



Research

Cite this article: Maureaud A, Hodapp D, van Denderen PD, Hillebrand H, Gislason H, Spaanheden Dencker T, Beukhof E, Lindegren M. 2019 Biodiversity–ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. *Proc. R. Soc. B* **286**: 20191189.
<http://dx.doi.org/10.1098/rspb.2019.1189>

Received: 22 May 2019

Accepted: 14 June 2019

Subject Category:

Ecology

Subject Areas:

ecology

Keywords:

fish biodiversity, ecosystem functioning, biomass, BEF relationship, dominance

Author for correspondence:

Aurore Maureaud

e-mail: auma@aqu.dtu.dk

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4551827>.

Biodiversity – ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness

Aurore Maureaud¹, Dorothee Hodapp², P. Daniël van Denderen¹, Helmut Hillebrand^{2,3}, Henrik Gislason⁴, Tim Spaanheden Dencker¹, Esther Beukhof¹ and Martin Lindegren¹

¹Centre for Ocean Life, National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark, Kemitorvet, Building 202, 2800 Kgs. Lyngby, Denmark

²Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Oldenburg, Germany

³Plankton Ecology Lab, Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University Oldenburg, Wilhelmshaven, Germany

⁴National Institute of Aquatic Resources (DTU Aqua), Technical University of Denmark, Kemitorvet, Building 202, 2800 Kgs. Lyngby, Denmark

ORCID AM, 0000-0003-4778-9443; DH, 0000-0001-5012-0199; PDv, 0000-0001-6351-0241; HH, 0000-0001-7449-1613; HG, 0000-0003-0242-3333; TS, 0000-0001-7804-0828; EB, 0000-0002-0350-9596; ML, 0000-0002-9185-951X

The relationship between biodiversity and ecosystem functioning (BEF) is a topic of considerable interest to scientists and managers because a better understanding of its underlying mechanisms may help us mitigate the consequences of biodiversity loss on ecosystems. Our current knowledge of BEF relies heavily on theoretical and experimental studies, typically conducted on a narrow range of spatio-temporal scales, environmental conditions, and trophic levels. Hence, whether a relationship holds in the natural environment is poorly understood, especially in exploited marine ecosystems. Using large-scale observations of marine fish communities, we applied a structural equation modelling framework to investigate the existence and significance of BEF relationships across northwestern European seas. We find that ecosystem functioning, here represented by spatial patterns in total fish biomass, is unrelated to species richness—the most commonly used diversity metric in BEF studies. Instead, community evenness, differences in species composition, and abiotic variables are significant drivers. In particular, we find that high fish biomass is associated with fish assemblages dominated by a few generalist species of a high trophic level, who are able to exploit both the benthic and pelagic energy pathway. Our study provides a better understanding of the mechanisms behind marine ecosystem functioning and allows for the integration of biodiversity into management considerations.

1. Introduction

The unprecedented loss of biodiversity worldwide is accelerating despite global conservation efforts to protect vulnerable species and habitats [1]. The extinction of species and shifts in community composition, either globally or locally, raises important questions regarding the consequences of biodiversity loss for the integrity, functioning, and services of ecosystems [2]. Consequently, there is a growing interest in ecology and conservation to understand the relationship between biodiversity and ecosystem functioning (BEF). Traditionally, the BEF relationship has been studied by experimentally investigating how the number of species occurring at a given site affects the total productivity [3]. Meta-analyses summarizing such experimental studies and field studies

have demonstrated a generally positive and saturating effect of species richness on ecosystem processes [4–7]. In parallel, theoretical studies have provided more insight into the mechanisms underlying these effects [8–11]. Through those complementary approaches, two mechanisms at the origin of BEF relationships have been identified: the ‘complementarity’ mechanism by which more species lead to higher ecosystem functioning and the ‘selection’ mechanism by which the dominance of species or traits lead to higher ecosystem functioning [12]. The BEF concept has expanded to account for links between multiple aspects of biodiversity (e.g. the variety of genes, species, and functional traits) and ecosystem functioning (e.g. biomass production, nutrient cycling, ecosystem metabolism, and physical engineering) [13]. Furthermore, the field of research has broadened considerably to encompass a range of organisms and trophic levels across terrestrial, freshwater, and marine ecosystems [7,14–16].

However, a fundamental limitation of our current knowledge on BEF is the degree to which relationships hold in real ecosystems, characterized by complex trophic interactions, highly variable environmental conditions, and vast spatio-temporal scales [17,18]. This is particularly important because the environment, including heterogeneity in resource supply and landscapes, is thought to have a direct influence on BEF relationships [19,20]. The effects of biodiversity and environment on ecosystem functioning also appear to be scale-dependent [21,22]. Hence, combining and analysing large observational datasets of biodiversity and ecosystem functioning is needed in order to ground truth BEF expectations with empirical evidence. Such analyses require statistical tools capable of handling the increasing size and resolution of data available and the complexity of interactions between biodiversity, ecosystem functioning, and environmental drivers [18]. Structural equation modelling (SEM) is an appropriate statistical framework to account for some of this complexity since it allows testing hypotheses about causality between multiple drivers and response variables simultaneously [18,23].

In this study, we empirically test the BEF concept by exploring the existence of links between biodiversity, ecosystem functioning, and the environment using SEM and a comprehensive collection of scientific survey data on marine demersal (bottom-living) fish species sampled across western European seas. This large geographical area represents an ideal case study to test the BEF concept in a natural marine environment thanks to its pronounced gradients in diversity and environmental conditions [24]. Furthermore, European seas are exposed to multiple human stressors including fishing, eutrophication, and warming. More specifically, coastal European shelf seas are perturbed systems, where historical fishing has modified marine communities and ecosystems in the past century [25,26]. Consequently, understanding the cumulative effects of the environment and stressors on the diversity, functions, and services of European seas is of major concern to resource managers, policymakers, and the general public. To test whether relationships between biodiversity metrics and ecosystem functioning (here represented by the total demersal fish biomass) hold, we set out to answer the following research questions: (i) is there a relationship between multiple metrics of fish biodiversity and community biomass? (ii) Which mechanism mostly explains fish community biomass (complementarity or selection)? (iii) What is the

relative importance (both direct and indirect effects) of different metrics of biodiversity and environmental conditions to explain fish community biomass? (iv) What are the key characteristics of fish communities in terms of species composition and traits leading to high or low biomass?

2. Methods

(a) Data and case study

The analysis was conducted within the European seas and was based on scientific bottom-trawl survey data available from the International Council for the Exploration of the Sea (ICES) online database (datras.ices.dk). Six winter-time bottom-trawl surveys were combined from 1997 to 2016, covering the North Sea, the eastern English Channel, the Scottish west coast, the Celtic Sea, and the Bay of Biscay (electronic supplementary material, S1). For each survey haul (i.e. sampling unit), the species were identified, the number of individuals were counted, and their length was measured, representing an indirect measure of abundance in number of individuals at size caught per species and haul. Hauls last approximately 30 min and the data was converted into abundance per hour fishing. Only taxonomic groups for which the species names were specified were kept, and scientific names were checked with the World Register of Marine Species [27]. All invertebrates and strictly pelagic species were excluded, limiting the analysis to demersal and other bottom-related fish species. To standardize for haul duration, only hauls with duration over 20 min were retained. A minimum hauling depth of 20 m was selected to exclude samples from coastal or estuarine areas, as these areas were not adequately sampled in the surveys [24]. A spatial grid with cells of $\frac{1}{2}$ degree latitude and longitude was created, resulting in 526 grid cells. Hauls from all surveys and years were assigned to their corresponding grid cell. Our dataset included in total 20 400 hauls and 204 species.

(b) Biodiversity and ecosystem functioning metrics

The total fish biomass per grid cell was used as a proxy for ecosystem functioning. The biomass was estimated from the survey abundances and length of individuals using species-specific length–weight relationships available from FishBase [28], which was then transformed into tons per hour trawled. Although methods to standardize for swept area exist [29], missing information on the duration of hauls, the speed of the vessel, and the opening of the gear would have resulted in a loss of a third of the data. Therefore, data standardized by swept area was used only as a sensitivity test while the main analysis used all available data.

The number of samples (e.g. hauls) per grid cell for all years was highly uneven, varying from just a few to more than a hundred. This heterogeneity in sampling effort can affect the biodiversity measurements, especially species richness [30]. In order to standardize for sampling effort, we constructed Species Accumulation Curves (SACs) [31,32] for each grid cell with the ‘vegan’ R package [33]. We then fitted nonlinear Michaelis–Menten curves to each of the SACs and estimated the minimum number of hauls required to reach the 50% threshold of the derived asymptotic species richness for each grid cell, integrating all years from 1997 to 2016. Finally, we randomly selected the minimum required number of hauls identified above for each grid cell, calculated the metrics of interest, repeated the process 100 times, and calculated the average of each metric per grid cell. This technique is further detailed in electronic supplementary material, S2.

In order to take multiple facets of biodiversity into account, several commonly used biodiversity indices were estimated

from the information contained in the randomly selected hauls. First, we estimated species richness as the mean number of species recorded in the randomly selected hauls within each grid cell. Since the dominance of species can reflect other patterns than richness [34], we also estimated the mean Simpson's evenness based on species abundance [35]. Furthermore, for each iteration, we quantified differences in species composition between grid cells with the average Jaccard dissimilarity index based on species presence-absence per site [36], using the 'betapart' R package [37]. For each grid cell and iteration, we calculated the mean dissimilarity to all other cells in the sampling grid in order to reflect the distinctness of the local species assemblages. Because the differences in community composition might be related to differences in trait composition as well, we calculated community-weighted mean (CWMs) traits of species linked to their diet (type of diet [generalist/benthivorous/piscivorous/planktivorous] and trophic level weighted by species biomass, electronic supplementary material, S3), using the R package 'FD' [38], and a collection of species traits [39].

(c) Environmental and fisheries data

To assess the contribution of abiotic variables explaining the spatial variation in total biomass, a number of environmental predictors were included in the analysis. Mean sea surface temperatures (SST) were estimated based on average monthly values for 1997–2016 available from the Hadley's Centre [40] (HadISST). To account for seasonality, a proxy for the stability of the environment, we used the coefficient of variation of monthly mean SST (SST.sea). Depth was taken from the ETOPO1 model (ngdc.noaa.gov/mgg/global/). To account for diversity in seafloor habitats, we also quantified the seafloor diversity by calculating Pielou's evenness based on the mean proportions of sand/gravel/mud for each grid cell [41]. High seafloor evenness indicates an even distribution of the three types of bottom habitats whereas a low evenness indicates the dominance of one of the categories in the grid cell. To quantify the productivity of the ecosystems in each grid cell, we used chlorophyll *a* concentration (mg Chl/m³/day) from the GlobColour data, as a mean of the years 1997–2016 [42] (globcolour.info, GSM merged data from various satellite observations, Garver, Siegel, Maritorena Model). Finally, we accounted for fishing impacts by investigating potential effects of spatial fishing effort estimates using the fished swept area in 1/year, gathered from the Vessel Monitoring System [43] as a mean of the years 2010–2012, and the Global Fishing Watch database where we estimated the fishing effort in kWh/year [44], as a mean of the years 2012–2016. All environment and fisheries data are presented in more detail and plotted in electronic supplementary material, S4.

(d) Statistical analysis

We used a SEM to test for potential spatial relationships between mean values of total biomass, biodiversity (i.e. species richness, evenness, dissimilarity), environmental conditions (i.e. depth, SST, seasonality in SST, seafloor diversity), and food availability (e.g. chlorophyll *a* concentration) across all grid cells in the study area. Since hypotheses on causal links in the system have to be established *a priori*, we postulated that total biomass (i.e. the primary response variable) could be explained by all the different biodiversity metrics and environmental drivers. In this analysis, we are interested in whether realized productivity (biomass) is driven by species niche complementarity (e.g. more species lead to higher biomass), or by selection (e.g. dominance of species/traits lead to higher biomass). We acknowledge that the hypothesized relationships between biodiversity and biomass might be bi-directional [45], especially across large-scale environmental gradients [46]. The number of species in a system can be a result of the potential productivity of a system, but is highly variable and has been debated [47]. However, we

restricted the focus of the study and the structure of the SEM to the research questions that we are interested in. Richness and evenness are non-independent components of diversity [48,49], we found a correlation between them, and as a result included a non-causal correlation between the variables in the model (electronic supplementary material, S5). The same was done with richness and dissimilarity; and evenness and dissimilarity. The three biodiversity indices were thus response variables (we allowed environmental variables to explain biodiversity) as well as explanatory variables of biomass. The model construction and hypotheses are further discussed in electronic supplementary material, S5.

We explored the relationships between fishing effort, biomass, and biodiversity metrics. The patterns observed led us to rule out fishing effort from the model for several reasons. First, fishing effort data was only available for recent years (from 2010), did not cover the entire time series of the analysis, or did not distinguish between pelagic and bottom-trawl fishing gears. As such, any historical fishing effort effect on the current spatial distribution of biodiversity and biomass cannot be identified. Second, the only significant relationship found for fishing was between fishing effort and evenness, where fishing effort is high when fish community dominance is high. *A priori*, it might be expected that intense fishing decreases the abundance of dominant species, but we find the opposite pattern in our analysis. This suggests that fishing occurs in communities with very abundant species, resulting in a causal relationship from evenness to fishing effort (and not vice versa). Since the directionality of the observed fishing effect is uncertain, we did not include fishing effort in the main model, but present the analysis in electronic supplementary material, S5.

Before fitting linear generalized least squares *gls* models (there were four models explaining biomass, richness, dissimilarity, and evenness), we used the natural logarithm transformation of some variables (biomass, evenness, depth, and chlorophyll *a*). As the analysis is based on spatial patterns, we tested for spatial autocorrelation and selected the best covariance structure for each relationship before running the SEM. To account for non-linearity of some of the links, we included quadratic terms with the following transformation $(x - \text{mean}(x))^2$ [50]. The non-linear relationships were explored *a priori* and included in the final SEM if they were statistically significant and improved the explained variance of each *gls* model. In order to reduce complexity and avoid model saturation, we evaluated the goodness-of-fit with the Fisher's statistic test after removing non-significant pathways between environmental variables and biodiversity or biomass from the SEM. We kept all biodiversity links in the model and biomass pathways, links that related to our main research hypotheses whether they were significant or not. We created and ran all models with the R package 'piecewiseSEM' [51]. Model validation of residuals of each relationship was performed *a posteriori* (electronic supplementary material, S5).

(e) Sensitivity analyses

The sensitivity of results to differences in sampling design were tested on the model residuals in order to verify the potential effects of mean sampling duration (min), gear opening (m), vessel speed (knots), the sampling season (summer, winter, or both), the type of gear, and the total number of samples. These variables were introduced as predictors in linear regressions against each of the four *gls* model residuals including richness, dissimilarity, evenness, and biomass. Also, the SEM was repeated with prior swept area standardization on a sub-dataset. To explore the consistency of the derived patterns and relationships between biomass and biodiversity through time, we tested the sensitivity of the relationships when fitted over each 5-year period from 1997 to 2016. Furthermore, we checked for the consistency of relationships regarding the effect of seasonality by comparing results with an

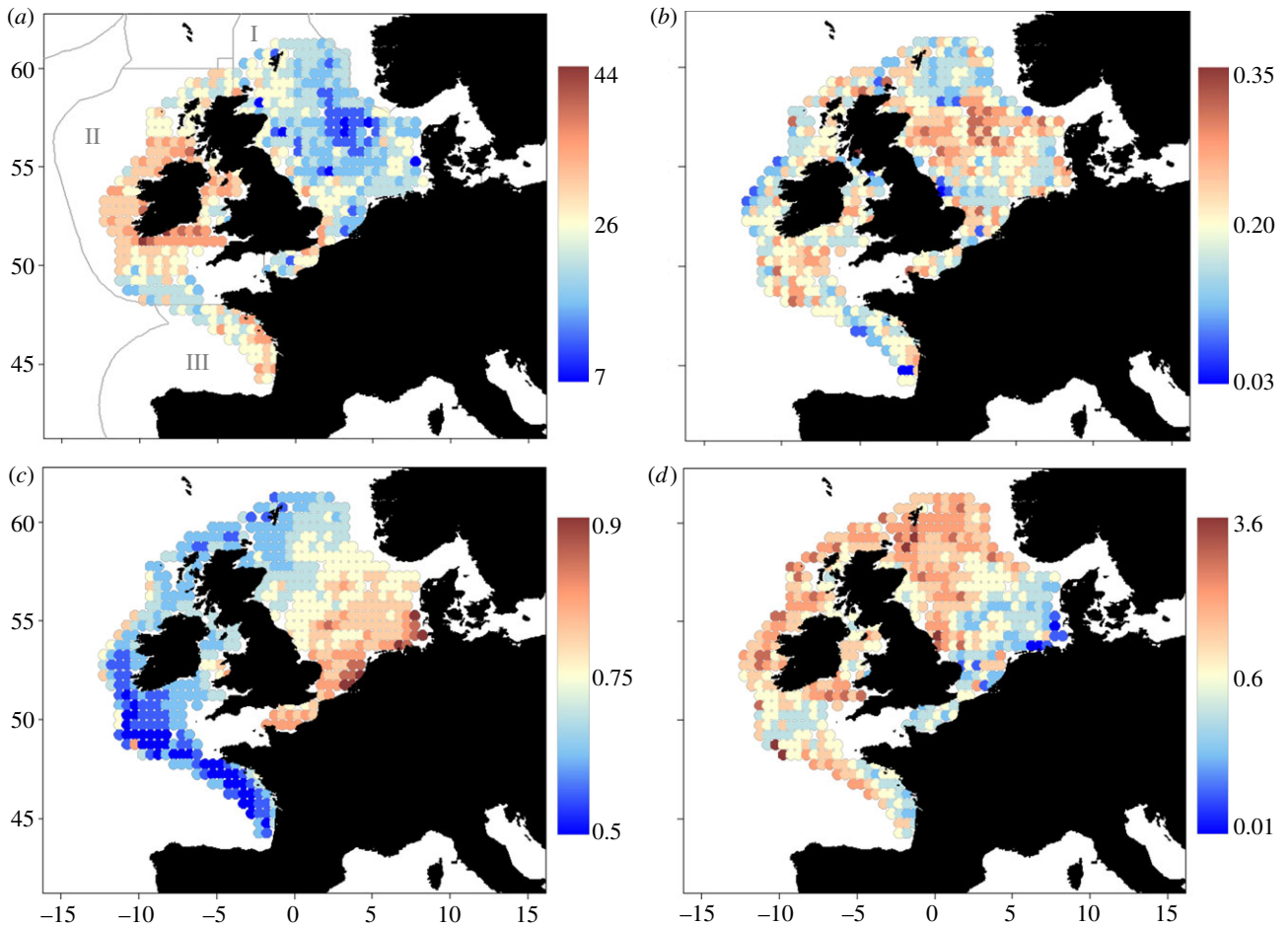


Figure 1. Large-scale patterns of demersal fish biodiversity and functioning across European seas, including the North Sea (I), the Celtic Sea (II), and the Bay of Biscay (III). The spatial patterns are illustrated by the standardized distribution of: (a) species richness (i.e. mean standardized number of species representing 50% of the estimated asymptotic richness per grid cell), (b) log-transformed species evenness (i.e. Simpson's evenness calculated with species abundances), (c) differences in species composition (i.e. beta-diversity based on Jaccard dissimilarity of species presence-absences), and (d) total fish biomass (expressed in log(tonnes/hour fishing)). (Online version in colour.)

analysis using fish survey data collected during summer, available for the North Sea. Finally, we checked for the consistency of our results in the North Sea when considering the catchability of the gear for different species using published estimates [52]. The sensitivity analyses are described in electronic supplementary material, S5 and S6.

3. Results

The geographical patterns in standardized species richness show large spatial variability with relatively lower numbers of species in the central North Sea compared to the Celtic Sea and Bay of Biscay (figure 1a). European fish communities are characterized by an uneven distribution of species abundances (except in the central North Sea and the Celtic Seas) and the highest evenness is only 0.35 (figure 1b), indicating strong dominance in most European demersal fish communities. The spatial patterns in community composition indicate the presence of a clearly distinguished community in the southern North Sea compared to the rest of the European seas as well as high dissimilarity overall (Jaccard > 0.5 , figure 1c). However, the Bay of Biscay shows lower dissimilarity, indicating that it is inhabited by species that are present throughout the area. Finally, there is a marked south-north gradient in total fish biomass. The highest values are found in the northern North Sea and along the west coast of Scotland, while the coastal areas of the Bay

of Biscay, the Celtic Seas, and the southern North Sea show considerably lower values (figure 1d).

The final SEM, including spatial autocorrelation, explains a moderate to large degree of spatial variation in total biomass (50%), species richness (29%), and dissimilarity (64%), whereas evenness is poorly explained (5%). The Fisher statistic test shows a satisfying goodness-of-fit of the model ($p = 0.48$). Furthermore, the results are robust to a number of potential confounding effects, including differences in sampling gear, duration, seasons, and number of hauls (electronic supplementary material, S5 and S6). The SEM is also reproduced with a prior standardization of abundance and biomass by the swept area, without changing the main results (electronic supplementary material, S6). We find a significant negative relationship between biomass and evenness and a non-significant relationship between biomass and species richness (figure 2a,b, electronic supplementary material, S5). The strongest links in the model are between temperature seasonality and biomass (estimated slope from the SEM: -0.42 , figure 2c), and temperature seasonality and dissimilarity (0.62, figure 2e). We find high fish biomass where evenness is low (i.e. high dominance), where dissimilarity and seasonality are at an intermediate level (figure 2c,d), and where temperature and chlorophyll *a* (as a proxy for primary productivity) are low (figure 2a). In terms of species richness, we find more species in areas with high temperature, high primary productivity, a diverse

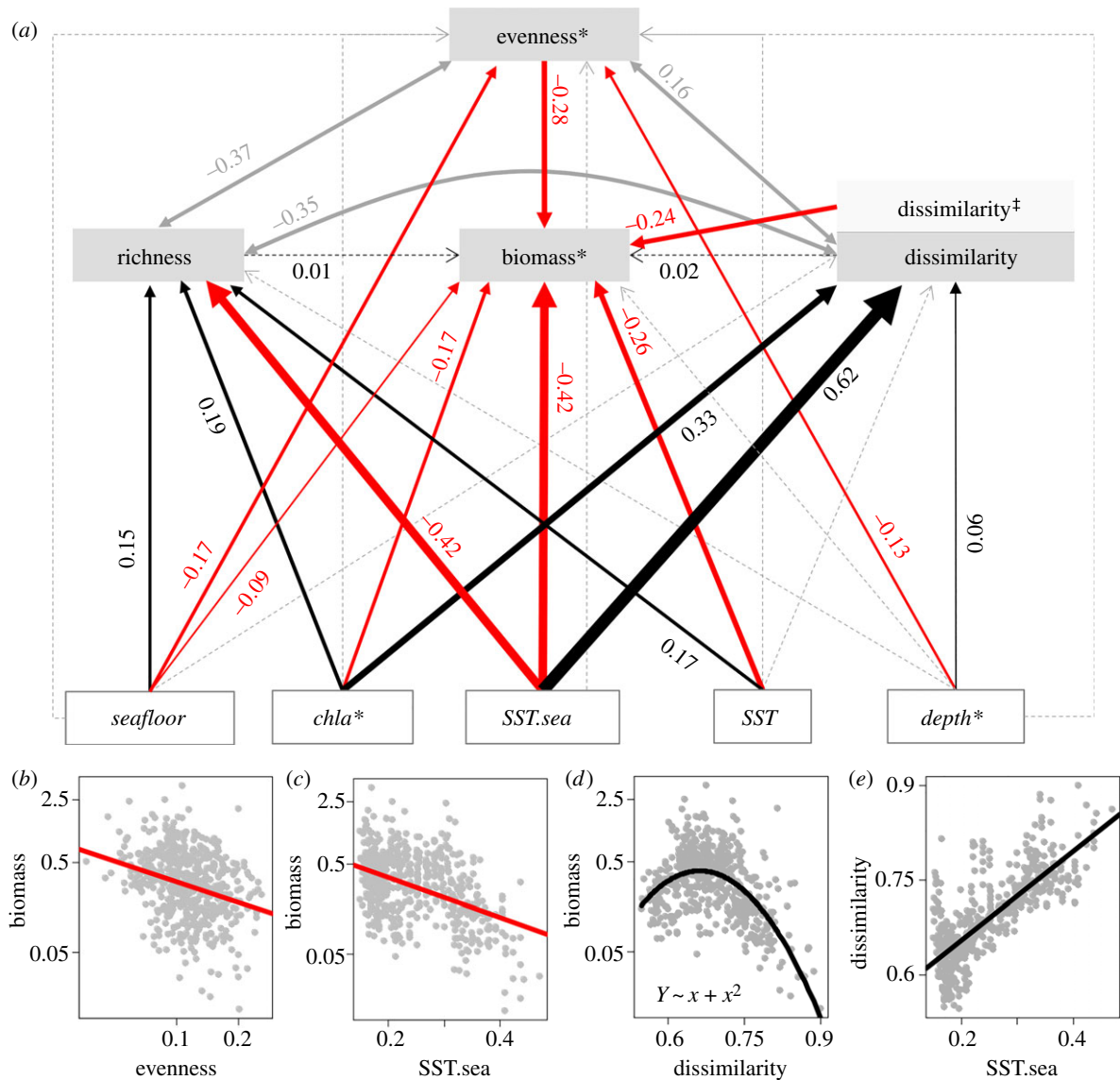


Figure 2. Results from the structural equation model (SEM) and main observed relationships. (a) The final SEM including the causal relationships between metrics of biodiversity, ecosystem functioning, and the environment. Variables in grey represent the four response variables and variables in italic the explanatory variables. Asterisk indicates if the variable was log-transformed with natural logarithm. † indicates if the variable was transformed following: $(x - \text{mean}(x))^2$. Black arrows represent positive causal links, red arrows negative causal links, grey arrows non-causal correlations between diversity indices, and dotted arrows show the non-significant relationships (grey if removed from the model, e.g. the environment). Standardized parameter estimates are shown next to each arrow. (b) Biomass and evenness relationship included in the model. (c) Biomass and seasonality of SST (SST.sea). (d) Biomass and dissimilarity (e) dissimilarity and SST.sea. The lines on b, c, d, and e represent regressions performed separately before the SEM and illustrate nonlinear links (d). (Online version in colour.)

seafloor habitat, and a low degree of seasonality. Conversely, we find low evenness (i.e. high dominance) prevailing in deeper environments and less diverse seafloor habitats. The largest differences in species composition occur in highly seasonal and productive areas. The SEM also includes indirect effects. For instance, depth does not significantly affect fish biomass but it is negatively related to evenness (-0.13). The net effect of depth on biomass calculated from the standardized coefficients is found to be weakly positive ($-0.13 \cdot (-0.28) = 0.04$). Seafloor evenness, on the other hand, affects biomass both directly and indirectly (through evenness), and the net effect of seafloor evenness is negative (-0.04).

The identity and trait characteristics of the dominant species can bring additional information on the potential biomass of communities in different environments. We identified several interactions between diversity, the environment, and biomass (figure 3). First, communities with a low evenness and high biomass (figure 3a) are dominated

primarily by gadoid species, such as Norway pout (*Trisopterus esmarkii*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). These communities are found in environments with a moderate degree of seasonality and beta-diversity (figures 2c,d and 3a). These communities are also characterized by a low proportion of benthivorous species and an overall higher mean trophic level (figure 3b,c). Conversely, areas with low evenness but low biomass, are primarily dominated by benthivorous flatfish species, such as common dab (*Limanda limanda*) and European plaice (*Pleuronectes platessa*), that occur in more shallow and seasonal environments. The differences in biomass between communities dominated by gadoids or flatfish are consistent even after correcting abundance and biomass by the gear catchability in the North Sea (electronic supplementary material, S6). The third group, demonstrating low biomass, is primarily found in warm environments with a low degree of seasonality and is characterized by a high

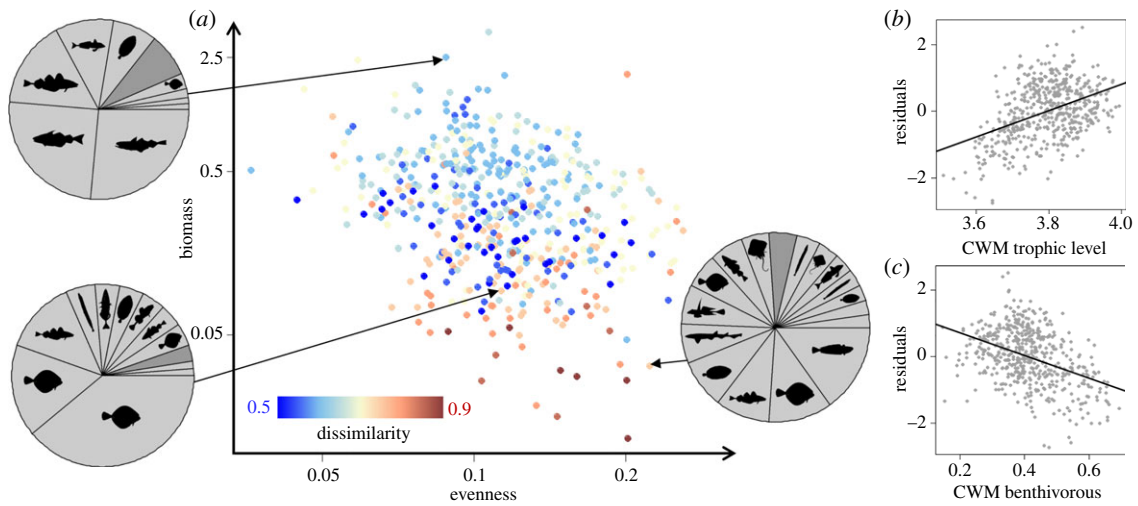


Figure 3. Links between biomass, species composition, and feeding traits. (a) Relationship between biomass (log(tons/hour fishing)) and log-transformed evenness where the colour scale shows the Jaccard dissimilarity index. The pie charts illustrate three distinct communities in terms of composition and relative abundances (species names are available in electronic supplementary material, S7). The dark grey sectors indicate ‘Other’ species contributing to less than 1% of the total abundance. A fitted linear relationship of the residuals of the biomass–evenness relationships (derived from a) against community-weighted mean (CWM) traits of the trophic level (b) and the proportion of benthivorous species (c), respectively. (Online version in colour.)

richness of more equally abundant species. This in turn gives rise to higher evenness and a lower degree of dissimilarity in species composition compared to the other areas.

4. Discussion and conclusion

Species richness is a simple and commonly used measure of diversity employed in many experimental and field studies where a higher number of species increase ecosystem processes (via niche complementarity), such as biomass production [4,7]. Support from natural systems for the positive effect of species richness on community biomass is developing [7,53], including large-scale observational studies demonstrating higher reef fish biomass with increasing richness [54,55]. Contrary to these findings, we found a non-significant relationship of species richness on fish biomass across north-western European seas. Our findings are supported by a temporal study on North Sea demersal fish species where no relationship between number of species and biomass was found [29]. Similarly, weak or even negative relationships between richness and biomass have been found in regional studies, for instance for phytoplankton [56] and benthic macrofauna [57], indicating that a universal positive relationship between species richness and biomass is not necessarily to be expected in natural marine environments.

Several reasons might explain the absence of a species richness–biomass relationship. First, we studied exploited marine systems with a long and intense history of fishing, especially in the North Sea. Fishing has been shown to cause local declines and extinctions of rare and sensitive species such as sharks and skates [58,59], and has, as a result, altered the natural composition and diversity of fish communities. Consequently, past effects of fishing might have disrupted a previously existing richness–biomass relationship. Unfortunately, we cannot test for such an effect as no historical records of fishing effort or species composition exist at the spatial scale and resolution needed. Second, a richness–biomass relationship is perhaps absent as it is a scale-dependent relationship and present foremost along significantly larger richness gradients, as demonstrated by previous studies and meta-analyses

[7,54,55]. Third, the relationship may be absent in the studied region as there are fundamental differences in richness–biomass dynamics compared to areas where a positive relationship has been observed.

Our results show for the first time that greater dominance (e.g. low evenness in distribution of species abundances) is related to higher total biomass of marine fish at a large spatial scale. Interestingly, not all uneven communities are characterized by high biomass, and relationships between species composition and environmental conditions need to be accounted for to understand these differences. Evenness and dominance have been thought to more directly affect the functioning of ecosystems [17,34], as large and numerically abundant species are suggested to promote productivity via the ‘selection effect’ [12,60]. Yet, the metric is rarely used in BEF studies [61]. Recently, evenness was discovered as an important driver of ecosystem functioning in plankton [56,62,63], macrophytes [64], and in benthic communities [65].

More specifically, the identity and performance of the dominating species and their associated traits may explain ecosystem functioning [34,66]. We found that highly uneven communities composed of species with a high mean trophic level and a low proportion of benthivory (e.g. gadoids and generalist/piscivorous species) had considerably higher total biomass under moderate seasonality and low temperatures. On the contrary, equally uneven communities but with low total biomass contained lower trophic level species primarily feeding on benthos (e.g. flatfish) and were found in more seasonal environments. This indicates that demersal fish communities consisting of generalist species, that are able to feed on both benthos and pelagic fish, may use a larger food supply [67] than specialist species primarily adapted to feed on benthos. Hence, we argue that environments where high trophic level fish species utilize both the pelagic and benthic energy pathway have considerably higher densities and population sizes of demersal species compared to areas with mostly benthivorous consumers that primarily utilize the benthic food chain. The reliance on the benthic food chain may explain the dominance of

benthivorous species in the southern North Sea where the biomass of benthic macrofauna was shown to be greatest [57]. In addition to higher food availability, the prevalence of benthivorous species in the southern North Sea may be due to lower competition and predation from large gadoids that follow a lower temperature envelope and therefore reside primarily in the deeper, colder northern North Sea. Consequently, the specific adaptations and traits of these species in terms of their feeding and habitat preferences can largely be explained by the different types of environments in which they dominate. This environmental filtering process is indicated by pronounced differences in mean temperature, degree of seasonality, productivity, and depth between the habitats preferred by the distinct communities [24].

The importance of these environmental factors in determining not only differences in species and trait composition, but the overall diversity and biomass of fish communities is clearly evidenced by their pronounced direct and indirect effects in the SEM. The higher relative importance of environmental factors compared to the effect of biodiversity on biomass alone is well in accordance with the idea that large-scale patterns are more environmentally driven than in local and regional systems [46]. In particular, the SEM emphasizes higher biomass in cooler, moderately seasonal, less productive, and deeper environments. This differs from a previous study conducted on reef fish communities, where high biomass was found in warm and less seasonal waters [55]. Additionally, higher biomass of benthic macrofauna was found in the warmer and more productive southern parts of the North Sea [57]. The contrasting spatial patterns and relationship between the environment and biomass in these studies might reflect differences in: (i) the spatial and temporal scale of the analyses, (ii) the environmental conditions and potential productivity between the ecosystems and habitats considered, (iii) and/or a fundamental difference in the way traits of different organism groups determine diets, resource use, and biomass potential.

While many of the environmental variables demonstrated strong, direct, and indirect effects on biomass, we found no significant relationship between fishing effort and biomass (electronic supplementary material, S4). On the contrary, we found a negative correlation between fishing effort and evenness, suggesting that fishing effort is higher in areas where a few species are dominant and potentially reflecting preference of fishery for dominant target species. As such, fishing seems to have a limited impact on the spatial distribution of biomass, richness, and evenness, as also suggested in a previous regional study [68] (electronic supplementary material, S5). Additionally, we found that the slope of the biomass–evenness relationship remained stable over time (electronic supplementary material, S6), indicating that fishing is not significantly modifying this relationship, despite pronounced changes in fishing effort and exploitation rates of individual fish stocks throughout the time period considered [43,69,70]. On the other hand, historical changes in community evenness have been demonstrated indicating that fisheries-induced changes may have occurred well before the time period of our analysis [71], and the results observed in the data might be a result of historical fishing activities. Moreover, recent climate warming has changed the diversity and species assemblages in western European seas [72,73], and caused an increase in the number of species [68,74], with a gradual displacement of gadoid species

towards northern, deeper, and colder waters [72,75]. Such warming and fishing-induced effects on fish communities ecosystem functioning are still unknown.

In summary, our observational study of demersal fish assemblages in a naturally variable environment illustrates that the potential relationships between biodiversity, ecosystem functioning, and the surrounding environment are highly context dependent and far from universally applicable [17,18]. In particular, we have shown that species richness, the most commonly applied biodiversity metric, may provide a poor proxy for ecosystem functioning, defined here as the total biomass of demersal fish. Instead, we found the environment (notably, seasonality) and evenness to be good predictors of biomass, as greater dominance and intermediate seasonality gave rise to considerably higher fish biomass. However, not all uneven communities had high biomass, since the identity of the dominant species and their feeding traits seemed to determine the actual level of demersal biomass. This relates to the specific morphological and behavioural adaptations of species to the available food resources in their preferred environments and habitats. Hence, environmentally driven heterogeneity in the availability of resources may determine community composition, diversity (i.e. channelled through traits and assembly processes), and biomass, which in turn affects ecosystem processes and the associated services for human well-being [2]. Finally, we wish to emphasize that while our analysis demonstrated strong and significant relationships between evenness, environmental drivers, and fish community biomass, these relationships may not necessarily hold for other ecosystem functions, spatial-temporal scales, ecosystem types, or taxonomic groups. Hence, we stress the need to further explore and test the BEF concept using simulations, large-scale observational data, and suitable statistical tools to better account for the complex interactions across multiple metrics of biodiversity, ecosystem functioning, and environmental conditions. Only then can we better understand the underlying processes and mechanisms by which biodiversity creates and maintains the structure and integrity of ecosystems and predict the impacts of biodiversity loss and climate change on ecosystems and human wellbeing.

Data accessibility. All data used in this study are freely available online and sources are described in the electronic supplementary material. Data used in this study are available to reproduce figures and statistical analyses from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j76d7t2> [76]. An R code is available, with a link provided in the electronic supplementary material.

Authors' contributions. A.M. and M.L. designed the study. A.M., E.B., H.G., P.D.v.D., and T.S.D. contributed to data collection and treatment. Statistics were performed by A.M., D.H., and P.D.v.D. Interpretation of the results included A.M., M.L., D.H., H.H., P.D.v.D., and H.G. The first manuscript was written by A.M. and was reviewed by all co-authors.

Competing interests. We declare we have no competing interests.

Funding. A.M. received funding from VILLUM research grant awarded to M.L. (No. 13159). E.B. has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 675997 (ITN MARmaED).

Acknowledgements. We wish to thank Ken H. Andersen, Marie-Christine Rufener, and Laurene Pecuchet for their constructive comments on the project, and Ole R. Eigaard for providing and helping with the European fishing effort dataset. A.M., M.L., P.D.v.D., T.S.D., and E.B. conducted the work within the Centre for Ocean Life, a Villum Kann Rasmussen Center of Excellence supported by the Villum Foundation.

- Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016 Biodiversity: the ravages of guns, nets and bulldozers. *Nature* **536**, 143–145. (doi:10.1038/536143a)
- Cardinale BJ *et al.* 2012 Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67. (doi:10.1038/nature11148)
- Tilman D, Wedin D, Knops J. 1996 Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720. (doi:10.1038/379718a0)
- Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B. 2006 Quantifying the evidence for biodiversity effects on ecosystem functioning and services: biodiversity and ecosystem functioning/services. *Ecol. Lett.* **9**, 1146–1156. (doi:10.1111/j.1461-0248.2006.00963.x)
- Cardinale BJ, Srivastava DS, Emmett Duffy J, Wright JP, Downing AL, Sankaran M, Jouseau C. 2006 Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**, 989–992. (doi:10.1038/nature05202)
- Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN. 2015 Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos* **124**, 252–265. (doi:10.1111/oik.01549)
- Duffy JE, Godwin CM, Cardinale BJ. 2017 Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**, 261–264. (doi:10.1038/nature23886)
- Schneider FD, Brose U, Rall BC, Guill C. 2016 Animal diversity and ecosystem functioning in dynamic food webs. *Nat. Commun.* **7**, 12718. (doi:10.1038/ncomms12718)
- Poisot T, Mouquet N, Gravel D. 2013 Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecol. Lett.* **16**, 853–861. (doi:10.1111/ele.12118)
- Thebault E, Loreau M. 2003 Food-web constraints on biodiversity–ecosystem functioning relationships. *Proc. Natl Acad. Sci. USA* **100**, 14 949–14 954. (doi:10.1073/pnas.2434847100)
- Fung T, Farnsworth KD, Reid DG, Rossberg AG. 2015 Impact of biodiversity loss on production in complex marine food webs mitigated by prey-release. *Nat. Commun.* **6**, 6657. (doi:10.1038/ncomms7657)
- Loreau M, Hector A. 2001 Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76. (doi:10.1038/35083573)
- Strong JA *et al.* 2015 Marine biodiversity and ecosystem function relationships: the potential for practical monitoring applications. *Estuar. Coast. Shelf Sci.* **161**, 46–64. (doi:10.1016/j.ecss.2015.04.008)
- Bell T, Newman JA, Silverman BW, Turner SL, Lilley AK. 2005 The contribution of species richness and composition to bacterial services. *Nature* **436**, 1157–1160. (doi:10.1038/nature03891)
- Maynard DS, Crowther TW, Bradford MA. 2017 Competitive network determines the direction of the diversity–function relationship. *Proc. Natl Acad. Sci. USA* **114**, 11 464–11 469. (doi:10.1073/pnas.1712211114)
- Tylianakis JM, Rand TA, Kahmen A, Klein A-M, Buchmann N, Perner J, Tschardt T. 2008 Resource heterogeneity moderates the biodiversity–function relationship in real world ecosystems. *PLoS Biol.* **6**, e122. (doi:10.1371/journal.pbio.0060122)
- Duncan C, Thompson JR, Pettoelli N. 2015 The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. *Proc. R. Soc. B* **282**, 20151348. (doi:10.1098/rspb.2015.1348)
- Daam MA, Teixeira H, Lillebø AI, Nogueira AJA. 2019 Establishing causal links between aquatic biodiversity and ecosystem functioning: status and research needs. *Sci. Total Environ.* **656**, 1145–1156. (doi:10.1016/j.scitotenv.2018.11.413)
- Loreau M, Mouquet N, Gonzalez A. 2003 Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl Acad. Sci. USA* **100**, 12 765–12 770. (doi:10.1073/pnas.2235465100)
- Hodapp D, Hillebrand H, Blasius B, Ryabov AB. 2016 Environmental and trait variability constrain community structure and the biodiversity–productivity relationship. *Ecology* **97**, 1463–1474. (doi:10.1890/15-0730.1)
- Thompson PL, Isbell F, Loreau M, O'Connor MI, Gonzalez A. 2018 The strength of the biodiversity–ecosystem function relationship depends on spatial scale. *Proc. R. Soc. B* **285**, 20180038. (doi:10.1098/rspb.2018.0038)
- Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J. 2018 Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* **359**, 791–793. (doi:10.1126/science.aao2117)
- Grace JB. 2006 *Structural equation modeling and natural systems*. Cambridge, UK: Cambridge University Press.
- Pecuchet L *et al.* 2017 From traits to life-history strategies: deconstructing fish community composition across European seas. *Glob. Ecol. Biogeogr.* **26**, 812–822. (doi:10.1111/geb.12587)
- Gascuel D *et al.* 2016 Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish. Fish.* **17**, 31–55. (doi:10.1111/faf.12090)
- Jennings S, Kaiser MJ. 1998 The effects of fishing on marine ecosystems. In *Advances in Marine Biology*, pp. 201–352. Elsevier. (doi:10.1016/S0065-2881(08)60212-6)
- WoRMS Editorial Board. 2017 World Register of Marine Species. See <http://www.marinespecies.org> at VLIZ. Accessed 2017. (doi:10.14284/170)
- Froese R, Pauly D. (eds) 2019 FishBase. World Wide Web electronic publication. www.fishbase.org, version (04/2019).
- Greenstreet SPR, Fraser HM, Rogers SI, Trenkel VM, Simpson SD, Pinnegar JK. 2012 Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community. *ICES J. Mar. Sci.* **69**, 8–22. (doi:10.1093/icesjms/fsr188)
- Greenstreet S, Piet G. 2008 Assessing the sampling effort required to estimate α species diversity in the groundfish assemblages of the North Sea. *Mar. Ecol. Prog. Ser.* **364**, 181–197. (doi:10.3354/meps07499)
- Gotelli NJ, Colwell RK. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391. (doi:10.1046/j.1461-0248.2001.00230.x)
- Gotelli NJ, Colwell RK, Magurran AE, McGill BJ. 2011 Estimating species richness. In *Biological diversity: frontiers in measurement and assessment* (ed. BJ McGill), pp. 39–54. Oxford, UK: Oxford University Press.
- Oksanen J *et al.* 2017 vegan: Community Ecology Package. R package version 2.4-4. <https://CRAN.R-project.org/package=vegan>.
- Hillebrand H, Bennett DM, Cadotte MW. 2008 Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**, 1510–1520. (doi:10.1890/07-1053.1)
- Hill MO. 1973 Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**, 427–432. (doi:10.2307/1934352)
- Baselga A. 2010 Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–143. (doi:10.1111/j.1466-8238.2009.00490.x)
- Baselga A, Orme CDL. 2012 betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812. (doi:10.1111/j.2041-210X.2012.00224.x)
- Laliberté E, Legendre P, Shipley B. 2014 FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package Version 10-12.
- Beukhof E, Dencker TS, Palomares MLD, Maureaud A. 2019 A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas. See <https://doi.pangaea.de/10.1594/PANGAEA.900866>.
- Rayner NA, Parker DE, Horton EB, Folland CK, Alexander LV, Rowell DP, Kent EC, Kaplan A. 2003 Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res. Atmos.* **108**, D14. (doi:10.1029/2002JD002670)
- Wilson RJ, Speirs DC, Sabatino A, Heath MR. 2018 A synthetic map of the north-west European Shelf sedimentary environment for applications in marine science. *Earth Syst. Sci. Data* **10**, 109–130. (doi:10.5194/essd-10-109-2018)
- Maritorena S, D'Andon OHF, Mangin A, Siegel DA. 2010 Merged satellite ocean color data products using a bio-optical model: characteristics, benefits and issues. *Remote Sens. Environ.* **114**, 1791–1804.
- Eigaard OR *et al.* 2016 The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865. (doi:10.1093/icesjms/fsw194)

44. Kroodsm DA *et al.* 2018 Tracking the global footprint of fisheries. *Science* **359**, 904–908. (doi:10.1126/science.aao5646)
45. Worm B, Duffy JE. 2003 Biodiversity, productivity and stability in real food webs. *Trends Ecol. Evol.* **18**, 628–632. (doi:10.1016/j.tree.2003.09.003)
46. Loreau M. 2001 Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808. (doi:10.1126/science.1064088)
47. Adler PB *et al.* 2011 Productivity is a poor predictor of plant species richness. *Science* **333**, 1750–1753. (doi:10.1126/science.1204498)
48. Jost L. 2010 The relation between evenness and diversity. *Diversity* **2**, 207–232. (doi:10.3390/d2020207)
49. Soininen J, Passy S, Hillebrand H. 2012 The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. *Oecologia* **169**, 803–809. (doi:10.1007/s00442-011-2236-1)
50. Cardinale BJ, Bennett DM, Nelson CE, Gross K. 2009 Does productivity drive diversity or vice versa? A test of the multivariate productivity–diversity hypothesis in streams. *Ecology* **90**, 1227–1241. (doi:10.1890/08-1038.1)
51. Lefcheck JS. 2016 PIECEWISESEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579. (doi:10.1111/2041-210X.12512)
52. Walker ND, Maxwell DL, Le Quesne WJF, Jennings S. 2017 Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES J. Mar. Sci.* **74**, 1448–1457. (doi:10.1093/icesjms/fsw250)
53. Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Fraschetti S, Vanreusel A, Vincx M, Gooday AJ. 2008 Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Curr. Biol.* **18**, 1–8. (doi:10.1016/j.cub.2007.11.056)
54. Mora C *et al.* 2011 Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol.* **9**, e1000606. (doi:10.1371/journal.pbio.1000606)
55. Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ. 2016 Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl Acad. Sci. USA* **113**, 6230–6235. (doi:10.1073/pnas.1524465113)
56. Lehtinen S, Tamminen T, Ptacnik R, Andersen T. 2017 Phytoplankton species richness, evenness, and production in relation to nutrient availability and imbalance: phytoplankton species richness, evenness, and production. *Limnol. Oceanogr.* **62**, 1393–1408. (doi:10.1002/lno.10506)
57. Heip C *et al.* 1992 Trends in biomass, density and diversity of North Sea macrofauna. *ICES J. Mar. Sci.* **49**, 13–22. (doi:10.1093/icesjms/49.1.13)
58. Dulvy NK, Sadovy Y, Reynolds JD. 2003 Extinction vulnerability in marine populations. *Fish Fish.* **4**, 25–64. (doi:10.1046/j.1467-2979.2003.00105.x)
59. Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA. 2005 Biology of extinction risk in marine fishes. *Proc. R. Soc. B* **272**, 2337–2344. (doi:10.1098/rspb.2005.3281)
60. Mulder CPH, Bazeley-White E, Dimitrakopoulos PG, Hector A, Scherer-Lorenzen M, Schmid B. 2004 Species evenness and productivity in experimental plant communities. *Oikos* **107**, 50–63. (doi:10.1111/j.0030-1299.2004.13110.x)
61. Hillebrand H, Matthiessen B. 2009 Biodiversity in a complex world: consolidation and progress in functional biodiversity research: consolidation and progress in BDEF research. *Ecol. Lett.* **12**, 1405–1419. (doi:10.1111/j.1461-0248.2009.01388.x)
62. Hodapp D, Meier S, Muijers F, Badewien T, Hillebrand H. 2015 Structural equation modeling approach to the diversity-productivity relationship of Wadden Sea phytoplankton. *Mar. Ecol. Prog. Ser.* **523**, 31–40. (doi:10.3354/meps11153)
63. Filstrup CT, Hillebrand H, Heathcote AJ, Harpole WS, Downing JA. 2014 Cyanobacteria dominance influences resource use efficiency and community turnover in phytoplankton and zooplankton communities. *Ecol. Lett.* **17**, 464–474. (doi:10.1111/ele.12246)
64. Engelhardt KA, Ritchie ME. 2001 Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature* **441**, 687–689. (doi:10.1038/35079573)
65. Dangles O, Malmqvist B. 2004 Species richness-decomposition relationships depend on species dominance: biodiversity and dominance in ecosystems. *Ecol. Lett.* **7**, 395–402. (doi:10.1111/j.1461-0248.2004.00591.x)
66. Brose U, Hillebrand H. 2016 Biodiversity and ecosystem functioning in dynamic landscapes. *Phil. Trans. R. Soc. B* **371**, 20150267. (doi:10.1098/rstb.2015.0267)
67. van Denderen PD, Lindegren M, MacKenzie BR, Watson RA, Andersen KH. 2018 Global patterns in marine predatory fish. *Nat. Ecol. Evol.* **2**, 65–70. (doi:10.1038/s41559-017-0388-z)
68. Dencker TS, Pecuchet L, Beukhof E, Richardson K, Payne MR, Lindegren M. 2017 Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: causes and consequences. *PLoS ONE* **12**, e0189731. (doi:10.1371/journal.pone.0189731)
69. Engelhard GH, Lynam CP, García-Carreras B, Dolder PJ, Mackinson S. 2015 Effort reduction and the large fish indicator: spatial trends reveal positive impacts of recent European fleet reduction schemes. *Environ. Conserv.* **42**, 227–236. (doi:10.1017/S0376892915000077)
70. Blanchard J, Dulvy N, Jennings S, Ellis J, Pinnegar J, Tidd A, Kell L. 2005 Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES J. Mar. Sci.* **62**, 405–411. (doi:10.1016/j.icesjms.2005.01.006)
71. Rijnsdorp A. 1996 Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES J. Mar. Sci.* **53**, 1054–1062. (doi:10.1006/jmsc.1996.0132)
72. Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. 2008 Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* **45**, 1029–1039. (doi:10.1111/j.1365-2664.2008.01488.x)
73. Perry AL. 2005 Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915. (doi:10.1126/science.1111322)
74. Hiddink JG, ter Hofstede R. 2008 Climate induced increases in species richness of marine fishes. *Glob. Change Biol.* **14**, 453–460. (doi:10.1111/j.1365-2486.2007.01518.x)
75. Engelhard GH, Righton DA, Pinnegar JK. 2014 Climate change and fishing: a century of shifting distribution in North Sea cod. *Glob. Change Biol.* **20**, 2473–2483. (doi:10.1111/gcb.12513)
76. Maureaud A, Hodapp D, van Denderen PD, Hillebrand H, Gislason H, Spaanheden Dencker T, Beukhof E, Lindegren M. 2019 Data from: Biodiversity–ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. Dryad Digital Repository. (<https://doi.org/10.5061/dryad.j76d7t2>)