Prioritising Functionally Distinct and Globally Endangered (FuDGE) sharks for conservation action

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Abstract

Robust species-level methods for quantifying ecological differences have yet to be incorporated into conservation strategies. Here, we describe a new approach to measure the unique contribution of species to overall functional diversity and incorporate it into an actionable conservation metric. The Functionally Distinct and Globally Endangered (FuDGE) metric directs conservation action to species whose extinction would result in significant losses of irreplaceable functional diversity. We apply FuDGE to the world's sharks and compare it with the phylogeny-based Evolutionarily Distinct and Globally Endangered (EDGE) metric to highlight shared and divergent priorities for conservation. Identifying threatened species revealed that functionally distinct species are disproportionately threatened, with 17-24% of extant shark trait space at risk of extinction. We show that exploitation by humans threatens to disproportionately erode shark trait space, with 70% of trait space at risk. We hope our FuDGE metric will be used to guide the conservation of functionally irreplaceable species in the face of human impacts.

Introduction

The biodiversity crisis is driving species declines and losses across landscapes and aquascapes, threatening the functioning of healthy ecosystems and the services they provide (*1*). Efforts to mitigate declines in biodiversity require strategic decision-making and often utilise established metrics of risk or priority, such as conservation status (*2*), taxonomic diversity (*3*), endemism (*4*), climate vulnerability (*5*, *6*) and evolutionary history (*7*). However, relatively little progress has been made at incorporating the variation of functional traits of species, measured as functional diversity (*8*, *9*), into conservation decision-making (*10*). For example, Goal A of the United Nations Convention on Biological Diversity (CBD) Kunming-Montreal Global Biodiversity Framework (GBF) focuses on maintaining, restoring and enhancing biodiversity to improve functions and services (*11*), yet the accompanying monitoring framework contains no means for tracking progress towards recovery of functional diversity.

Measuring the functional diversity of species assemblages can help to inform how species loss might impact ecosystem functions and services (*12*), through establishing a better understanding of species' individual functionality within a system, and the uniqueness or redundancy of that role in comparison to other related or co-occurring taxa. Recent studies suggest that loss of species that exhibit functionally unique traits will drive homogenisation and erosion of ecological communities (*13*, *14*). However, current prioritisation metrics that consider taxonomic or phylogenetic information alone do not adequately capture functional diversity (*15*, *16*).

Advances in metrics that prioritise species for conservation based on phylogenetic diversity (the sum of phylogenetic branch lengths connecting a set of taxa (*17*)) have produced approaches that are based on the established conceptual framework of averting expected losses of the most imperilled biodiversity (*18*–*22*). For example, the Evolutionarily Distinct and Globally Endangered (EDGE) metric, based on the EDGE2 protocol (*18*), prioritises species based on the amount of threatened phylogenetic diversity their conservation would secure. In contrast, proposed metrics to prioritise species for conservation based on functional diversity (e.g. (*23*, *24*)) often lack fundamental conceptual and mathematical foundations (*25*), with rare exception (*26*). However, growing focus on the maintenance of functionally diverse systems for conservation[8,9], the increasing availability of trait data across the tree of life (*16*, *27*), and established methods to quantify functional diversity (*28*) provide the opportunity to develop a mechanistic prioritisation approach to guide the conservation of functionally irreplaceable species.

Functional trait and extinction risk data are now available for the world's sharks (Selachimorpha). Sharks are among the most evolutionarily distinct (*29*) and functionally unique (*24*) vertebrate lineages and perform a range of ecological roles (including apex predators and mesopredators) across global marine ecosystems, and some estuarine and freshwater habitats. However, sharks are one of the most imperilled vertebrate clades (30% of species threatened with extinction)(*2*, *30*), and many species are experiencing population declines due to overexploitation, habitat degradation and climate change (*31*). Overfishing is one of the primary threats faced by sharks (*32*) and species targeted by humans might be distinct in different biodiversity facets (*33*, *34*). These declines threaten the stability and

health of aquatic ecosystems globally and require focused conservation action to prevent irreversible loss (*35*, *36*).

Here, we set out to develop a method that prioritises functionally irreplaceable and threatened species for conservation. We present the Functionally Distinct and Globally Endangered (FuDGE) metric, which quantifies the expected loss of species functional diversity that can be averted through species-focused conservation action. We apply FuDGE to the world's sharks and explore the relationship between FuDGE and its phylogenetic equivalent, EDGE (Evolutionarily Distinct and Globally Endangered)(*18*). We also examine whether species threatened by overexploitation are particularly functionally or evolutionarily distinct, and explore how conservation strategies to prioritise distinct sharks perform at safeguarding overexploited species. These results provide a major new advance in conservation prioritisation and have wider implications for creating policy-relevant functional indices.

Results

Erosion of shark functional diversity

To quantify the trait space occupied by the world's sharks, we selected eight traits that characterise a variety of functional guilds (maximum body length, maximum depth in the water, trophic level, reproductive guild, vertical position in the water, growth ratio, and the first two principal component axes from an analysis of body shape; see Methods) for 557 species (>99% of all sharks). Taxonomic coverage of these eight traits was high overall (mean coverage = 81.6%, median = 89.8%; Table S1). Trophic level and reproductive guild had the lowest taxonomic coverage, with 49.9% and 61.4% trait coverage respectively. All other traits had coverage of 84.2% or higher, with vertical position having 100% coverage, and we used random forest models to impute missing trait values to attain 100% coverage for all traits (see Methods).

To estimate the projected impact of extinction on shark trait space, we calculated the proportion of trait space that would be lost with the extinction of all 167 currently threatened species (Vulnerable [VU], Endangered [EN], Critically Endangered [CR] on the IUCN Red List). We define trait space occupied by extant sharks by condensing the dissimilarity distance matrix of compiled traits using a principal coordinate analysis (PCoA), and extracting the first four axes, which together represent 45.28% of total variation. We used trait probability densities (TPDs)(*37*) to account for the probabilistic nature of species traits (see Methods). We found that 17.18% of global shark trait space is at risk of extinction, potentially increasing to 23.58% if we were to also consider all Data Deficient [DD] and Not Evaluated [NE] species as at risk of extinction.

Functionally Distinct and Globally Endangered (FuDGE) species

The FuDGE metric aims to identify and prioritise threatened species whose extinction is expected to represent disproportionately large losses of unique functional trait space. FuDGE estimates the functional distinctiveness of a species by calculating its expected future unique contribution to overall trait space given the extinction risk and functionality of

all other species in the same trait space. FuDGE is calculated as the product of the functional distinctiveness and probability of extinction of a species, and indicates the expected future loss to trait space that could be averted through conservation action (i.e., if the species does not go extinct) (Fig. 1).

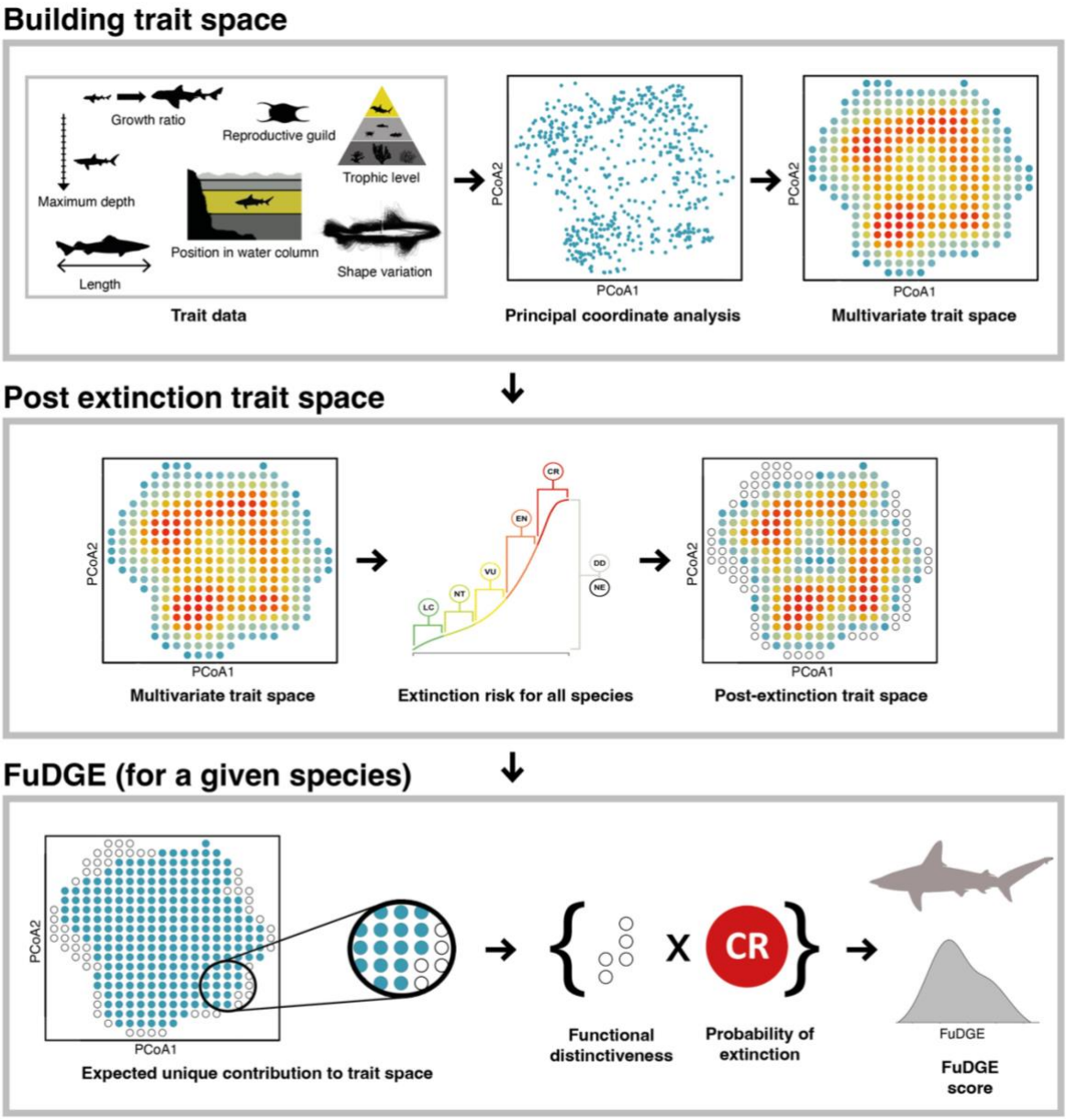

Fig. 1| Calculating the Functionally Distinct and Globally Endangered (FuDGE) metric. Procedure used to calculate FuDGE. Top panel: Building trait space requires trait data to quantify functional distances between species using a principal coordinate analysis (PCoA). Probabilistic trait space is estimated from the PCoA and an estimated variability using the TPD package (v1.1.0)(*38*). Middle panel: Post-extinction trait space is calculated by removing species predicted to go extinct in a given iteration following an extinction scenario, whereby species become extinct or survive based on their probability of extinction. This step is repeated over 1000 iterations to derive a distribution of uncertainty in extinction scenarios. IUCN Red List categories are used to represent the probability of extinction, following Gumbs et al.(*18*): Critically Endangered = 0.97, Endangered = 0.485, Vulnerable =0.2425, Near Threatened = 0.12125, and Least Concern = 0.060625. Bottom panel: The functional distinctiveness of a species is calculated as the distinct contribution of that species (which is immune to extinction during the calculation of its own functional distinctiveness score) to post-extinction trait space. The FuDGE of a species is then calculated as the product of its functional distinctiveness and probability of extinction, and this is calculated 1,000 times to capture the distribution of outcomes from the probability of extinction.

Shark functional distinctiveness and risk

To facilitate comparability between functional distinctiveness scores calculated from different trait spaces, we present the scores as the percentage of total trait space. The most functionally distinct shark is the Basking Shark (*Cetorhinus maximus*), which has a functional distinctiveness score of 0.64%, compared with the mean functional distinctiveness across the entire shark dataset of 0.07%. The top 5% of functionally distinct species (28 spp.) together occupy 10.85% of unique trait space (Fig. 2). Overall, 46% of the top 5% functionally distinct species are threatened with extinction, compared with 30% of all sharks being threatened with extinction (*2*). The shark orders Hexanchiformes, Echinorhiniformes and Lamniformes have the highest average functional distinctiveness scores of 0.20% (sd = 0.21), 0.18% (sd = 0.01) and 0.18% (sd = 0.18) respectively (Fig. 3a). The orders with the lowest average functional distinctiveness score are Squatiniformes and Carcharhiniformes, which both have an average functional distinctiveness score of 0.06% (sd = 0.07 and 0.09, respectively) (Fig. 3a). We compared our functional distinctiveness measure against other approaches to quantifying species-specific contributions to overall functional diversity (*38*, *39*), and found significant but only moderate positive relationships between them (Fig. S1; see Methods).

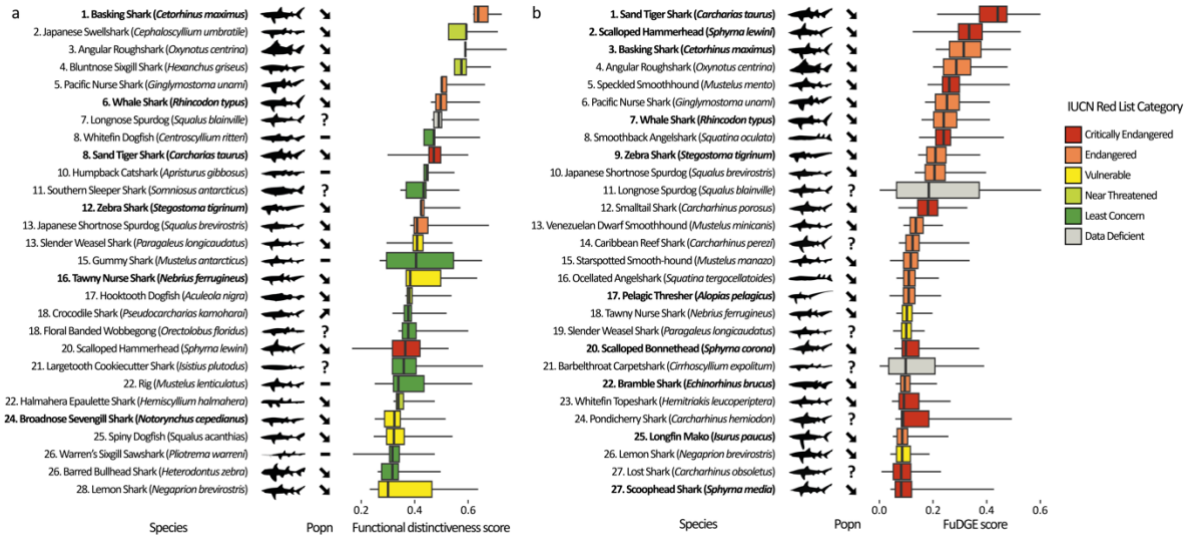

Fig. 2| The top 5% functionally irreplaceable sharks. The top 5% highest ranked (a) functionally distinct and (b) Functionally Distinct and Globally Endangered (FuDGE) shark species. Numbers represent the (a) functionally distinct and (b) FuDGE rank of each species, where species with the same median value have the same rank. Boxplots represent the range, interquartile range and median of (a) functional distinctiveness and (b) FuDGE scores calculated over 1000 iterations. IUCN Red List population trends (Popn) are denoted with arrows to represent increasing or decreasing population trends, a dash to represent stable population trends, and a question mark to represent unknown population trends. Species in bold text fall in the top 5% of both (a) functional distinctiveness and evolutionary distinctiveness scores and (b) FuDGE and EDGE scores. Box colours represent IUCN Red List categories (red = Critically Endangered, orange = Endangered, yellow = Vulnerable, light green = Near Threatened, green = Least Concern, grey = Data Deficient).

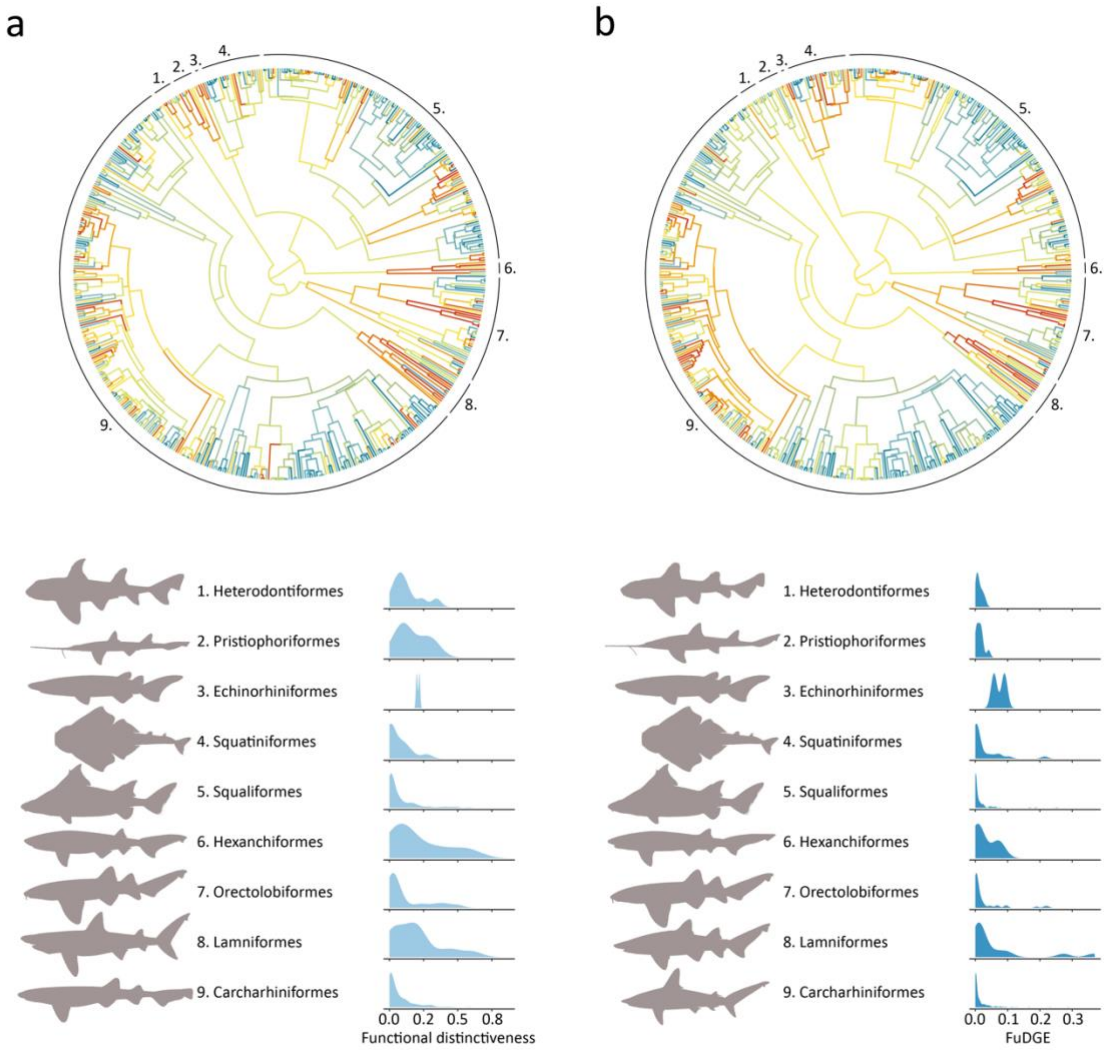

Fig. 3| Distribution of functional distinctiveness and FuDGE across the tree of life. A phylogenetic tree of all sharks with branches coloured to represent the median (a) functional distinctiveness and (b) FuDGE of all descendant species across the shark tree of life. Numbers indicate shark orders. Density plots represent the distribution of (a) functional distinctiveness and (b) FuDGE scores in each order, both on log scale. Illustrations represent the shark species with the highest (a) functional distinctiveness and (b) FuDGE score in their respective order. Shark species: (a) 1. Barred Bullhead Shark (*Heterodontus zebra*), 2. Warren's Sixgill Sawshark (*Pliotrema warreni*), 3. Bramble Shark (*Echinorhinus brucus*), 4. Smoothback Angelshark (*Squatina oculata*), 5. Angular Roughshark (*Oxynotus centrina*), 6. Bluntnose Sixgill Shark (*Hexanchus griseus*), 7. Pacific Nurse Shark (*Ginglymostoma unami*), 8. Basking Shark (*Cetorhinus maximus*), 9. Japanese Swellshark (*Cephaloscyllium umbratile*), (b) 1. Horn Shark (*Heterodontus francisci*), 2. Anna's Sixgill Sawshark (*Pliotrema annae*), 3. Bramble Shark (*Echinorhinus brucus*), 4. Smoothback Angelshark (*Squatina oculata*), 5. Angular Roughshark (*Oxynotus centrina*), 6. Broadnose Sevengill Shark (*Notorynchus cepedianus),* 7. Pacific Nurse Shark (*Ginglymostoma unami*), 8. Sand Tiger Shark (*Carcharias taurus*), 9. Scalloped Hammerhead (*Sphyrna lewini*). The phylogenetic tree was selected at random from the set of 1,000 phylogenetic trees used in this study to calculate EDGE scores.

Priority FuDGE species

The species with the highest FuDGE scores are the Sand Tiger Shark (*Carcharias taurus*; representing 0.44% avertable expected loss of trait space), Scalloped Hammerhead (*Sphyrna lewini*; representing 0.33% avertable expected loss) and Basking Shark (0.31%). Shark orders Echinorhiniformes and Lamniformes have the highest average FuDGE scores of 0.08% (sd = 0.02) and 0.07% (sd = 0.12), respectively (Fig. 3b). In total, 12 species were included in both the top 5% functionally distinct and FuDGE lists (Fig. 2). We identified 78 shark species as priority 'FuDGE' species, defined as threatened sharks for which we have 95% certainty that they are above median FuDGE (mirroring the approach to identifying priority 'EDGE species' (*18*)).

Relationship between FuDGE and EDGE

We applied the EDGE2 protocol (*18*) to calculate evolutionary distinctiveness (ED; see Methods) and EDGE scores for sharks, and compare functional distinctiveness and FuDGE with their phylogenetic equivalents. Functional distinctiveness and evolutionary distinctiveness had a weak but significant positive correlation (Pearson's correlation: $r = 0.18$, $p < 0.001$; Fig. 4a). Six species – the Basking Shark, Whale Shark (*Rhincodon typus*), Sand Tiger Shark, Zebra Shark (*Stegostoma tigrinum*), Tawny Nurse Shark (*Nebrius ferrugineus*) and Broadnose Sevengill Shark (*Notorynchus cepedianus*) – were in both the top 5% of functionally distinct and evolutionarily distinct species (Fig. 2a and Fig. 4a). Conversely, two species – the Spined Pygmy Shark (*Squaliolus laticaudus*) and Viper Dogfish (*Trigonognathus kabeyai*) – were in the top 5% of evolutionarily distinct species but the bottom 5% of functionally distinct species, and three species – the Gummy Shark (*Mustelus antarcticus*), Rig (*Mustelus lenticulatus*) and Southern Sleeper Shark (*Somniosus antarcticus*) – were in the top 5% functionally distinct species but the bottom 5% of evolutionarily distinct species (Fig. 4a).

FuDGE and EDGE had a significant positive correlation (Pearson's correlation: $r = 0.51$, $p < 0.001$; Fig. 4b). Ten species were in the top 5% of both FuDGE and EDGE, and we classify these species as the most Extremely Distinct and Globally Endangered (ExDGE) shark species on Earth (species in bold in Fig. 2b). The highest-ranking species across both EDGE and FuDGE are the Sand Tiger Shark (FuDGE rank 1, EDGE rank 1), Basking Shark (FuDGE rank 3, EDGE rank 2) and Scalloped Hammerhead (FuDGE rank 2, EDGE rank 9).

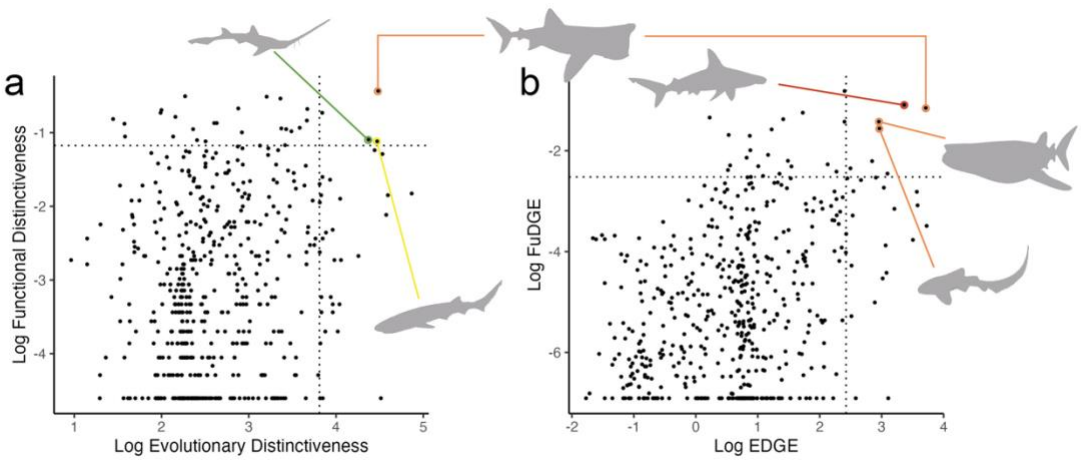

Fig. 4| Correlation between prioritisation metrics. Correlations between (a) evolutionary distinctiveness and functional distinctiveness and (b) Evolutionarily Distinct and Globally Endangered (EDGE) and Functionally Distinct and Globally Endangered (FuDGE) scores. Dotted lines represent the upper 5% of scores for each metric. Illustrations represent examples of species that fall within the top 5% of (a) evolutionary and functional distinctiveness and (b) EDGE and FuDGE. Colours of the lines represent the species' IUCN Red List assessment categories (red = Critically Endangered, orange = Endangered, yellow = Vulnerable). Shark species: 1. Broadnose Sevengill Shark (*Notorynchus cepedianus*), 2. Zebra Shark (*Stegostoma tigrinum*), 3. Basking Shark (*Cetorhinus maximus*), 4. Scalloped Hammerhead (*Sphyrna lewini*).

FuDGE and exploited sharks

There are 468 shark species (84.0% of all shark species) with biological resource use listed as a threat on the IUCN Red List (*2*). Of these species, 170 (30.5% of all shark species) are categorised as intentionally exploited and 298 (53.5% of all shark species) are categorised as unintentionally exploited (see Methods). To determine whether different prioritisation strategies effectively highlight species targeted for exploitation, we selected sets of species of increasing richness with their selection driven by functional distinctiveness, evolutionary distinctiveness, FuDGE, EDGE (i.e., species with higher scores in a given metric had a greater probability of being selected in a set), or randomly selected (see Methods). All prioritisation strategies performed significantly better than random at highlighting intentionally exploited species (Fig. 5; ANOVA with Tukey's test all $p < 0.001$ compared with random; all pairwise comparison results available in Table S2). Functional distinctiveness highlighted more intentionally exploited species than evolutionary distinctiveness at all sample sizes (Fig. 5; Table S2). At all sample sizes, species sets weighted by FuDGE highlighted significantly more intentionally exploited species than functional distinctiveness (Fig. 5; Table S2) and evolutionary distinctiveness (Fig. 5; Table S2), which is to be expected given FuDGE's increased weighting towards threatened species (for which the predominant threat is use), but also significantly more than species sets weighted by EDGE for 20%-50% sample sizes (Fig. 5; Table S2). Intentionally exploited species had significantly higher functional distinctiveness, evolutionary distinctiveness, FuDGE and EDGE scores than unintentionally exploited species ($p < 0.01$ for all comparisons; Table S3). We found that 27.11% (compared to an average random sample of 11.52%; sd = 1.25) of global shark trait space and a median of 3358.60 (compared to 2520.99 random sample, sd = 390.63) million years of evolutionary history is at risk from intentional exploitation. When we considered both intentional and unintentional exploitation of shark species, the risk increased to 70.39% (57.63% random sample; sd = 1.75) of global shark trait space and a median of 10802.42 (9675.31 random sample; sd = 1273.03) million years of evolutionary history.

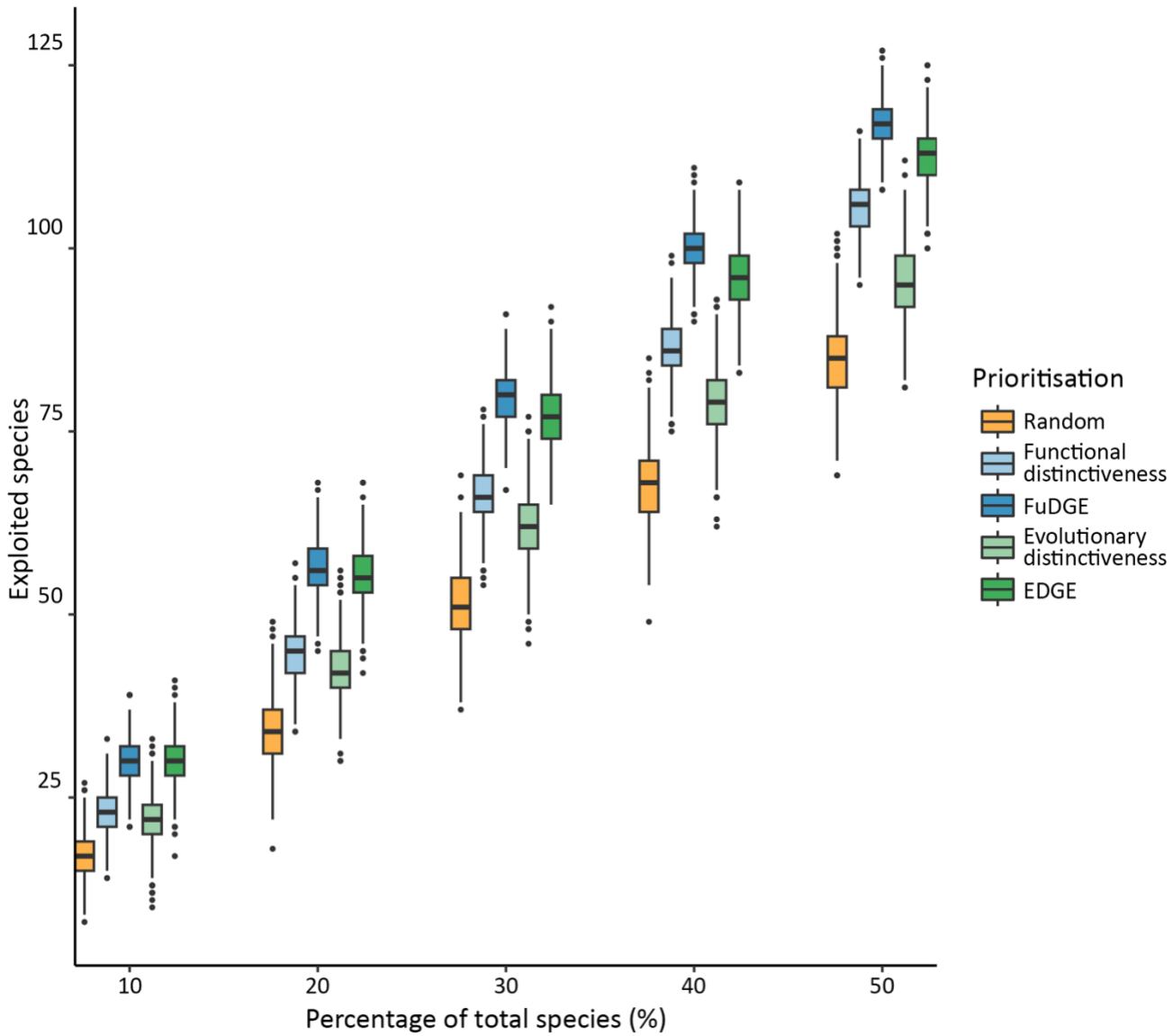

Fig. 5| Performance of different prioritisation approaches at capturing intentionally exploited shark species. The number of intentionally exploited shark species highlighted when 5%-50% of species are selected for conservation based on weighted random draws from different distributions corresponding to different conservation strategies: uniform (fully random; orange), weighted by functional distinctiveness (light blue), weighted by FuDGE (blue), weighted by evolutionary distinctiveness (light green) or weighted by EDGE (dark green). Boxplots represent median value (solid line), 25th and 75th percentiles (box edges), and 5th and 95th percentiles (whiskers) from 1000 iterations.

Discussion

Here we outline FuDGE, a novel approach for identifying species for conservation action, whose extinction would result in significant losses of irreplaceable functional diversity. Given the wealth of evidence linking functional diversity to the provision of functions and services, it is vital to prevent further erosion of functional trait space (*39–41*). We show that over one-sixth of shark trait space is currently at risk of being lost. Using the FuDGE framework we identify 78 sharks that are globally threatened and have above-median FuDGE scores. Our results show that 100% of the top 28 FuDGE sharks and 78.6% of the top 28 functionally distinct sharks have declining or unknown population trends, based on Red

List data (*2*). One Critically Endangered species in the top 28 FuDGE sharks, the Lost Shark (*Carcharhinus obsoletus*), is Possibly Extinct, and has not been recorded since 1934 (*42*).

By implementing a functional diversity-based approach, FuDGE identifies species whose loss would have large impacts on the functioning of ecosystems they inhabit. For example, filter-feeding species, such as the Basking Shark, Whale Shark and Megamouth Shark (*Megachasma pelagios*), all have high functional distinctiveness scores, with all three species in the 75th percentile of functional distinctiveness. Filter-feeding sharks are among the largest living marine vertebrates and play crucial roles in marine ecosystems through regulation of plankton populations and nutrient cycling (*43*).

The weak correlation between shark functional and evolutionary distinctiveness echoes recent studies that challenge the longstanding assumption that phylogenetic diversity should be employed as a surrogate for functional diversity (*17*, *44*). Instead, phylogenetic diversity and functional diversity are associated yet distinct dimensions of biodiversity, the conservation of which is of value to both ecosystems (*40*, *45*, *46*) and human wellbeing (*33*, *34*). Indeed, our work further highlights the complex and non-linear relationship between major adaptive change and evolutionary time (*47*–*49*). Three species were in the top 5% of functional distinctiveness but the bottom 5% of evolutionary distinct species. Exploring the distribution of these species in trait space highlights that there are multiple clusters in trait space that are occupied by many species. However, though these three species were clustered with their congeners, they occupy areas on the periphery of their respective genus clusters. Their unique trait combinations cause these species to occupy low density areas, in at least one dimension of trait space, which is not occupied by many other species (Fig. S2).

The stronger correlation between FuDGE and EDGE is driven by the incorporation of extinction risk in both metrics. We highlighted species that are in the top 5% of both FuDGE and EDGE scores as species of particular interest that represent distinctiveness across multiple dimensions of biodiversity. However, outliers in these correlations highlight distinctive species in one dimension that may be overlooked by prioritising the other. Prioritising a single biodiversity facet alone thus risks overlooking species that may significantly contribute to ecological or phylogenetic aspects of biodiversity.

Previous studies on plants (*33*, *50*) and birds (*34*) indicate that functionally and evolutionarily distinct species are disproportionately utilised by humans. Our work shows the same is true in sharks with respect to both functional distinctiveness and evolutionary distinctiveness. Sets of shark species selected based on FuDGE and EDGE scores highlight more species threatened by exploitation than selecting species at random. This is to be expected given the interplay of extinction risk, exploitation, and FuDGE and EDGE scores. However, we also demonstrate that sets of sharks selected by their functional and evolutionary distinctiveness alone (i.e. without extinction risk weightings) also highlight a greater number of exploited species than random sets. The effect is stronger for FuDGE and functional distinctiveness than it is for their evolutionary-based counterparts. These findings support earlier work that suggests that functionally distinct species are targeted by hunting (*51*, *52*), fishing (*51*, *52*) and the pet trade (*53*). Beyond targeted fishing and exploitation, incidental catch is also a problem for many marine species (*30*, *54*). When considering all species that are threatened by exploitation (intentional and unintentional), we show that

70.39% of globals shark trait space and 10802.42 million years of evolutionary history is at risk. Transitioning to the sustainable use and protection of species that are currently overexploited is essential to maintain the benefits provided to people through ecosystem services.

Prominent approaches to integrate functional traits into conservation prioritisation metrics have often focused on an analogue of the original EDGE metric (*7*). EcoDGE (*23*) uses functional dendrograms to replace phylogenetic trees in the original EDGE calculation. FUSE (*24*) adapts the original EDGE calculation, creating a functional index by summing two measures, functional uniqueness and functional specialisation, both of which are independently weighted by an ordinal ranking of extinction risk. These methods follow the original EDGE approach by weighting one or more measures of distinctiveness by an index of extinction risk in an *ad hoc* manner. As such, these metrics are not prioritisation tools with obvious mechanistic meaning (*25*). However, the EDGE approach has evolved into a mechanistic tool that is based on the concept of expected loss (*18*), where species are measured on their expected contribution to biodiversity and how much of this contribution is at risk of being lost through extinction. Our FuDGE metric, which measures the expected contribution of species to overall trait space, embeds the conservation of functional diversity in an expected loss framework.

Our calculation of FuDGE for sharks uses a binary approach to the occupation of trait space by a given species; a species occupies a region of trait space or it does not. However, the framework is designed to allow FuDGE to be calculated in the context of changes to the probability of occupancy across trait space with the expected loss of constituent species. FuDGE also presents further opportunities beyond species prioritisation. The framework allows us to not only measure the erosion of trait space following extinction, but also quantify the changes in the probability of occupancy in regions of trait space under changing risk of loss. We can monitor these changes over time to look at the shrinking of trait space and reduction in probability of occupancy as extinctions occur. This method would allow us to adopt a functional diversity indicator to monitor the effective safeguarding of functional diversity, akin to the phylogenetic diversity indicator outlined in Gumbs et al. (*55*). Here we calculate FuDGE for sharks globally; however, our method can also be calculated at regional, national or community levels. These complementary levels of analysis would allow us to identify species whose function within specific ecosystems or localities is expected to be distinct and at risk of being lost (*56*, *57*).

As TPDs use kernels to represent the probabilistic distribution of species in trait space, additional work to explore the sensitivity of these approaches to kernel parameters is needed. One aspect that was not possible to explore with sharks is the potential for intraspecific variation in trait data to inform the size and shape of the kernel. As trait data availability increases across taxonomic groups (*58–63*), the number and types of traits used to inform trait space will vary and will require careful consideration. An important aspect of shark life history that we were unable to include due to trait availability is changes through different life stages . Many species will display changes in functional and behavioural features, such as shifts in trophic position and foraging location (*65*) throughout their lifetime, and future work should aim to incorporate these and other trait dynamics to

understand the relationship between ecological function and extinction risk more comprehensively.

Our new FuDGE method demonstrates how we can effectively prioritise species to avert the greatest impending losses of functional diversity. EDGE has been able to galvanise conservation action through prioritising highly evolutionarily distinct and threatened species for practical conservation (*18*). We hope that FuDGE lists will inform conservation in a similar light to guide the effective prioritisation of imperilled functional diversity. This can bring a much discussed but perennially overlooked dimension of biodiversity to the forefront of species conservation planning, policy and action. The erosion and reorganisation of ecological assemblages is already widespread (*66–68*), with local and global declines of species happening at an unprecedented rate (*69*). The integration of species with distinct functional roles into conservation strategies is critical to maintain diverse, resilient ecosystems and support human wellbeing. We propose that FuDGE could provide a mechanistically justified approach to support these important goals.

Methods

Functionally Distinct and Globally Endangered (FuDGE) calculations

The Functionally Distinct and Globally Endangered (FuDGE) metric identifies species whose effective conservation will avert the greatest expected losses of functional diversity. To do this, for each species, FuDGE combines two components: (i) functional distinctiveness, the expected unique contribution of a given species to overall trait space into the future, based on the extinction risk of all other species and (ii) Global Endangerment (GE), the extinction risk of the species.

Species coverage of trait space

One way to measure functional diversity, the property we are trying to maximise through our prioritisation scheme, is to find the hypervolume of trait space where a given trait probability density (TPD) summed across all species is non-zero. More generally, however, we could say that functional richness is given by;

$$\sum_{v \in V} \left(1 - \prod_{i \in S} \left(1 - x_{i,v} \right) \right)$$

where $x_{i,v}$ is the probability that species i is present in a section v of trait space, S is the set of all species and V is the set of all possible parts of trait space (these could be voxels in n-dimensional space). In the simpler calculation that we use in practice here, we effectively constrain $x_{i,v}$ to be either 1 or 0 when it could in practice take intermediate values based on intraspecific variability and/or total abundance of the species if such data becomes available in the future.

When using the TPD package applied here (see main text) the probability density of a single species must sum to one. This assumes that there is no intraspecific variability and that a

species only occupies more than one position in trait space because of uncertainty about the one position it occupies in reality. future work may go beyond this and provide a species' probability of occupying each position in trait space which sum to an amount greater than one because we expect the species to occupy several (probably nearby) areas simultaneously though intraspecific trait variation. Species with large abundances could, if known, occupy larger areas of trait space. None of these improvements would change the formula given above, they would require us to use a different method to get the data on what areas each species occupies in trait space.

Irreplaceable species-specific trait space (functional distinctiveness)

To quantify the expected contribution of a given focal species to total functional diversity in the future, we measured the trait space that is expected to be occupied solely by the focal species, given the extinction risk to all other species comprising the trait space. If the focal species overlaps in trait space with few other species that are at high risk of extinction, it is likely that this focal species will be the sole inhabitant of that region of trait space in the future. In contrast, if the focal species overlaps in trait space with many other species or with species that have low risk of extinction, then it is very unlikely that the focal species will be the sole inhabitant of that region of trait space in the future. Our method for the functional distinctiveness is based on three steps and is performed on every species (summarised in Fig. 1 of the main text).

Step 1: Calculate the volume of trait space occupied by all species in the analysis.

Step 2: Stochastically simulate the removal of species based on their extinction risk but with the constraint that the focal species does not go extinct. We followed the Gumbs et al.(*18*) weighting of IUCN Red List categories (*70*) to estimate probability of extinction for each species. IUCN Red List categories were converted to represent probability of extinction; CR = 0.97, EN = 0.485, VU =0.2425, NT = 0.12125, and Least Concern [LC] = 0.060625. Species that were not assessed or had IUCN Red List category listed as Data Deficient, were randomly sampled from other IUCN Red List categories.

Step 3: Calculate a post-extinction trait space with the focal species present, and again with the focal species removed. Calculate the difference between these two values and divide the result by total trait space (step 1) to give the species of interest's distinct relative contribution to trait space.

Avertable loss (FuDGE). To capture the avertable loss of irreplaceable functional diversity we multiplied the functional distinctiveness of each species by its probability of extinction (GE) to quantify the expected loss of functional diversity given the extinction risk of the species. We calculated GE, as a probability of extinction, using the same IUCN Red List weightings as the functional distinctiveness calculation.

Final functional distinctiveness and FuDGE values. We calculate functional distinctiveness and FuDGE over 1000 repeat iterations to capture a distribution of uncertainty in the extinction scenarios. The final functional distinctiveness and FuDGE values are given by the median value of the sampled distribution. It would be possible to calculate the result

precisely by evaluating the formula given above, but we opt not to do this because it would require looping over every possible species and every possible position in (four dimensional) trait space, all of which would be computationally prohibitive. A stochastic simulation with 1000 repeats as we do here is a much more practical way of quickly converging to the same result as a precise evaluation of the formula.

Comparing functional metrics. To investigate the variations between different metrics, we use Pearson's correlation to compare functional distinctiveness against other metrics that measure functional diversity (Fig. S1). We investigate correlations between functional distinctiveness, functional uniqueness (FUn), functional distinctiveness (FDis) and functional uniqueness measured in probabilistic trait space (FU). FU is calculated as the functional distance to the nearest neighbour of the species of interest, using the uniqueness function in the funrar package (v. 1.5.0)(*71*). FDis is calculated as the average functional distance from a species to all the others in the given community, using the distinctiveness function in the funrar package (v. 1.5.0)(*71*). FU is calculated as the mean overlap of species in probabilistic trait space, using the uniqueness function in the TPD package (v. 1.1.0)(*38*).

Calculating FuDGE for sharks

Data collection

We collated published data for extinction risk, traits and evolutionary history of sharks (Selachimorpha). We limited our study to sharks, omitting other clades of Chondrichthyes (Batoidea and Holocephali), due to limited availability of comparable data for several key traits, including body shape. To taxonomically match species information from different datasets, we used nomenclature from FishBase (accessed 11/2023)(*62*), which included 557 species. All database manipulation and analyses were performed using R statistical software (v. 4.3.1)(*72*).

Extinction risk data. We use the IUCN Red List of Threatened Species (v. 2023.1)(*2*) to obtain information of species extinction risk. This includes assessment data for 540 species, including 467 data sufficient species (Least Concern, LC; Near Threatened, NT; Vulnerable, VU; Endangered, EN; or Critically Endangered, CR) and 73 categorised as Data Deficient (DD). The remaining 17 species in our dataset are Not Evaluated on the Red List.

Evolutionary history data. We used the EDGE2 protocol (*18*) to calculate evolutionary distinctiveness (ED; the expected contribution of a species to overall evolutionary history given the extinction risk to all other species) and Evolutionarily Distinct and Globally Endangered (EDGE; the amount of expected loss of evolutionary history that can be conserved by averting the extinction of a given species) scores for all sharks. Evolutionary distinctiveness and EDGE are the phylogenetic equivalents of functional distinctiveness and FUDGE, and we used the same weightings of extinction risk for EDGE and FUDGE calculations. ED and EDGE scores were calculated as the median scores from a sample of 1000 phylogenetic trees generated from the Stein et al.(*29*) tree distribution of 10,000 Chondrichthyes trees, where species absent from the phylogenies were inserted based on taxonomy using the same approach as Gumbs et al.(*73*).

Trait data. We collated eight traits for our analysis, obtained from FishBase (*62*) and Sharks of the World: A Complete Guide (*74*). We selected traits based on data availability and representation of functional guilds (*75*)(Table S1). These traits relate to body size (maximum body length), diet/predator-prey relationship (trophic level, body shape PC1 and PC2), reproduction (reproductive guild), metabolism (growth ratio) and habitat preference (maximum depth and vertical position in the water). To measure body shape, we modify methods shown in Siders et al.(*76*), which uses Elliptical Fourier analysis (EFA) to represent variation in shark body shape. We collected 515 illustrated images from Sharks of the World: A Complete Guide[65] to measure the variation in shark body shape using EFAs. These images were first converted into outlined silhouettes using photoshop (v. 23.5.5)(*77*). Using the R package Momocs (v. 1.4.1)(*78*) each outline was scaled and centred on a matrix (Fig. S3) and EFA was performed on the outlines, using 16 harmonics (Fig. S4). Results of the EFA were condensed using Principal Component Analysis (PCA). PC1 and 2 collectively explain 62% of total variation and were used to represent body shape for our analysis (Fig. S5), PC1 represents 43% variation and PC2 represents 19% variation.

Imputing missing data. Our compiled database contained 557 species. To complete missing values in the trait database, we imputed missing data using the missForest function in the missForest R package (v. 1.5)(*79*). This method uses a random forest trained on the observed values of the trait matrix to impute missing values. It can be used to predict both continuous and categorical data.

Quantifying trait space

Distance matrix. Prior to quantifying a distance matrix, we log transformed, scaled and centred continuous traits to ensure normal distribution and prevent overweighting. We calculated a dissimilarity distance matrix using the function gawdis (v. 0.1.5)(*12*). This approach prevents disproportionate weighting of categorical traits to produce multi-trait dissimilarity with more uniform contributions of different traits (*12*).

Principal coordinate analyses. Using the dudi.pco function in the ade4 package (v. 1.7.22)(*80*) we summarised the functional dissimilarity matrix with PCoA to quantify distances in trait space between species. Multivariate trait space was built by extracting the first four PCoA axes.

Multidimensional trait space. We use TPDs to account for intraspecific trait variability when describing functional space[71]. TPDs represent each species in functional trait space as a multivariate kernel density estimation. We approximated TPD values using the measured traits available in the analysis and an estimated variability using the TPD package (v. 1.1.0)(*38*). Each species occupancy is estimated in the same field defined by the four axes of the PCoA, and trait space is held constant following removal of species in subsequent analyses.

Functional distinctiveness/FuDGE. We apply the methods stated above to calculate functional distinctiveness and FuDGE values for all sharks. Following the EDGE2 protocol (*18*) and applying it to our FuDGE metric, we defined sets of priority FuDGE sharks as being those that are both assessed as threatened on the IUCN Red List and above the median,

75th percentile, and 95th percentile of functional distinctiveness with 95% confidence (i.e. in 95% or more of the iterations of FuDGE calculation).

Relationship between FuDGE and EDGE

We used Pearson's correlation to examine the relationship between functional distinctiveness and evolutionary distinctiveness scores and between FuDGE and EDGE scores. To determine species that are of particularly high priority for conserving irreplaceable functional and phylogenetic diversity we identified species that are in the top 5% of both functional and evolutionary distinctiveness as well as FuDGE and EDGE.

To better understand patterns of high functional distinctiveness in highly speciose groups (i.e. many close evolutionary relatives) we investigated the distribution of three species—the Gummy Shark (*Mustelus antarcticus*), Rig (*Mustelus lenticulatus*) and Southern Sleeper Shark (*Somniosus antarcticus*)—and their congeners in trait space. We plot each dimension of trait space and highlight the three species and their congeners in trait space (Fig. S2).

FuDGE and exploited sharks

We identified exploited shark species using the IUCN Red List threats classification scheme (https://www.iucnredlist.org/resources/threat-classification-scheme)(*2*), where threat type was listed as Biological resource use Fishing & harvesting aquatic resources (5.4). We consider a species intentionally exploited when the species being assessed is the target, as codifined under Intentional use: subsistence/small scale (5.4.1) and Intentional use: large scale (5.4.2). Unintentionally exploited species were those indicated as being impacted by Unintentional effects: subsistence/small scale (5.4.3) and Unintentional effects: large scale (5.4.4). Species that were listed as both intentional use and unintentional effects were not included in the unintentionally exploited categorisation. No sharks are coded as having motivation unknown or unrecorded (5.4.6).

To explore the potential of different prioritisation strategies at safeguarding intentionally exploited species, we selected 10%, 20%, 30%, 40% and 50% of all shark species, weighted by different prioritisation measures: evolutionary distinctiveness score; EDGE score; functional distinctiveness score; FuDGE score and randomly selected species, repeated this 1000 times for each approach and compared the number of intentionally exploited species captured by each approach for each sample size. We included EDGE and FuDGE in this analysis to investigate how effectively prioritisation strategies that aim to protect threatened evolutionary diversity and functional diversity capture threatened and intentionally exploited species. To test if prioritisation strategies differed significantly at safeguarding intentionally exploited species we used ANOVA with Tukey's Honestly Significant Difference post hoc test to test the pairwise difference between strategies.

To consider species that are unintentionally exploited we compare functional and evolutionary distinctiveness scores of species using t-tests. To investigate the potential impact of human exploitation on shark functional diversity and phylogenetic diversity, we removed species categorised as i) intentionally exploited and ii) both intentionally and unintentionally exploited to identify the loss of trait space and cumulative years of

evolutionary history. We compared the loss of trait space and evolutionary history in exploited species to a randomly selected sample of species of the same number.

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