximised true-skill statistic. We produced three sets of maps for each species: a map of habitat suitability (continuous from 0 to 1), presence (binary 0 or 1), and expected biomass (continuous value in grams)—these maps were combined with species-specific micronutrient estimates as described below. Whilst biomass was mapped at 0.25° resolution, the gram values indicate the biomass on an average local SCUBA survey (gram per 500m<sup>2</sup>). Note that we accounted for dispersal limitations, and avoided strong spatial extrapolations, by predicting habitat suitability and biomass only within Spalding's Provinces already containing the focal species (Spalding et al., 2007).

### 2.3 | Micronutrient properties of species and communities

Micronutrient reference nutrient intake (RNI) (mass of micronutrient per 100 g raw fish muscle) were obtained from FishBase (FishNutrient database 2022; <https://fishbase.de/Nutrients/NutrientSearch.php>), which represents an updated version of the micronutrient predictions first developed in Hicks et al. (2019). The updated database used here

includes >3500 measurements for 610 fish species. Note that this dataset is expanded by >60% from that used in Hicks et al. (2019) who covered 367 species and includes new nutrient analyses of tropical coral reef species (Robinson, Maire, et al., 2022). These values were derived using a Bayesian hierarchical modelling approach relating micronutrient content to species' diet, energy demand, thermal regime and phylogenetic history, in addition to observation effects relating to methodological differences among sample collectors (model details have been documented at <https://github.com/mamacneil/NutrientFishbase>; accessed 21.07.2021). Model diagnostics indicate 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. Taking a broad-scale perspective, we did not include intraspecific variation in micronutrient concentrations which are expected to be a more minor source of variation compared with interspecific variation in micronutrient concentrations and biomass variation among species (Budge et al., 2002).

We further simplified our analysis by focusing on three minerals (calcium, iron, and zinc), in addition to vitamin A, which are relevant due to high PII globally in these micronutrients (Afshin et al., 2019; Beal et al., 2017). Micronutrient content units for calcium, iron, and zinc were in mg per 100g, and for vitamin A in µg per 100g. We expressed these concentrations as a percentage of micronutrient RNI from dietary reference intake tables. The RNI values indicate the daily intake level at which 97% to 98% of the nutritional requirements of children aged 1–3 years are met (calcium = 700 mg per day; iron = 7 mg per day; vitamin A = 300 µg per day; zinc = 3 mg per day; NASEM, 2017).

We combined the outputs of species distribution and biomass models with micronutrient information of each fish species. We converted species presences to micronutrient RNI by filling the species-by-site matrix with species micronutrient RNI when species were present. To obtain country-scale RNI estimates, we used a spatial intersection of countries' exclusive economic zones with our 0.25-degree site-by-species grid cells and mean-averaged micronutrient RNIs across all species present in countries' grid cells. We converted biomass to micronutrient mass by multiplying the species biomass (g) by species micronutrient RNI across the whole species-by-site matrix to give micronutrient mass per species per grid cell. As in other studies, we did not assess edible mass from biomass estimates or modification of nutrients through preservation or cooking (Hicks et al., 2019). We mean-averaged micronutrient mass for each species in all grid cells of each country to avoid summing larger values for larger countries, before summing micronutrient mass across all species per country.

### 2.4 | Coupling known reef fish catch and micronutrient ecosystem potential

Using the *Sea Around Us* reconstructed landings data for small-scale fisheries for 58 of 87 countries that reported catches, we

identified 251 out of 1081 fish species within these countries that also had species-level catch tonnage information available for comparison to modelled regional biomass estimates. Although low in number, we expect these focal species to be important biomass sources because they comprise 29% of the total global biomass in our models and formed 23% of species richness. Additionally, these species totalled 0.32 million tonnes of catch for direct human consumption. We expect this tonnage to contribute non-trivially to food security because the amounts considered in our analysis are relatively large when compared to requirements from seafood-dependent peoples, such as the global estimate for Coastal Indigenous Peoples to catch 1.5 to 2.8 million tonnes (Cisneros-Montemayor et al., 2016). As such, the reef fishes considered in our analysis form an important food, even though a high level of taxonomic uncertainty and under-reporting exists in reef fish catch reporting (Derrick et al., 2023; Pauly & Zeller, 2016; Zeller et al., 2015). This is also indicated in our analysis by the 48% of total catch tonnage for the reef-associated countries that are identified above the species level (e.g., genus, family, order). We expected that if countries target the most nutritious species, then micronutrient RNI and micronutrient mass will be related to catch tonnage in the *Sea Around Us* data. To see if there was a broad correspondence between these variables, we estimated the Spearman's rank correlation ( $\rho$ ) and the R-squared of a linear model. In the above, all biomass and micronutrient mass values were log-transformed prior to analysis.

## 2.5 | Micronutrient optimality and selectivity

In the above analysis, we were limited by available species-level catch data. To overcome this limitation, we used our species distribution and biomass models to broaden our approach by including all targeted reef species defined in both *Sea Around Us* and FishBase ( $n=1081$ ). From these models, we estimated the availability of micronutrients from a modelled regional source pools of species, assuming model adequacy. We defined two metrics to compare the micronutrients fished and those potentially available in a country's reef fisheries: micronutrient optimality and micronutrient selectivity. We estimated these metrics for both micronutrient RNI and micronutrient mass. Thus giving 4 metrics for investigation: RNI optimality, RNI selectivity, mass optimality and mass selectivity. These metrics are based on evaluating micronutrients in subsets of the source pool that contain the same number of species that are in countries catches. These metrics indicate the proportion of micronutrients in source pools that are fished (optimality), and whether current fishing is selective for micronutrients compared to randomised simulations (selectivity). We present our results separately for optimality and selectivity.

To define these properties, we calculated the micronutrients of species observed to be fished in each country for each micronutrient and called this  $MN_{\text{fished}_i}$  whereby MN stands for micronutrients. Next,

to estimate our metrics of optimality and selectivity we had to simulate an optimised and randomised fishing strategy, from all species present in the modelled regional pool, and we called this  $MN_{\text{max}}$  and  $MN_{\text{null}}$  respectively. To estimate these properties, we had to define the number of fished species ( $n$ ) per country ( $i$ ). We then calculated the mean micronutrient RNI and total micronutrient mass for these three sets of species per country: (i) micronutrients in  $n_i$  targeted fish species (i.e., reported as caught at a country-level),  $MN_{\text{fished}_i}$ , (ii) the  $n_i$  species with the highest micronutrient value in the regional species pool,  $MN_{\text{max}_i}$ , and (iii) the average micronutrients of 999 randomised subsets of  $n_i$  species from the regional species pool,  $MN_{\text{null}}$ . Note that *ii* and *iii* are species that are not necessarily reported as caught at a country level but could be expected to be present in countries' ecosystems based on species distribution and biomass models.

We defined the 'micronutrient optimality' as the percentage of maximum micronutrients available in the modelled regional species pool that are reported as caught in fished species,  $\frac{MN_{\text{fished}_i}}{MN_{\text{max}_i}}$ , for both micronutrient RNI and micronutrient mass. Optimality can take a maximum value of 100% whereby the most nutritious set of species is fished. We also defined the 'micronutrient selectivity' of a fishery as the extent to which current fisheries target species with high-micronutrient RNI and micronutrient mass. To calculate selectivity, we compared the optimality of micronutrient selection in the fished pool to random samples of available species:  $\frac{MN_{\text{fished}_i}}{MN_{\text{max}_i}} - \frac{MN_{\text{null}}}{MN_{\text{max}_i}}$ , thus indicating if micronutrient values are similar to a random selection of available species. Micronutrient selectivity is positive if current fishing practices are closer to the optimal fishing strategy compared with a random selection from the available species pool. Selectivity is expressed as a percentage, being the percentage difference between optimality of fished and random fishing scenarios.

These investigations were undertaken for 58 of the 87 reef-associated countries that had more than one species with landings in the *Sea Around Us* reconstructed catch data. Note that these simulated scenarios occur completely within our modelled system, but using species and congeners identified as caught in the *Sea Around Us* data (for the analysed 58 countries in the *Sea Around Us* data  $n_i=116 \pm 90$  with a range of  $n_i=3$  to 336 species). As such, there is no bias introduced by comparing micronutrient properties from different data sources, and our analyses benefitted from including more species than those only available in the reconstructed catch data. For these scenarios, we kept constant the total number of species fished to avoid selecting scenarios with higher richness and thus simulating scenarios that deplete biodiversity. We did not constrain biomass extracted in our scenarios because lower biomass extraction for a higher micronutrient RNI for the same number of species is beneficial for species conservation. Note that we did not consider biomass production rate (e.g., productivity) variation among species that determines stock sustainability (Morais et al., 2020) and assume that stocks can be sustainably fished. We further checked whether optimising for micronutrients modified overall biomass supplied by comparing the average biomass of ' $n$ ' fishes in simulated catch with biomass of micronutrient RNI optimised catch and micronutrient mass optimised catch. It is important to note that this

set of simulations are a heuristic exercise to better understand the micronutrient structure of regional source pools and micronutrient targeting in available catch data, but context-dependent fisheries monitoring and management plans are best placed to assess the local reality of food systems supported by fisheries (see Section 4).

## 2.6 | Sensitivity to under-sampling

In general, data availability limitations led to reductions in sample sizes throughout our analysis, indicating we likely under-sampled many properties of reef fish biodiversity and fisheries landings. We therefore simulated these under-sampling biases as we could not easily increase the input data. Two important sources of under-sampling exist in defining  $MN_{\text{fished}}$ ,  $MN_{\text{null}}$  and  $MN_{\text{max}}$  which could therefore compromise our estimates of micronutrient optimality and selectivity: (i) incomplete biodiversity sampling leading to under-sampled country species pools (defining  $MN_{\text{null}}$  and  $MN_{\text{max}}$ ), and (ii) incomplete catch datasets (defining  $MN_{\text{fished}}$ ). Challenges in representatively sampling marine biodiversity are well-known (Montes et al., 2021; Webb et al., 2010), with strong consequences even for relatively simple global patterns in biodiversity such as latitudinal richness gradients (Menegotto & Rangel, 2018). Using the *Sea Around Us* data should decrease under-reporting issues that exist with FAO reported catches (Chuenpagdee et al., 2006; Pauly & Zeller, 2016; Zeller et al., 2015), however under-sampling issues still exist, especially in species-level identifications in catch statistics. To test the influence of these joint issues we randomly reduced the number of species considered at a country level by 50%, doing so for both the species distribution and biomass model-derived species pools and the *Sea Around Us* species pool, and recalculated all statistics. In addition, we checked for differences in our metrics calculated from modelled habitat suitability and biomass values compared with the same set of metrics derived from observed mean biomass on local SCUBA transects that recorded the species identity, abundance and body size standardised to 500 m<sup>2</sup> (see Appendix S2). The number of investigated countries for which we also have SCUBA records of captured and recorded fishes was 13 at the genus level and 15 at the family level (Tables S4 and S5).

## 3 | RESULTS

### 3.1 | Defining regional micronutrient species pools

Our presence-only models had good predictive accuracy when assessed using spatially blocked out-of-sample cross-validations (Figure S2;  $n=1081$ ; sensitivity= $0.89 \pm 0.05$ ; specificity= $0.74 \pm 0.08$ ; true-skill statistic= $0.63 \pm 0.11$ ; AUC= $0.83 \pm 0.06$ ). Comparing observed local species' biomass and model predicted biomass, we observed acceptable performance in terms of discrimination metrics for only 139 species (Spearman's rank correlation  $\rho=0.31 \pm 0.09$ ; Figure S2). Our models broadly capture biomass distributions of reef

fishes among countries, confirmed by relating country-level modelled fish biomass to country-level reconstructed reef fish catch from the *Sea Around Us* data (Pauly & Zeller, 2016). At this broader scale, we found a significant positive correlation between modelled biomass and caught biomass ( $\rho=0.40$ ,  $p<0.001$ ; Figure S3), which supports the expectation that countries disproportionately catch species with high rather than low local biomass, and additionally supports that our models broadly predict the biomass distribution of a regional species pool in each country. However, we noted substantial variation between modelled biomass and caught biomass remains unexplained.

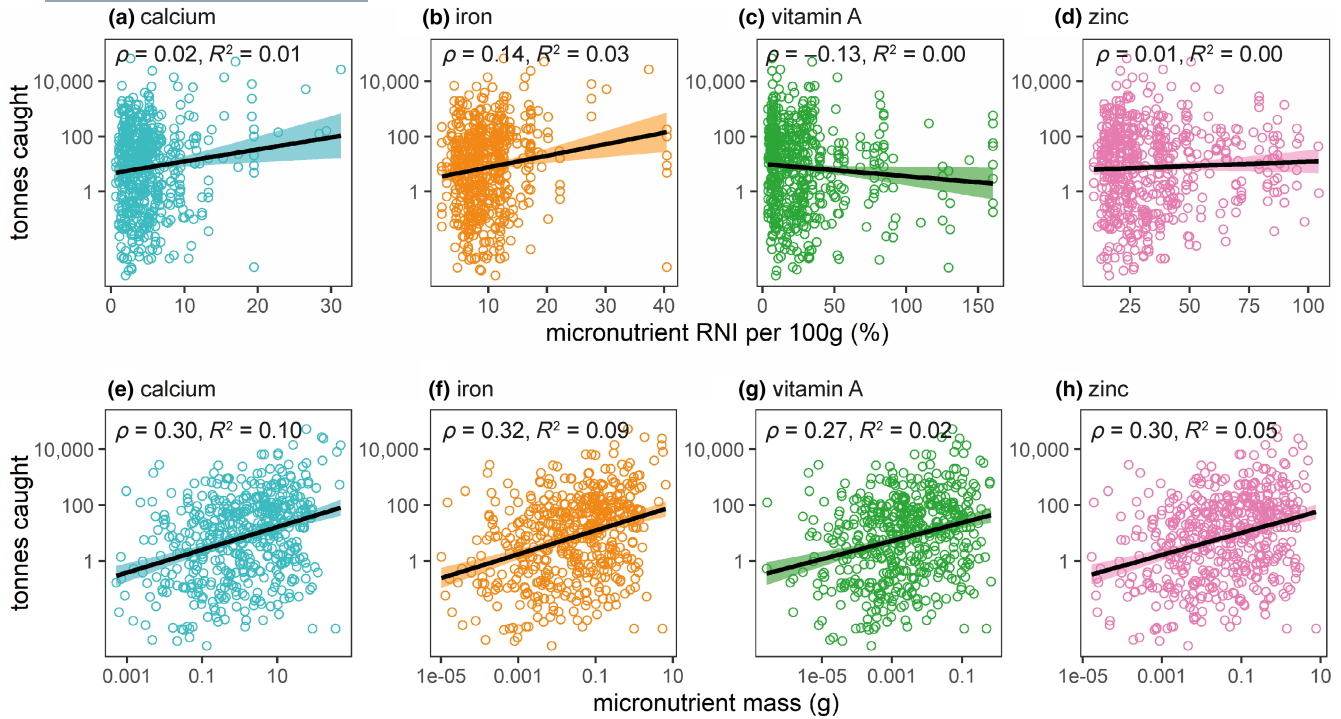
### 3.2 | Coupling reef fisheries catch and micronutrient ecosystem potential

We expected that if countries would consider the micronutrient content of fish in their fisheries policies and practices, a positive relationship would exist between species' catch tonnage and micronutrient RNI or mass. A positive relationship for all micronutrients would be optimal from a human nutrition standpoint, whereby species having the highest multi-micronutrient contents and mass also dominate the catch volumes. However, we found species' catch tonnage and micronutrient RNI (% RNI per 100g) were weakly positively related for calcium and iron, while vitamin A had a negative relationship and zinc was unrelated to catch tonnage (Figure 1a–d). Across all micronutrients, species' catch tonnage and micronutrient mass were positively related (Figure 1e–h, as in Figure S3). In general, species' catch tonnage and micronutrient mass were more positively related than species' catch tonnage and micronutrient RNI (Figure 1). We emphasise that our micronutrient calculations are completely independent of the *Sea Around Us* project data, which indicates fisheries appear to somewhat select species with high locally available micronutrient mass, probably because these targeted species also have high standing stock biomass. We caution that although a positive relationship between catch tonnage and reef fish micronutrients exists, the relationship explains only a small amount of variation (Figure 1), suggesting at best a weak coupling between catch and micronutrients. Additionally, the variation explained was lower for micronutrient RNI compared to micronutrient mass, again indicating a weaker coupling between catch tonnage and micronutrient content than catch tonnage and micronutrient mass.

### 3.3 | Low micronutrient optimality and selectivity of global reef fish catches

Micronutrient optimality of fisheries catches was generally low across both micronutrient RNI and micronutrient mass. That is, for the same number of species that are reported as caught, we model a higher amount of micronutrients potentially available in a different composition of species but keeping the same species richness. Therefore, only a small percentage of the potential maximum micronutrient RNI and micronutrient mass was contained within the caught species, compared to the species available in the modelled



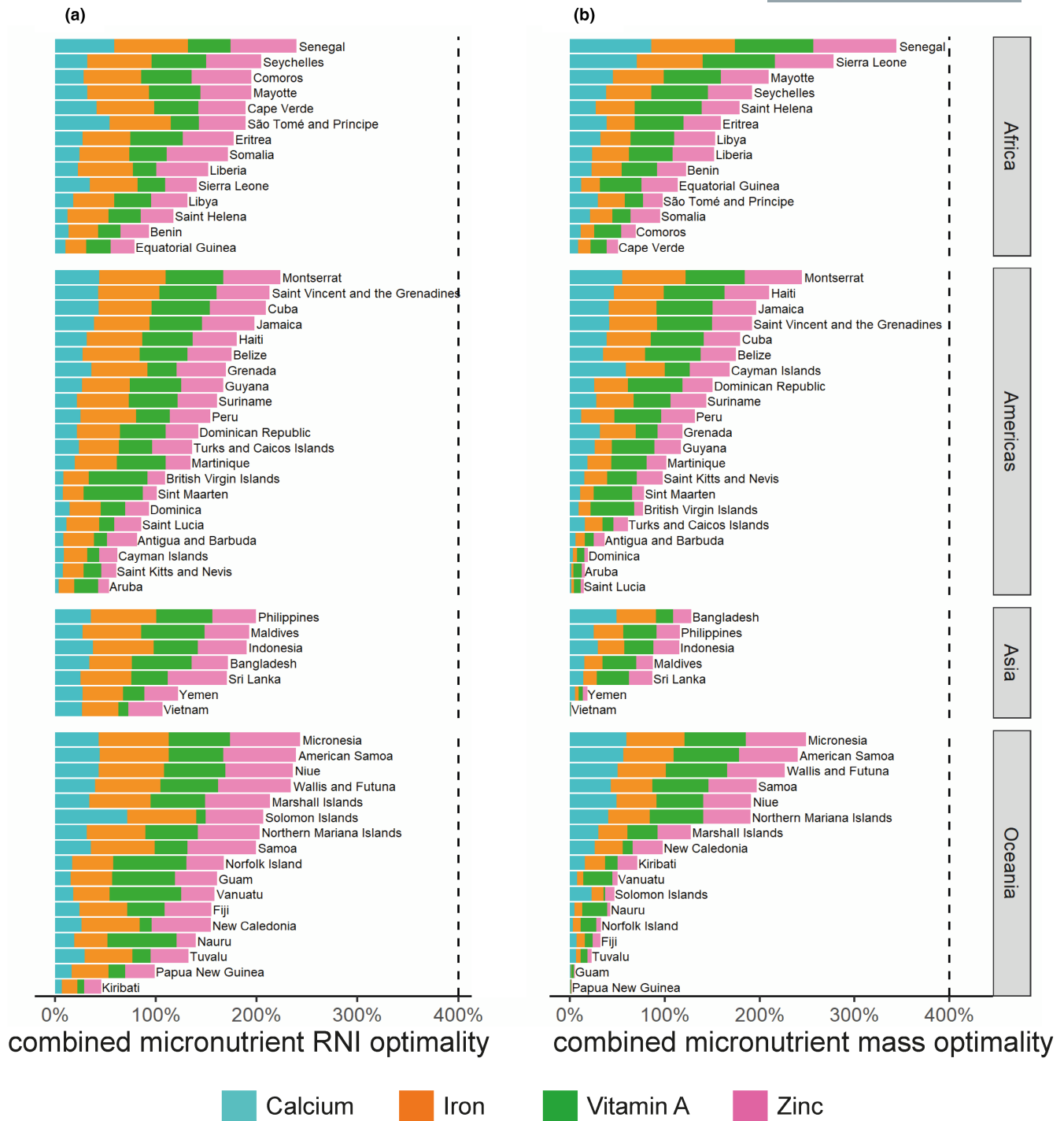


**FIGURE 1** Relationship between potential species micronutrients as a % of reference nutrient intake (RNI) values (a–d) and potential total micronutrient mass in a reef fish community (e–h), as modelled using species distribution and biomass models, compared to a country's actual total tonnes caught (as per Sea Around Us data). Each dot represents a species ( $n=251$ ) caught by a country ( $n=58$ ), although not all species are caught by all countries. Note that micronutrient mass and tonnes caught are shown here on a log<sub>10</sub> scale. Linear models were used to relate micronutrient mass and realised catch tonnage with mean predictions and  $\pm 95\%$  CI indicated by lines and shaded intervals. Spearman's rank correlations ( $\rho$ ) and variation explained ( $R^2$ ) are presented in panels.

regional pool (Figure 2). The per micronutrient optimality values ranged between 29% and 50% for micronutrient RNI and between 29% and 39% for micronutrient mass. However, optimality of micronutrient mass capture (Figure 2b) was much more variable between countries compared to micronutrient RNI capture (Figure 2a). Simulating a micronutrient-“optimal” fishing scenario, micronutrient RNI per 100g portion of fish ranged between 35% and 80% across all micronutrients, but at present known-to-be fished species per country contained only 8% to 34% micronutrient RNI per 100g portion across all micronutrients (Table 1). Some countries had low optimality across multiple micronutrients, for example, micronutrient RNI optimality ranged between 7% and 18% for all micronutrients in Kiribati, and calcium, iron and zinc RNI optimality ranged between 3% and 16% in Aruba despite having high-micronutrient RNI  $MN_{max}$  of 81% across these micronutrients in these two countries. On the other hand, fisheries catch sometimes optimised certain micronutrients over others. For instance, catches in the Solomon Islands had high optimality for calcium (72%) and iron (69%) but not vitamin A (9%) (Figure 2a). Some countries had high optimality across multiple micronutrients, including São Tomé and Príncipe, Micronesia, Senegal, and American Samoa all having multiple micronutrients with >50% optimality, but in such cases the maximum RNI available was lower, averaging only 27% across all micronutrients in these examples (Figure 2a). Further, some countries had very high micronutrient optimality for mass, for example, Senegal, Sierra Leone,

Micronesia and American Samoa all had >50% mass optimality for all micronutrients (Figure 2b). It is important to note that optimising for micronutrient RNI led to the selection of lower biomass species compared to currently targetted species, and optimising for micronutrient mass led to the selection of higher biomass compared to currently targetted species, indicating trade-offs and co-benefits of optimising towards the different micronutrient properties of RNI and mass (Figure S4). Overall, our optimality results indicate, on average, reported fisheries catches represent less than half the micronutrients in modelled reef fish assemblages, but at a country scale even larger potential gaps and trade-offs can exist between reported fisheries catches and modelled-as-available fishes.

Micronutrient selectivity was low, on average, for both micronutrient RNI and micronutrient mass in most countries, indicating that fisheries are not positively selective towards the most nutritious fishes from the available species pool (Figure 3; Table 1). Although selectivity was low in general, we found substantial variation between countries, ranging from -31% to +49% for micronutrient RNI and from -24% to +81% for micronutrient mass (Figure 3; Table 1). Some countries fisheries had positive selectivity for micronutrients; for example, domestic catches in the Solomon Islands had high-micronutrient RNI selectivity for calcium (49%) and iron (36%) and selectivity for vitamin A in Vanuatu, Norfolk Island and Nauru was ~40% (Figure 4a). Some countries also positively selected for some micronutrients but negatively for



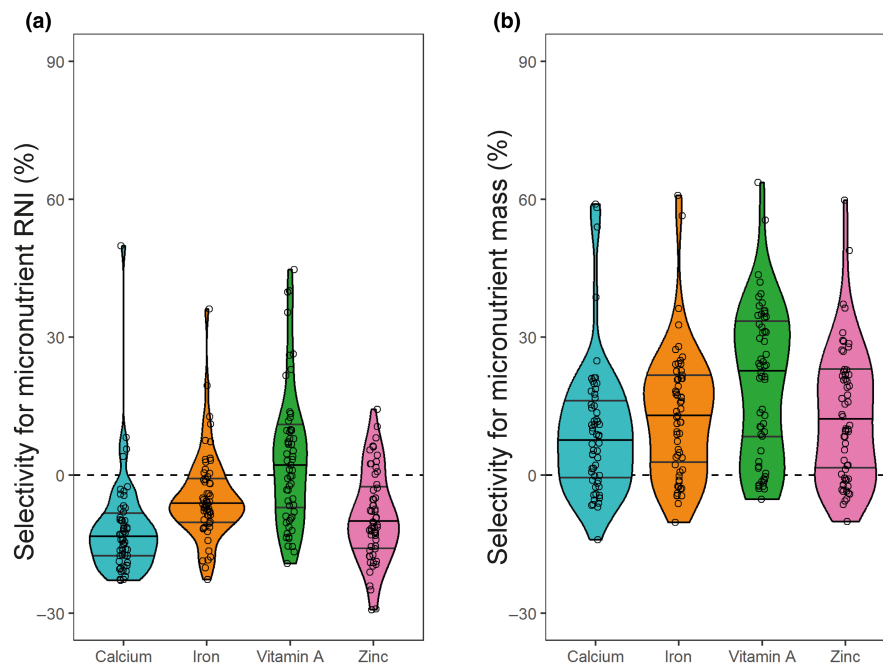
**FIGURE 2** Optimality of reef fisheries for micronutrient capture. Micronutrient optimality represents whether the micronutrients available in the modelled regional species pool are captured in fisheries. More specifically, we calculated the optimality as the proportion of a country's potential micronutrients ( $MN_{max}$ ) reported as caught ( $MN_{fished}$ ). Each micronutrient then has a maximum total optimality of 100% and a summed optimality of 400% across all four micronutrients. (a) Optimality of micronutrient reference nutrient intake (RNI) and (b) optimality of micronutrient mass. Micronutrient RNI is calculated as the average micronutrient RNI across all species in a country. Micronutrient mass is calculated as the average of a species micronutrient mass within a country and sums all species averages to provide a total value per country.

others; for example, domestic catches in the Sint Maarten had a positive selectivity of +27% for vitamin A but a selectivity of -24% for zinc (Figure 4a). In terms of micronutrient mass, a few countries had consistently positive selectivity (>25%) across multiple

micronutrients such as Senegal, Sierra Leone, Eritrea, Libya, and the Cayman Islands (Figure 4b). In contrast, Cape Verde, Saint Lucia and Guam had negative micronutrient mass selectivity for all micronutrients but only to an average negative selectivity of

**TABLE 1** Mean  $\pm$  one standard deviation for micronutrient metrics across 58 countries. All reference nutrient intake values (RNI) values are expressed as percentages. For micronutrient mass values of maximum micronutrient potential of a country's species pool ( $MN_{max}$ ), micronutrient potential of species caught ( $MN_{fished}$ ) and micronutrient potential from a randomised fishing strategy ( $MN_{null}$ ) are expressed as the sum of micronutrients across all mean-average species micronutrient values within a country (see Section 2), and micronutrient optimality and selectivity are percentages as defined in the text.

Micronutrient	$MN_{max}$	$MN_{fished}$	$MN_{null}$	Optimality (%)	Selectivity (%)
<b>RNI</b>					
Calcium (mg)	21 $\pm$ 8.9	5.3 $\pm$ 3.7	7.4 $\pm$ 1.2	29 $\pm$ 16	-11 $\pm$ 12
Iron (mg)	22 $\pm$ 7.9	10 $\pm$ 3.1	11 $\pm$ 0.94	50 $\pm$ 17	-4.4 $\pm$ 11
Vitamin A ( $\mu$ g)	72 $\pm$ 31	28 $\pm$ 16	26 $\pm$ 4.3	42 $\pm$ 18	2.6 $\pm$ 15
Zinc (mg)	80 $\pm$ 24	34 $\pm$ 12	41 $\pm$ 6.8	45 $\pm$ 17	-9.5 $\pm$ 10
<b>Mass</b>					
Calcium (mg)	29,000 $\pm$ 34,000	11,000 $\pm$ 18,000	7100 $\pm$ 12,000	29 $\pm$ 22	11 $\pm$ 17
Iron (mg)	550 $\pm$ 600	210 $\pm$ 310	130 $\pm$ 210	33 $\pm$ 23	15 $\pm$ 18
Vitamin A ( $\mu$ g)	62,000 $\pm$ 82,000	29,000 $\pm$ 53,000	14,000 $\pm$ 28,000	39 $\pm$ 25	21 $\pm$ 20
Zinc (mg)	870 $\pm$ 1100	350 $\pm$ 670	210 $\pm$ 390	33 $\pm$ 23	15 $\pm$ 18



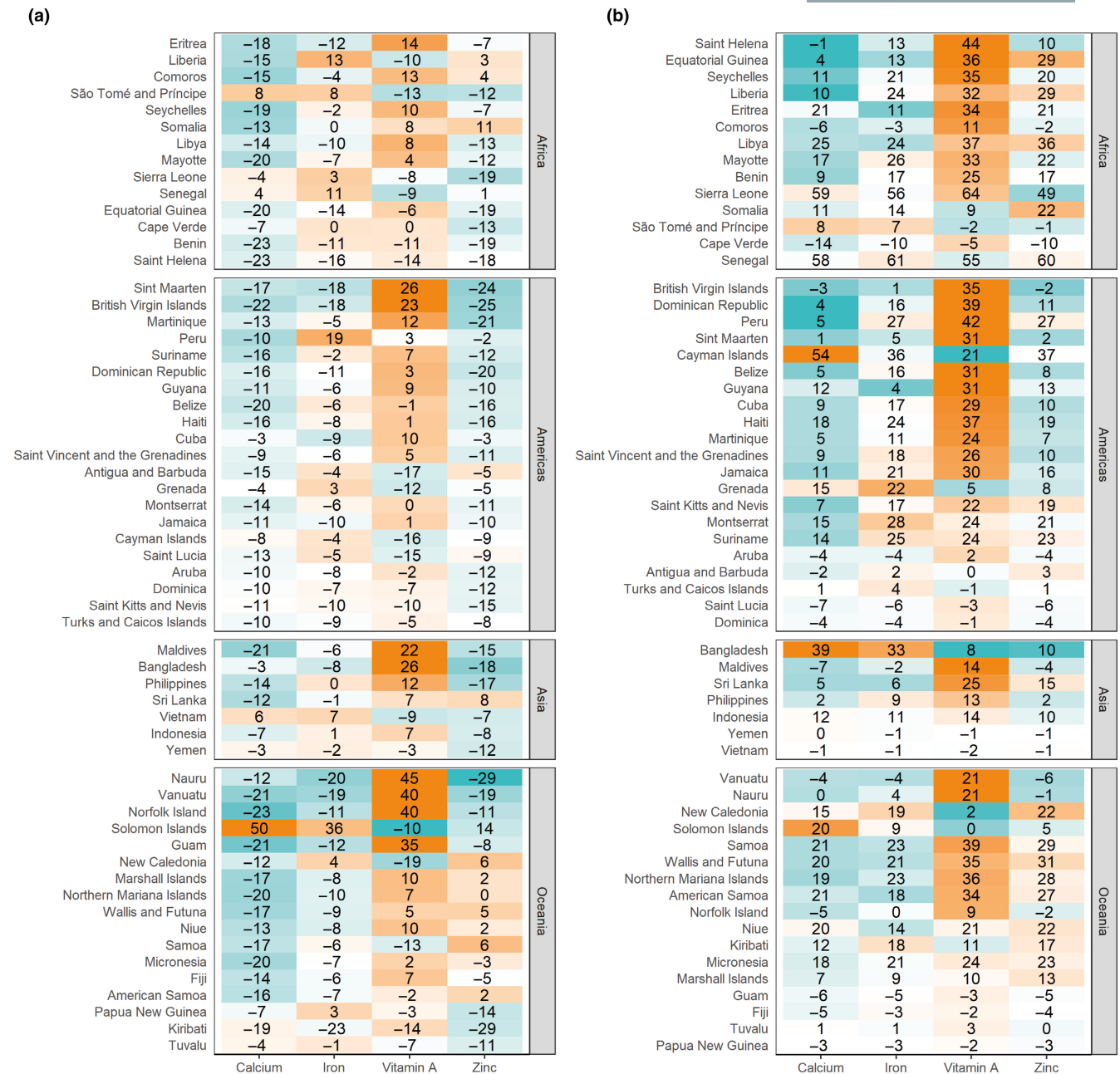
**FIGURE 3** The selectivity of fisheries-derived micronutrients for micronutrient reference nutrient intake (RNI) and micronutrient mass. Micronutrient selectivity is defined as the difference between the micronutrient potential of species caught by a given country and the micronutrient potential from a randomised fishing strategy ( $MN_{fished} - MN_{null}$ ) as a percentage of the maximum micronutrient potential of a country's species pool ( $MN_{max}$ ). Micronutrient selectivity is positive if current fishing practices are closer to the optimal fishing strategy compared with a random selection from the available species pool, i.e., compared to random fisheries selected for micronutrients. Selectivity is shown for micronutrient RNI (a) and micronutrient mass (b) across 58 countries. Points show mean values across 999 null simulations (to generate  $MN_{null}$ ) with violin-width corresponding to the density of points at a given selectivity. Bars across violins show median and 25th to 75th percentiles.

around -11% (Figure 4b). However, we must note that there was a trade-off between micronutrients, when one was positively selected for another was negatively selected against, and these trade-offs appeared in multiple constellations (Figure 4a,b). Many countries were positively selective for vitamin A but against other micronutrients, especially in terms of micronutrient mass (Figure 4b). In contrast, Bangladesh, the Cayman Islands, and the Solomon Islands had low selectivity for vitamin A, but instead

selected for Calcium and Iron. New Caledonia and Kiribati were selective for Iron and Zinc but against vitamin A (Figure 4a,b). As such, the relatively consistent average selectivity values across all countries and micronutrients, as seen in micronutrient mass selectivity, belie a complex assortment of micronutrient trade-offs between any given countries fisheries.

Our results were robust to uncertainty in the sets of species that defined the optimal fishing strategy ( $MN_{max}$ ), current fishing strategy





**FIGURE 4** Trade-offs between different micronutrients in the selectivity of fisheries-derived micronutrients. Orange coloured values indicate higher selectivity of a micronutrient for a country compared to the other three micronutrients, and blue the opposite. Within-country divergences that are masked in Figure 3 are shown here. Text values inside boxes indicate selectivity for micronutrient Reference Micronutrient Intake (a) and mass (b) whereas colours represent the difference between selectivity values for each micronutrient and the mean across all micronutrients, per country. To highlight trade-offs between micronutrients, countries are ordered by the deviation in selectivity between micronutrients separately in panels a and b, and separately in each region.

( $MN_{\text{fished}}$ ), and the randomised null pool of species ( $MN_{\text{null}}$ ). The quantitative magnitude and qualitative direction of micronutrient optimality and selectivity among countries in our main findings were robust to under-sampling issues when we simulated a decreased sampling to only 50% of the species in any of the species pools (Tables S1 and S2). In addition, evaluating selectivity when defining the fished species pool using a family-level classification (Table S3) and using local scuba transects rather than species distribution and biomass models for defining regional species pools (Tables S4 and S5) revealed

qualitatively consistent results although sample sizes are greatly reduced due to fewer countries having suitable data.

## 4 | DISCUSSION

Food insecurity and malnutrition have substantial negative impacts on human health. Small-scale fisheries in marine and inland areas already benefit population health by supporting half a billion people

economically and nutritionally—especially people outside formal markets (FAO et al., 2023). Biodiverse ecological systems can further contribute to food security by providing more diverse micronutrient pools. Yet for multi-species tropical reef fisheries, our results reveal the need for a better understanding of the mismatch between wild-potential versus harvested micronutrients. Overall, this finding supports others in reporting low realisation of micronutrient-sensitive food policies in agricultural and marine food systems and little recognition of the role of biodiverse food systems in human health (Lachat et al., 2017; Ruel et al., 2013; Vianna et al., 2020).

Fish are a valuable micronutrient source, and, as such, policies to increase consumption can improve human health. Fish from small-scale fisheries are increasingly advocated as important to help address micronutrient deficiencies, which are not declining in line with sustainable development goals. For example, approximately 320 million more people in 2020 are without reliable access to food compared with 2019 (FAO et al., 2023). The health benefits of fish consumption include lower rates of childhood stunting, higher birth weight and reduced risk of cardiovascular disease (Headey et al., 2018; Muthayya et al., 2009). Yet, while closing micronutrient gaps by increasing consumption of micronutrient-rich fishes has been shown to improve the nutritional quality of food sources, our results highlight new challenges in quantifying and comparing fisheries and ecosystem nutrients that should be further investigated to address health goals through fisheries (Bogard et al., 2015; Thilsted et al., 2016). Indeed, data gaps and discrepancies are associated with an increased likelihood of failing to meet policy targets (Jacob, 2017). In addition, many fisheries are already overexploited, leading to potential practical challenges in sustainably increasing fisheries catch to obtain micronutrients (MacNeil et al., 2015). Promisingly, the positive selectivity of micronutrient mass of fisheries in many countries indicates that countries often fished the species with relatively high micronutrient mass in the ecosystem (Figure 3). We also found some countries had low selectivity for micronutrients. Empirical data can indicate some fisheries capture a highly biased portion of available fish biomass, such as spearfishing in the Moorea, French Polynesia, which could lead to the micronutrient mismatches between availability and catch that we observe here (Rassweiler et al., 2020). However, optimising for micronutrient mass may not be necessary or feasible in non-selective reef fisheries, and, as such, retention and use of available micronutrients may be the only option (Hicks et al., 2021). Policies focussing on the use of available micronutrient mass through targeting access, redistribution and consumption of fish are therefore well poised to capitalise on the already selective fisheries for micronutrient mass (Koehn et al., 2022). However, the use of available micronutrient mass must acknowledge the trade-offs we reveal here between micronutrients that benefit health in different ways (Figure 4). One proposed solution to such trade-offs is evaluating locally available non-fish micronutrient sources, and, as such, a food system perspective beyond fisheries is required, as indicated by the trade-offs revealed herein (Halpern et al., 2019).

Broadly, interventions to improve micronutrient intake from biodiverse food sources include assessing micronutrient availability in

terms of biomass and species compositions, improving access via price and market distribution, and increasing awareness via food choices. It may be difficult to choose between these interventions if insufficient information exists on the in situ biodiversity that determines micronutrients available for consumption. To date, nutritional content of non-commercialised fishes in human food systems is not well-considered, and disaggregated species-specific data would improve the design of micronutrient-sensitive policies (Halpern et al., 2019). Our results highlight how catch under-reporting and under-sampling of expected biodiversity can impact micronutrient content estimates provided by fisheries and biodiversity models or surveys (which we jointly compare here), leading to a relatively weak correlation among these data sources. Further comparison and ground-truthing of the mismatch between potentially available and caught micronutrients in natural systems will benefit potential decisions between micronutrient-sensitive policy levers. More broadly, localised surveys and data integration across socio-economic and ecological systems are a key knowledge gap in how small-scale fisheries can contribute to health outcomes to better achieve sustainable development goals (FAO et al., 2023).

Our findings raise a key question: why are data sources incomplete to address nutritional mismatches between ecosystems and fisheries? Fisheries monitoring continues to perceive fisheries through an economic commodity rather than a public health lens—which in turn affects available fisheries data compiled by national and international organisations. This fundamental economic framing leads to weak consideration and incorporation of nutrition in the managing and targeting of fish species and stocks (Driscoll & Chan, 2022; Koehn et al., 2022), and can even lead to negative micronutrient yields (Driscoll & Chan, 2022; Willer et al., 2022). The fact that fisheries policies under-prioritise nutritional resources in fisheries may explain the large gaps in nutritional optimality and selectivity observed here. If small-scale fisheries catches are not perceived as a fundamental human health resource, then economic and policy incentives for their capture and domestic retention are weak because these fish are relatively cheap (Robinson, Mills, et al., 2022), and instead fish may be sold for fishmeal or traded internationally. Indeed, a recent global study revealed trade as a major mediator of micronutrient supply (Nash et al., 2022). There are potential health costs if economic incentives divert fish away from human consumption (Marinda et al., 2018), so viewing fisheries through a public health lens and addressing associated incentive structures is critical to manage fisheries for human health.

Trade-offs emerge between different goals for food supply systems, such as: economic development goals around income generation; sustainable development goals around food supply, human health, and nutrition; and environmental goals around reducing biodiversity loss and recovering depleted populations. These trade-offs are critical to consider if modifying food systems towards any one goal (Béné et al., 2016; Koehn et al., 2022). One key trade-off could be that micronutrient goals can only be met through wide-scale depletion of species diversity. Importantly, our simulations suggest that more nutritionally rich species are available for the

same species richness during capture, which implies low conflict between different sustainability targets. This is especially true when targeting micronutrient mass because a few species often dominate communities in terms of biomass (Figure S4). However, targeting micronutrient mass leads to the selection of higher biomass species which could lead to further total reef fish biomass and abundance depletion and potential reductions in dimensions of biodiversity such as genetic diversity and ecosystem stability (Benkwitt et al., 2020; Cinner et al., 2020; Leffler et al., 2012). Given the expected increase in demand for seafood to feed and nourish a global population approaching 10 billion people by 2050, multiple sustainability goals could be better achieved if the trade-offs explored here are considered more deeply than at present (Costello et al., 2020).

Our work highlights two approaches to move towards sustainability of small-scale aquatic food systems: (i) increase the limited information on micronutrient content and species-level diversity, and (ii) develop micronutrient-orientated policies to maximise micronutrient mass. We took the perspective that biodiversity forms a reservoir, or pool, of available micronutrients and focussed on the potential of a modelled system, rather than what is reported as currently fished (Cantwell-Jones et al., 2022; Powell et al., 2015). Species with different ecological traits have distinct micronutrient profiles that are complementary, therefore more biodiverse human diets are expected to increase the nutritional content that is consumed (Bernhardt & O'Connor, 2021). Indeed, micronutrient adequacy can be more strongly related to species richness in the human diet than the consumption of adequate calories or multiple food groups (Lachat et al., 2017). As such, managing fisheries to obtain maximum micronutrient mass has been advocated (Robinson, Nash, et al., 2022). However, our work reveals that estimates of micronutrients caught are likely inadequate at present to assess micronutrient mass optimisations completely. This problem is also highlighted by a recent global report on small-scale fisheries where only 63% of marine and 40% of inland fisheries catches are identified to family level, not to mention the vast proportion unidentified to species level (FAO et al., 2023). Resolving data to the species level is essential to link species identities to the variation in life history and feeding ecology that contributes to the micronutrient composition of individuals. Improvements in taxonomic resolution of catch data and better biodiversity inventories are therefore required to design micronutrient-oriented fisheries policies.

We observed trade-offs in micronutrient selection which may challenge effective fisheries policies to change micronutrient supply. We reveal these trade-offs to be specific to each country's fisheries. In general, selecting iron and calcium does not necessarily lead to high levels of all micronutrients, because zinc and vitamin A's RNI were decoupled from iron and calcium's RNI (Bernhardt & O'Connor, 2021). Ideally, fishers could selectively target an optimal yet minimal set of high-micronutrient species with a complementary micronutrient profile, but this strategy comes with problems (Bell et al., 2009). Small-scale fisheries are often multi-species with non-selective methods, have low capital investment and individual

fishers use few gear types that select a consistent subset of the community (Dalzell et al., 1996; Selgrath et al., 2018). In reality, the most impactful interventions may be in actions that: (i) reduce and eliminate harmful subsidies to large-scale fisheries that outcompete small-scale fisheries, (ii) financially support well-managed sustainable small-scale fisheries that provide fish with higher micronutrient content to local communities, (iii) reduce market incentives that facilitate the export of local catch or fishmeal processing, (iv) increase the use of micronutrient-rich bycatch, (v) reduce micronutrient loss through handling, processing and storage of fish, (vi) increase the awareness of the health benefits of fish for infants, children and mothers, and (vi) rebuild collapsed and overfished stocks (Andreoli et al., 2023; FAO et al., 2023; Hicks & McClanahan, 2012; Pauly & Zeller, 2016; Schuhbauer et al., 2017; Selgrath et al., 2018; Sumaila et al., 2019). Yet, our results also indicate that many of the above actions would still require or benefit from more robust species-specific country-level data and biodiversity assessments. It must also be acknowledged that any micronutrient-sensitive fisheries policy must focus on micronutrients that have high human physiological importance, with established micronutrient deficits, and where micronutrients have high concentrations in fish relative to other dietary sources (Zamborain-Mason et al., 2023).

#### 4.1 | Limitations

We attempted to inventory biodiversity to first establish the hypothetically available biodiversity pool that could be fished. This ecosystem-based perspective attempts to quantify the capture of micronutrients by fisheries relative to the availability in the wider ecosystem (Robinson, Nash, et al., 2022), allowing our definitions of optimality and selectivity. Here, we aimed to provide a first broad overview of micronutrient optimality and selectivity using comparable methods across different countries. We therefore chose the approach of using models at large spatial scales to define our available species pool, and the country-level *Sea Around Us* data to define our fished species pool. Species distribution and biomass models would further benefit from the inclusion of local-scale environmental variables, for example, using local benthic and pelagic habitat variables such as coral and algae cover, water turbidity, wave exposure and terrestrial run-off (Lyons et al., 2024; Violet et al., 2024). While we did not aim to model intra-country variation in species presence and biomass, doing so is an important future step that could provide a more accurate comparison between fisheries catch and source pools at smaller spatial scales. Furthermore, here we consider standing biomass but determining spatial drivers of ecosystem productivity, as a rate, would provide a better estimate of micronutrient availability through time (Morais et al., 2020; Robinson et al., 2023). Likewise, the *Sea Around Us* data as well as the data reported by countries to the FAO on which *Sea Around Us* data are based (Zeller et al., 2016) would benefit immensely from better species-specific data being collected and reported on by the contributing countries. Further, accounting for intraspecific variation in species micronutrient

compositions, for example, driven by body size or local ecological conditions, could improve micronutrient concentration estimates. Our work provides only a heuristic exercise that is suboptimal for country-level or local applications and policy reform but hints at a large potential for micronutrient optimality and selectivity to be further investigated using better taxonomically resolved biodiversity and local fisheries and supply chain information (Thilsted et al., 2016). Recent reports from international bodies support this conclusion by highlighting the localised nature of wild-fish food supply systems that support micronutrient accessibility and economic benefits for people living nearer to fisheries (FAO et al., 2023).

The optimality and selectivity gaps identified here arise at least partly because the *Sea Around Us* data remain a conservative estimate of tonnage and species diversity landed, even though it is more comprehensive than the officially reported data as presented by the FAO on behalf of countries (Pauly & Zeller, 2016). As such, we likely underestimate  $MN_{\text{fished}}$  as well as optimality and selectivity, compared with reality. Additionally, we would underestimate  $MN_{\text{max}}$  if species are missing or are under-represented globally in fisheries records, which would then underestimate the potential to extract fish and thus micronutrients from ecosystems. Furthermore, baselines of historically available or more common species that were depleted before current fishery monitoring efforts developed could also impact our findings. Our sensitivity tests suggested only a modest effect of under-sampling. However, it is important to note that we could only sample species from existing data, which might result in a biased view of catch records for or against certain species and functional groups. In interpreting this work, we must remember a multitude of reef fish are caught and eaten and this is only partially represented in our data (Dalzell et al., 1996; Mbaru et al., 2020; Zeller et al., 2015). Additionally, accounting for the effect of food processing and preparation on micronutrient content, as well as the micronutrient contributions from non-muscle portions that are often consumed, would further refine our micronutrient estimates. Our perspective that regional biodiversity forms a reservoir of nutrients will have the greatest impact when combined with high-quality local catch records that contain fewer false negatives. A large proportion of catch data is not resolved to species level, which is probably the main limitation in applying the optimality and selectivity metrics defined here, but also a key result revealed by comparison across information sources.

## 5 | CONCLUSIONS

Overall, we report that reef fisheries have a high availability of micronutrients that already contribute substantially to health and nutrition. More robust species-level localised catch data would benefit micronutrient-sensitive fisheries policies and address the currently low selectivity for the most nutritious species within the ecosystem. Our analysis focussed on the Global South but the challenges outlined here are also prevalent across Global North fisheries, thus likely exist independently from economic resources available to monitor fisheries and biodiversity (Driscoll & Chan, 2022,

2023; Willer et al., 2022). We thus support recent international calls to recognise wild-capture fisheries as a critical source of nutrition and one pillar of sustainable development (FAO et al., 2023). Efforts to shift fisheries policies must be cognisant of historical and ongoing declines in biomass, changes in biodiversity and ecosystem function on coral reefs that are undermining the long-term contributions of these ecosystems to people beyond fisheries (Eddy et al., 2021; Edgar et al., 2014; Lefcheck et al., 2021). It will be a challenge for future food policies to balance potential biodiversity losses and human well-being benefits, and a lack of species-level knowledge in fisheries and their contributions to nutrition only makes this harder. Use of local knowledge involving participatory processes and knowledge co-production should help ensure policy change is equitable (Cinner et al., 2019; van Kerkhoff & Lebel, 2015). The decoupling between nutrients in ecosystems and in fisheries catches indicates that social, economic, and biodiversity policies are not yet shaped around nutrients, but this is key to fostering a sustainable and healthy planet for both people and nature.

## AUTHOR CONTRIBUTIONS

Conor Waldoock, Eva Maire, David Mouillot and Loic Pellissier conceived the ideas and designed the methodology, Vania Andreoli, Maria Beger, David A. Feary, Sebastian C. A. Ferse, Andrew Hoey, Maria Lourdes Palomares, Santiago de la Puente, Mark Tupper, Shaun Wilson, Laure Velez, Dirk Zeller collected or supported data collection and distribution, Conor Waldoock analysed the data and led the writing of the manuscript with input from Eva Maire, David Mouillot, Loic Pellissier, Camille Albouy, Sebastian C. A. Ferse, Vania Andreoli and Dirk Zeller. David Mouillot, Loic Pellissier and Camille Albouy led funding acquisition. All authors contributed critically to the manuscript and gave final approval for publication.

## AFFILIATIONS

<sup>1</sup>Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland; <sup>2</sup>Unit of Land Change Science, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; <sup>3</sup>Division of Aquatic Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland; <sup>4</sup>Department of Fish Ecology and Evolution, Center for Ecology, Evolution and Biogeochemistry, Eawag—Swiss Federal Institute of Aquatic Science and Technology, Kastanienbaum, Switzerland; <sup>5</sup>Lancaster Environment Centre, Lancaster University, Lancaster, UK; <sup>6</sup>MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Montpellier, France; <sup>7</sup>Sea Around Us—Indian Ocean, School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia; <sup>8</sup>Faculty of Biological Sciences, School of the Environment, University of Leeds, Leeds, UK; <sup>9</sup>Centre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, Queensland, Australia; <sup>10</sup>ENTROPIE, Univ. La Réunion, IRD, IFREMER, Univ. Nouvelle-Calédonie, CNRS, CUFR Mayotte, Saint-Denis, Réunion, France; <sup>11</sup>Global Institute of Sustainability and Innovation, Center for Biodiversity Outcomes, Arizona State University, Tempe, Arizona, USA; <sup>12</sup>General Organization for Conservation of Coral Reefs and Turtles, Red Sea, Jeddah, Saudi Arabia; <sup>13</sup>Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany; <sup>14</sup>Marine Ecology Department, Faculty of Biology and Chemistry, University of Bremen, Bremen, Germany; <sup>15</sup>Faculty of Fisheries and Marine Sciences, Bogor Agricultural University (IPB), Bogor, Indonesia; <sup>16</sup>Australian Research Council Centre of Excellence for Coral Reef Studies and College of Science and Engineering, James Cook University, Townsville, Queensland, Australia; <sup>17</sup>Department of Biology and Marine Biology, Center for Marine



Science, University of North Carolina Wilmington, Wilmington, USA; <sup>18</sup>The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, South Australia, Australia; <sup>19</sup>Laboratoire de Sciences Animales et Halieutique, Unité de Recherche en Aquaculture et Gestion des Pêches, Ecole d'Aquaculture, Université Nationale d'Agriculture, Porto-Novo, Benin; <sup>20</sup>Sea Around Us Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada; <sup>21</sup>Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada; <sup>22</sup>Norwegian Institute for Water Research, Oslo, Norway; <sup>23</sup>Centre for National Parks and Protected Areas, Institute of Science and Environment, University of Cumbria, Ambleside, UK; <sup>24</sup>Terra Nexus, Dubai, United Arab Emirates; <sup>25</sup>Department of Biodiversity, Conservation and Attractions, Perth, Western Australia, Australia; <sup>26</sup>Oceans Institute, University of Western Australia, Crawley, Western Australia, Australia and <sup>27</sup>Department of Nutrition, Harvard T.H. Chan School of Public Health, Boston, Massachusetts, USA

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All data to reproduce the findings in the manuscript are provided at <https://doi.org/10.6084/m9.figshare.26347909> and code is archived at <https://github.com/cwaldock1/reef-futures-nutrient>.

## ORCID

Conor Waldock  <https://orcid.org/0000-0002-2818-9859>

Vania Andreoli  <https://orcid.org/0000-0001-9163-011X>

Katie L. Cramer  <https://orcid.org/0000-0001-8760-180X>

Andrew Hoey  <https://orcid.org/0000-0002-4261-5594>

Nicolas Loiseau  <https://orcid.org/0000-0002-2469-1980>

M. Aaron MacNeil  <https://orcid.org/0000-0001-8406-325X>

Matthew McLean  <https://orcid.org/0000-0001-6518-6043>

Camille Mellin  <https://orcid.org/0000-0002-7369-2349>

Santiago de la Puente  <https://orcid.org/0000-0002-6189-9596>

Dirk Zeller  <https://orcid.org/0000-0001-7304-4125>

Loïc Pellissier  <https://orcid.org/0000-0002-2289-8259>

## REFERENCES

- Afshin, A., Sur, P. J., Fay, K. A., Cornaby, L., Ferrara, G., Salama, J. S., Mullany, E. C., Abate, K. H., Abbafati, C., Abebe, Z., Afarideh, M., Aggarwal, A., Agrawal, S., Akinemiju, T., Alahdab, F., Bacha, U., Bachman, V. F., Badali, H., Badawi, A., ... Murray, C. J. L. (2019). Health effects of dietary risks in 195 countries, 1990–2017: A systematic analysis for the global burden of disease study 2017. *The Lancet*, 393, 1958–1972.
- Andreoli, V., Meeuwig, J. J., Skerritt, D. J., Schuhbauer, A., Sumaila, U. R., & Zeller, D. (2023). Fisheries subsidies exacerbate inequities in accessing seafood nutrients in the Indian Ocean. *npj Ocean Sustainability*, 2, 1–9.
- Angkasa, D., Tambunan, V., Khusun, H., Witjaksono, F., & Agustina, R. (2017). Inadequate dietary  $\alpha$ -linolenic acid intake among Indonesian pregnant women is associated with lower newborn weights in urban Jakarta. *Asia Pacific Journal of Clinical Nutrition*, 26, S9–S18.
- Auber, A., Waldock, C., Maire, A., Goberville, E., Albouy, C., Algar, A. C., McLean, M., Brind'Amour, A., Green, A. L., Tupper, M., Vigliola, L., Kaschner, K., Kesner-Reyes, K., Beger, M., Tjiputra, J., Toussaint, A., Violle, C., Mouquet, N., Thuiller, W., & Mouillot, D. (2022). A functional vulnerability framework for biodiversity conservation. *Nature Communications*, 13, 4774.
- Barneche, D. R., Rezende, E. L., Parravicini, V., Maire, E., Edgar, G. J., Stuart-Smith, R. D., Arias-González, J. E., Ferreira, C. E. L., Friedlander, A. M., Green, A. L., Luiz, O. J., Rodriguez-Zaragoza, F. A., Vigliola, L., Kulbicki, M., & Floeter, S. R. (2019). Body size, reef area and temperature predict global reef-fish species richness across spatial scales. *Global Ecology and Biogeography*, 28, 315–327.
- Beal, T., Massiot, E., Arsenault, J. E., Smith, M. R., & Hijmans, R. J. (2017). Global trends in dietary micronutrient supplies and estimated prevalence of inadequate intakes. *PLoS One*, 12, e0175554.
- Bell, J. D., Kronen, M., Vunisea, A., Nash, W. J., Keeble, G., Demmke, A., Pontifex, S., & Andréfouët, S. (2009). Planning the use of fish for food security in the Pacific. *Marine Policy*, 33, 64–76.
- Béné, C., Arthur, R., Norbury, H., Allison, E. H., Beveridge, M., Bush, S., Campling, L., Leschen, W., Little, D., Squires, D., Thilsted, S. H., Troell, M., & Williams, M. (2016). Contribution of fisheries and aquaculture to food security and poverty reduction: Assessing the current evidence. *World Development*, 79, 177–196.
- Benkwitt, C. E., Wilson, S. K., & Graham, N. A. J. (2020). Biodiversity increases ecosystem functions despite multiple stressors on coral reefs. *Nature Ecology & Evolution*, 4, 919–926.
- Bernhardt, J. R., & O'Connor, M. I. (2021). Aquatic biodiversity enhances multiple nutritional benefits to humans. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e1917487118.
- Boettiger, C., Lang, D. T., & Wainwright, P. C. (2012). Rfishbase: Exploring, manipulating and visualizing FishBase data from R. *Journal of Fish Biology*, 81, 2030–2039.
- Bogard, J. R., Hother, A.-L., Saha, M., Bose, S., Kabir, H., Marks, G. C., & Thilsted, S. H. (2015). Inclusion of small indigenous fish improves

- nutritional quality during the first 1000 days. *Food and Nutrition Bulletin*, 36, 276–289.
- Budge, S. M., Iverson, S. J., Bowen, W. D., & Ackman, R. G. (2002). Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 886–898.
- Cantwell-Jones, A., Ball, J., Collar, D., Diazgranados, M., Douglas, R., Forest, F., Hawkins, J., Howes, M. J. R., Ulian, T., Vaitla, B., & Pironon, S. (2022). Global plant diversity as a reservoir of micronutrients for humanity. *Nature Plants*, 8, 225–232.
- Cashion, T., Le Manach, F., Zeller, D., & Pauly, D. (2017). Most fish destined for fishmeal production are food-grade fish. *Fish and Fisheries*, 18, 837–844.
- Cheung, W. W. L., Maire, E., Oyinlola, M. A., Robinson, J. P. W., Graham, N. A. J., Lam, V. W. Y., MacNeil, M. A., & Hicks, C. C. (2023). Climate change exacerbates nutrient disparities from seafood. *Nature Climate Change*, 13, 1242–1249.
- Chuenpagdee, R., Liguori, L., Palomares, M. L. D., & Pauly, D. (2006). *Bottom-up, global estimates of small-scale marine fisheries catches*. Fisheries Centre Research reports, 14. Fisheries Centre, University of British Columbia.
- Cinner, J. E., Lau, J. D., Bauman, A. G., Feary, D. A., Januchowski-Hartley, F. A., Rojas, C. A., Barnes, M. L., Bergseth, B. J., Shum, E., Lahari, R., Ben, J., & Graham, N. A. J. (2019). Sixteen years of social and ecological dynamics reveal challenges and opportunities for adaptive management in sustaining the commons. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 26474–26483.
- Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan, T., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A. S., Gurney, G. G., Feary, D. A., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., ... Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences of the United States of America*, 115, E6116–E6125.
- Cinner, J. E., Zamborain-Mason, J., Gurney, G. G., Graham, N. A. J., MacNeil, M. A., Hoey, A. S., Mora, C., Villéger, S., Maire, E., McClanahan, T. R., Maina, J. M., Kittinger, J. N., Hicks, C. C., D'agata, S., Huchery, C., Barnes, M. L., Feary, D. A., Williams, I. D., Kulbicki, M., ... Mouillot, D. (2020). Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science*, 368, 307–311.
- Cisneros-Montemayor, A. M., Pauly, D., Weatherdon, L. V., & Ota, Y. (2016). A global estimate of seafood consumption by coastal indigenous peoples. *PLoS One*, 11, e0166681.
- Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M. Á., Free, C. M., Froehlich, H. E., Golden, C. D., Ishimura, G., Maier, J., Macadam-Somer, I., Mangin, T., Melnychuk, M. C., Miyahara, M., de Moor, C. L., Naylor, R., Nøstbakken, L., Ojea, E., O'Reilly, E., Parma, A. M., ... Lubchenco, J. (2020). The future of food from the sea. *Nature*, 588, 95–100.
- Dallas, T. A., & Santini, L. (2020). The influence of stochasticity, landscape structure and species traits on abundant-centre relationships. *Ecography*, 43, 1341–1351.
- Dalzell, P., Adams, T. J. H., & Polunin, N. V. C. (1996). Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: An Annual Review*, 34, 395–531.
- Derrick, B., Burns, K., Zhu, A., Andreoli, V., Zeller, D., & Pauly, D. (2023). Small-scale fisheries catch and fishing effort in the Socotra Archipelago (Yemen) between 1950 and 2019. *Frontiers in Marine Science*, 10, 1201661.
- Dormann, C. F., Calabrese, J. M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoň, K., Beale, C. M., Ciuti, S., Elith, J., Gerstner, K., Guelat, J., Keil, P., Lahoz-Monfort, J. J., Pollock, L. J., Reineking, B., Roberts, D. R., Schröder, B., Thuiller, W., Warton, D. I., ... Hartig, F. (2018). Model averaging in ecology: A review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs*, 88, 485–504.
- Driscoll, J., & Chan, K. M. A. (2022). Net negative nutrient yields in a bait-consuming fishery. *Environmental Research Letters*, 17, 084024.
- Driscoll, J., & Chan, K. M. A. (2023). Assessing fisheries nutrient yields: The Northwest Atlantic, 1950–2014. *Ambio*, 52, 271–284.
- Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, 4, 1278–1285.
- Edgar, G. J., Cooper, A., Baker, S. C., Barker, W., Barrett, N. S., Becerro, M. A., Bates, A. E., Brock, D., Ceccarelli, D. M., Clausius, E., Davey, M., Davis, T. R., Day, P. B., Green, A., Griffiths, S. R., Hicks, J., Hinojosa, I. A., Jones, B. K., Kininmonth, S., ... Stuart-Smith, R. D. (2020). Establishing the ecological basis for conservation of shallow marine life using Reef Life Survey. *Biological Conservation*, 252, 108855.
- Edgar, G. J., & Stuart-Smith, R. D. (2014). Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, 1, 140007.
- Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. C., Försterra, G., Galván, D. E., Irigoyen, A. J., Kushner, D. J., ... Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506, 216–220.
- FAO, Duke University, & WorldFish. (2023). *Illuminating Hidden Harvests—The contributions of small-scale fisheries to sustainable development*.
- Farmery, A. K., Allison, E. H., Andrew, N. L., Troell, M., Voyer, M., Campbell, B., Eriksson, H., Fabin, M., Song, A. M., & Steenbergen, D. (2021). Blind spots in visions of a “blue economy” could undermine the ocean's contribution to eliminating hunger and malnutrition. *One Earth*, 4, 28–38.
- Froese, R., & Pauly, D. (2024). *FishBase*. [www.fishbase.org](http://www.fishbase.org)
- Gao, J. (2017). Downscaling global spatial population projections from 1/8-degree to 1-km grid cells. NCAR Technical Notes, NCAR/TN-537+STR, National Center for Atmospheric Research.
- Gearty, W., & Chamberlain, S. (2022). *rredlist: 'IUCN' Red List Client*. R package version 0.7.1. <https://CRAN.R-project.org/package=rredlist>
- Golden, C. D., Allison, E. H., Cheung, W. W. L., Dey, M. M., Halpern, B. S., McCauley, D. J., Smith, M., Vaitla, B., Zeller, D., & Myers, S. S. (2016). Nutrition: Fall in fish catch threatens human health. *Nature*, 534, 317–320.
- Halpern, B. S., Cottrell, R. S., Blanchard, J. L., Bouwman, L., Froehlich, H. E., Gephart, J. A., Sand Jacobsen, N., Kuempel, C. D., McIntyre, P. B., Metian, M., Moran, D. D., Nash, K. L., Többen, J., & Williams, D. R. (2019). Putting all foods on the same table: Achieving sustainable food systems requires full accounting. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 18152–18156.
- Headey, D., Hirvonen, K., & Hoddinott, J. (2018). Animal sourced foods and child stunting. *American Journal of Agricultural Economics*, 100, 1302–1319.
- Hicks, C. C., Cohen, P. J., Graham, N. A. J., Nash, K. L., Allison, E. H., D'Lima, C., Mills, D. J., Roscher, M., Thilsted, S. H., Thorne-Lyman, A. L., & MacNeil, M. A. (2019). Harnessing global fisheries to tackle micronutrient deficiencies. *Nature*, 574, 95–98.
- Hicks, C. C., Graham, N. A. J., Maire, E., & Robinson, J. P. W. (2021). Secure local aquatic food systems in the face of declining coral reefs. *One Earth*, 4, 1214–1216.
- Hicks, C. C., & McClanahan, T. R. (2012). Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, sea-grass and coral reef fishery. *PLoS One*, 7, e36022.
- Jacob, A. (2017). Mind the gap: Analyzing the impact of data gap in millennium development goals' (MDGs) indicators on the progress toward MDGs. *World Development*, 93, 260–278.

- Jones, B., & O'Neill, B. C. (2016). Spatially explicit global population scenarios consistent with the Shared Socioeconomic Pathways. *Environmental Research Letters*, *11*, 084003.
- Kawarazuka, N., & Béné, C. (2011). The potential role of small fish species in improving micronutrient deficiencies in developing countries: Building evidence. *Public Health Nutrition*, *14*, 1927–1938.
- Koehn, J. Z., Allison, E. H., Villeda, K., Chen, Z., Nixon, M., Crigler, E., Zhao, L., Chow, M., Vaitla, B., Thilsted, S. H., Scholtens, J., Hicks, C. C., & Andrew, N. (2022). Fishing for health: Do the world's national policies for fisheries and aquaculture align with those for nutrition? *Fish and Fisheries*, *23*, 125–142.
- Kulbicki, M., Parravicini, V., Bellwood, D. R., Arias-González, E., Chabanet, P., Floeter, S. R., Friedlander, A., McPherson, J., Myers, R. E., Vigliola, L., & Mouillot, D. (2013). Global biogeography of reef fishes: A hierarchical quantitative delineation of regions. *PLoS One*, *8*, e81847.
- Lachat, C., Raneri, J., Smith, K., Kolsteren, P., Van Damme, P., Verzelen, K., Penafiel, D., Vanhove, W., Kennedy, G., Hunter, D., Oduor, F., Ntandou-Bouzitou, G., De Baets, B., Ratnasekera, D., The, K., Remans, R., & Termote, C. (2017). Dietary species richness as a measure of food biodiversity and nutritional quality of diets. *Proceedings of the National Academy of Sciences*, *115*, 201709194. <https://doi.org/10.1073/pnas.1709194115>
- Lefcheck, J. S., Edgar, G. J., Stuart-Smith, R. D., Bates, A. E., Waldock, C., Brandl, S. J., Kininmonth, S., Ling, S. D., Duffy, J. E., Rasher, D. B., & Agrawal, A. F. (2021). Species richness and identity both determine the biomass of global reef fish communities. *Nature Communications*, *12*, 6875.
- Leffler, E. M., Bullaughey, K., Matute, D. R., Meyer, W. K., Ségurel, L., Venkat, A., Andolfatto, P., & Przeworski, M. (2012). Revisiting an old riddle: What determines genetic diversity levels within species? *PLoS Biology*, *10*, e1001388.
- Liu, G., Heron, S. F., Eakin, C. M., Muller-Karger, F. E., Vega-Rodriguez, M., Guild, L. S., de la Cour, J., Geiger, E., Skirving, W., Burgess, T., Strong, A., Harris, A., Maturi, E., Ignatov, A., Sapper, J., Li, J., & Lynds, S. (2014). Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA coral reef watch. *Remote Sensing*, *6*, 11579–11606.
- Lyons, M. B., Murray, N. J., Kennedy, E. V., Kovacs, E. M., Castro-Sanguino, C., Phinn, S. R., Acevedo, R. B., Alvarez, A. O., Say, C., Tudman, P., Markey, K., Roe, M., Canto, R. F., Fox, H. E., Bambic, B., Lieb, Z., Asner, G. P., Martin, P. M., Knapp, D. E., ... Roelfsema, C. M. (2024). New global area estimates for coral reefs from high-resolution mapping. *Cell Reports Sustainability*, *1*, 100015.
- MacNeil, M. A., Graham, N. A. J., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., Newman, S., Friedlander, A. M., Jupiter, S., Polunin, N. V. C., & McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, *520*, 341–344.
- Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., & Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters*, *19*, 351–360.
- Maire, E., Graham, N. A. J., MacNeil, M. A., Lam, V. W. Y., Robinson, J. P. W., Cheung, W. W. L., & Hicks, C. C. (2021). Micronutrient supply from global marine fisheries under climate change and overfishing. *Current Biology*, *31*, 4132–4138.e3.
- Marinda, P. A., Genschick, S., Khayeka-Wandabwa, C., Kiwanuka-Lubinda, R., & Thilsted, S. H. (2018). Dietary diversity determinants and contribution of fish to maternal and under-five nutritional status in Zambia. *PLoS One*, *13*, e0204009.
- Mbaru, E. K., Graham, N. A. J., McClanahan, T. R., & Cinner, J. E. (2020). Functional traits illuminate the selective impacts of different fishing gears on coral reefs. *Journal of Applied Ecology*, *57*, 241–252.
- Mellin, C., Hicks, C. C., Fordham, D. A., Golden, C. D., Kjelleve, M., MacNeil, M. A., Maire, E., Mangubhai, S., Mouillot, D., Nash, K. L., Omukoto, J. O., Robinson, J. P. W., Stuart-Smith, R. D., Zamborain-Mason, J., Edgar, G. J., & Graham, N. A. J. (2022). Safeguarding nutrients from coral reefs under climate change. *Nature Ecology & Evolution*, *6*, 1808–1817.
- Menegotto, A., & Rangel, T. (2018). Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nature Communications*, *9*, 4713.
- Micha, R., Khatibzadeh, S., Shi, P., Andrews, K. G., Engell, R. E., Mozaffarian, D., & Global Burden of Diseases Nutrition and Chronic Diseases Expert Group (NutriCoDE). (2015). Global, regional and national consumption of major food groups in 1990 and 2010: A systematic analysis including 266 country-specific nutrition surveys worldwide. *BMJ Open*, *5*, e008705.
- Montes, E., Lefcheck, J. S., Guerra-Castro, E., Klein, E., & Kavanaugh, M. T. (2021). Optimizing large-scale biodiversity sampling effort: Toward an unbalanced survey design. *Oceanography*, *34*, 80–91.
- Morais, R. A., Connolly, S. R., & Bellwood, D. R. (2020). Human exploitation shapes productivity-biomass relationships on coral reefs. *Global Change Biology*, *26*, 1295–1305.
- Muthayya, S., Dwarkanath, P., Thomas, T., Ramprakash, S., Mehra, R., Mhaskar, A., Mhaskar, R., Thomas, A., Bhat, S., Vaz, M., & Kurpad, A. V. (2009). The effect of fish and omega-3 LCPUFA intake on low birth weight in Indian pregnant women. *European Journal of Clinical Nutrition*, *63*, 340–346.
- NASEM. (2017). *Dietary reference intakes tables and application*. National Academies of Sciences, Engineering and Medicine.
- Nash, K. L., MacNeil, M. A., Blanchard, J. L., Cohen, P. J., Farmery, A. K., Graham, N. A. J., Thorne-Lyman, A. L., Watson, R. A., & Hicks, C. C. (2022). Trade and foreign fishing mediate global marine nutrient supply. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, e2120817119.
- Pauly, D., & Charles, A. (2015). Counting on small-scale fisheries. *Science*, *347*, 242–243.
- Pauly, D., & Zeller, D. (2016). Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications*, *7*, 10244.
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*, 181–197.
- Powell, B., Thilsted, S. H., Ickowitz, A., Termote, C., Sunderland, T., & Herforth, A. (2015). Improving diets with wild and cultivated biodiversity from across the landscape. *Food Security*, *7*, 535–554.
- Rassweiler, A., Lauer, M., Lester, S. E., Holbrook, S. J., Schmitt, R. J., Madi Moussa, R., Munsterman, K. S., Lenihan, H. S., Brooks, A. J., Wencélius, J., & Claudet, J. (2020). Perceptions and responses of Pacific Island fishers to changing coral reefs. *Ambio*, *49*, 130–143.
- Righetti, D., Vogt, M., Gruber, N., Psomas, A., & Zimmermann, N. E. (2019). Global pattern of phytoplankton diversity driven by temperature and environmental variability. *Science Advances*, *5*, eaau6253.
- Robinson, J. P. W., Darling, E. S., Maire, E., Hamilton, M., Hicks, C. C., Jupiter, S. D., Aaron MacNeil, M., Mangubhai, S., McClanahan, T., Nand, Y., & Graham, N. A. J. (2023). Trophic distribution of nutrient production in coral reef fisheries. *Proceedings of the Royal Society B: Biological Sciences*, *290*, 20231601.
- Robinson, J. P. W., Maire, E., Bodin, N., Hempson, T. N., Graham, N. A. J., Wilson, S. K., MacNeil, M. A., & Hicks, C. C. (2022). Climate-induced increases in micronutrient availability for coral reef fisheries. *One Earth*, *5*, 98–108.
- Robinson, J. P. W., Mills, D. J., Asiedu, G. A., Byrd, K., Mancha Cisneros, M., Cohen, P. J., Fiorella, K. J., Graham, N. A. J., MacNeil, M. A., Maire, E., Mbaru, E. K., Nico, G., Omukoto, J. O., Simmance, F., & Hicks, C. C. (2022). Small pelagic fish supply abundant and affordable micronutrients to low- and middle-income countries. *Nature Food*, *3*, 1075–1084.
- Robinson, J. P. W., Nash, K. L., Blanchard, J. L., Jacobsen, N. S., Maire, E., Graham, N. A. J., MacNeil, M. A., Zamborain-Mason, J., Allison, E.



- H., & Hicks, C. C. (2022). Managing fisheries for maximum nutrient yield. *Fish and Fisheries*, 23, 800–811.
- Ruel, M. T., Alderman, H., & Maternal and Child Nutrition Study Group. (2013). Nutrition-sensitive interventions and programmes: How can they help to accelerate progress in improving maternal and child nutrition? *Lancet*, 382, 536–551.
- Schuhbauer, A., Chuenpagdee, R., Cheung, W., Greer, K., & Sumaila, R. (2017). How subsidies affect the economic viability of small-scale fisheries. *Marine Policy*, 82, 114–121.
- Selgrath, J. C., Gergel, S. E., & Vincent, A. C. J. (2018). Shifting gears: Diversification, intensification, and effort increases in small-scale fisheries (1950–2010). *PLoS One*, 13, e0190232.
- Sing Wong, A., Vrontos, S., & Taylor, M. L. (2022). An assessment of people living by coral reefs over space and time. *Global Change Biology*, 28, 7139–7153.
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience*, 57, 573–583.
- Sumaila, U. R., Ebrahim, N., Schuhbauer, A., Skerritt, D., Li, Y., Kim, H. S., Mallory, T. G., Lam, V. W. L., & Pauly, D. (2019). Updated estimates and analysis of global fisheries subsidies. *Marine Policy*, 109, 103695.
- Teh, L. S. L., Teh, L. C. L., & Sumaila, U. R. (2013). A global estimate of the number of coral reef fishers. *PLoS One*, 8, e65397.
- Thilsted, S. H., Thorne-Lyman, A., Webb, P., Bogard, J. R., Subasinghe, R., Phillips, M. J., & Allison, E. H. (2016). Sustaining healthy diets: The role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. *Food Policy*, 61, 126–131.
- Vaitla, B., Collar, D., Smith, M. R., Myers, S. S., Rice, B. L., & Golden, C. D. (2018). Predicting nutrient content of ray-finned fishes using phylogenetic information. *Nature Communications*, 9, 3742.
- van Kerkhoff, L. E., & Lebel, L. (2015). Coproductive capacities: Rethinking science-governance relations in a diverse world. *Ecology and Society*, 20, 14.
- VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist*, 174, 282–291.
- Vianna, G. M. S., Zeller, D., & Pauly, D. (2020). Fisheries and policy implications for human nutrition. *Current Environmental Health Reports*, 7, 161–169.
- Violet, C., Boyé, A., Dubois, S., Edgar, G. J., Oh, E. S., Stuart-Smith, R. D., & Marzloff, M. P. (2024). From local seafloor imagery to global patterns in benthic habitat states: Contribution of citizen science to habitat classification across latitudes (p. 2024.02.18.580891). *bioRxiv*. <https://doi.org/10.1101/2024.02.18.580891>
- Waldock, C., Stuart-Smith, R. D., Albouy, C., Cheung, W. W. L., Edgar, G. J., Mouillot, D., Tjiputra, J., & Pellissier, L. (2022). A quantitative review of abundance-based species distribution models. *Ecography*, 2022, e05694. <https://doi.org/10.1111/ecog.05694>
- Waldock, C., Stuart-Smith, R. D., Edgar, G. J., Bird, T. J., & Bates, A. E. (2019). The shape of abundance distributions across temperature gradients in reef fishes. *Ecology Letters*, 22, 685–696.
- Webb, T. J., Berghe, E. V., & O'Dor, R. (2010). Biodiversity's big wet secret: The global distribution of marine biological records reveals chronic under-exploration of the deep Pelagic Ocean. *PLoS One*, 5, e10223.
- Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F., & Grelle, C. E. V. (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, 40, 817–828.
- Willer, D. F., Robinson, J. P. W., Patterson, G. T., & Luyckx, K. (2022). Maximising sustainable nutrient production from coupled fisheries-aquaculture systems. *PLOS Sustainability and Transformation*, 1, e0000005.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., & NCEAS Predicting Species Distributions Working Group. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 14, 763–773.
- Zamborain-Mason, J., Viana, D., Nicholas, K., Jackson, E. D., Koehn, J. Z., Passarelli, S., Yoo, S. H., Zhang, A. W., Davin, H. C., Duggan, C. P., Schmidhuber, J., & Golden, C. D. (2023). A decision framework for selecting critically important nutrients from aquatic foods. *Current Environmental Health Reports*, 10, 172–183.
- Zeller, D., Ansell, M., Andreoli, V., & Heidrich, K. (2023). Trends in Indian Ocean marine fisheries since 1950: Synthesis of reconstructed catch and effort data. *Marine and Freshwater Research*, 74, 301–319.
- Zeller, D., Harper, S., Zylich, K., & Pauly, D. (2015). Synthesis of under-reported small-scale fisheries catch in Pacific Island waters. *Coral Reefs*, 34, 25–39.
- Zeller, D., Palomares, M. L. D., & Pauly, D. (2023). Global fisheries science documents human impacts on oceans: The Sea Around Us Serves Civil Society in the twenty-first century. *Annual Review of Marine Science*, 15, 147–165.
- Zeller, D., Palomares, M. L. D., Tavakolie, A., Ang, M., Belhabib, D., Cheung, W. W. L., Lam, V. W. Y., Sy, E., Tsui, G., Zylich, K., & Pauly, D. (2016). Still catching attention: Sea Around Us reconstructed global catch data, their spatial expression and public accessibility. *Marine Policy*, 70, 145–152.

## DATA SOURCES

- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43, 1223–1232.
- Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., Dornelas, M., & Schipper, A. M. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology & Evolution*, 4, 927–933.
- Asch, R. G., Cheung, W. W. L., & Reygondeau, G. (2018). Future marine ecosystem drivers, biodiversity, and fisheries maximum catch potential in Pacific Island countries and territories under climate change. *Marine Policy*, 88, 285–294.
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3, 327–338.
- Barneche, D. R., Rezende, E. L., Parravicini, V., Maire, E., Edgar, G. J., Stuart-Smith, R. D., Arias-González, J. E., Ferreira, C. E. L., Friedlander, A. M., Green, A. L., Luiz, O. J., Rodríguez-Zaragoza, F. A., Vigliola, L., Kulbicki, M., & Floeter, S. R. (2018). Body size, reef area and temperature predict global reef-fish species richness across spatial scales. *Global Ecology and Biogeography*, 28, 315–327.
- Boettiger, C., Lang, D. T., & Wainwright, P. C. (2012). rfishbase: Exploring, manipulating and visualizing FishBase data from R. *Journal of Fish Biology*, 81, 2030–2039.
- Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, 275, 73–77.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.
- Briggs, J. C., & Bowen, B. W. (2012). A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, 39, 12–30.
- Broennimann, O., Di Cola, V., & Guisan, A. (2020). *ecospat: Spatial ecology miscellaneous methods*. R package Version 3.1. <https://CRAN.R-project.org/package=ecospat>
- Brooks, M. E., Kristensen, K., Benthem, K. J., van Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.
- Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R. O., Wang, Z., & Zimmermann, N. E. (2020). Model complexity affects species distribution



- projections under climate change. *Journal of Biogeography*, 47(1), 130–142. <https://doi.org/10.1111/jbi.13734>
- Buisson, L., Thuiller, W., Casajus, N., Lek, S., & Grenouillet, G. (2010). Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, 16, 1145–1157.
- Burrows, M. T., Bates, A. E., Costello, M. J., Edwards, M., Edgar, G. J., Fox, C. J., Halpern, B. S., Hiddink, J. G., Pinsky, M. L., Batt, R. D., García Molinos, J., Payne, B. L., Schoeman, D. S., Stuart-Smith, R. D., & Poloczanska, E. S. (2019). Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change*, 9, 959–963.
- Cheung, W. W. L., Frölicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, G., Rodgers, K. B., Rykaczewski, R. R., Sarmiento, J. L., Stock, C., & Watson, J. R. (2016). Building confidence in projections of the responses of living marine resources to climate change. *ICES Journal of Marine Science*, 73, 1283–1296.
- Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan, T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A. S., Gurney, G. G., Feary, D. A., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., ... Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences of the United States of America*, 115(27), E6116–E6125. <https://doi.org/10.1073/pnas.1708001115>
- Dallas, T. A., & Hastings, A. (2018). Habitat suitability estimated by niche models is largely unrelated to species abundance. *Global Ecology and Biogeography*, 27, 1–9.
- Edgar, G. J., Barrett, N. S., & Morton, A. J. (2004). Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology*, 308, 269–290.
- Edgar, G. J., & Stuart-Smith, R. D. (2014). Systematic global assessment of reef fish communities by the reef life survey program. *Scientific Data*, 1, 140007.
- Evans, D. H., & Claiborne, J. B. (2008). Osmotic and ionic regulation in fishes. In K. W. Beyenbach & P. M. Piermarini (Eds.), *Osmotic and ionic regulation: Cells and animals* (pp. 295–366). CRC Press.
- Evans, D. H., Piermarini, P. M., & Choe, K. P. (2005). The multifunctional fish gill: Dominant site of gas exchange, osmoregulation, acid-base regulation, and excretion of nitrogenous waste. *Physiological Reviews*, 85, 97–177.
- Fasiolo, M., Goude, Y., Nedellec, R., Wood, S. N., & Edf, R. (2017). *Fast calibrated additive quantile regression*. <https://arxiv.org/abs/1707.03307>.
- Feeley, K. J., & Silman, M. R. (2011). Keep collecting: Accurate distribution modelling requires more collections than previously thought. *Diversity and Distributions*, 17, 1132–1140.
- Froese, R., & Pauly, D. (2000). *FishBase 2000: Concepts, design and data sources*. ICLARM.
- Glynn, P. W., & D'Croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs*, 8, 181–191.
- Heuer, R. M., & Grosell, M. (2014). Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology*, 307, R1061–R1084.
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., & Hatzioi, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–1742.
- Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, 546, 82–90.
- Kaschner, K., Kesner-reyes, K., Garilao, C., Segschneider, J., Rius-Barile, J., Rees, T., et al. (2019). *AquaMaps: Predicted range maps for aquatic species*. <https://www.aquamaps.org>
- Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 3, 18–22.
- Lindén, A., & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, 92, 1414–1421.
- Liu, G., Heron, S. F., Eakin, C. M., Muller-Karger, F. E., Vega-Rodriguez, M., Guild, L. S., De La Cour, J. L., Geiger, E. F., Skirving, W. J., Burgess, T. F. R., Strong, A. E., Harris, A., Maturi, E., Ignatov, A., Sapper, J., Li, J., & Lynds, S. (2014). Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA coral reef watch. *Remote Sensing*, 6(11), 11579–11606. <https://doi.org/10.3390/rs6111579>
- Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models. *Computational Statistics and Data Analysis*, 55, 2372–2387.
- Mellin, C., Matthews, S., Anthony, K. R. N., Brown, S. C., Caley, M. J., Johns, K. A., Osborne, K., Puotinen, M., Thompson, A., Wolff, N. H., Fordham, D. A., & MacNeil, M. A. (2019). Spatial resilience of the great barrier reef under cumulative disturbance impacts. *Global Change Biology*, 25, 2431–2445.
- Merow, C., Smith, M. J., Edwards, T. C., Jr., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., Wüest, R. O., Zimmermann, N. E., & Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, 37(12), 1267–1281. <https://doi.org/10.1111/ecog.00845>
- Mora, C., Aburto-Oropeza, O., Bocos, A. A., Ayotte, P. M., Banks, S., Bauman, A. G., Beger, M., Bessudo, S., Booth, D. J., Brokovich, E., Brooks, A., Chabanet, P., Cinner, J. E., Cortés, J., Cruz-Motta, J. J., Magaña, A. C., DeMartini, E. E., Edgar, G. J., Feary, D. A., ... Zapata, F. A. (2011). Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biology*, 9(4), e1000606. <https://doi.org/10.1371/journal.pbio.1000606>
- Neves, L. M., Teixeira-Neves, T. P., Pereira-Filho, G. H., & Araújo, F. G. (2016). The farther the better: Effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. *PLoS One*, 11, e0166679.
- Payne, N. L., Morley, S. A., Halsey, L. G., Smith, J. A., Stuart-Smith, R., Waldock, C., & Bates, A. E. (2021). Fish heating tolerance scales similarly across individual physiology and populations. *Communications Biology*, 4, 264.
- Phillips, S. J., Dudik, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19, 181–197.
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, 341, 1239–1242.
- Ploton, P., Mortier, F., Réjou-Méchain, M., Barbier, N., Picard, N., Rossi, V., Dormann, C., Cornu, G., Viennois, G., Bayol, N., Lyapustin, A., Gourlet-Fleury, S., & Péliissier, R. (2020). Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nature Communications*, 11, 1–11.
- Ready, J., Kaschner, K., South, A. B., Eastwood, P. D., Rees, T., Rius, J., Agbayani, E., Kullander, S., & Froese, R. (2010). Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, 221, 467–478.
- Righetti, D., Vogt, M., Gruber, N., Psomas, A., & Zimmermann, N. E. (2019). Global pattern of phytoplankton diversity driven by temperature and environmental variability. *Science Advances*, 5, 1–11.
- Roger, K. (2021). *quantreg: Quantile regression*. R package Version 5.83.
- Scornet, E. (2017). Tuning parameters in random forests. *ESAIM: Proceedings and Surveys*, 60, 144–162.
- Sunday, J. M., Fabricius, K. E., Kroeker, K. J., Anderson, K. M., Brown, N. E., Barry, J. P., Connell, S. D., Dupont, S., Gaylord, B., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday, P. L., Russell, B. D., Sanford, E., Thiagarajan, V., Vaughan, M. L. H., Widdicombe, S., & Harley, C. D. G. (2017). Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. *Nature Climate Change*, 7, 81–85.
- Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18, 944–953.
- Tessarolo, G., Rangel, T. F., Araújo, M. B., & Hortal, J. (2014). Uncertainty associated with survey design in species distribution models. *Diversity and Distributions*, 20, 1258–1269.
- Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Arroita, G. (2019). *block cv: An R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models*. *Methods in Ecology and Evolution*, 10, 225–232.
- VanDerWal, J., Shoo, L. P., Graham, C., & Williams, S. E. (2009a). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, 220, 589–594.
- VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009b). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist*, 174(2), 282–291. <https://doi.org/10.1086/600087>
- Vito, M. R. M. (2008). *Segmented: An R package to fit regression models with broken-line relationships*.
- Voeten, C. C. (2020). *buildmer: Stepwise elimination and term reordering for mixed-effects regression*.
- Waldock, C., Stuart-Smith, R. D., Albouy, C., Cheung, W. W. L., Edgar, G. J., Mouillot, D., Tjiputra, J., & Pellissier, L. (2022). A quantitative review of abundance-based species distribution models. *Ecography*, 2022, 1–18.
- Waldock, C., Stuart-Smith, R. D., Edgar, G. J., Bird, T. J., & Bates, A. E. (2019). The shape of abundance distributions across temperature gradients in reef fishes. *Ecology Letters*, 22, 685–696.

- Webb, T. J., Lines, A., & Howarth, L. M. (2020). Occupancy-derived thermal affinities reflect known physiological thermal limits of marine species. *Ecology and Evolution*, *10*, 7050–7061.
- Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F., & Grelle, C. E. V. (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, *40*, 817–828.
- Wenger, A. S., Williamson, D. H., da Silva, E. T., Ceccarelli, D. M., Browne, N. K., Petus, C., & Devlin, M. J. (2016). Effects of reduced water quality on coral reefs in and out of no-take marine reserves. *Conservation Biology*, *30*, 142–153.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*, 763–773.
- Wittmann, A. C., & Pörtner, H. O. (2013). Sensitivities of extant animal taxa to ocean acidification. *Nature Climate Change*, *3*, 995–1001.
- Wood, S. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, *73*, 3–36.
- Wood, S. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Chapman and Hall/CRC.
- Yancovitch Shalom, H., Granot, I., Blowes, S. A., Friedlander, A., Mellin, C., Ferreira, C. E. L., Arias-González, J. E., Kulbicki, M., Floeter, S. R., Chabanet, P., Parravicini, V., & Belmaker, J. (2020). A closer examination of the 'abundant centre' hypothesis for reef fishes. *Journal of Biogeography*, *47*, 2194–2209.
- Yang, W., Ma, K., & Kreft, H. (2014). Environmental and socio-economic factors shaping the geography of floristic collections in China. *Global Ecology and Biogeography*, *23*, 1284–1292.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Supporting tables and figures.

**Appendix S2.** Species distribution modelling further methods and materials.

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