

Threatened fish species in the Northeast Atlantic are functionally rare

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Abstract

Aim: The criteria used to define the International Union for Conservation of Nature (IUCN) Red List categories are essentially based on demographic parameters at the species level, but they do not integrate species' traits or their roles in ecosystems. Consequently, current IUCN-based protection measures may not be sufficient to conserve ecosystem functioning and services. Some species may have a singular combination of traits associated with unique functions. Such functionally distinct species are increasingly recognized as a key facet of biodiversity since they are, by definition, functionally irreplaceable. The aim of this study is to investigate whether threatened species are also functionally rare and to identify which traits determine extinction risk.

Location: European continental shelf seas.

Time period: 1984–2020.

Major taxa studied: Marine fish.

Methods: Using newly compiled trait information of 425 marine fish species in European waters, and more than 30 years of scientific bottom trawl surveys, we estimated the functional distinctiveness, restrictedness and scarcity of each species and cross-referenced it with their IUCN conservation status.

Results: In European continental shelf seas, 38% of the species threatened with extinction (9 out of 24 species) were identified as the most functionally distinct. By mapping extinction risk in the multidimensional species trait space, we showed that species with the greatest risk of extinction are long-lived and of high trophic level. We also identified that the most functionally distinct species are sparsely distributed (4% of the total area on average) and have scarce abundances (<1% of the relative mean abundance of common species).

Main Conclusions: Because a substantial proportion of threatened species are functionally distinct and thus may play unique roles in ecosystem functioning, we stress that species traits—especially functional rarity—should become an indispensable step in the development of conservation management plans.

KEYWORDS

distinctiveness, extinction risk, functional rarity, IUCN, marine fish, species trait, threatened

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1 | INTRODUCTION

Global changes and increasing anthropic pressures are causing a rapid and unprecedented loss of biodiversity (Ceballos et al., 2015; IPBES, 2019). This so-called 'biodiversity crisis' not only threatens unique habitats and biota worldwide, but also the provisioning of key goods and services for human well-being (Halpern et al., 2008; Pecl et al., 2017). To ensure that biodiversity is preserved and that natural resources are used in an equitable and sustainable manner, the International Union for Conservation of Nature (IUCN) encourages and assists societies to preserve the integrity and diversity of nature. This includes providing assessments of the extinction risk of species across the globe to define the IUCN Red List used as a benchmark to support policymakers, government agencies, wildlife departments and nongovernmental organizations in the elaboration of conservation actions and priorities (Alaniz et al., 2019). Red List categories are defined according to quantitative thresholds using five criteria that incorporate the geographical range of the species and population size/trends, known for only a few well-monitored species (IUCN, 2022). The IUCN Red List does not currently integrate species traits that provide insights into their contribution to ecosystems through physiological, morphological, reproductive or behavioural characteristics (Tilman, 2001; Violle et al., 2017), making it difficult to integrate ecosystem functioning into conservation plans.

Traits provide a mechanistic understanding of species responses to environmental forcing and their effects on ecosystem functioning (Gagic et al., 2015; McGill et al., 2006). Trait-based indexes can detect community responses earlier than indexes based on taxonomic characteristics (McLean et al., 2019; Mouillot, Bellwood, et al., 2013; Pécuchet et al., 2017), allowing more efficient conservation plans. Moreover, trait-based approaches are helpful to anticipate which species are the most sensitive to climatic (Jones & Cheung, 2018), and/or anthropogenic (e.g. fishing; Cheun et al., 2005) pressures, to implement targeted protection measures, even before species are impacted (Hare et al., 2016). For example, the use of trait-based metrics has shown that seabirds with narrow habitat breadths, and fast reproduction strategies, are impacted by human-induced habitat degradation worldwide (Richards et al., 2021). Species traits can serve as a valuable tool in assessing species extinction risk (Carmona et al., 2021), especially when demographic data are lacking (Luiz et al., 2016; Walls & Dulvy, 2020). By incorporating species traits, it becomes easier to align species richness hotspots with functional concerns (Grenié et al., 2018), an approach more in line with a precautionary attitude (Dulvy et al., 2021; Lyons et al., 2005). This is especially evident for marine fish such as skates, classified as non-threatened or data deficient species, but identified as highly sensitive to trawling based on their life-history parameters, body shape and habitat (Rindorf et al., 2020). Using different scenarios based on the IUCN species' extinction risk assessments, a recent study projected a global erosion of the functional spectra of larger species with slower pace of life (Carmona et al., 2021). Although considering functional trait information for more than 75,000 species

worldwide, marine fishes were not included despite their important ecological and socio-economical roles and benefits to human health and well-being, from protein supply to climate regulation to recreation (Guerry et al., 2010). Many of these services rely—to some extent—on the presence of only a few functionally distinct species that provide pivotal functions within ecosystems (Bracken & Low, 2012; Dee et al., 2019; Leitão et al., 2016).

These key functions are generally achieved through a combination of traits that provide species-specific capabilities: while some combinations are widespread in marine ecosystems (e.g. invertivorous diet, demersal water-column position, diurnal active period, solitary behaviour and small-to-medium body size; McLean et al., 2021), other trait compositions are more distinct and supported predominantly by species with no functional equivalent; this results in low functional redundancy (Violle et al., 2017). The classical approach that consists of using biomass or total productivity as an indicator of ecosystem functioning, where dominant species are assumed to drive ecological processes and low-abundant species are assumed to contribute weakly (Grime, 1998), has led to disregarding low-abundant species that may be functionally distinct. Nevertheless, it is generally accepted that even when they are low in abundance, top predators can have a disproportionate impact on ecosystem functioning. Therefore, it should be acknowledged that the loss of species with unique functional traits (i.e. functionally distinct species; Violle et al., 2017), can have major impacts on ecosystem stability and functioning if no other species can compensate for the potentially lost functions (Mouillot et al., 2013a, 2013b). Shifts in energy and/or nutrient inputs in ecosystems or disequilibrium in the structure of trophic webs have already been documented in response to the loss of these species (Carmona et al., 2021; Colares et al., 2022; McLean et al., 2019).

Functionally distinct species are under-represented in the IUCN categories because of a lack of species trait information, including distinctiveness, in the classification (Loiseau et al., 2020), which may lead to mismatches between hotspots of functional fish distinctiveness and the implementation of protection measures such as marine protected areas (Grenié et al., 2018; Trindade-Santos et al., 2022). When functionally distinct species are also spatially restricted or poorly abundant, ecosystem stability may be even more fragile in the sense that stability depends on a few key species having disproportionate impacts on the ecosystem relative to their biomass (i.e. functionally rare species; Violle et al., 2017). For example, the giant moray eel (*Gymnothorax javanicus*) is a large sedentary nocturnal benthic specialized predator, with few potential challengers to this role in coral reef ecosystems (Mouillot, Bellwood, et al., 2013). This species is no longer just functionally distinct, it is also functionally rare within communities (Violle et al., 2017), as are most predators. Unfortunately, distinctiveness is thought to be an evolutionary response to a spatially and temporally stable environment, so functionally distinct species—especially species with specific dietary needs—may be more vulnerable to abrupt environmental and anthropogenic changes than those carrying more common traits (Clavel et al., 2011). Protecting functionally rare species is therefore

crucial to maintaining the ecological integrity of ecosystems while helping to identify which sites to prioritize for conservation. It should also allow for the protection of a large assemblage of species, by focussing efforts on only a few, which can be a considerable advantage in establishing management plans (Astudillo-Scalia & de Albuquerque, 2019).

Based on approximately four decades of scientific bottom trawl surveys in European seas, we first identified which species are functionally distinct and what are the traits that characterize them. We then quantified to what degree threatened species are the most functionally rare by assessing their functional distinctiveness, restrictedness and scarcity. Finally, we argue for greater integration of traits in the assessment of species extinction risk, as the use of traits also allows the identification of functionally distinct species which, by definition, contribute to vulnerable functions performed by few species (Violle et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study area and bottom trawl surveys

The study area covers most of the European continental shelf seas, including the Baltic Sea, the North Sea, the English Channel, the Scottish west coast, the Celtic Sea, Rockall and Porcupine Banks, the Irish Sea, Bay of Biscay and the Portuguese coast and is divided into 1° longitude by 0.5° latitude grid cells (hereafter 'rectangles') as defined by the International Council for the Exploration of the Sea (ICES) (Figure 1). Abundance data were collated from 20 scientific bottom trawl surveys (see Supporting Information Appendix S1–Table S1) during the last four decades, from 1984 to 2020. Sampling was carried out during daylight at an average speed of 4 knots for at least 20 min. Although gears and sampling schemes differ between surveys (see Supporting Information Appendix S1–Table S1), all captured individuals were identified at the finest taxonomic level possible and reported in a standardized number of individuals per species caught per hour of trawling, including potadromous species that may be caught in brackish water (Kawamura, 2008). The abundance dataset we used was obtained from the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark. (<https://datras.ices.dk>) and includes 425 species across 536 standard ICES rectangles. Due to the absence of reporting on non-commercial species from Spanish surveys, we did not include these surveys. Since the total number of hauls per rectangle is spatially heterogeneous (from 3 to 1070; see Supporting Information Appendix S2–Figure S1a), we standardized sampling effort by means of species accumulation curves (SACs) (Chao, 1987) for each rectangle, considering each haul as a sampling unit, using the 'vegan' R package (Oksanen et al., 2008). Nonlinear Michaelis–Menten curves were fitted to each of the SACs. When the total number of hauls was lower than the estimated number of hauls necessary to achieve 65% of the asymptotic species richness, we discarded the rectangle (59 rectangles

out of 536) following the approach of Maureaud et al. (2019) (see Supporting Information Appendix S2–Figure S1b).

2.2 | Species traits and gap filling

We selected traits that reflect habitat use, life-history and trophic ecology of species expected to be implicated in the response of species to environmental changes and ecosystem functioning (see Supporting Information Appendix S1–Table S2 for reasoning; Beukhof, Dencker, Pecuchet, & Lindegren, 2019; McLean et al., 2019, Murgier et al., 2021). Among the selected traits, eight are continuous (trophic level, age at sexual maturity, length at sexual maturity, fecundity, offspring size, Von Bertalanffy growth coefficient K, maximum length and length infinity) and three are categorical (position in the water column, feeding mode and spawning type). Trait data for the 425 species were initially collected by extracting trait values from the North Atlantic and Northeast Pacific shelves dataset collated by Beukhof, Dencker, Palomares, and Maureaud (2019). Our obtained trait dataset had 38% missing trait values (1289 out of 3386), explained by the presence of missing data in Beukhof, Dencker, Palomares, and Maureaud (2019) and because some species we studied were not in Beukhof et al. (2019b). We filled missing values by following the procedure undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019) and by using the predictive life-history model developed by Thorson et al. (2017).

Continuous traits were supplemented with information extracted from FishBase (Froese & Pauly, 2020) restricted to the Northeast Atlantic and completed by scientific literature as undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019). For 'trophic level', 'offspring size' and 'fecundity' traits not available at the species levels, we averaged the trait values at the genus level or family level if genus was not available, following Beukhof, Dencker, Palomares, and Maureaud (2019). Additionally, 'age at maturity', 'size at maturity', 'Von Bertalanffy's growth coefficient K' and 'infinite size' traits were completed (171 values) using the data-integrated predictive life-history model (Thorson et al., 2017) made available in the 'FishLife' R package. This model estimates life-history parameters by incorporating existing data and life-history correlations between related species into a multivariate random walk model. Three life-history traits per species must be known to accurately predict the remaining life-history variables. Predictions are more accurate for species with many measurements than those for which only a few measurements were made. Therefore, we were unable to predict all of the missing life-history traits and applied the note accompanying the FishBase 'Growth' table advising to keep species life-history parameters only when the predicted infinite size is not more or less than one-third different from the maximum reported size for the species. For categorical traits, missing traits were extracted from FishBase, completed by scientific literature and finally assigned according to the trait values of a species of the same genus or family when information was available. After completion, only 4% of the values (i.e. 139 of the 3386) were missing and scattered

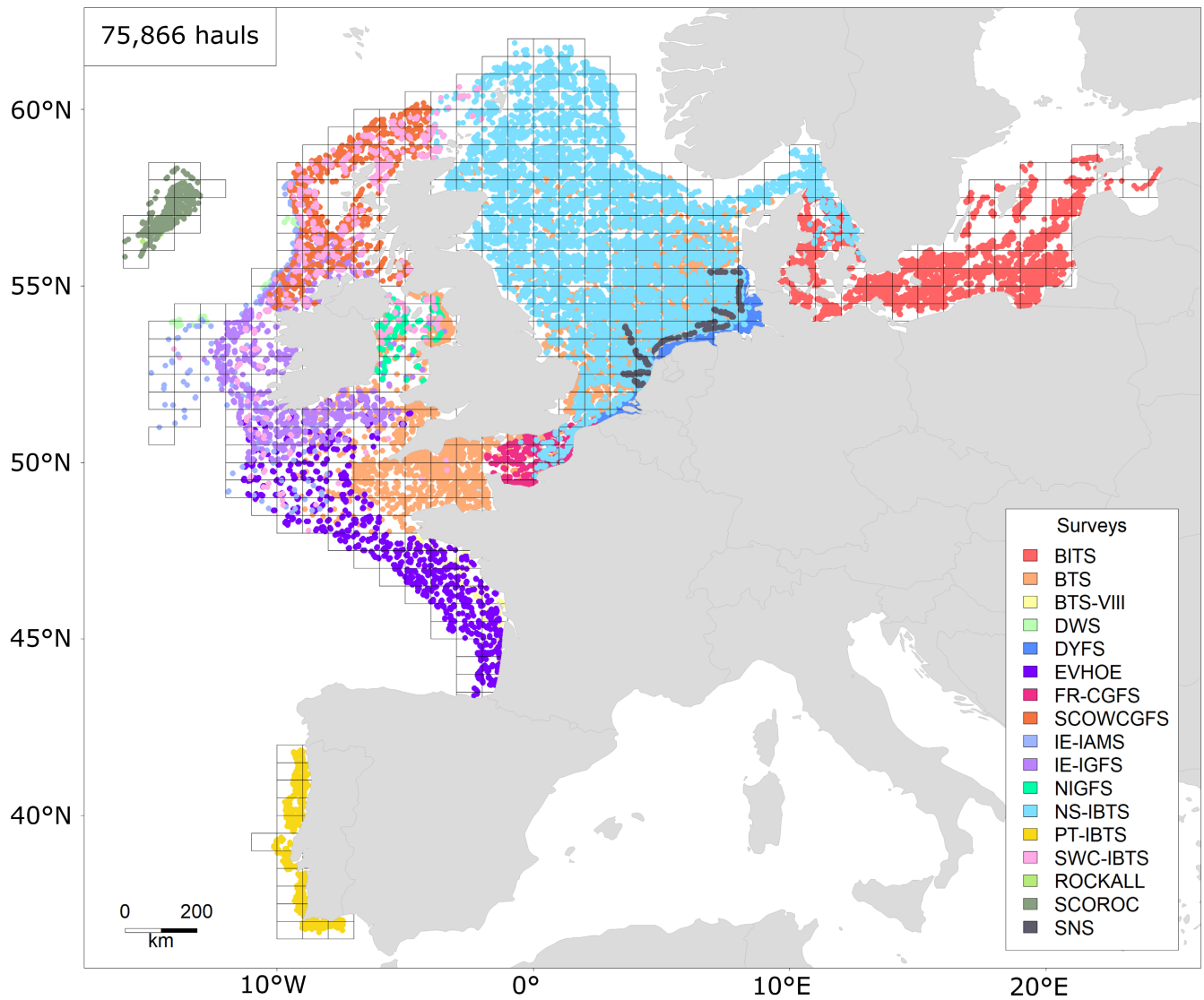


FIGURE 1 Map of the available bottom trawl surveys of demersal fish communities across northwest European continental shelf seas obtained from the International Council for the Exploration of the Sea data portal (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Coloured dots locate the individual hauls, with one colour per survey. ICES rectangles (1° longitude by 0.5° latitude grid cells) are represented. See Supporting Information Appendix S1—Table S1 for detailed information about bottom trawl surveys and their acronyms.

within the different trait types with less than 10% missing values, at most, per trait. Our final database contains 339 species fully informed. The resulting trait database is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1 (see also Appendix 1—Data sources).

2.3 | Functional distinctiveness, restrictedness and scarcity

The functional rarity framework developed by Violle et al. (2017) provided a definition and quantification of functional rarity that considers both trait distinctiveness, species abundance and species distribution. According to this concept, functionally rare species have low abundances and are the most distinct and spatially restricted

in local areas, while functionally common species have the highest abundances, common trait values and larger spatial distributions. The functional distinctiveness D_i of species i is an index calculated independently of species abundance, quantifying how a species i is functionally dissimilar to all other species in the community (Violle et al., 2017), considering one combination of traits:

$$D_i = \frac{\sum_{j=1, j \neq i}^S d_{ij}}{S - 1} \quad (1)$$

with S the total number of species within the study area and d_{ij} the dissimilarity between species i and j . A species with a high D_i value is considered functionally distinct compared with the rest of the pool (Violle et al., 2017). Because identifying the relevant number of traits to correctly describe ecological functions is difficult and subjective

(Lepš et al., 2006; Petchey & Gaston, 2002), we computed an integrative version of the functional distinctiveness index (IntDi) that not only considers one combination of traits (i.e. the combination of all available traits) but all possible combinations of available traits. This index therefore provides a more robust assessment of species distinctiveness (see Supporting Information Appendix S1–Table S3) and a more objective ranking between species according to their functional distinctiveness; it ensures that a species has a high distinctiveness value not because of a single extreme trait value but because it has several uncommon trait values (Grenié et al., 2017). The R code is freely available at Figshare public data repository 10.6084/m9.figshare.22317643.v1 (see also Appendix 1–Data sources). We calculated the dissimilarity matrix (i.e. dissimilarities between species based on their traits) of each possible combination of traits among the 11 traits selected for this study, considering that a minimum of 4 is needed to characterize the difference between species (Petchey & Gaston, 2002). This procedure therefore provides a total of 1816 dissimilarity matrices. We then calculated the IntDi value of each species from the integrated dissimilarity matrix itself computed as the average between the 1816 matrices (see Supporting Information Appendix S2–Figure S2 for example). Additionally, to prevent any disproportionate contribution of categorical traits in dissimilarity matrices and thus on distinctiveness computation, we applied the approach developed by de Bello et al. (2021) using the 'gawdis' package. Functional distinctiveness was standardized so that it ranges between 0 and 1. We followed the same procedure for the resulting trait database, the database with no missing data, and the database with missing data predicted with the R package 'missForest' (Stekhoven & Buehlmann, 2012). We developed two linear models (Supporting Information Appendix S2–Figure S3; $R_1^2=0.9954$ & $R_2^2=0.9982$) and calculated the percentage of variation between the rankings to ensure the robustness of the ranking made from the integrated distinctiveness calculation (refer to Supporting Information Appendix S1–Table S4). The 425 species were then grouped on the basis of their IntDi values: the first group (D1, the most functionally common species) was defined according to the first decile of IntDi,

while the last group (D10, the most functionally distinct species) was defined according to the last decile. This division into deciles was done a posteriori according to the number of groups allowing to best isolate the most functionally distinct species according to the distribution of distinctiveness values (Figure 2). We then performed Spearman correlation tests to assess the relationship between each continuous trait and species distinctiveness. For categorical traits, differences in functional distinctiveness between trait modalities were computed using Wilcoxon post hoc tests.

A Principal Coordinate Analysis (PCoA) was performed on the average dissimilarity matrix to summarize interspecific dissimilarities in a biplot referred to as a 'trait space'. We calculated the functional dissimilarity between the species of a functional distinctiveness group (e.g. D2) and all other species from all other groups (for this example: all groups without D2) to test for the difference between functional distinctiveness groups (D1 to D10 distribution deciles), according to their dissimilarities. We then tested whether this functional dissimilarity was lower or higher than expected by chance given the number of species in each functional distinctiveness group. The functional dissimilarity between the species of a functional distinctiveness group and all other species was calculated using the R function 'dissim' of the package 'TPD' (Carmona et al., 2019). It reflects the degree of functional dissimilarity between the probabilistic distributions of species in the trait space between the two assemblages and ranges from 0 (complete overlap) to 1 (no overlap). We used a TPD (Trait probability density; 'TPD' package; Carmona et al., 2019) approach—estimation of the probabilistic distribution of the species within the trait space—by performing multivariate kernel density estimations. We divided the 2-dimensional space into 40,000 cells, that is, 200 per dimension. For each species, the kernel was a multivariate normal distribution centred in the coordinates of the species in the trait space and bandwidth was chosen using unconstrained bandwidth selectors from the 'Hpi' R function in the 'ks' package (Chacón & Duong, 2018). We then compared the

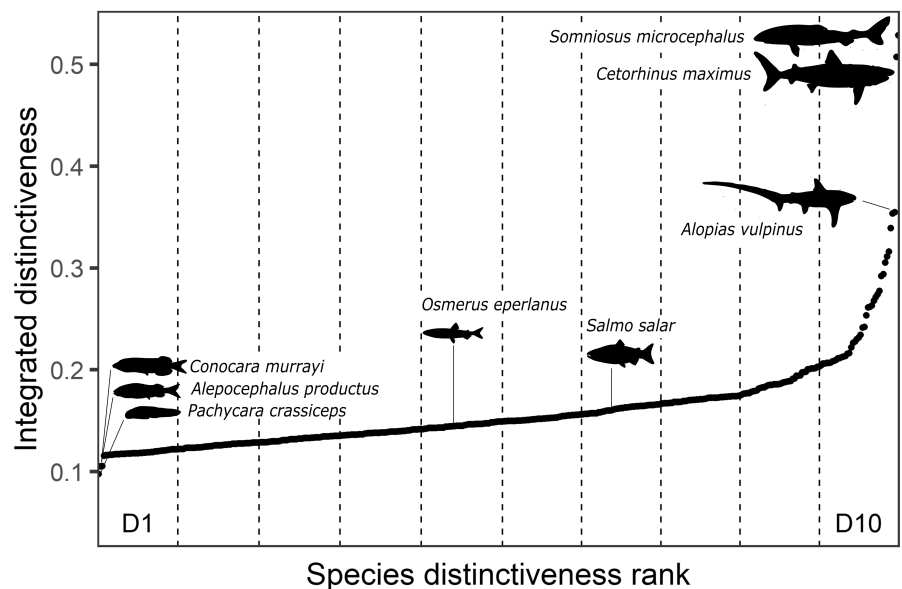


FIGURE 2 Integrated distinctiveness index per species showing that most species are rather functionally common and only a few are very distinct. The grey dotted lines separate species according to distinctiveness deciles, from D1 (the most functionally common species) to D10 (the most functionally distinct species).

observed functional dissimilarity to a null model where the functional distinctiveness groups were randomly assigned to species, keeping the number of species in each group constant. We drew 999 simulated assemblages and compared simulated and observed functional dissimilarities. We calculated standardized effect sizes (SES) as the difference between the observed value and the mean of the simulated values after standardization by their standard deviations: p -values higher (lower) than 0.975 (0.025) indicate that the observed functional dissimilarity is significantly lower (higher) than expected by chance (using a 5% threshold), given the number of species in each group.

We then turned to the complementary components of functional distinctiveness to define functional rarity, that is, the scarcity and spatial restrictedness of species in the study area. Although initially defined at local and regional spatial scales, the indexes can be calculated at the same study scale to capture both aspects of functional rarity: being low in abundance and being spatially poorly distributed (Grenié et al., 2017; Ricotta et al., 2016). This is because both range size and local abundance influence extinction risk; species with small ranges can avoid extinction if their local abundance is high, while species with low local abundance can avoid extinction if they are widespread; species with both small ranges and low local abundance should be at high risk (Johnson, 1998). For a given species, we compared its geographical range with the geographical extent of the entire study area. The spatial restrictedness R_i is an index between 0 and 1 based on species occurrence (Violle et al., 2017) (weakly impacted by gear selectivity) and is computed as follows:

$$R_i = 1 - \frac{K_i}{K_{tot}} \quad (2)$$

with K_i the number of ICES rectangles where species i occurs and K_{tot} the total number of ICES rectangles in the dataset. R_i nearly equals one when a species is present in a single site and 0 when the species is present in all sites (Grenié et al., 2017). Because there are differences in sampling effort between the 536 ICES rectangles, we computed the restrictedness to prevent under or overestimation. The restrictedness was computed for each grid cell by randomly selecting the minimum number of hauls to catch 65% of the asymptotic number of species with enough sampling effort (477 rectangles out of 536). For a given species, the procedure was repeated 100 times. The integrated restrictedness (IntRi) was calculated as the average of restrictedness values.

The scarcity index Sc_i , which ranges between 0 and 1, measures the relative abundance of species i in the community (Violle et al., 2017):

$$Sc_i = \left(-S \times \ln(2) \times Ab_i \right) \quad (3)$$

with S the total number of species in the study area and Ab_i the relative abundance of species i (i.e. the mean abundance of the species divided by the mean abundance of all species in the Northeastern

community). A species with a low relative abundance will have a scarcity value close to 1, while dominant species will tend toward 0. Since scientific bottom trawl surveys are conducted with bottom trawls and not pelagic trawls, we also calculated the scarcity index excluding the 24 pelagic species. For both restrictedness and scarcity, a unilateral Welch's t -test was performed to compare the restrictedness/scarcity between the most functionally common and distinct species (D1 and D10, respectively). We also implemented two Generalized Linear Mixed Models (GLMM) using the 'lme4' R package (Bates et al., 2015) using the restrictedness/scarcity index as a response, the deciles (D1 and D10) as predictors and the species family as a random factor.

2.4 | Relationship between extinction risk, functional distinctiveness and traits

Regional IUCN Red List statuses of species were obtained using the 'rredlist' R package (Chamberlain & Salmon, 2018) and manually verified thanks to the IUCN Red List of Threatened Species (IUCN, 2022). Only species with IUCN status (and not 'Data Deficient' status; 362 out of 425 species) and complete trait information (294 out of 425 species) were selected for the rest of the study. We converted IUCN status into two threat categories: (i) 'not threatened', which grouped together 'least concern' (LC) and 'near-threatened' (NT) species, and (ii) 'threatened', that encompassed 'vulnerable' (VU), 'endangered' (EN) and 'critically endangered' (CR) species. A unilateral Welch's t -test was performed to assess whether species assigned as 'threatened' have a higher distinctiveness than 'non-threatened' species. We then mapped species conservation status in trait space using a trait probability density approach, following Carmona et al. (2021): we set up a Generalized Additive Model (GAM), using the species conservation status as a response, the corresponding position in the different dimensions of the trait space (PCoA axes) as predictors. Model predictions (i.e. the probability of species being threatened) were done for the different PCoA axes without extrapolation. By representing predictions on the different axis, we mapped the complete functional space and therefore offer a visualization of how extinction risk was distributed across trait combinations.

We finally performed a down-sampled Random Forest classification (RF; 'randomForest' R package, Breiman, 2011), recommended when classes are unbalanced (Freeman et al., 2012) to assess the contribution of individual traits on species conservation status. Instead of a bootstrap sample from the entire dataset, each tree of the forest during down-sampling is built from a bootstrap sample from the rare class, along with a sub-sample of the same size from the more common class (Chen et al., 2004). Species threat (1: threatened, 24 species; 0: not threatened, 270 species) was the response variable, and species trait values were the predictors.

The flowchart of the methodology developed for our analyses is presented in Supporting Information Appendix S2—Figure S4.

3 | RESULTS

3.1 | Functionally rare species and their traits

Species rank based on distinctiveness is very robust to missing data, in particular for defining the ranks of the most common and distinct species (see Supporting Information Appendix S1–Table S4), but the absolute value of the distinctiveness decreases more for the most distinct species (see Supporting Information Appendix S2–Figure S3; $R_1^2=0.9954$ & $R_2^2=0.9982$). The integrated distinctiveness (IntDi; Figure 2; see Supporting Information Appendix S1–Table S5) of Northeastern Atlantic marine fish ranges from 0.10 for *Pachycara crassiceps* to 0.51 and 0.53 for Basking Shark (*Cetorhinus maximus*) and Greenland Shark (*Somniosus microcephalus*), respectively, followed by Thresher Shark (*Alopias vulpinus*) with a IntDi value of 0.35. With a median integrated distinctiveness value of 0.14, most species of the European continental shelf are quite functionally common and only a few species are very functionally distinct. The first functional distinctiveness group (D1; 42 species), defined according to the first decile of the integrated distinctiveness indexes distribution, encompasses the most functionally common species with IntDi values ranging from 0.10 to 0.12. Almost all D1 species are 'non-guarder' (one value is missing) and 'demersal' (40 out of 43 species). They spawn a very large number of tiny eggs (median offspring size = 0.96 mm; median fecundity = 50,000) (see Supporting Information Appendix S2–Figure S5). On the opposite part of the distribution (Figure 2), D10 species (42 species, of which 41% are elasmobranchs with 16 sharks and one skate, and a significant number of deep-sea species) groups together the most functionally distinct species with IntDi values between 0.20 and 0.53.

Species that belong to D10 represent between 0 and 17% of the total number of species per ICES rectangle, the maximum number being observed on Porcupine Bank (see Supporting Information Appendix S2–Figure S6). They present particularly high restrictedness values (IntRi = 0.960 ± 0.097), indicating a spatial restriction with significantly more limitations than for D1 species (IntRi = 0.860 ± 0.219 ; unilateral Welch's *t*-test; $p=0.003$; see Supporting Information Appendix S1–Table S5). At the scale of the European continental shelf seas, D10 species are present on average in 4% of the ICES rectangles, the most common species being present on average in 14% of the rectangles. Functionally distinct species (D10 species) also present very high scarcity values (Sci = 0.863 ± 0.278), which is significantly higher (unilateral Welch's *t*-test; $p=0.011$; see Supporting Information Appendix S1–Table S5) than for functionally common species (D1 species; Sci = 0.590 ± 0.450): the relative mean abundance of functionally distinct species corresponds to 0.86% of the relative mean abundance of common species. When pelagic species are removed from the calculation of the scarcity index, the same conclusions are reached (unilateral Welch's *t*-test; $p=0.003$). In addition, the variance of the family random effect is less than the residual variance of each GLMM showing that significant differences in restrictedness/

scarcity between D1 and D10 species are not due to a family effect. In other words, this means that whatever the family, functionally distinct species are also scarce and geographically restricted, resulting in functionally rare species.

The first two axes of the PCoA (57.3% of the total variance; Figure 3a), and tests for the relationship between each trait and the species integrated distinctiveness (see Supporting Information Appendix S2–Figure S5), show that functionally rare species are mainly characterized by slow individual growth, large body size (i.e. length at infinity and maximal length), high trophic level, late sexual maturity, low fecundity and that they provide high parental investment to their progeny in comparison to functionally common species. These species are also mainly not demersal.

3.2 | Extinction risk and functional distinctiveness

Thirty species have not yet been assigned a European IUCN status and 33 species have a 'Data-Deficient' status. These species are distributed in each of the functional distinctiveness groups (see Supporting Information Appendix S2–Figure S7). Of the 294 species considered in this section, 24 are classified as 'threatened' (see Supporting Information Appendix S1–Table S5). Using a unilateral Welch's *t*-test to test whether 'threatened' and 'nonthreatened' species have distinct IntDi values, we show that 'threatened' species have a significantly higher distinctiveness ($p=0.003$) than 'non-threatened' species (see Supporting Information Appendix S2–Figure S8). Indeed, 37.5% of the 'threatened' species are functionally rare species (D10 species) and this percentage increases further (58.3%) if we include D9 species, the second most functionally distinct group. These correspond to elasmobranchs (D9 and D10 species) classified as 'vulnerable', 'endangered' and 'critically endangered' on the IUCN Red List; European Sturgeon (*Acipenser sturio*) classified as 'critically endangered' (D10 species) and Beaked Redfish (*Sebastes mentella*) classified as 'endangered' (D9 species); 100% of the most common species (D1 species) are 'non-threatened' species. However, some threatened species are classified into the rather common functional groups (D2, D3 and D4 species): Sandy Ray (*Leucoraja circularis*, EN), Shagreen Ray (*Leucoraja fullonica*, VU), European Eel (*Anguilla anguilla*, CR), European Whitefish (*Coregonus lavaretus*, VU) and Roundnose Grenadier (*Coryphaenoides rupestris*, EN).

Species with the greatest risk of extinction belong to the group with the highest dissimilarity in trait space (SES = 0.78; Supporting Information Appendix S1–Table S6), a dissimilarity greater than that expected by chance (SES = 14.78, $p=1$). The subspace they occupy is mostly characterized by slow pace-of-life species (i.e. slow individual growth, late sexual maturity, low fecundity, high parental care and larger offspring size; Figure 3b), large maximum size and high trophic levels with a piscivorous feeding mode. These traits are also the most important for assessing the risk of extinction of species according to the down-sampled random forest (error rate = 7.14%; see Supporting Information Appendix S2–Figure S9) with species in the 'threatened'

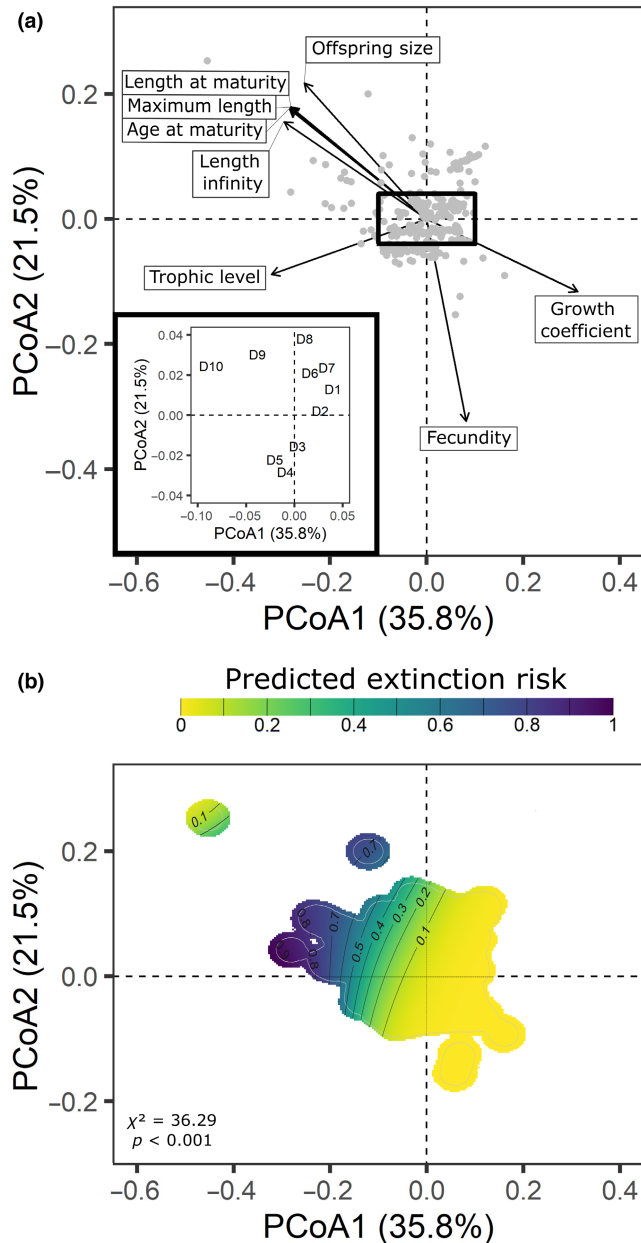


FIGURE 3 Sorting of species along the two principal axes of the principal coordinate analysis (PCoA) of the Northeastern Atlantic marine fish trait data. (a). Functionally rare species are long-lived species. Annotations from D1 (the most common species) to D10 (the most distinct species) refer to the centroids of each functional group. Categorical factors are not represented for convenience and given their low explanatory power. (b). Threatened fish species are functionally rare. Extinction risk in the trait space of the Northeastern Atlantic marine fish. Probability of species being classified as threatened according to the Generalized additive model (GAM) (with binomial distribution; χ^2 and p -values are shown), using the position of species in the functional space as predictors. Yellow tones indicate a low risk of extinction. Purple tones indicate a high risk of extinction. The grey line indicates the 0.99 quantile of the spectra of each group, considering only species with known extinction risk and traits (294 out of 425).

category having larger maximum length and much larger offspring size (see Supporting Information Appendix S2—Figure S10), followed by body size coefficients, fecundity and trophic level.

4 | DISCUSSION

Our aim was to evaluate whether threatened fish species are functionally rare and identify traits that make them vulnerable. To do so, we used IUCN species status, species traits and abundance data from bottom trawl surveys to define the functional rarity of 425 fish species in the European seas. Here we both demonstrate that (i) a substantial proportion (38%) of threatened fish are functional distinct, spatially restricted and present high abundance scarcity and (ii) that the functional distinctiveness of these species is primarily associated with slow pace-of-life strategies. Our results are analogous to similar studies on freshwater fishes (Su et al., 2019), or on terrestrial mammals and birds (Loiseau et al., 2020), demonstrating a general trend to devote efforts to protect species with unique functional traits and supporting key functions within ecological processes (Dee et al., 2019; Leitão et al., 2016; Mouillot, Bellwood, et al., 2013).

The most functionally distinct species identified in our analysis tend to occupy a higher trophic position in the food web to the extent that some, such as Porbeagle (*Lamna nasus*) that feeds mainly on teleost fish and cephalopods (Stevens, 2010), are known to be apex predators (Wallach et al., 2015). Because top predators exert top-down regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), their decline or disappearance may destabilize ecosystems functioning through cascade reactions (Leitão et al., 2016; Mouillot, Graham, et al., 2013; Murgier et al., 2021; Violle et al., 2017). Top predators may also be linked to other ecosystem functions, such as transporting nutrients and carbon through the layers of the ocean (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018). For example, Swordfish (*Xiphias gladius*) feed near the surface at night (0–90m) and up to 650m depth during the day on myctophid fish and squid (Chancollon et al., 2006). Species with a high trophic level may also facilitate the acquisition of organic matter for other species both during their lifetime through their feeding practices (e.g. bioturbation of skates; O'Shea et al., 2012) and after their death when the sinking of their carcass provides food for mobile scavengers over extended periods of time ranging from several weeks to months (e.g. Porbeagle or Thresher Shark; Higgs et al., 2014). Species, such as Turbot (*Scophthalmus maximus*), Brill (*Scophthalmus rhombus*) and Blue Shark (*Prionace glauca*), can also support ecosystem services including food supply (Simpfendorfer et al., 2011) and tourism (Cisneros-Montemayor et al., 2013; Gonzáles-Mantilla et al., 2022). Associating the extinction risk to the impact of a given species on the entire food web—like the complexity of its interactions with other species—would be relevant to move toward efficient ecosystem conservation plans.

Functionally distinct species (D10 species) also reach sexual maturity later, at a larger size, and carry few larger eggs or offspring to which they provide parental care, thus having an overall slower pace of life. Among these species, there are 16 external brooding and internal live-bearing sharks whose new-born pups are very large (28–175 cm), such as Blue Shark that has evolved placentae with gestation lasting from 9 to 12 months (Dulvy & Reynolds, 1997). The 'bearer' type (i.e. external brood and internal live-bearer type) occurs

when the benefits of increased offspring survival outweigh the costs of reduced fertility, mobility and increased metabolic demands of carrying offspring through development (Goodwin et al., 2002). Two teleost species (Ribbonfish: *Trachipterus arcticus* and European Sturgeon), distinguished by very high fecundity in contrast to older ages at maturity are also among the most functionally distinct species. Similarly, by studying more than 75,000 species of vascular plants, mammals, birds, reptiles, amphibians and freshwater fish, Carmona et al. (2021) showed that species with long-lived functional strategies, living in stable environments in which investment in juvenile survival is more effective in maintaining the population, are more likely to be threatened with extinction.

Furthermore, we show that distinct species (D10 species) are mostly poorly geographically distributed and low in abundance. Unfortunately, species that have small population sizes, restricted geographical ranges (or habitat extent) and, often, narrow environmental niches, are especially vulnerable to extinction (Casey et al., 2021; Davies et al., 2004; Harnik et al., 2012; Johnson, 1998; Loiseau et al., 2020). Some of the most spatially restricted species (see restrictedness index) are evolving at great depths (e.g. *Melanostigma atlanticum*; *Maulisia microlepis*; *Benthocometes robustus*; *Normichthys operosus*), including deep-sea sharks (e.g. sharpnose sevengill shark (*Heptranchias perlo*) and *Somniosus* sp.), therefore having a low probability of being encountered on the continental shelf due to biological constraints. Large pelagic species such as Thresher Shark and Swordfish rank among the least abundant species in European seas, as indicated by the scarcity index. By contrast, seven small pelagic fishes (out of a total of 29 pelagic species in our dataset) including European Sprat (*Sprattus sprattus*), Atlantic Horse Mackerel (*Trachurus trachurus*), Atlantic Mackerel (*Scomber scombrus*) and European Anchovy (*Engraulis encrasicolus*) are among the most abundant species. The International Bottom Trawl Survey (IBTS) has been previously shown effective for examining the temporal dynamics of both demersal and pelagic fishes (Hiddink & Ter Hofstede, 2008; McLean et al., 2018). Furthermore, bottom trawl surveys, including the IBTS surveys, are reliably used for pelagic stock assessment (HAWG, 2022; Heessen et al., 1997; ICES, 2007, 2022; Monnahan et al., 2021). Therefore, other species traits such as size and body shape or behaviour must be considered to further explain differences in abundance (Walker et al., 2017). What is certain is that less abundant species are less resilient to abrupt environmental changes (Bell & Gonzalez, 2011), and anthropogenic pressure such as habitat degradation and overfishing—that we can be related to the anthropogenic Allee effect; for example, Courchamp et al. (2006)—due to a limited supply of beneficial mutations and interspecific competition with more common species that have already undergone such beneficial mutation (Bell, 2017; van Eldijk et al., 2020) and competitive exclusion as they are less able to exploit their habitat (Segre et al., 2014). Here, we reveal that the abundance of the most functionally distinct species is low across the Northeast Atlantic, with maximum richness and abundance being found on the Porcupine Bank (see Supporting Information Appendix S2—Figure S5), although this region is one of the less well sampled of the European

seas. Specific surveys conducted in this region between 2006 and 2009, O'Hea et al. (2020) sampled 21 species of deep-sea sharks (we counted seven deep-sea sharks in our datasets), the greatest number of individuals being constrained in deep habitats (~500 m depth). Porcupine Bank and adjacent areas support an important European demersal fishery, which makes these deep-sea species highly vulnerable to bottom trawl bycatch (Oliver et al., 2015), especially those for which abundance data do not support the implementation of management measures (ICES, 2021).

Our study reveals that the species facing the greatest risk of extinction are frequently functionally distinct species (D10 species), often contributing to unique niches and functions in the ecosystem (Hammerschlag et al., 2019). We showed that 38% of the species threatened with extinction according to the IUCN Red List in European seas (9 out of 24 species) are the most functionally distinct species (D10 species) with eight sharks belonging to both. If the second most functionally distinct group of species is added, the number of species increases up to 58% (14 species out of 24) and also includes one skate and one ray. Already alarming, this result is certainly underestimated because of the 'Data Deficient' classification of six D10 species (e.g. Forkbeard, *Phycis phycis*; Ocean Sunfish, *Mola mola*; Arrowhead Dogfish, *Deania profundorum*; Sharpnose Sevengill Shark; Little Sleeper Shark, *Somniosus rostratus* and Atlantic Torpedo Ray, *Tetronarce nobiliana*) (Dulvy et al., 2021). Dulvy et al. (2021) estimated that one-third of chondrichthyan fishes worldwide were threatened with extinction, the largest sharks and rays being in the most peril, especially those living in shallow waters that are more accessible to fisheries, and more impacted by habitat degradation and pollution (Dulvy et al., 2021; Pacoureaux et al., 2021). This risk is mainly related to their greater body size—a determining trait in the rate of extinction of animal species since the Pleistocene—(Cardillo et al., 2005; Carmona et al., 2021) and may result from a higher hunting pressure, a higher requirement for resources and a slower response to changes in conditions; nuances exist, however (see review by Chichorro et al., 2019). Moreover, sharks and skates are especially threatened in the Northeast Atlantic due to non-selective fishing techniques (Smith & Garcia, 2014; Walls & Dulvy, 2020) that may have led to local extinctions, such as occurred with Common Skate (*Dipturus batis*) (Brander, 1981) and angel sharks *Squatina* spp. (Lawson et al., 2020). If functionally rare species were to disappear, we could see significant changes in the functioning of ecosystems in connection with irreparable losses of functions (Carmona et al., 2021). Looking back to the unique functions already mentioned, such as highly specialized predation (Mouillot, Bellwood, et al., 2013), top-down trophic regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), transfer of matter through the ocean layers (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018), access facilitation to organic matter (Higgs et al., 2014; O'Shea et al., 2012), protein supply (Simpfendorfer et al., 2011) and ecotourism (González-Mantilla et al., 2022), we realize that entire ecosystems are at stake, from coral reefs to abyssal plains to the continental shelves on which our marine resource

exploitation relies. We also should highlight that several non-threatened species were functionally distinct, such as deep-sea lizardfish (*Bathysaurus ferox*), Alepocephaliformes, Stomiiformes, that can perform vertical migrations (e.g. *Vinciguerria poweriae*). Species expressing this behaviour influence ecological processes (e.g. grazing and predation pressure) in the upper water column by altering the composition of assemblages between day and night, and also participate in the organic matter transport from the surface to the seafloor (Angel & Pugh, 2000), thus enhancing the efficiency of the biological pump (Bianchi et al., 2013). Certainly ecologically unique—yet overlooked in conservation strategies—functionally distinct deep-sea species deserve greater attention for their conservation (Davies et al., 2007), especially in the context of climate change and carbon sequestration (Birch et al., 2016; De Stasio et al., 1993; Pinti et al., 2023).

The way we identify functionally distinct species is independent of species selectivity but can be influenced by both the selection of traits and the initial set of studied species (Legras et al., 2020). This means that whether a species is distinct or not is context and area dependent, conditioned by the regional species pool and their prevailing set of traits and adaptations. We therefore caution that our conclusions are limited to the spatial scale, species pool and trait combination we used. The inclusion of traits related to species' ecological versatility, such as thermal preference or range and vulnerability to acidification, could have been relevant to identifying species whose narrow ecological niches may make them particularly vulnerable to climate change (Jones & Cheung, 2018), with global declines observed in functionally distinct species predicted by niche theory (Clavel et al., 2011). For example, some functionally distinct but abundant and widely distributed species that were not identified as functionally rare in this study may become so if they exhibit increased sensitivity to environmental variation. Conversely, some species identified as low abundant and sparsely distributed but functionally common and therefore redundant in the ecosystem could become functionally rare if other species collapse. Second, highly specific life-history traits, such as amphidromy, could have been used to define distinct species (e.g. European Eel; European Whitefish; Salmon, *Salmo salar*), with amphidromic recruitment leading to movement of biomass from marine to freshwater systems, which may have important ramifications for riverine and estuarine trophic ecology and production (Jenkins et al., 2010). The inclusion of amphidromia would also be of particular interest as amphidromous species are at risk of extinction, mainly due to stream alteration (e.g. in-stream barriers, Cooney & Kwak, 2013; flow modifications, Kwak et al., 2013). Although there are many examples of very low abundance species having a disproportionate impact on their ecosystems (e.g. Canadian Beaver, *Castor canadensis*; bass, *Micropterus* spp.; gophers, *Geomys bursarius*, *Thomomys bottae* and Snow Geese, *Chen caerulescens*, as documented by Power et al., 1996), it should be noted that functionally distinct species are not always scarce. Neither are they always threatened, as evidenced for Brill (*Scophthalmus rhombus*): classified as a functionally distinct

species (D10), Brill is present in over 38% of our study area, is one of the 100 most abundant species and belongs to the 'least concern' category. It is important to distinguish functional distinctiveness from functional rarity, which encompasses both the concept of functional distinctiveness and the notion of low abundance and spatial distribution. Lastly, we cannot reject a null effect of the selectivity of the trawling gears on scarcity results. The gears used during scientific surveys, primarily designed to sample commercial fish species, have varied over time with the improvement of fishing techniques; and they vary spatially at the scale of the different surveys, which may bias the assessment of spatial diversity patterns (O'Neill & Mutch, 2017).

Further research is needed to better understand the responses of functionally distinct species to past and current environmental changes and anthropogenic stressors. This will allow us to anticipate ecosystem responses and to develop management plans and strategies tailored to the responses of distinct species that will almost certainly determine future ecosystem structure and function. Such work should include understanding their responses to pressures in both recent (Osgood et al., 2021) and past periods (e.g. paleontological studies; Paillard et al., 2021; Stein et al., 2018). Identifying sustainable fishing strategies that reduce the impacts on functionally distinct species, for example, by limiting disturbance on critical life stages/areas, is also an essential prerequisite.

Our study highlights the importance of considering the conservation significance of functionally distinct species with unique combinations of ecological traits known to preserve ecosystem structure and function, a too often-overlooked facet of biodiversity. The life-history strategy of the most functionally rare species makes them particularly vulnerable to both natural variability and the drivers of global change, increasing the need for adaptive conservation efforts. In the context of the biodiversity crisis, there is an urgent need to complement the indicators used to guide species management and conservation policies, such as the IUCN Red List. Including the functional component of biodiversity would help better identify species that deserve special conservation attention due to their functional role, with respect to ecosystem functioning and balance.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The trait dataset that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1. The abundance data that support the findings of this study are available on the ICES Database of Bottom Trawl Surveys (DATRAS) at <https://datras.ices.dk>. IUCN statutes that support the findings of this study are available on The IUCN Red List of Threatened Species (Version 2022-2) at <https://iucnredlist.org>. The R code used to calculate the integrated distinctiveness index that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.22317643.v1.

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SUPPORTING INFORMATION

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

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APPENDIX 1

DATA SOURCES

A.1 | THREATENED FISH SPECIES IN THE NORTHEAST ATLANTIC ARE FUNCTIONALLY RARE

Trait dataset

The sources used to build the dataset of traits for marine fish taxa observed during international scientific bottom-trawl surveys in the Northeast Atlantic are listed here. This dataset, which completes the one presented by Beukhof et al. (2019), is freely available at the Figshare public data repository (<https://doi.org/10.6084/m9.figshare.19833304.v1>).

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Abundance dataset

The Database of Trawl Surveys (DATRAS) is a repository for data collected primarily from bottom trawl fish surveys coordinated by ICES expert groups. These surveys cover a wide range of areas, including the Baltic Sea, Skagerrak, Kattegat, North Sea, English Channel, Celtic Sea, Irish Sea, Bay of Biscay, and the eastern Atlantic from the Shetlands to Gibraltar. The current dataset includes more than 45 years of continuous time series data, which is continuously updated by national institutions. Users can freely download both data products (such as CPUE) and raw data in accordance with the ICES Data Policy on the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark, via the DATRAS website at <https://datras.ices.dk>.

IUCN statutes

The IUCN Red List Categories and Criteria were developed for assessing the extinction risk of species. This system provides information on a variety of factors, including range, population size, habitat and ecology, use and/or trade, threats, and conservation actions. This information can inform conservation decisions and actions. The IUCN Red List of Threatened Species provides free access to the latest IUCN Red List Categories and Criteria. Users can download the most recent version of the IUCN Red List at the following website: <https://www.iucnredlist.org>, Version 2022-2.

Integrated distinctiveness R code

The R code is freely available at Figshare public data repository <https://doi.org/10.6084/m9.figshare.22317643.v1>.