

Title: Global change in the functional diversity of marine fisheries exploitation over the past 65 years

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Abstract: Overexploitation is recognised as one of the main threats to global biodiversity. Here we report widespread change in the functional diversity of fisheries catches from the Large Marine Ecosystems (LMEs) of the world over the past 65 years (1950 to 2014). The spatial and temporal trends of functional diversity exploited from the LMEs were calculated using global reconstructed marine fisheries catch data provided by the Sea Around Us initiative (including subsistence, artisanal, recreational, industrial fisheries and discards) and functional trait data available in FishBase. Our analyses uncovered a substantial increase in the functional richness of both ray-finned fishes (80% of LMEs) and cartilaginous species (sharks and rays) (75% of LMESs), in line with an increase in the taxonomic richness, extracted from these ecosystems. The functional evenness and functional divergence of these catches have also altered substantially over the time span of this study, with considerable geographic variation in the patterns detected. These trends show that global fisheries are increasingly targeting species that play diverse roles within the marine ecosystem and underline the importance of incorporating functional diversity in ecosystem management.

Keywords: Biodiversity, Large Marine Ecosystems, Fisheries Management, Overexploitation, Actinopterygii,

Elasmobranchii

Introduction

It is widely recognised that fisheries are putting global marine ecosystems under severe pressure [1, 2]. Nearly 30% of fish stocks are overexploited and 17% have collapsed [3-7]. Selective exploitation of large predators has led to concerns about ‘fishing down the food chain’ [8], and an increasing number of marine taxa, including a quarter of all sharks, are considered to be at an elevated risk of extinction [9]. As human food security is underpinned by the sustainable use of natural resources [10], most attention to date has focused on maintaining fisheries catches [11, 12]. It is becoming clear, however, that maintenance of taxonomic diversity and biomass of the most economically important species is not enough to sustain ecosystem resilience, and that functional diversity should also be taken into consideration [13-15]. Fish species have the most diverse life histories and the highest functional diversity of all vertebrates [14, 16]. Given the growing demand for fish as a food source, coupled with the development of fishing gears and fleets [17], and the spatial expansion of the fisheries industry [18, 19], it seems likely that there has been an increase in the extent to which functional diversity is being extracted from marine ecosystems around the world [20]. To quantify this, we analyse temporal trends in the functional diversity of marine catches in 66 Large Marine Ecosystems (LMEs – see Figure S1) from 1950 to 2014.

Fish species have a plethora of different traits which reflect their varying functional roles in the ecosystem as a whole [21, 22]. Functional diversity is measured by examining the distribution of these species in multivariate trait space [23], with this trait space being computed on the basis of the characteristics of all the species that are potentially present. Different attributes of trait space are captured by a range of summary diversity metrics [24]. Here we focus on three informative measures: functional richness - the fraction of overall trait space occupied by

an assemblage at a given point in time; functional evenness - a measure of how evenly spread the species are in trait space; and functional divergence - the extent to which more abundant species are located towards the margins of trait space [15, 23] (see Functional Diversity Indices section and Figure S5 in the supplementary material). Unlike functional richness, measures of functional evenness and divergence take account of species abundances. To quantify change in functional diversity, we evaluated temporal trends in each metric for both Actinopterygii (ray-finned fish) and Elasmobranchii (cartilaginous fish such as sharks and rays) species in all LMEs.

Decreases in the abundance of traditionally important species have led to diversification of target species [17, 25], to include more mesopelagic and deep sea fish [26]. This shift leads us to predict that most LMEs will have experienced an increase in both the functional and taxonomic richness of catches over the more than six decades for which reconstructed catches have been compiled [17]. In other words, we expect fish with a wider variety of traits to be represented in more recent catches relative to earlier ones. Any change in functional evenness will reflect change in how evenly species in the reported catches are distributed in functional space [15, 27, 28]. In light of pressures on the stocks of historically important populations, any moves by fishers to target species with a wider range of traits, could reduce the functional evenness of catches. However, temporal shifts in the functional divergence of these catches may depend on the extent to which local conditions have favoured catches of species with different combinations of traits, suggesting that there will be marked geographic variation in trends in this metric.

Materials and Methods

All data and code used in our analysis can be accessed at: (<http://biotime.st-andrews.ac.uk/LME/links.php>). We also provide a workflow illustration in the supplementary material detailing our steps in each stage of the methods (see Figure S3, A and B).

Data Compilation

We combined data from three sources to produce the data frames (assemblage matrix, trait & distance matrix and catch matrix) required for the calculation of functional diversity indices.

The assemblage matrix was created using the composition of species potentially present (occurrence data) in each of the 66 LMEs (see Figure S1 for map information). These data were provided by AquaMaps [29], an online database consisting of geo-referenced occurrences from the Global Biodiversity Information Facility [30] and the Ocean Biogeographic Information System [31], combined with information taken from FishBase [32] and SeaLifeBase [33]. In total, the number of species present across all systems is 11,178 marine Actinopterygii (ray finned fishes) and 820 Elasmobranchii (cartilaginous fish).

The trait matrix was built using FishBase [32], which includes information on biology, taxonomy, trophic ecology, life history, uses and historical data. We selected 11 ecologically relevant traits (7 continuous and 4 categorical, see the Functional Traits Selection section in the supplementary material and Tables S2 and S3). We divided the traits into 4 categories: 1 *Environmental Traits* (position in water column, mean temperature preference, maximum depth); 2 *Morphological Traits* (body shape and swimming mode); 3 *Life History Traits* (trophic level, life span, growth coefficient (k) and food consumption (Q/B)); 4 *Reproductive Traits* (Length of first maturity and reproductive guilds). These traits are largely uncorrelated with one another (see Figure S11).

Lack of knowledge regarding species functional traits is known as a “Raunkiaeran shortfall” [34] and this type of data gap represents a major challenge in analyses such as ours. To deal with this problem we used random forest algorithms [35, 36] to impute the missing information (for further detail on this process see supplementary material). After this process we generated a distance matrix to find the specific position of each species in the multidimensional functional space (convex hull volume) based upon its trait values. This was done using the function *quality_funct_space* developed by Maire et al [37] which results in a final species x coordinate matrix (in order to preserve the quality of functional space represented we use three PCoA axes).

The catch matrix was compiled using the amount of biomass annually exploited by global fisheries in metric tonnes (m.t.) from each LME. These data come from the Sea Around Us project [38], and contain catch data from multiple fishing sectors including industrial, artisanal, subsistence, recreational and discards (see supplementary material for further detail). For our analyses we used the combined catch data from all these sectors, including discards. Catches were summed for each species (or higher taxonomic groups) by 5-year time steps to give a species x time matrix from 1950-54 until 2010-14 (13 time periods). When the catch data were resolved above

species level, e.g. genus or family level, we used the average of the coordinates of the species associated with these different levels (see Data Compilation, section 3.1 Catch Data Processing, and Figure S6 for detailed information).

We used these catch data to calculate the amount of functional diversity fisheries have extracted from the LMEs [39] (see supplementary material and Figures S4 and S5 for more detail and examples). The final step was to combine the separate files into one data frame. At the end of this process we had single long form csv file which was used for subsequent analyses (this file is available at <http://biotime.st-andrews.ac.uk/LME/links.php>). See Figure S3A for the full Data Compilation workflow illustration.

Functional Diversity Indices

Functional diversity is a facet of biodiversity that quantifies the complexity of a system with regard to how individual species traits influence their performance and ecosystem functioning [40]. Here we use three complementary indices to calculate the functional diversity of assemblages: functional richness, functional evenness and functional divergence (see Figure S5 for graphic exemplification).

Functional Richness

Within an assemblage each species will occupy a different position in the multidimensional functional space based on the combination of its individual traits. Functional richness represents the proportion of functional space (convex hull volume) [23] filled by all Actinopterygii (or Elasmobranchii) species in each LME. This index takes into account the role that each species plays within its assemblage [23, 41]. Assemblages with high functional richness possess species with a greater range of functional traits and which play many different roles within the ecosystem.

Functional Evenness

Functional evenness integrates the regularity of spacing of species within multidimensional functional space and the evenness of distribution of abundance across species [23, 42]. Depending on the combination of traits and the relative abundances (of all species within a specific assemblage), species placement in functional space can be more (high functional evenness) or less regular (low functional evenness).

Functional Divergence

Functional divergence integrates both the level of complexity in the combination of species traits and how biomass is distributed among the generalist or specialist species [24, 42]. This index therefore represents the deviation of species biomass from the centre of the multidimensional functional space [15]. High functional divergence will be found in assemblages where the greatest biomass of species is located on the borders of the functional space [24].

Taxonomic Richness

To relate the trends in functional diversity to taxonomic shifts in catches, we additionally computed taxonomic richness by quantifying the number of taxa, e.g. species, family or genus, present in the catch data in each time step (see section 3.1 Catch Data Processing at the Supplementary Material and Figure S6). Catch data were identified to species level in 60% of cases and the remaining 40% were identified to genus or family. In some instances we could potentially be counting the same taxon twice, e.g. there may be occasions where *Thunnus sp.* is the name provided rather than *Thunnus albacares*. In such cases we made the decision to count these as different taxa and applied this decision consistently in all analyses.

Calculating the Functional Diversity Indices

We calculated the indices using a function called *multidimFD* [15]. For further information see supplementary material (code is available at <http://biotime.st-andrews.ac.uk/LME/links.php>).

Calculating Slopes and Detecting Trends

To detect trends, we first fitted a linear regression model to each of the metrics using a simple Ordinary Least Squares regression model. We calculated slopes of change for biomass of catch (see map in Figure S7) and taxonomic richness (see map in Figure S8), as well as each of the functional diversity metrics over the 65 year period (Figure 1). Regression plots, with confidence intervals, for the functional diversity trends in each LME can be found in the Appendix of the supplementary materials and are also available at <http://biotime.st-andrews.ac.uk/LME/links.php>. We then used scatter plots with marginal histograms to visualise how the trends

(standardised regression slopes) for each functional diversity index changed in relation to trends found for biomass of catch (Figure 2) and taxonomic richness (Figure 3). To provide an insight into the strength of these relationships we identify the fraction of trends where $p < 0.05$ (see SM Tables S4, S5 and S6). As a final step, for each metric, we computed the overall ordinary least squares (OLS) regression slope of all LMEs combined and overlaid these on the individual trends (Figure S13). In addition, we constructed time series plots using the `acf()` function in base R [43] to assess the extent of temporal autocorrelation in the functional diversity analyses; these plots (see the Appendix section at the SM) reassured us that temporal autocorrelation was unlikely to have a major influence on the interpretation of our results (<http://biotime.st-andrews.ac.uk/LME/links.php>). We also checked for spatial autocorrelation by computing distance decay plots between LMEs (see Figure S12). Finally, we examined correlations between functional indices using Spearman's rank coefficient (see Figures S3B and S10).

Results

The three functional diversity indices used in our analysis highlight the different ways in which the functional traits of fish captured from global marine ecosystems have changed over a timescale of decades. As expected, the functional richness of catches has risen substantially over time, for both Actinopterygii and Elasmobranchii (around 73% of all LMEs) (Figure 1, A and B) (see Table S4 for percentages of significant trends for all metrics and Table S6 for summary statistics for individual LMEs). In 66% of LMEs an increase in functional richness was detected in both classes of fish. These results were supported by the overall (global) OLS regression analyses of all LMEs combined (Figure S13). Thus, fish with a wide range of functional traits are increasingly represented in catches from most of the marine ecosystems in the world. At the same time, the functional evenness of catches, for both Actinopterygii (33% of all LMEs) and Elasmobranchii (21%) decreased (Figure 1, C and D, and Table S4), with 43% of these LMEs undergoing a decrease for both taxa – a result reinforced by the overall model (Figure S13). The expected temporal shifts in response to exploitation found for functional richness and evenness correspond with our initial expectation (see Functional Diversity Indices section in the supplementary material and Figure S5 for further details).

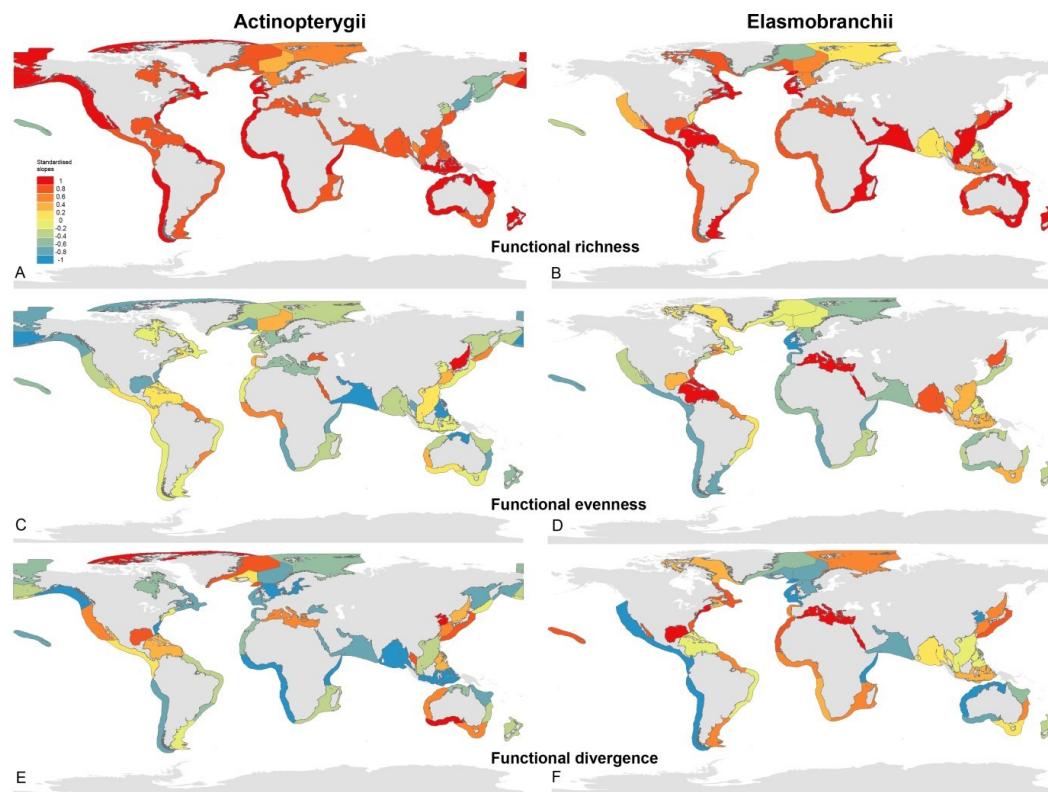


Figure 1. Change in the functional diversity of marine fisheries catches from the Large Marine Ecosystems (LMEs) in the period 1950 to 2014. The map shows, for each LME, the standardised slope of each metric computed against time (see supplementary material for more detail). Increasing trends (slope > 0.2 in the

standardised regression) are coloured red–orange, decreasing ones (<-0.2) as green–blue (see scale). 73% of LMEs exhibited a significant trend in Actinopterygii functional richness, with a further 10% showing a non-significant increase (see Table S4). The equivalent figures for increasing functional richness trends in Elasmobranchii were 72% (significant) plus 15% (non-significant). Functional evenness increased in 14% (7% significant + 7% non-significant) of Actinopterygii LMEs and 49% (26% + 23%) of Elasmobranchii LMEs; decreasing functional evenness was detected in 71% Actinopterygii LMEs (33% + 38%) and in 53% Elasmobranchii LMEs (21% + 32%). Functional divergence increased in 30% (15% + 15%) of Actinopterygii LMEs and 49% (26% + 23%) of Elasmobranchii LMEs; it declined in 60% (42% + 18%) of Actinopterygii LMEs and 36% (30% + 6%) of Elasmobranchii LMEs. Please note that we use the conventional $p < 0.05$ threshold to infer significance, and hence to strength of the relationship, to provide information on uncertainty. For the overall model see Table S5 and Figure S13 in the supplementary material.

With functional divergence we found mixed results. We detected a significant decrease in functional divergence (42% for Actinopterygii and 30% for Elasmobranchii (Figure 1, E and F)), but in only 13% of LMEs did this decrease involve both classes. The overall model reported a significant increase in functional divergence for Actinopterygii but not for Elasmobranchii (Figure S13). We found the greatest increase in functional divergence of catches on the Yellow Sea and South Australian Shelf for Actinopterygii, and in the Red Sea and Northeast U.S. Continental Shelf for Elasmobranchii. Meanwhile the LMEs with the sharpest decrease in the functional divergence of catches were the Guinea Current and Southeast U.S. Continental Shelf for Actinopterygii, whilst for Elasmobranchii the most pronounced decreases were observed on the Celtic-Biscay Shelf and Yellow Sea.

As Figure 2A shows, an increase in functional richness in catches of Actinopterygii was associated with an increase in the size of the catch (top right quadrant of the plots). However, the pattern was more mixed for the Elasmobranchii where a rise in the functional richness of catches within an LME occurred alongside temporal reductions as well as temporal increases in catch (Figure 2B, see the upper histogram on the plots). Over time, the global marine fisheries exploitation from most of the LMEs became less functionally even for both groups (Figure 2, C and D, see the right side histogram of the plot, with a greater distribution of LMEs at the two bottom quadrants). Mixed patterns are seen for the functional divergence from catches (Figure 2, E and F).

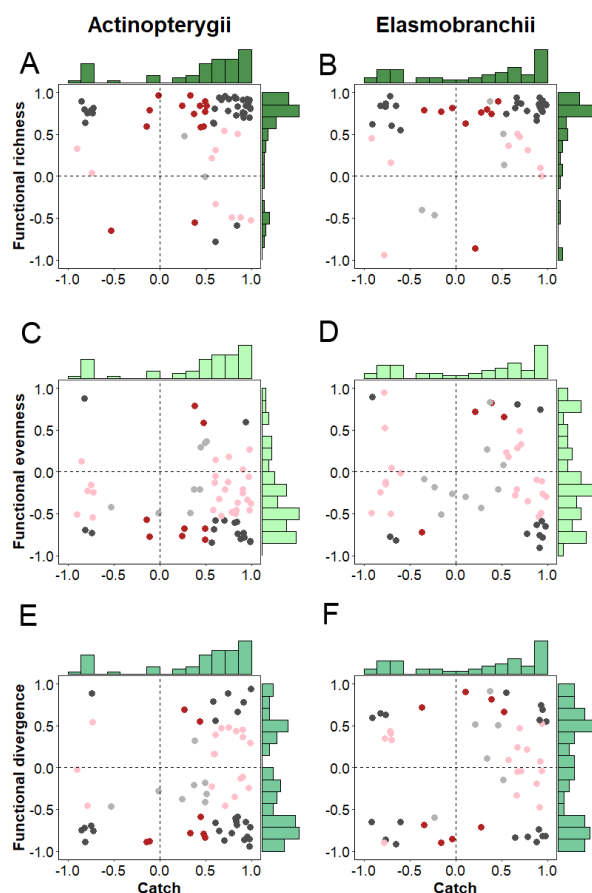


Figure 2. Scatter plots illustrating the relationship between the trends in catch and metric for Actinopterygii and Elasmobranchii. Trends are computed as standardised slopes (see Figure 1). The marginal histograms illustrate the distribution of these variables. Top left quadrant: catch decreases and the functional index increases, top right: catch increases and index increases, bottom left: catch decreases and index decreases, bottom right: catch increases and index decreases. Each point in the plot corresponds to one LME and these are shaded by significance of trend (dark grey – both trends significant; dark red for significant only on y axis; pale red for significant only on x axis; light grey – significant in neither). Summary statistics and error bars for each of the can be found in Tables S4, S5 and S6).

Over the time frame of the study, 85% of LMEs for Actinopterygii and 73% for Elasmobranchii experienced an increase in the taxonomic richness of catches (see Figure 3, the upper histogram on the plots). This increase coincided with increases in functional richness (Figure 3, A and B) and decreases in functional evenness (Figure 3, C and D) for both groups. The relationship between temporal change in taxonomic richness and functional divergence was heterogeneous (Figure 3, E and F). Finally, distance decay plots (Figure S12) show that the pattern of trends across LMEs is not related to the spatial distance between them, in other words suggests that spatial autocorrelation does not explain the results.

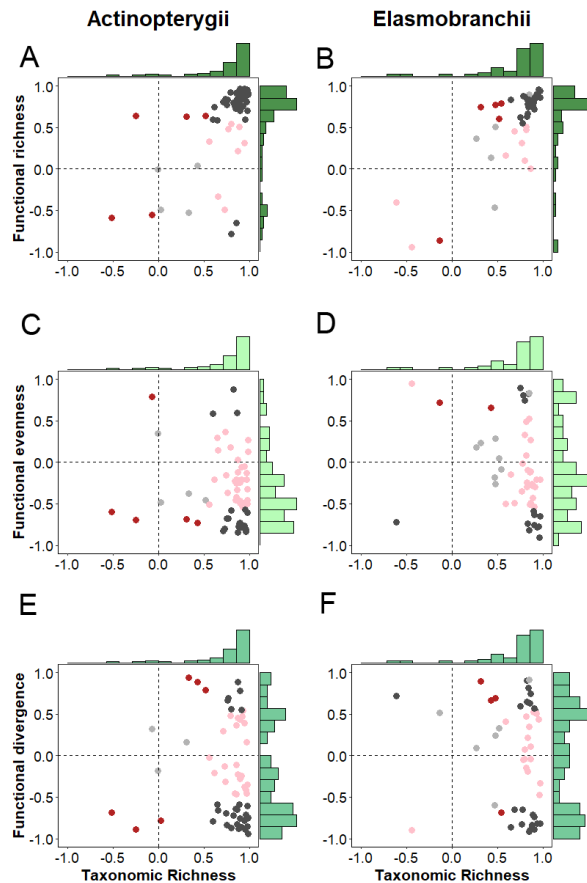


Figure 3. Scatter plots illustrating the relationship between the trends in taxonomic richness and functional diversity metrics for Actinopterygii and Elasmobranchii. Trends are computed as standardised slopes (see Figures 1 and 2). The marginal histograms illustrate the distribution of these variables. Top (A and B) show that as taxonomic richness increases, functional richness also increases. Middle (C and D) functional evenness tends to decrease as taxonomic richness increases. Bottom (E and F) shows a mixed pattern for functional divergence. Each point in the plot corresponds to one LME. Colour coding as in Figure 2.

Discussion

Our results uncovered marked shifts in the functional diversity of global fisheries over the 65 years of our study. In particular, we detected a sharp increase in the functional richness of both bony and cartilaginous fish being extracted from the majority of LMEs (Figure 1, A - B). We also found a strong association between increases in the functional richness and the taxonomic richness of catches, supporting the expectation that these trends in functional richness arise because the fishing industry is exploiting a wider taxonomic range of fish - in part through targeting habitats, such as the deep seas, which previously were not exploited. A marked increase in fisheries catches over the last 65 years, for Actinopterygii (58% of all LMEs ($p\text{-value} < 0.05$)) and Elasmobranchii (47%) (see Figure S7 and Table S4), could also partly explain the patterns we report. (We note that although catches began to decline sharply after 1996 (see Figure S2) we nonetheless detect an overall increasing trend in catch over the time frame of our analyses.). However, an increase in functional richness can occur even where there has been a decrease in marine fisheries catches; the North Sea along with another 20 LMEs are examples of this pattern.

The functional evenness and functional divergence of these catches have also changed, with considerable geographic variation in the patterns detected (Figure 1, C - F). Although there was a tendency for an increase in the functional richness of catches to be associated with a decrease in functional evenness within an LME, this negative correlation was relatively small (around -0.17 for both groups of species, (Figure S10)). Fisheries target

certain parts of the multidimensional functional space by exploiting species that share similar combinations of traits, such as size [44], predatory behaviour [45], and trophic level [8]. Spatio-temporal changes in functional evenness from catches could be due to increased exploitation of particular subgroups of taxa (with certain functional traits) within the LMEs and/or less availability of fishes belonging to particular subgroups of taxa. The exploitation of a wider range of species playing different roles (higher functional richness) and at the same time increasing catches of certain groups of species will additionally contribute to a reduction in functional evenness. This pattern was evident in our analysis, with most LMEs exhibiting a decreasing pattern of functional evenness in catches (Figure 2, C and D, and see Functional Diversity Indices section at the Supplementary Materials for rationale).

Temporal trends in functional divergence were notably heterogeneous and not tightly linked to temporal trends in the overall catch within LMEs (Figure 2, E and F), nor to trends in taxonomic richness (Figure 3, E and F). An increase in the functional divergence of catches within an LME points towards the exploitation of species that possess unusual combinations of traits (e.g. functionally specialist species), whereas a decrease means specialist species have reduced representation in recent catches relative to older ones. It is possible that spatial heterogeneity in the extent to which mesopelagic and deep sea fishes have been incorporated in catches contribute [26] to these patterns in functional divergence. Taken together these findings show that a rise in the functional richness of catches can occur alongside an increase, decrease or even little change in functional evenness and divergence. Indices that take into account the species traits and their abundances or biomass, such as functional divergence, can change independently of species local extinctions, and thus have considerable potential to act as early-warning signals in exploited ecosystems [15].

While directional change in the magnitude, and taxonomic composition, of the catch over the duration of the study is likely to contribute to the changing functional diversity of global fish catches, it is not the whole story. Climate change [46] and other anthropogenic impacts will also affect these assemblages [47], and these impacts may interact in complex ways with fishing practices. For example, increased targeting of specialist species could further reduce ocean resilience in the face of climate change. These threats are in addition to the already documented pressures on biodiversity in the Anthropocene [48]. The complementary functional diversity metrics used here (Figures S5 and S9) extend insights based on single species and taxonomic based indices [49] as well as those from previous work on geographical heterogeneity in the functional diversity of marine catches in most of the world's LMEs in a single year [28]. It is already clear that the pattern is a multifaceted one. A better appreciation of the consequences of the ways in which changes in the different metrics of functional diversity relate to ecosystem functioning is urgently needed, particularly in light of the increase in specialist species targeted by fisheries. A deeper conceptual understanding of the linkage between shifts in 'classic' taxonomic metrics (such as the taxonomic richness measure used here) and functional diversity measures will also help explain the geographic patterns we detected in this study. However, great care needs to be taken in making inferences about change in the functional diversity of the ecosystems themselves, based on analyses of the sub-set of fish extracted from them [50]. To link change in the functional diversity of catches with change in the marine ecosystem it will be necessary to conduct detailed investigations of those LMEs for which scientific survey data are also available.

There are a number of wider implications to these findings. Better understanding of the link between biodiversity, ecosystem services and resilience is the *sine qua non* for conservation and natural resource management [51, 52], particularly in an era of pervasive global transformations (such as overexploitation and climate change) [48, 53, 54]. Functional diversity is a key facet of biodiversity but we know much less about how it is changing over space and time than we do for taxonomic diversity. As our investigation has now made clear, there have been substantial shifts in the functional diversity of exploited marine fish over the last 65 years. Even so, we barely comprehend the consequences of these shifts for ecosystem function. This is a pressing research challenge for the coming years. In addition, our results also have implication for stewardship of the seas, and underline the importance of Ecosystem Based Fisheries Management (EBFM). Whereas traditional fisheries management has focused on commercially valuable taxa, often on a population by population basis, EBFM adopts a holistic approach in which all the species in the ecosystem are considered in the same framework [55, 56]. Since functional diversity indices take account of species interactions [52, 57, 58] as well as the structure of the communities and ecosystems within which the species are embedded [24] they have an important role to play in informing fisheries policy and protecting the resilience of systems in the years to come. Global fisheries management urgently needs to consider multiple facets of biodiversity to promote the conservation and management of this vital natural resource. Better understanding of how biodiversity changes in space and time [59] will underpin improved decision making in relation to the establishment of protected areas and fisheries management. Future analyses should also consider how functional diversity responds in fisheries that are deemed to be recovering as this will provide an important test of the effectiveness of restoration policy. Finally, public awareness campaigns to promote the sustainability

of seafood will need to place greater emphasis on the roles that species play in ecosystems, as well as on the vulnerability of stocks.

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