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Integrating functional diversity into the global conservation agenda

Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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Statement of Originality

I, Ceri Webster, declare that this thesis entitled, “Integrating functional diversity into the global conservation agenda”, and the work presented within are my own, unless stated here. Chapters 1 and 5 were written by me with comments from my principal supervisor, James Rosindell. I wrote chapter 2 with comments from my supervisors James Rosindell, Rikki Gumbs and Nathalie Pettorelli. Chapter 3 was written by me, and comments from Rikki Gumbs, James Rosindell, Nathalie Pettorelli, Michael Hoffmann, David Curnick, Samuel Turvey, Matthew Gollock, James Hansford, Patrick Walkden and Joanna Barker on drafts of the chapter prepared for publication were incorporated here. Chapter 4 was written by me, with comments from James Rosindell and Rikki Gumbs. All analyses outlined in all chapters were conducted by me. All tables and figures were produced by me.

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Abstract

Biodiversity is declining at an unprecedented rate, driven largely by anthropogenic pressures. This thesis explores the multifaceted nature of biodiversity, focusing on phylogenetic diversity (PD) and functional diversity (FD), to provide insights into the current and future state of global biodiversity. Using comprehensive datasets on sharks, rays, and birds, I examine the relationship between PD and FD, revealing that these facets often diverge, particularly when decoupled from species richness, and are therefore complementary rather than interchangeable. Building on these findings, I develop the FuDGE framework to prioritise species for conservation based on their functional distinctiveness and extinction risk. This framework incorporates intraspecific trait variation, future trait space predictions, and uncertainties in extinction risk, providing a robust tool for identifying species whose loss would result in irreplaceable functional deficits. Applying this framework to sharks highlights 76 species with high functional distinctiveness that are threatened with extinction, offering actionable priorities for conservation efforts. Finally, I introduce a probabilistic approach to quantify expected FD losses under current extinction trajectories. By simulating potential erosion of trait space, I identify vulnerable ecological strategies and regions at heightened risk. This research underscores the urgency of protecting species that contribute disproportionately to FD, especially in marine ecosystems where overexploitation and climate change are accelerating biodiversity loss. The findings presented in this thesis highlight the need to move beyond taxonomic measures to capture the full breadth of biodiversity. By integrating PD and FD metrics, and by prioritising functionally irreplaceable species, this work aims to provide critical tools to inform policy and enhance global conservation strategies. These advances will offer new insights into the global decline of FD and safeguarding ecological strategies essential for human well-being.

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Chapter 1 – Introduction

1 – 1 Biodiversity in the face of global change

The stability of the natural world is maintained through countless complex biotic and abiotic interactions. Such interactions structure and balance ecological communities; from tiger sharks sustaining seagrass ecosystems through predation (Heithaus et al., 2002) to bare-nosed wombats forming habitats through burrowing (Old et al., 2018). Biodiverse ecosystems not only preserve the equilibrium of the earth's biomes but also provide a multitude of essential benefits and services that humanity relies on (Scheffers et al., 2016). Healthy functioning ecosystems are essential for human existence, playing a critical role in the provision of food, energy and materials, climate regulation and protection against natural disasters (IPBES, 2019).

Marine ecosystems offer direct benefits to people, with over a third of the global population living in coastal zones (Barbier, 2017) and approximately 10-12% relying on fishing and aquaculture for their livelihood (HLPE, 2014). The ocean is vital to the global economy, with up to 75% of worldwide trade relying on sea routes (Lane and Pretes, 2020) and ocean-based industries annual value ranging from US$1.5 trillion to US$2.5 trillion (Sumaila et al., 2021). The marine realm also encompasses a diverse range of cultural and spiritual importance to coastal communities around the world (Boswell, 2022).

The ocean benefits humanity indirectly, by absorbing over 90% of excess heat released into the atmosphere and 20-30% of anthropogenic CO2 emissions (IPCC, 2022).

Over the past 500 years, as human populations have grown, and industry has expanded, our growing exploitation of the ocean has increasingly modified marine biodiversity (Lotze, 2021; Rick and Erlandson, 2008). In the past 50 years alone, 40% of the ocean has been severely altered by human activities (IPBES, 2019). Physical and chemical stress factors have accelerated the decline and extinction of marine species (Lotze et al., 2006; Pimm et al., 2014). Direct human impact such as unsustainable fishing practices, coastal development and pollution are disrupting the balance of ecosystems and threaten the abundance of resources the ocean provides (Le Quéré et al., 2018; Tessnow-von Wysocki and Vadrot, 2020). This issue is further exacerbated by climate change causing increased ocean temperatures, ocean acidification and reduced oxygen concentration (Talukder et al., 2022).

Marine communities connect and function through biological interactions such as nutrient cycling, intricate food webs, competition and facilitation. Any shifts in abundance, behaviour or range of a species could affect these processes to the extent of altering the structure of an entire ecosystem (Doney et al., 2012). Loss of biodiversity in the ocean will not only reduce ecosystem function but also the availability of resources and services that are essential to society (Cardinale et al., 2012; CBD, 2022). These consequences are already apparent, as seen through widespread coral bleaching (Hughes et al., 2018), collapsing marine ecosystems (IPBES, 2019), and declining fish stocks (FAO, 2024). In a United Nations (UN) report released in 2016, the First Global Integrated Marine assessment, it was concluded that we are almost out of time to start managing the ocean sustainably (Inniss et al., 2016). With less than 4% of funding to natural science allocated to ocean science (Ryabinin et al., 2019) and only 8.35% of the ocean covered, at varying degrees, by marine protected areas (MPAs; UNEP-WCMC, 2024), it is clear that urgent and focused conservation action is needed to combat biodiversity loss in the ocean.

In response to the continued declines in biodiversity, governments and independent organizations worldwide have undertaken efforts to halt or reverse these trends (CBD, 2022; IPBES, 2019; Nations, 2015; UNESCO-IOC, 2021). The Convention on Biological Diversity (CBD) developed the Kunming-Montreal Global Biodiversity Framework (KMGBF), which sets ambitious targets and goals to address biodiversity loss and sustainable development (CBD, 2022). Within this framework includes goals to restore at least 30% of degraded ecosystems, halt human induced extinction and ensure sustainable use of biodiversity. Following the failed legacy of previous international agreements (CBD, 2020; Tittensor et al., 2014), and the continuously shrinking window of opportunity for action (Inniss et al., 2016) successfully realising the defined biodiversity targets will require a clear understanding of biodiversity at a global scale.

Although species richness is relatively well understood at large scales, other aspects of biodiversity are still poorly described (R. Henriques et al., 2020; Safi et al., 2011). However, technological advances and huge efforts from the scientific community have aided an unprecedented availability of biological and environmental data (Gagné et al., 2020). This provides new opportunities to understand ecological interactions, patterns and processes on different spatial and temporal scales.

For example, increased availability of trait data has allowed researchers to better understand how climate drives functional variation in plant communities (Bruelheide et al., 2018; Kambach et al., 2023). Studies integrating large-scale data on satellite imagery and human pressures reveal that only 40% of remaining forests have high ecosystem integrity (Grantham et al., 2020), whilst aggregated population trend data shows a 73% decline in vertebrate populations since 1970 (WWF, 2024).

To successfully bend the curve of biodiversity loss, focused action is needed to optimally allocate seriously limited resources (Mace et al., 2018). As such, numerous measures and indicators have been developed to prioritise species and regions for conservation action. Prioritisations have focused on extinction risk (IUCN Red List of Threatened Species, 2023), ecosystem services (Chavanich et al., 2015), ecosystem integrity (Grantham et al., 2020; Newbold et al., 2015) and evolutionary history (Gumbs et al., 2023a, 2023b; Isaac et al., 2007). Yet, maximising conservation impact will require use of measures that represent all areas of biodiversity (Davies and Cadotte, 2011). Recent expansions of data and biodiversity monitoring offer new opportunities to meaningfully measure unrepresented areas of diversity as well as formerly underrepresented taxa and regions (Ledger et al., 2023).

One such area that lags behind in conservation efforts is the marine realm. Compared to terrestrial systems, knowledge on the extent of biodiversity in marine ecosystems falls considerably short (Gagné et al., 2020; Lotze, 2021). Marine systems are highly dynamic, interconnected and contain extensive areas outside any national jurisdiction (Lotze, 2021). Additionally, many marine ecosystems exist that are timely, expensive and difficult to access. Yet the use of technology such as satellite imagery, acoustic monitoring and baited remote underwater video systems are overcoming these limitations (Bicknell et al., 2016). These advances have significantly increased the availability of ecological data in the marine realm, enabling more in-depth research into marine biodiversity and providing better tools to measure the success of conservation efforts.

Overall, there is increasing agreement on the need for more comprehensive representations of biodiversity, encompassing both different dimensions of biodiversity and improved taxonomic and geographic representation (Díaz et al., 2020; Mace et al., 2014). In this thesis, I focus on marine species to explore biodiversity realms that were previously difficult to study. By addressing these understudied areas, this research will contribute to the development of truly global biodiversity studies and strengthen existing theories.

As threats to marine ecosystems intensify, it is becoming increasingly important to understand the structure and functionality of ocean systems shaped by human activity. Sharks and rays play key roles in shaping communities, influencing ecosystem processes, and enhancing resilience across multiple ecosystem types (Dedman et al., 2024). Their functional contributions span a wide range, from scavengers and parasites to apex predators, with species ranging in size from 20 cm to 18 meters (Heithaus et al., 2022). Many species exhibit ontogenetic shifts, occupying different ecological roles over their lifetimes, along with varying habitat preferences, sizes, and movement patterns (Heupel et al., 2014). In addition to their ecological importance, sharks and rays hold significant social,

economic, and cultural value for human societies (Dedman et al., 2024). However, sharks and rays have been increasingly exploited for resources such as food, medicine, and cosmetics (Pacoureau et al., 2021). This exploitation, compounded by other pressures like climate change, habitat degradation, and the industrialization of aquascapes, continues to accelerate the decline in shark populations (Dedman et al., 2024). To understand large scale patterns of diversity in sharks and rays and assess the impact of their decline, leveraging global datasets will be essential.

1 – 2 Phylogenetic diversity conservation

Conserving evolutionary history and the tree of life is a concept that has been long considered in the scientific literature (e.g. Davies & Cadotte, 2011; Mace et al., 2003; Purvis et al., 2005; Purvis & Hector, 2000; Tucker et al., 2017) and has recently been incorporated into international conservation assessments and targets (CBD, 2022; Gumbs et al., 2023a; IPBES, 2019). Measures of evolutionary history, such as phylogenetic diversity (PD), aim to capture variation in the tree of life. PD measures the total evolutionary history represented by a set of taxa, typically by summing the branch lengths that link a group of species to the root of their phylogenetic tree (Faith, 1992).

In developing the PD metric, Faith (1992) theorised that by capturing greater phylogenetic distances between species, PD would embody a larger range of species characters and 'features'. As such, species with few close relatives on the tree of life will have less shared 'features' than species that have more recently split from their closest relatives. Such evolutionarily isolated species are likely to have forms and functions that are distinct from other species (Faith, 1992; Faith, 2018). This concept has been well documented as a justification for the use PD as a proxy for functional diversity (FD; Cadotte & Davies, 2010; Collen et al., 2011; Winter et al., 2013). The underlying assumption that closely related species express similar traits has frequently been challenged using theoretical models of evolution (e.g. Cadotte et al., 2017; Letten & Cornwell, 2015; Tucker et al., 2018) and empirical data (e.g. Devictor et al., 2010; Kelly et al., 2014; Mazel et al., 2018) yet, there is still uncertainty as to how well PD captures FD. Additionally, Owen et al. (2019) warn against the synonymous use of the terms "feature-diversity" and "functional diversity", arguing that the two concepts are distinct, with feature diversity encompassing all evolutionary features (known and unknown), rather than a selection of measurable functional traits.

PD represents the living variation across a community by quantifying the evolutionary links between a set of species (Collen et al., 2011; Jetz et al., 2014). Maintaining variation in living organisms expands the capacity of future evolutionary options in biological systems (option value), increasing their potential to adapt to novel environmental conditions (Collen et al., 2011; Forest et al., 2007). As uncertainties about the state of nature and future ecosystems increase, enhancing the likelihood of species to adapt to new environments will help build resilience against unpredictable changes (Tucker et al., 2019). Option value also refers to the evolutionary features that will benefit humanity, that are not yet fully understood or discovered (Gumbs et al., 2023c; IPBES, 2019; Molina-Venegas et al., 2021). Since these benefits are currently unknown, evaluating whether evolutionary history helps to maintain future options is limited, however some studies have shown that maximizing PD can

safeguard a larger number and wider variety of known benefits (Forest et al., 2007; Gumbs et al., 2023c; Molina-Venegas et al., 2021).

While PD has garnered considerable attention in the scientific literature since its conception in the 1990s (Faith, 1992; Vane-Wright et al., 1991), its use as a biodiversity measure in conservation practice has been slow to catch up. The most notable example of PD's integration into conservation is the EDGE of existence programme (ZSL EDGE of Existence, 2022). Established in 2007, the EDGE of existence programme was the first of its kind to prioritise threatened PD for conservation action (Isaac et al., 2007; Owen et al., 2019). The EDGE of existence programme supports 'on the ground' conservation to prevent the loss of entire branches of the tree of life, combining scientific priorities with practical conservation strategies to have a meaningful impact on global biodiversity (ZSL EDGE of Existence, 2022).

The programme's metric, the EDGE (Evolutionarily Distinct and Globally Endangered) metric is a valuable tool used to identify species whose extinction would lead to significant losses of unique PD. It combines species-specific measures of evolutionary distinctiveness (ED) and global endangerment (GE) to highlight species that are both at high risk of extinction and represent a considerable portion of evolutionary history. Initial formulations of EDGE were calculated, for a given species, as;

$$\log(1 + ED) + GE \log(2)$$

Where ED is measured as the proportion of PD that a species represents, calculated by dividing the length of each branch by the number of species that share that branch, then summing the total branch lengths from the species to the root of the phylogenetic tree (Isaac et al., 2007). GE reflects the species' extinction risk, as assessed by the IUCN Red List categories (IUCN Red List of Threatened Species, 2023), where each increment in Red List ranking corresponds to a doubling of extinction probability (Least Concern [LC] = 0, Near Threatened [NT] = 1, Vulnerable [VU] = 2, Endangered [EN] = 3, and Critically Endangered [CR] = 4; Isaac et al., 2007).

A decade after the conceptualisation of EDGE, in light of advances in research based on phylogenetically informed conservation (Steel et al., 2007), a workshop was held to update the EDGE metric while still retaining the same foundation of phylogenetic irreplaceability and vulnerability (Gumbs et al., 2023b). Advances in the metric include consideration of uncertainties with phylogenies by incorporating a distribution of 1000 trees, as well as the incorporation PD complementarity, where the extinction risk of species that share internal branches is considered. For example, if a sister species has a high risk of extinction, then the ED value of the measured species will be higher as they are likely to represent more evolutionary history in future (Gumbs et al., 2023b). The updated EDGE metric also incorporates uncertainty of extinction risk values for species where discrete IUCN Red List categories are used to generate a distribution of extinction risk values. A species' probability of extinction is randomly selected from the distribution of extinction probabilities defined by their IUCN Red List categories, and repeated 1000 times to capture uncertainty about species exact extinction risk value (Gumbs et al., 2023b).

Priority lists of EDGE species are used to highlight species based on their phylogenetic irreplaceability and vulnerability. The original criteria for an EDGE species were an above-median ED score and threatened IUCN Red List categorisation (VU, EN, CR). The new EDGE approach outlines

that EDGE species have an above-median EDGE score, with 95% certainty after incorporating uncertainties in phylogeny and extinction risk and are categorised as threatened on the IUCN Red List. As well priority lists of EDGE species, the new approach also includes borderline lists, research lists and watch lists to incorporate reduction of the certainty threshold, species with insufficient extinction risk and species not threatened on the IUCN Red List (IUCN Red List of Threatened Species, 2023) respectively (Gumbs et al., 2023b). Such lists have been developed for all jawed vertebrates and can be used for practical conservation prioritisation (Gumbs et al., 2024).

Recently, PD has also been recognised by international policy initiatives as an important and fundamental component of biodiversity conservation. In recognition of the value of future options, PD has been incorporated into the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as an indicator of PD represented by threatened species (PD indicator; IPBES, 2019) to monitor the status of the tree of life. The KMGBF has incorporated indicators that monitor evolutionary history (CBD, 2022). Goal A, which focuses on restoring and enhancing ecosystem integrity by 2050, includes the expected loss of PD as a complementary indicator and a measure of the state of evolutionary distinct and globally endangered (EDGE) species (EDGE index) as a component indicator (Gumbs et al., 2023a). Goal B, which aims to ensure biodiversity is sustainably used and managed by 2050, includes the expected loss of PD as a complementary indicator. Target 4, which aims to halt extinction and protect genetic diversity by 2030, includes the EDGE index as a complementary indicator (Gumbs et al., 2023a).

1 – 3 Functional diversity conservation

Despite recent progress in integrating various dimensions of biodiversity into international policy, FD—a key aspect of biodiversity—has been largely overlooked (Díaz et al., 2020). FD reflects the diversity and distribution of species' traits, shedding light on the variation of species' functional roles within ecosystems (Cadotte et al., 2011). However, FD is of major conservation concern, with potential extinctions threatening the homogenization, erosion, and rearrangement of ecological strategies across the tree of life (Ali et al., 2023; Carmona et al., 2021). Recent studies indicate that FD is often not adequately captured by other conservation approaches (Oliveira et al., 2020), and prioritizing species based solely on extinction risk or evolutionary history does not adequately protect threatened FD (Pollock et al., 2017). Therefore, effectively conserving FD will require dedicated and targeted strategies (Pollock et al., 2017).

FD has been linked to ecosystem function, as communities with a broader range of traits are likely to use a wider variety of resources (McGill et al., 2006). Studies have shown that FD improves resource-use efficiency, increases ecosystem stability, and enhances the potential for ecosystem services in multiple taxa, including plants, animals, and bacteria (Díaz and Cabido, 2001; Escalas et al., 2019; Hiraiwa and Ushimaru, 2024). Furthermore, empirical evidence has demonstrated that FD provides a better explanation of ecosystem function than species richness (Gagic et al., 2015; Petchey et al., 2004; Tilman et al., 1997). Ecosystems with greater FD have capacity to exploit a wider range of resources, enhancing their ability to adapt to environmental changes (McGill et al., 2006; Worm et al., 2006).

Measuring FD relies on functional traits—characteristics that impact a species' fitness through growth, reproduction and survival (Violle et al., 2007). However, functional traits are often poorly understood, difficult to measure or unavailable (Cadotte et al., 2011; Estes et al., 2011) In their absence, it is recognised that other measurable traits—individual properties or characteristics of a species—can inform species functional guilds and thus their ecological role within ecosystems (de Bello et al., 2021b; Pigot et al., 2020) facilitating an understanding of communities beyond their taxonomic identity. Historically, the lack of comprehensive ecological data for large groups of species has limited FD studies, leading to broad functional assumptions (Kohli and Jarzyna, 2021). However, recent advances in the collection and availability of functional trait data across various taxonomic groups (e.g. Froese & Pauly, 2023; Jones et al., 2009; Kattge et al., 2020; Meiri, 2024; Tobias et al., 2022) and the development of tools to quantify and visualise FD (Carmona et al., 2024; Mammola et al., 2021) enable more detailed characterisation of FD across multiple clades, providing richer insights into ecosystem functioning (Kohli and Jarzyna, 2021).

Estimating FD from a suite of species and traits requires interpreting these multivariate data, usually by defining trait space where species are considered as objects and traits as variables (Schmera et al., 2023). Many methods exist for computing trait space, including distance-based dendrograms (Petchey and Gaston, 2002), multidimensional axes (Villéger et al., 2008) and density-based estimations (Blonder et al., 2014; Carmona et al., 2016). After building a trait space, there is a broad selection of metrics available to quantify FD (e.g. functional richness, Rao's quadric entropy and functional divergence; Botta-Dukát, 2005; Cornwell et al., 2006; Villéger et al., 2008). Although the huge availability of techniques offers opportunities to answer questions about different functional aspects of species and ecosystems, few studies have compared these approaches (Mammola et al., 2021). This can provide uncertainty over which methods should be used to address specific questions (Carmona et al., 2016). Additionally, there has been some contention over the term functional diversity without the use of all functional traits that directly explain ecosystem function (Streit and Bellwood, 2022; Volaire et al., 2020). However, capturing the diversity of trait combinations within a community has significant value and will still reflect the intricate realities of ecosystems (Carmona, 2023). There has been some push for use of the term trait diversity over FD, however in this thesis I will use the term FD to describe measures used to capture the variation of traits—and approximate functionality in a community—to stay consistent with the existing literature.

A recent study by Cooke et al. (2020) demonstrates that threatened bird and mammal species are more likely to be ecologically distinct. While studies that simulated extinction scenarios reveal that current extinction trajectories will lead to large declines of FD and greatly reduce variance among species traits in bird, mammals and amphibians (Cooke et al., 2019b; Oliveira et al., 2020). Investigating the detail of these projections show that some specific traits, such as large size, slow pace, slow reproduction and herbivory are particularly vulnerable to future extinction (Ali et al., 2023; Carmona et al., 2021; Cooke et al., 2019b; Newbold et al., 2013; Rodríguez-Caro et al., 2023). These studies predict erosion and reorganisation of functional space, with the global functional spectra of multiple clades shifting towards small, fast-lived generalist species (Cooke et al., 2019b; Toussaint et al., 2021). Assessments of FD across different biogeographical realms reveal that the

Indo-Malayan and Palearctic realms are particularly vulnerable to FD loss in the future, with the extent of functional decline varying by realm and taxonomic group (Toussaint et al., 2021). Forecasting the functional consequences of biodiversity decline is fundamental for predicting and mitigating the loss of ecological strategies. These studies emphasise the importance of understanding how extinctions may erode functional aspects of diversity for effective conservation planning.

Species-specific measures of FD can help identify species with unique trait combinations and irreplaceable ecological roles. Species with unique functional traits will enhance ecosystem performance and adaptability (Devictor et al., 2010; Pimiento et al., 2020; Pollock et al., 2017). Additionally, growing evidence indicates that functionally unique species provide people with diverse and distinct benefits (Gumbs et al., 2023c; Molina-Venegas, 2021; Molina-Venegas et al., 2021). The loss of species with unique ecological strategies will have a greater impact on ecosystem functioning compared to those with more common strategies (Cooke et al., 2020). Identifying functionally unique species that are at risk of extinction is crucial to prevent further erosion of the global functional spectrum (Ali et al., 2023; Carmona et al., 2021; Cooke et al., 2019b; Toussaint et al., 2021).

Advances in metrics that incorporate FD and extinction risk have been proposed to prioritise species for conservation. Hidasi-Neto et al. (2015) developed the ecologically distinct and globally endangered (EcoDGE) metric which uses functional dendrograms to describe trait space and calculates EcoDGE using the original EDGE framework. However, there is some evidence that dendrogram-based FD indices may lead to biased distribution of ecological distances and inaccurate ecological conclusions (Villéger et al., 2017). Pimiento et al. (2020) also adapted the EDGE metric to integrate functional traits into conservation prioritisation, establishing the functionally unique, specialized and endangered (FUSE) metric. This metric uses functional uniqueness (FUn)— the overall isolation of species within trait space —and functional specialisation (FSp)— the species' distance from the centre of trait space —to quantify a species functional irreplaceability and combines this with ranked IUCN Red List scores (global endangerment; GE) to calculate vulnerability:

$$\log\left(1 + 4\frac{FSp}{\max(FSp)}GE\right) + \log\left(1 + 4\frac{FUn}{\max\,(FUn)}GE\right)$$

This method has received some criticism, since summing two measures of species functional contribution—both weighted by an ordinal ranking of extinction risk—for a single quantitative score raises conceptual and mathematical concerns (Gouhier and Pillai, 2020). Pavoine and Ricotta (2023) recently proposed a parametric framework for the measurement of functional distinctiveness, based on the functional dissimilarities among species and their extinction probability. However, these metrics are yet to be incorporated into conservation prioritisation initiatives.

In recent decades, there has been a rapidly growing interest in quantifying FD for conservation (Cardoso et al., 2024). Many studies have used FD to examine patterns and processes structuring biological communities, and the impact of biodiversity loss on ecosystem functioning and services. Despite numerous international agendas citing FD as an essential biodiversity facet, there remains a lack of integration into conservation strategies (e.g., none of the proposed indications in the KMGBF monitoring directly incorporate FD; CBD, 2022). This could, in part, be due to a lack of available data,

misconceptions in terminology and an uncertainty over which methods best align with policy goals (Zhu et al., 2024). However, with new monitoring technologies, data sharing practices and huge interest from the scientific community, we are presented with new opportunities for the integration of FD into conservation prioritisation.

1 – 4 Summary of data chapters

Quantifying the consequences of extinction is critical to understand the impact of global change on the natural world. Understanding how biodiversity loss will erode and reorganise evolutionary and ecological dimensions of biodiversity will be fundamental in implementing coordinated action to mitigate decline. This is particularly pertinent when one facet of biodiversity is used as a surrogate for another (Oliveira et al., 2020; Veron et al., 2021). Additionally, investigating realms where large scale studies were historically not possible will expand the relevance to global conservation and international goals of bending the curve of biodiversity loss. The overall theme of this thesis is to explore functional and phylogenetic diversity in the marine realm. Using the best available global data on sharks and rays, I first seek to unpick the relationships between different biodiversity measures. I then develop a framework that prioritises functionally irreplaceable and threatened species for conservation. With this framework I propose an indicator that monitors trends in global FD represented by threatened species, to track the overall conservation status of FD.

In chapter 2, I explore the relationship between phylogenetic and functional diversity in sharks, rays and chimaeras. Using phylogenetic data generated from Stein et al.(2018) and trait data from FishBase (Froese and Pauly, 2023), I use different dimensions of diversity and different approaches to calculate phylogenetic and functional diversity. I compare these different dimensions and approaches to reveal varying levels of correlation between phylogenetic and functional diversity, with the strongest relationships occurring between richness-based diversity metrics. I represent functional and phylogenetic richness, independent of species richness to show a significant reduction in correlations of richness-based metrics.

In chapter 3, I present a novel framework to identify functionally irreplaceable and threatened species for conservation. This builds on from other species-specific conservation prioritisation measures (Gumbs et al., 2023b; Hidasi-Neto et al., 2015; Isaac et al., 2007; Pavoine and Ricotta, 2023; Pimiento et al., 2020) to quantify the amount of FD loss that can be averted through species-focused conservation action. I apply this framework to the world's sharks, adding additional trait data to the database created in chapter 2, to identify the most functionally distinct and endangered sharks. I calculate EDGE scores for all sharks, to identify species of high conservation priority that are both functionally and phylogenetically unique. This also highlighted species that significantly contribute to global FD that may have been overlooked by other conservation measures. Using data collated from the IUCN Red List, I identify how much FD and PD is at risk through overexploitation and explore how different conservation strategies perform at safeguarding overexploited species.

In chapter 4, I create a probabilistic global trait space for sharks and birds to project the predicted future erosion of each clade's functional spectrum based on species IUCN Red List assessment. Using historical IUCN Red List assessments, I develop an FD indicator to track progress in conserving global

functional diversity. This indicator highlights a significant increase in expected loss of functional diversity compared to historical expected loss for both sharks and birds. I highlight vulnerable areas of trait space and identify potential trait combinations at risk of extinction. Using simulated scenarios, I show that the current expected loss of global FD is greater than expected, if extinctions were randomly distributed across species. I assess the functional impacts of extinctions on both birds and sharks to demonstrate the application of an FD indicator on taxa with different qualities of data.

I hope that the methodological approaches and conservation priorities discussed in these chapters not only encourage further research into the conservation of FD, but also expand its practical application, making it more relevant for conservation practitioners and policymakers working to safeguard biodiversity across the planet.

Chapter 2 – A comparison of functional and phylogenetic diversity metrics as indicators of biodiversity in sharks, rays and chimaeras (Chondrichthyes)

2 – Abstract

Addressing the challenge of biodiversity decline requires metrics that reflect the complexity of ecological communities. However, current indicators often rely on taxonomic diversity, which overlooks the evolutionary and functional variation of ecological communities. FD, the variation of functional traits within communities is often considered the most salient biodiversity aspect to inform on ecosystem functioning but is often constrained by data requirements at broad taxonomic and geographic scales. Therefore, PD, which captures the living variation across a community by quantifying the evolutionary links between a set of species, is often suggested as a proxy for FD. However, there is still uncertainty as to how well PD captures FD, particularly when there is a large variety of phylogenetic and functional metrics available. In this chapter, I evaluate the relationship between PD and FD in a global study of sharks, rays, and chimaeras (Class Chondrichthyes). Using multiple dimensions of biodiversity (e.g., richness, divergence, and regularity) I assess correlations between phylogenetic and functional metrics to determine if evolutionary relationships serve as an effective proxy for FD. My results indicate that richness-based correlations between PD and FD are strongly influenced by species richness. However, the relationship between phylogenetic and functional metrics may vary across different conceptual aspects of biodiversity.

2 – 1 Introduction

The complex nature of biodiversity poses a challenge as we strive to combat its decline. Current indicators evaluating trends in nature overwhelmingly consider a single facet of biodiversity; taxonomic diversity (Jarzyna and Jetz, 2016). However, taxonomic diversity fails to acknowledge that communities in nature comprise species with a range of evolutionary history and ecological roles. With a new era of data availability and enhanced computational power comes the opportunity to explore more aspects of biodiversity (Pollock et al., 2020). New research increasingly encourages the use of metrics that consider PD and FD (Jarzyna and Jetz, 2016; Mammola et al., 2021; Tosa et al., 2021). As use of these metrics increases, it is important that we understand how they might relate to one another, and how helpful they are in predicting the consequences of species decline and extinctions on ecosystems (Petchey et al., 2004).

Phylogenetic metrics, defined as metrics based on phylogenetic relationships on the tree of life (Faith, 1992; Vane-Wright et al., 1991), measure the branch lengths connecting species, to quantify the phenotypic, genetic and phenological differences accumulated over time (Faith, 1992; Tucker et al., 2018). Preserving variation in living organisms expands the capacity of future evolutionary options in biological systems, increasing their potential to adapt to novel environmental conditions (Collen et al., 2011; Forest et al., 2007). Additionally, conserving evolutionary diversity increases 'future options for humanity', the likelihood of preserving features that will benefit humanity which are not yet fully understood or discovered (Hayward et al., 2022). With the development of genetic technologies, the data required to build phylogenies is expanding quickly, and evolutionary diversity is becoming one of the most prominent measures of biodiversity, with phylogenetic history increasingly incorporated into global conservation initiatives (CBD, 2022; Gumbs et al., 2024; IPBES, 2019).

Functional metrics, defined as metrics based on functional trait data (Botta-Dukát, 2005; Carmona et al., 2016; Cornwell et al., 2006; Villéger et al., 2008), aim to provide measurable values to generalise patterns in diversity (Streit and Bellwood, 2022) and offer simplified descriptions of complex ecosystems (de Bello et al., 2021b; Schmera et al., 2017). These approaches use traits to estimate functionality in an ecosystem (FD; Violle et al., 2007), which has led to an increase in popularity of functional metrics in studies that look to understand biodiversity decline and its implications (Mason et al., 2005; Mouillot et al., 2013; Petchey et al., 2004; Petchey and Gaston, 2006; Schleuter et al., 2010). Yet, there is little consensus on how best to measure FD and often the lack of trait availability prevents large scale analyses and encourages bias in species sampling.

Using PD as a measure of biodiversity may allow wider application of comparative studies as there is a more general consensus on which metrics to use (Tucker et al., 2019). Phylogenetic metrics may also address limited trait data and data bias concerns, as phylogenetic data is more broadly available. Additionally, original concepts in evolutionary diversity stated that preserving evolutionary history would preserve unique forms and functions (Faith, 1992; Vane-Wright et al., 1991), justifying the use of PD as a proxy for FD (Mazel et al., 2018). The question of whether PD captures FD has caused much debate in recent literature (Albouy et al., 2017; Lin et al., 2021; Mazel et al., 2018; Owen et al., 2019; Poff et al., 2006). Yet there is still little understanding of how different

phylogenetic and functional metrics correlate with one another, particularly in the marine realm, where the paucity of data seriously limits opportunities to assess how different biodiversity metrics correlate (Edgar et al., 2016)

While critical knowledge gaps on marine species are constantly being addressed, our understanding of global scale biodiversity in the ocean falls behind that of terrestrial communities. Attempts to tackle this lack of understanding of biodiversity metrics in the marine realm has led to studies investigating the relationship between taxonomic, functional and phylogenetic diversity in marine fish (D'agata et al., 2014; R. Henriques et al., 2020; Mazel et al., 2018), sharks (Cachera and Le Loc'h, 2017; Pimiento et al., 2023; Siders et al., 2022), corals (Ng et al., 2022; Wong et al., 2018) and molluscs (Tan et al., 2022). These studies reveal varying levels of correlation between different biodiversity metrics, yet much of this research is limited in taxonomic and geographic scope. Additionally, these studies are often limited to conceptual approaches associated with richness as a diversity index, which estimates the total amount of variation in a community. Other conceptual dimensions include divergence, which represents the average difference between species; and regularity, which represents the variance in differences between species. The latter diversity indexes are rarely used in analyses comparing PD and FD and our understanding of the relationship between them is limited (Schmera et al., 2017; Tucker et al., 2017).

In this chapter I construct a trait database of sharks, rays and chimaeras (Class Chondrichthyes; herein 'sharks and rays') to compare the relationship between phylogenetic and functional metrics at a global scale. I chose sharks and rays for my study as there is good coverage of phylogenetic and trait data, additionally, using a large clade for my analysis allows me to explore variations in communities beyond those closely related on the tree of life. I estimate PD and FD using different conceptual dimensions associated with richness, divergence and regularity. I explore the relationship between different biodiversity metrics and show that correlations between richness-based phylogenetic and functional metrics is mostly driven by species richness (SR). The relationship between PD and FD has received increased attention and been the subject of debate in recent literature (Letten and Cornwell, 2015; Mazel et al., 2018; Ng et al., 2022; Owen et al., 2019; Wicke et al., 2021). Bringing new study species to the debate will expand our understanding of this relationship. Additionally, comparing different conceptual dimensions and disentangling the relationship between richness-based diversity metrics offers a new perspective to understanding biodiversity metrics.

2 – 2 Methods

To examine the relationship between different biodiversity metrics, I used taxonomic, trait and phylogenetic data of Chondrichthyes species from around the world. For this analysis I have (i) compiled a database containing trait information for all Chondrichthyes, (ii) imputed missing data using random forest models, (iii) calculated PD and FD to analyse the correlation between randomly selected Chondrichthyan species. All database manipulation and analyses were performed using R statistical software (v 4.1.2; R Core Team 2021).

2 – 2.1 Data collation

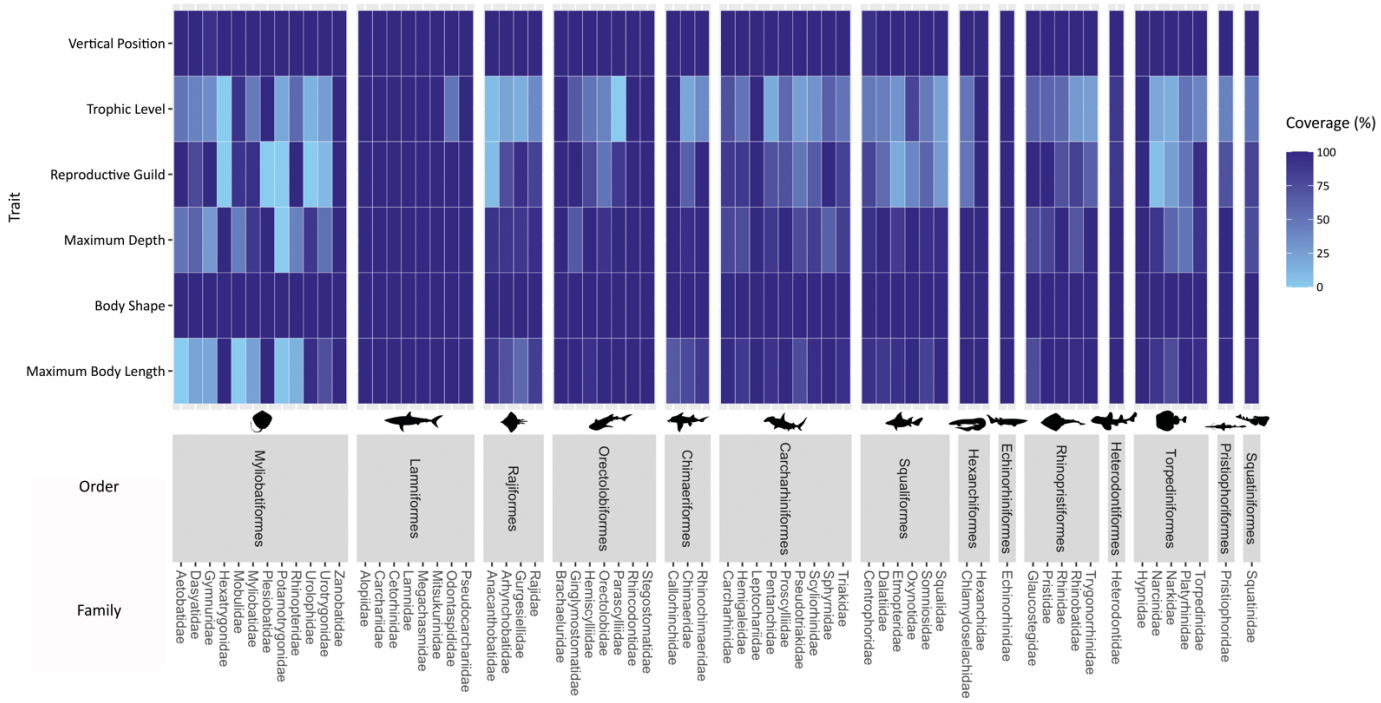
To taxonomically match species information from different datasets, I used nomenclature from FishBase, which comprises information for 34666 finfish species (Froese and Pauly, 2023). I accessed information from FishBase using the R package "rfishbase" (v 4.0.0; Boettiger et al., 2012). Using rfishbase I compiled a database containing the taxonomic information and 19 traits for 34666 finfish species (Fig. S1). After extracting the data, I standardised it and corrected any errors. I created a script to load all data in its original format, apply necessary corrections, and ensure consistency by addressing a predefined list of detected errors. I also relabelled columns when data clearly belonged to a different field than the one declared in the database, for example; a general information column populated with discrete reproductive mode categories. Duplicate rows were identified based on matching species names and codes; when duplicates contained identical information or one row was blank, I deleted the incomplete row. Additionally, rows with numeric values instead of species names were removed from the database.

2 – 2.1.1 Trait data

I extracted chondrichthyan species (N = 1323) from the cleaned FishBase database. For my analyses, I selected six traits, based on trait coverage (Fig. 1) and representation of a variety of functional guilds. Habitat preference can link to functional roles such as hunting and foraging behaviour (Sorenson et al., 2014); trophic level reflects the position occupied on food webs (Henderson et al., 2024); reproductive guild relates to life history strategies (Cortés, 2004); maximum depth represents vertical mobility and nutrient cycling (Andrzejaczek et al., 2022); body shape reflects morphological variation and predator-prey interactions (Sternes and Shimada, 2020) and length relates to body size and metabolism (Henderson et al., 2024).

2 – 2.1.2 Phylogenetic data

I obtained published phylogenetic data for Chondrichthyes from Stein et al. (2018). To capture uncertainty in phylogenetic relationships (Thomas et al., 2013), I selected a sample of 1000 phylogenetic trees generated from the Stein et al.(2018) tree distribution of 10000 Chondrichthyes trees. Where species in my database were absent from the phylogenies I imputed missing species into their genus using the congeneric.impute function in the R package pez (v. 1.2.4; Pearse et al., 2015) following methods outlined in Gumbs et al. (2023).



2 – Fig. 1 | Trait coverage. Summary of trait data coverage for the 1323 Chondrichthyan species. The percentage of data coverage for each family is indicated by colour, with darker blue indicating higher percentage of coverage.

2 – 2.2 Imputation of missing data

To complete missing values in the trait database, I used the missForest function in the missForest R package (v 1.5; Stekhoven and Bühlmann, 2012) to implement random forest imputations. Prior to imputation, I log transformed, scaled and centred continuous traits to ensure normal distribution and prevent overweighting. The missForest function 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.

To test the performance of the imputation I used species with complete information and simulated unknown trait data by artificially removing trait data from these species. I randomly removed species traits from each trait category, with the percentage of trait removal synonymous to the percentage of trait data missing from my database. I then handled the simulated missing data by either removing species that had unknown data or imputing the missing data using missForest. This gave me three datasets; a complete case containing all known trait data, a removed dataset where simulated missing data was removed and an imputed dataset where simulated missing data was imputed. I repeated the simulated removal of data 100 times to get a variable combination of missing values. Since I wanted to examine how imputation affected the estimation of FD, I calculated FD of the complete datasets, removed datasets and imputed datasets, using six different approaches (listed in section 2.4). I used two-sample T-tests to test the accuracy of the imputation methods by comparing FD values for the complete dataset with the simulated datasets (simulated dataset

FD/complete dataset FD).

2 – 2.3 Quantifying Trait Space

I calculated a dissimilarity distance matrix using the function gawdis (v. 0.1.5; de Bello et al., 2021), which allows the treatment of categorical and continuous trait data and prevents disproportionate weighting of categorical traits (de Bello et al., 2021a). Using the dudi.pco function in the ade4 package (v. 1.7.22; Dray & Dufour, 2007) I summarised the functional dissimilarity matrix with principal coordinate analyses (PCoA) to quantify distances in trait space between species. The first four axes of the PCoA accounted for 55% of the total variation. Since the subsequent axes only accounted for a small amount of the explained variance (less than 6%) but significantly increased computing times, I constructed trait space based on four axes.

2 – 2.4 Functional Diversity

FD was assessed using six metrics. I selected these metrics based on the variation in approaches to describe trait space (Table 1).

i) **Functional Richness (FRich)** – Functional richness represents accumulated variation among taxa by capturing the limits of functional space filled by a community and is conceptually analogous to other richness metrics (Cornwell et al., 2006; Mason et al., 2005). I calculated functional richness as the minimum convex hull volume occupying multivariate trait space using the convhulln function in the geometry package (v 0.4.6.1; Habel et al., 2022).

ii) **Functional Evenness (FEve)** – Functional evenness represents how regularly species are distributed in trait space and is conceptually analogous to other regularity metrics (Mason et al., 2003; Mason et al., 2005; Villéger et al., 2008). I calculated functional evenness as the average branch length of the minimal spanning tree that connects all species in multivariate trait space, using the func.eve function in the dispRity package (v 1.6.8; Guillerme, 2018).

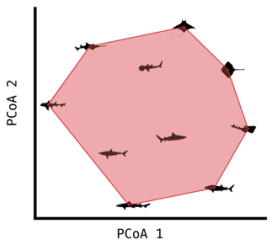
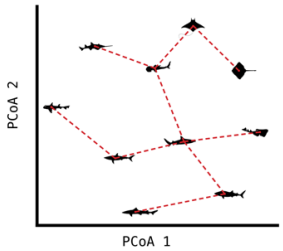
iii) **Functional Divergence (FDiv)** – Functional divergence measures how far species are distributed from the centre of the trait space occupied and is conceptually analogous to other divergence metrics (Mason et al., 2003; Mason et al. 2005; Villéger et al., 2008).I calculated functional divergence as the ratio of deviation from the centroid of multivariate trait space, using the func.div function in the dispRity package (v 1.6.8; Guillerme, 2018).

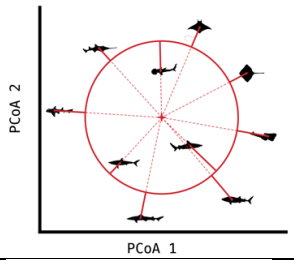
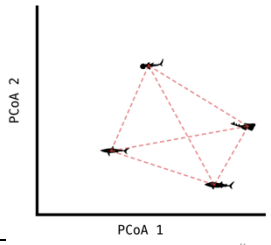
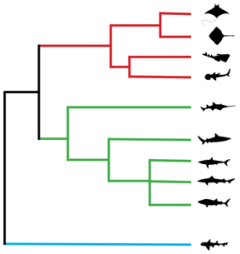
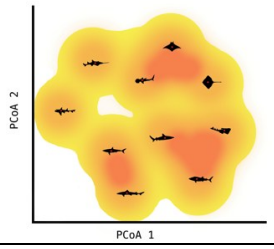
iv) **Rao's Quadric Entropy (Rao's Q)** – Rao's Q represents the expected dissimilarity between two species occupying trait space and conceptually represents both richness and divergence. I calculated Rao's Q as the mean pairwise distance between species in multivariate trait space (Botta-Dukát, 2005), using the pairwise.dist function in the dispRity package (v 1.6.8; Guillerme, 2018).

v) **Functional Dendrograms (FDend)** – Functional dendrograms represent trait space by describing the functional relationship among species through dendrograms (Mammola et al., 2021) and are calculated as the total branch length of the minimum-spanning tree that connects all the species in trait space (Petchey and Gaston, 2002). The total branch lengths of the trees represent functional richness and is conceptually analogous to other richness measures. To calculate functional dendrograms of a community, I first created a distance dissimilarity matrix using the gawdis function in the gawdis package (v 0.1.5; de Bello, Botta-Dukát, et al., 2021), to cluster species in trait space I used a hierarchical clustering method with unweighted pair group arithmetic mean and converted this into a tree using the function as.phylo from the ape package (v 5.6.2 Paradis & Schliep, 2019). From this hierarchical clustering tree, I calculated the FD of each community as total branch lengths.

vi) **Trait Probability Densities (TPDs)** – TPDs account for the probabilistic nature of species traits by considering intraspecific trait variability when describing functional space (Carmona et al., 2016). I approximated TPD values using the measured traits available in the analysis and an estimated variability. I then used the estimated TPD values to calculate functional richness, using the function REND in the TPD package (v 1.1.0; Carmona et al., 2019). I measured TPD richness to capture the total amount of variation in the probabilistic trait values, which can be conceptually comparable to other richness measures.

2 – Table 1 | Functional diversity metrics. The different metrics of functional diversity used in the analysis and the conceptual dimensions represented by each measure. The illustrations for functional richness, functional evenness, functional divergence, Rao's Q and TPD show the structure of two-dimensional trait space occupied by a set of species and a visualisation of how each metric is calculated. Functional dendrograms are represented by the hierarchical clustering method with each functional group denoted by different colours.

Functional metrics	Illustration	Dimensional category	Definition
Functional Richness		Richness	The minimum convex hull volume occupying multivariate trait space (Cornwell et al., 2006).
Functional Evenness		Regularity	The average branch length of the minimal spanning tree that connects all species in multivariate trait space (Villéger et al., 2008).

Functional Divergence		Divergence	The mean deviation from the centroid of multivariate trait space (Villéger et al., 2008).
Rao's Quadric Entropy		Richness, Divergence	The mean pairwise distance between species in multivariate trait space (Botta-Dukát, 2005).
Functional Dendrograms		Richness	The total branch length of the minimum-spanning tree that connects all the species in trait space (Petchey & Gaston, 2002).
Trait Probability Density Richness		Richness	The total amount of variation in functional trait space where each species is represented as a multivariate kernel density estimation (Carmona et al., 2016)

2 – 2.5 Phylogenetic Diversity

To measure biodiversity using phylogenetic data, I selected seven metrics, based on the variation in approaches of describing evolutionary relationships between sets of species in a community (Table 2). I calculated each of the seven metrics using a sample of 100 phylogenetic trees and take the median value to capture phylogenetic uncertainty.

i) **Faith's Phylogenetic Diversity (Faith's PD)** – Faith's PD measures the amount of evolutionary history represented by a selected group of species (Faith, 1992). I calculated PD as the total length of minimum spanning path that links the given group of species to the root of their phylogenetic tree. PD represents accumulation of evolutionary history in a community and is conceptually analogous to other richness metrics.

ii) **Evolutionary Heritage (EvoH)** – Whilst Faith's PD captures evolutionary history, this includes all the features that ever existed in the ancestry of a species. Some of these features may have been lost in extant species due to a process known as attrition (Behe, 2010). Evolutionary heritage (EvoH) aims to explicitly account for both the accumulation and attrition of features (Rosindell et al., 2024). Specifically, EvoH estimates only the

evolutionary history that is maintained in the living decendents of a group of species, thus accounting for the loss of features during the process of evolution. EvoH represents the evolutionary history expressed by the extant species in a community and conceptually reflects richness. I adapted code from Rosindell et al. (2024) to calculate EvoH, with a rho value of 0.001.

iii) **Mean Evolutionary Distinctiveness** – Mean evolutionary distinctiveness measures the mean evolutionary distinctiveness (ED) of all species in a community and conceptually represents divergence (Isaac et al., 2007; Redding, 2003). I calculated the mean of all species ED values, where ED was calculated for each species using the ed.calc function in the caper package (v. 1.0.2; Orme et al., 2023).

iv) **Mean Pairwise Distance (MPD)** – MPD measures the mean of pairwise phylogenetic distances between all possible pairs of species in a community (Clarke and Warwick, 1998). MPD reflects the distribution of species in a phylogenetic tree and is conceptually analogous to other divergence metrics (Tucker et al., 2017). I calculated the mean of pairwise distances, where pairwise distances were calculated using the cophenetic.phylo function in the ape package (v. 5.7.1; Paradis & Schliep, 2019).

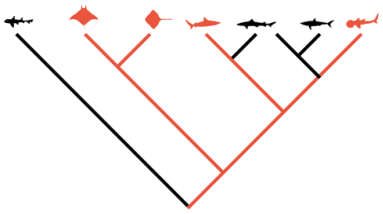
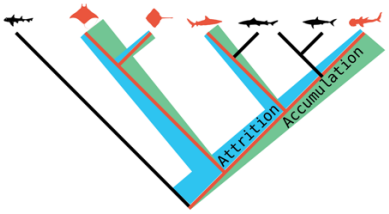
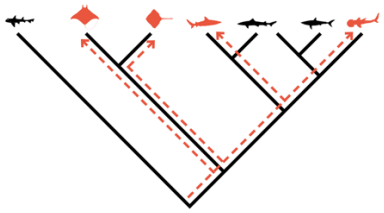
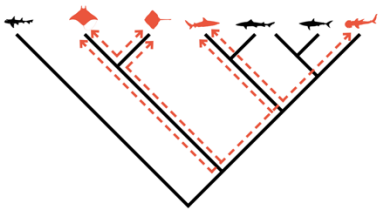
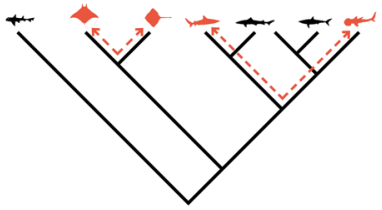
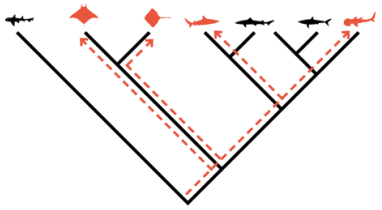
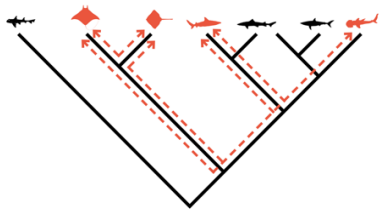
v) **Mean Nearest Taxon Distance (MNTD)** – MNTD measures the mean shortest distance between each species and their closest relative in a community (Webb et al., 2002). MNTD represents the distribution between species and their nearest neighbour and is conceptually analogous to other divergence metrics (Tucker et al., 2017). I calculated MNTD using the mntd function in the picante package (v. 1.8.2; Kembel et al., 2010).

vi) **Variance of ED** – Variance of ED measures the variance of ED of all species in a community and conceptually represents regularity (Isaac et al., 2007; Redding, 2003). I calculated the variance of all species ED values, where ED was calculated for each species using the ed.calc function in the caper package (v. 1.0.2; Orme et al., 2023).

vii) **Variance of Pairwise Distance (VPD)** – VPD measures the variance of pairwise phylogenetic distances between all possible pairs of species in a community (Clarke and Warwick, 2001). VPD reflects the evenness of a set species distributed in a phylogenetic tree and is conceptually analogous to other regularity metrics (Tucker et al., 2017). I calculated the variance of pairwise distances using the cophenetic.phylo function in the ape package (v. 5.7.1; Paradis & Schliep, 2019).

2 – Table 2 | Phylogenetic diversity metrics. The different metrics of phylogenetic diversity used in the analysis and the conceptual dimensions represented by each measure. The illustrations represent a phylogenetic tree with species in red representing the set of species included in the metric calculation.

Phylogenetic metrics	Illustration	Dimensional category	Definition

Faith's PD		Richness	The sum of total branch lengths that connects the set of species to each other across their phylogenetic tree (Faith, 1992).
Evolutionary Heritage		Richness	The evolutionary history that is maintained in only the living decendents of a group of species (Rosindell et al., 2024).
Mean Evolutionary Distinctiveness		Divergence	The mean of a set of species' evolutionary distinctiveness (Isaac et al., 2007; Redding, 2003).
Mean Pairwise Distance		Divergence	The mean pairwise phylogenetic distance between all possible pairs of species (Clarke & Warwick, 1998).
Mean Nearest Taxon Distance		Divergence	The mean phylogenetic distance between each species and its closest relative (Webb et al., 2002).
Variance of Evolutionary Distinctiveness		Regularity	The variance of a set of species' evolutionary distinctiveness (Isaac et al., 2007; Redding, 2003).
Variance of Pairwise Distance		Regularity	The variance of pairwise phylogenetic distance between all possible pairs of species (Clarke & Warwick, 2001).

2 – 2.6 Overview of Analyses

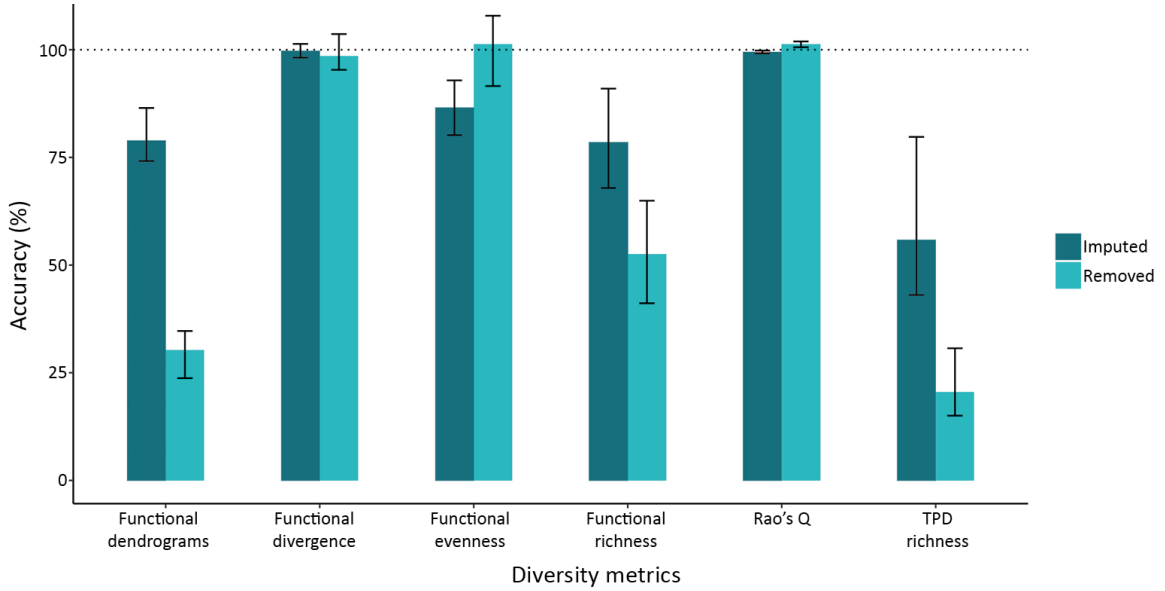
To compare the different phylogenetic and functional metrics, I randomly selected 1000 sets of species, ranging from 1% to 100% of the total species pool. For each set of species, I calculated seven phylogenetic metrics (Faith's PD, EvoH, Mean ED, MPD, MNTD, Variance of ED, VPD) and six functional metrics (FRich, FEve, FDiv, FDend, Rao's Q, TPD Richness). The relationship between SR and other richness-based metrics is expected to be positive, since increasing the number of species would not decrease the total amount of variation in a community (Pavoine and Bonsall, 2011; Wong et al., 2018). As richness-based phylogenetic and functional metrics are not independent from SR (Pavoine et al., 2013), I modelled each richness-based diversity metric as a function of SR and used the residuals of these models to represent SR-independent measures of each metric (Devictor et al., 2010; Pardo et al., 2017). I fitted linear, quadratic, cubic and logarithmic models and used Akaike information criterion (AIC) values to determine which model to use (Fig. S2 and Table S1). I used SR as the only model parameter to explain the relationship between richness-based metrics and SR, and identified the variation that can't be explained by SR. I removed Rao's Q from this analysis as it did not have a monotonic relationship with SR (Fig. S3). To understand the effect of sample size on the relationship between PD and FD I produced 800 sets of randomly selected species, 100 sets for each of eight different sizes of sample from the complete set: 1%, 2.5%, 5%, 10%, 20%, 30%, 40% and 50% of the total species pool. I calculated the Spearman rank correlation between each variable to compare the relationship between phylogenetic and functional metrics.

2 – 3 Results

2 – 3.1 Database

My database included 1323 species of chondrichthyans, of the six traits I used for my analysis, trait coverage for the majority of species was high, with a mean coverage of 76% (81% median). Trophic level and reproductive guild had the lowest coverage, with 33% and 59% trait coverage respectively. All other traits had coverage of 80% or higher (Fig. 1).

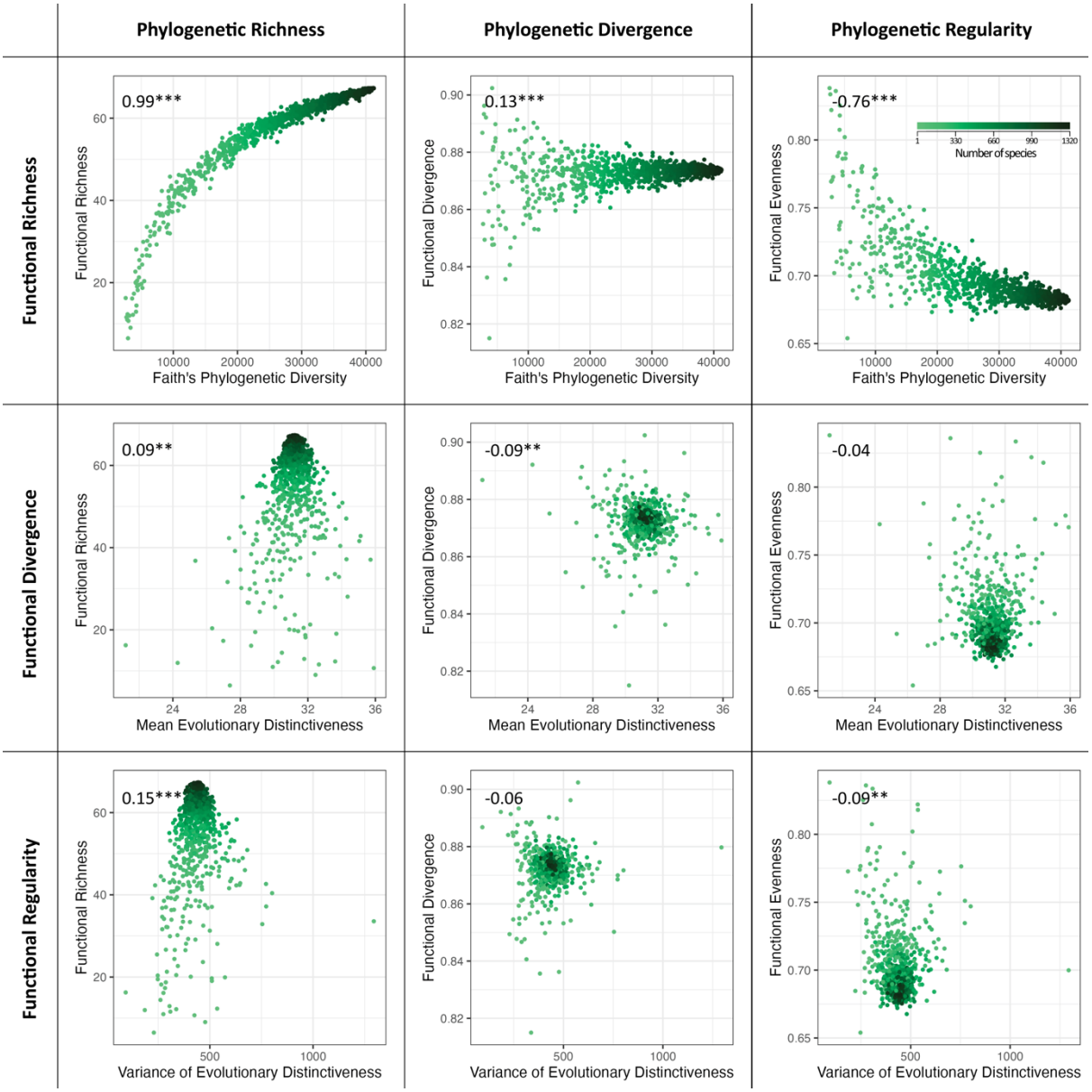
Imputing data using missForest increased the accuracy of all FD estimations except functional evenness when compared to removing species with missing data ($p < 0.001$ for all diversity metrics). FD estimates calculated from imputed datasets had lower values than estimates calculated using the complete dataset, in all metrics except FDiv (Fig. 2). TPD richness estimations had the greatest deviation from the complete data FD values with a median deviation of 44%, all other functional metrics deviated from the complete dataset by less than 21%. Though some data may not have been optimally imputed, I chose to continue using missForest for my analysis, as I wanted to include all Chondrichthyes species and random forest methods offer the best available performance for imputing data without incorporating phylogenetic information (May et al., 2023; Stewart et al., 2023).



2 – Fig. 2 | Imputation accuracy. Estimations of FD for simulated database where missing data was imputed (dark blue) or removed (light blue) compared to FD estimates calculated using the complete dataset (represented by the dotted line). Bars represent median values of 100 replicates where trait data was randomly removed from the complete dataset, error bars represent 95% confidence intervals. FD was calculated using six metrics; functional dendrograms, functional divergence, functional evenness, functional richness, Rao's Quadric Entropy (Rao's Q) and trait probability density (TPD) richness.

2 – 3.2 Overall comparisons of diversity metrics

Across the three conceptual dimensions for diversity metrics (richness, divergence and regularity) I used a single metric to represent each index and compare the relationship between PD and FD (Fig. 3). I present correlations between other phylogenetic and functional metrics in the supplementary material (Fig. S3). Of these metrics phylogenetic richness (Faith's PD) and functional richness (FRich) had the highest positive correlation (Spearman's coefficient = 0.99; p-value < 0.001), followed by phylogenetic regularity (Variance of ED) and functional richness (FRich; Spearman's coefficient = 0.15; p-value < 0.001) and phylogenetic richness (Faith's PD) and functional divergence (FDiv; Spearman's coefficient = 0.13; p-value < 0.001). There was a significantly strong negative correlation between functional regularity (FEve) and phylogenetic richness (Faith's PD; Spearman's coefficient = -0.76; p-value < 0.001).

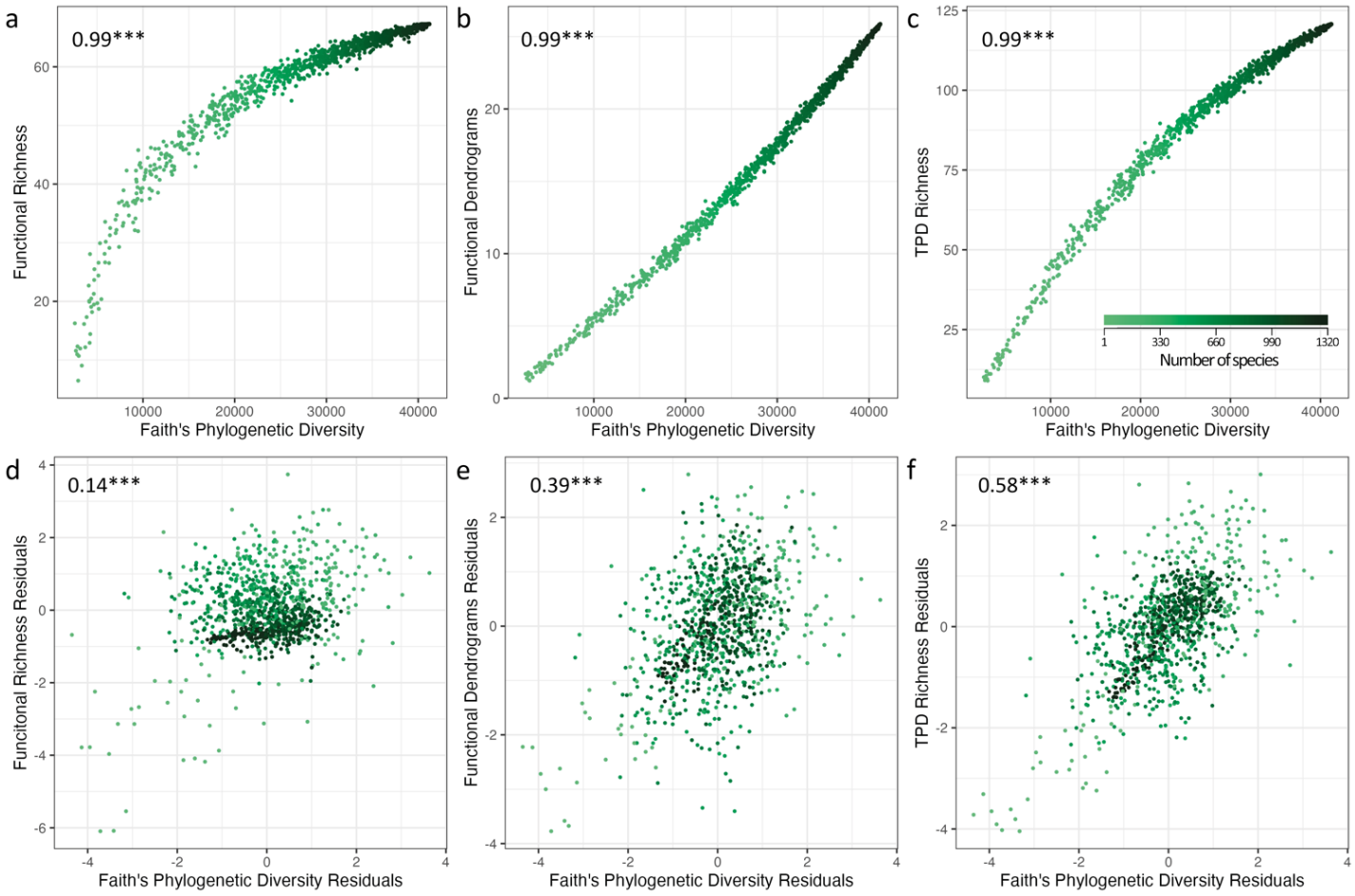


2 – Fig. 3 | Correlation between phylogenetic and functional metrics. Scatterplots to compare different conceptual dimensions for measuring PD and FD, with Spearman's coefficient values shown in the top left corner (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Colour represents species richness with light green tones indicating low species richness and dark green tones indicating high species richness. Richness-based diversity measures are represented by Faith's PD for PD and functional richness for FD. Divergence based diversity measures are represented by mean ED for PD and functional divergence for FD. Regularity based diversity measures are represented by variance of ED for PD and functional evenness for FD.

2 – 3.3 Richness metrics

When comparing richness measures without accounting for SR, Faith's PD had significantly high correlations with FRich, FDend and TPD richness (Fig. 4a, 4b and 4c). Across SR-independent measures of diversity, correlations were reduced (Fig. 4d, 4e and 4f). Correlations between Faith's PD residuals and TPD richness residuals and FDend residuals still had significant, moderately positive

correlations (Fig. 4e and 4f). As there was little difference between Faith's PD and EvoH correlations with functional richness metrics, I include the correlations for EvoH as supplementary material (Fig. S4). Across richness diversity metrics at different sample sizes, Spearman's correlations coefficient between phylogenetic and functional metrics were low, with sample sizes of 40% of the total species pool having consistently higher correlations (Table 3). Faith's PD ~ FDend and Faith's PD ~ TPD appeared to have the highest overall positive correlations of all the models tested (Table 3).



2 – Fig. 4 | Richness-based diversity metrics. Scatterplots to compare richness-based diversity metrics where PD and FD are measured with species richness not accounted for (a), (b) and (c) and species richness independent measures of PD and FD (d), (e) and (f). Spearman's coefficient values are shown in the top left corner (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Colour represents species richness with light green tones indicating low species richness and dark green tones indicating high species richness. Richness-based diversity measures are represented by Faith's PD for PD and functional richness, functional dendrograms and TPD richness for FD.

2 – Table 3 | Correlations between richness-based diversity metrics at different sample sizes. Spearman's rank correlations between phylogenetic richness-based metrics (Faith's phylogenetic diversity [PD] and evolutionary heritage [EvoH]); and functional richness-based metrics (functional richness [FRich], functional dendrograms [FDend], trait probability densities richness [TPD] and Rao's quadric entropy [RaosQ]). Significance values donated as * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001.

Model	1% Total Species	2.5% Total Species	5% Total Species	10% Total Species	20% Total Species	30% Total Species	40% Total Species	50% Total Species
PD ~ FRich	0.00	0.08	0.06	0.09	-0.10	0.07	0.17	-0.06
EvoH ~ FRich	0.00	0.11	0.08	0.08	-0.07	0.09	0.19	-0.04
PD ~ FDend	0.05	0.18	0.20*	0.14	0.03	0.09	0.30**	0.03
EvoH ~ FDend	0.11	0.15	0.19	0.11	0.03	0.16	0.32**	-0.04
PD ~ TPD	0.21*	0.13	0.31**	0.10	-0.01	-0.05	0.20*	0.09
EvoH ~ TPD	0.18	0.16	0.31**	0.11	-0.03	0.00	0.15	0.08
PD ~ RaosQ	-0.18	-0.06	-0.17	-0.08	-0.05	0.04	0.10	0.05
EvoH ~ RaosQ	-0.02	-0.07	-0.18	-0.06	-0.08	0.06	0.02	0.10

2 – 3.4 Divergence metrics

The Spearman's correlation coefficient between divergence diversity metrics was low, with no change in correlation between different sample sizes. The majority of correlations were slightly negative with only two significant slightly positive correlations between Rao's Q and Mean ED and MNTD (Table 4).

2 – Table 4 | Correlations between divergence-based diversity metrics at different sample sizes. Spearman's rank correlations between phylogenetic divergence-based metrics (mean pairwise distance [MPD] and mean evolutionary distinctiveness [MeanED]); and functional divergence-based metrics (functional divergence [FDiv] and Rao's quadric entropy [RaosQ]). Significance values donated as * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001.

Model	1% Total Species	2.5% Total Species	5% Total Species	10% Total Species	20% Total Species	30% Total Species	40% Total Species	50% Total Species
MPD ~ FDiv	0.03	-0.08	-0.05	-0.12	-0.21	-0.31**	-0.18	-0.17
MeanED ~ FDiv	-0.09	-0.11	-0.06	-0.20*	-0.16	-0.10	-0.26**	0.02
MNTD ~ FDiv	-0.10	0.03	0.01	-0.13	0.02	-0.10	-0.20*	-0.12
MPD ~ RaosQ	-0.18	-0.20*	-0.33***	-0.18	-0.19	-0.16	-0.16	-0.25*
MeanED ~ RaosQ	-0.06	0.25*	-0.08	-0.12	-0.05	0.06	0.01	0.02
MNTD ~ RaosQ	-0.14	0.12	-0.09	0.01	0.02	0.03	0.12	0.20*

2 – 3.5 Regularity metrics

Regularity diversity metrics had low Spearman's correlation coefficient, with no detectable pattern between sample size and correlation (Table 5).

2 – Table 5 | Correlations between regularity-based diversity metrics at different sample sizes. Spearman's rank correlations between phylogenetic regularity-based metrics (variance of pairwise distances [VPD] and variance of evolutionary distinctiveness [VarED]); and functional regularity-based metrics (functional evenness [FEve]). Significance values donated as * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001.

Model	1% Total Species	2.5% Total Species	5% Total Species	10% Total Species	20% Total Species	30% Total Species	40% Total Species	50% Total Species
VPD ~ FEve	-0.21*	-0.12	-0.18	-0.13	-0.07	0.06	-0.01	0.07
VarED ~ FEve	-0.05	-0.04	0.03	0.15	0.03	0.01	0.25*	-0.06

2 – 4 Discussion

In this chapter, I demonstrate that the outcome of measuring both PD and FD can vary hugely, depending on the metrics chosen and the dimension of biodiversity that they represent (Carmona et al., 2016; Mason et al., 2005; Villéger et al., 2008). Accurately characterising mechanisms underlying biodiversity is essential for understanding the impact of biodiversity loss, since different biodiversity facets may align with different conservation priorities. PD quantifies the amount of evolutionary variation and FD quantifies the variation of trait combinations within an assemblage. However, within these biodiversity measures there are multiple dimensions of variation that can be captured. Richness for example aims to capture the amount of diversity accumulated by assemblages, whereas divergence captures the spread of differences and regularity captures the distribution of an assemblage (Mammola et al., 2021). Here, I have shown that not only do these conceptual dimensions measure different facets of biodiversity but also the relationship between them varies significantly.

I have found strong correlations between richness-based phylogenetic and functional metrics, yet no strong correlations between divergence-based or regularity-based phylogenetic and functional metrics, demonstrating that methodological aspects such as the choice of diversity metrics can hugely influence correlations between phylogenetic and functional metrics. The influence of SR on diversity metrics should also be considered when selecting metrics. Here I demonstrate that correlations between richness-based phylogenetic and functional metrics were considerably reduced when accounting for SR, suggesting that these correlations were primarily driven by SR. Some relationships can be explained by the way different metrics are measured, for example there are positive correlations between Faith's PD and FDend even after accounting for SR. These methods both measure the total branch length of the minimum-spanning tree that connects all the species to represent hierarchical relationships between species, it is likely that these correlations occur due to the method of measuring diversity. Faith's PD and FEve have a strong negative correlation. As SR increases, the average distance between species in trait space is likely to decrease since there are more species existing within that space. Consequently, while Faith's PD increases with SR, FEve may decrease. In this study, I found that after accounting for SR, TPD richness residuals had the strongest relationship with PD residuals. Unlike other functional metrics, TPD richness incorporates intraspecific variation of species' traits. More of the total variation of species' traits may be explained when identifying each species' combination of traits as a probabilistic range of values, as represented in TPD richness, rather than representing trait variation as a single point. As such, PD correlates more closely with TPD richness, since PD captures all of trait variation (see chapter 1).

While some studies have found strong correlations between diversity metrics (Tucker et al., 2018), others have not (Cachera and Le Loc'h, 2017; Kelly et al., 2014). The lack of consistency in the relationship between PD and FD in empirical studies could depend on a number of different factors. For example, different assumed models of evolution or the shape of a clades phylogenetic tree could change the relationship between traits and phylogenies (Cadotte et al., 2017; Tucker et al., 2018). Previous work on this topic has also shown that correlations between PD and FD can be influenced by SR, the diversity metrics used, the type of traits selected (e.g. categorical or continuous data) and the number of traits used (Schmera et al., 2017; Tucker et al., 2018).

My results are consistent with recent papers that show a varying strength of correlation between measures of PD and FD (Kelly et al. 2014, Mazel et al. 2019). However, these studies that have included traits with categorical data, which will saturate at larger sample sizes. Studies using continuous data to observe the relationship between PD and FD have found a stronger correlation (Tucker et al. 2018). Relationships between diversity components will be contingent on the type, quality and quantity of trait data. Aligning traits to adequately represent ecosystem functions is essential for measuring FD in a meaningful way (Streit and Bellwood, 2022), however, data availability, especially when incorporating lesser studied clades, can limit the scope of traits to select from (Etard et al., 2020). For this study, I found that there was a limited number of traits with sufficient data to include in the analyses. Imputing data provides a practical way to overcome these limitations. Here I have used missForest to impute missing data as it makes no prior assumptions about the distributions of variables and does not incorporate phylogenetic relationships (Stekhoven and Bühlmann, 2012a). Since I am comparing the relationship between PD and FD it is important that missing data was not imputed using phylogenetic methods. Additionally, numerous studies have found a high degree of accuracy when imputing traits using random forest methods such as missForest (Gendre et al., 2024; May et al., 2023; Stewart et al., 2023). I found that imputing missing data increased the accuracy of FD estimates compared to removing species that had incomplete trait information. However, using published literature to reduce the amount of missing trait information would help to reduce the uncertainty in species contributions to trait space.

In this chapter I observe the correlation between PD and FD at the clade-level, this relationship may change as species are sorted into local communities (Mazel et al. 2017). Understanding how PD and FD correlate in geographical space would also provide a more direct reference for conservation action. Some studies have explored this relationship in terrestrial communities (Devictor et al., 2010; Safi et al., 2011), however different life histories, ecological interactions and taxonomic compositions in the marine realm may alter this relationship (Tessnow-von Wysocki and Vadrot, 2020). Indeed, large scale studies comparing biodiversity facets in multiple different communities in the marine realm may be complicated, due to a lack of consistent range data for marine species (Edgar et al., 2016). Additionally, species' ranges are defined vertically as well as horizontally, future work should consider how marine communities can be sorted over a three-dimensional scale, rather than just horizontal ranges (Andrzejaczek et al., 2022).

The contribution of a species to nature is a complicated concept and cannot be represented fully by a single metric (Griffin et al., 2020). This study highlights the importance of incorporating multiple metrics to measure biodiversity. The past two decades have seen exponential growth in trait

diversity studies (Mammola et al., 2021). With a jungle of information available for functional metrics, recent efforts have been made to summarise this theoretical information and connect with current practical methods available to apply trait based ecology (de Bello et al., 2021b; Mammola et al., 2021; Pavoine et al., 2009; Pavoine and Bonsall, 2011; Tucker et al., 2017). However, there is certainly scope for improvement when it comes to generalising FD methods to facilitate comparisons and coherence between different studies. Developments in both phylogenetic and functional metrics are occurring rapidly. With such developments come new opportunities to understand and identify patterns in biodiversity. This chapter identifies nuances between phylogenetic and functional metrics beyond what SR alone can capture. These findings emphasise the importance of directly studying FD, as PD cannot fully represent the variation of trait combinations in a community. This opens opportunities to refine methods that prioritise FD for conservation, as current approaches prioritising FD do not align with those used for PD.

2 – Supplementary information

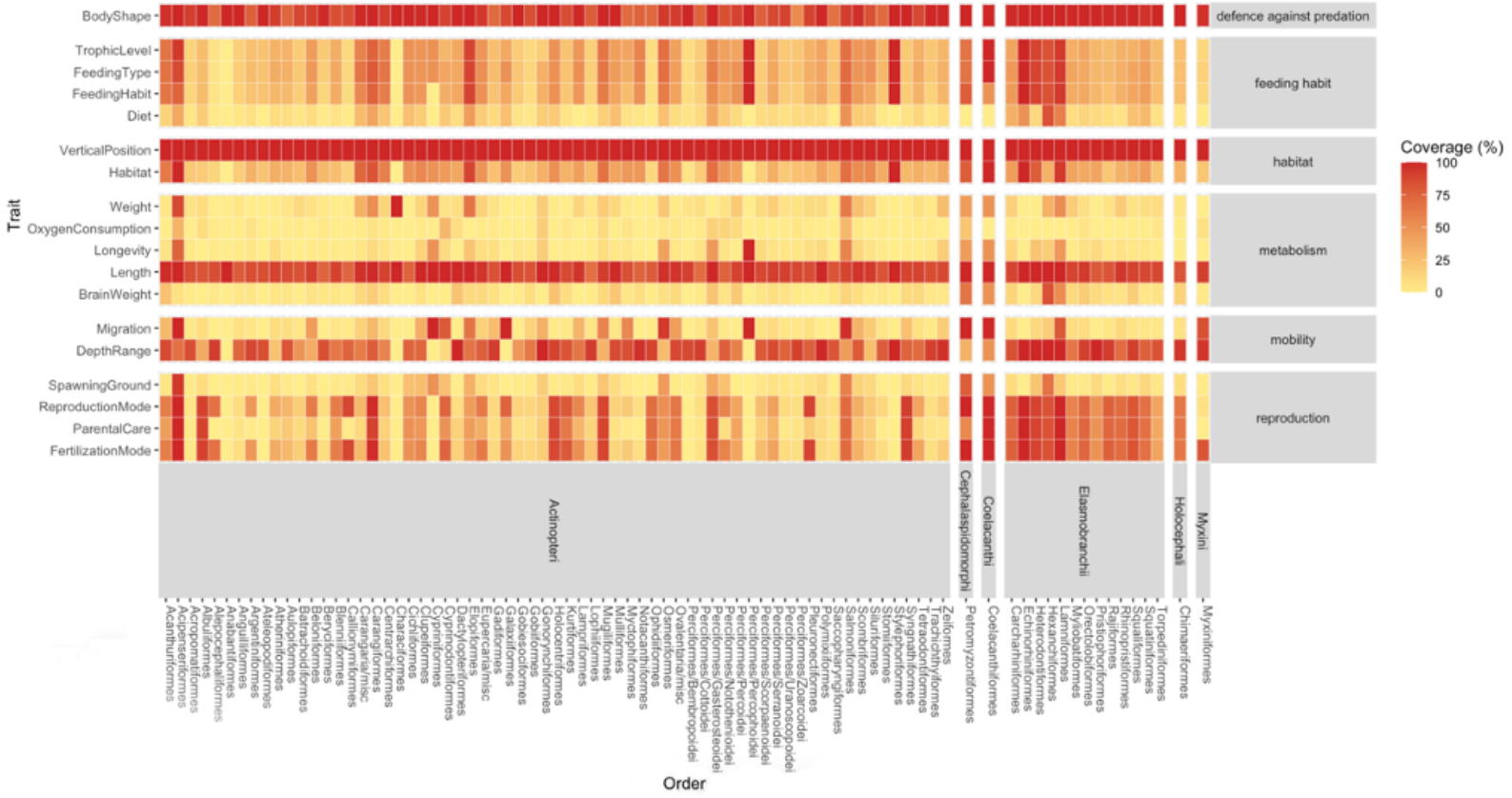


Fig. S1. Summary of trait data coverage for all 34666 finfish species in the FishBase database. The percentage of data coverage for each family is indicated by colour, with red indicating higher percentage of coverage.

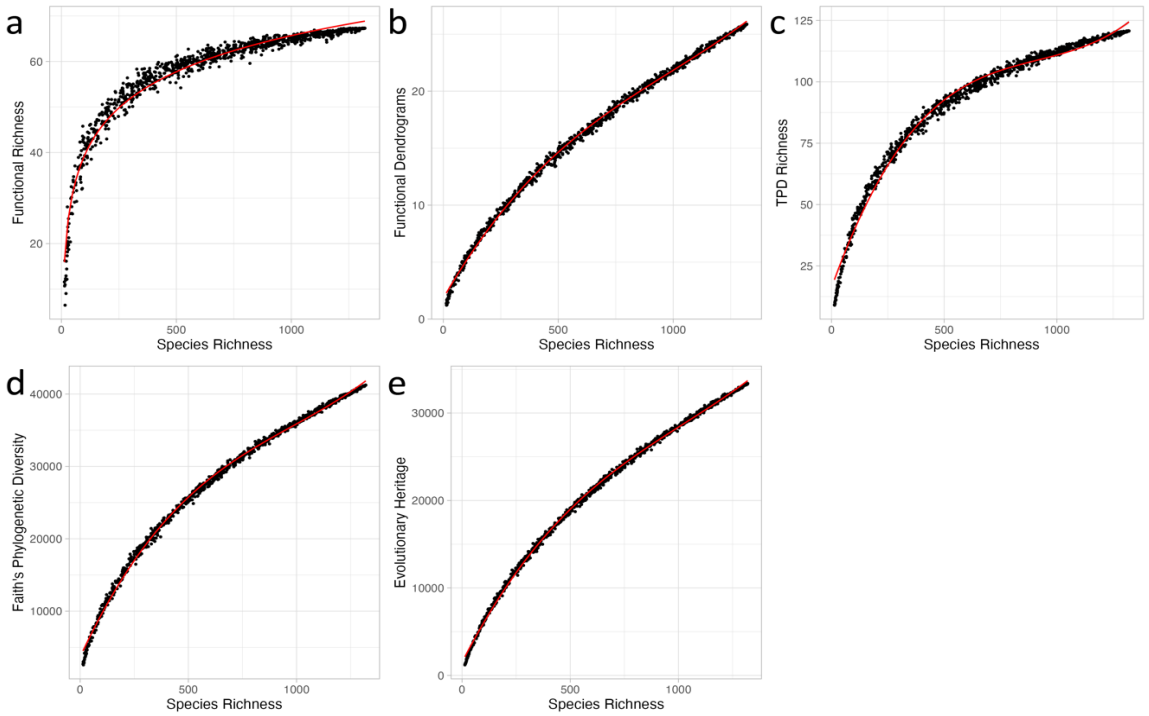


Fig. S2. Relationships between richness-based functional (a-c) and phylogenetic (d and e) metrics and species richness. Red line indicates regression models fitted using logarithmic (a) and cubic (b-e) models.

Table S1. Table of AIC values for linear, quadratic, cubic and logarithmic models between species richness (SR)

and five richness-based biodiversity metrics, functional richness (FRich), functional dendrograms (FDend), trait probability densities (TPD), phylogenetic diversity (PD) and evolutionary heritage (EvoH). Models that minimise the AIC are highlighted in bold.

Model parameters	***Model***	***df***	***AIC***
FRich ~ SR	Linear	3	6409.99605
	Quadratic	4	5563.60607
	Cubic	**5**	**4907.9865**
	Logarithmic	3	4185.85113
FDend ~ SR	Linear	3	2967.49137
	Quadratic	4	1233.73565
	Cubic	**5**	**445.874411**
	Logarithmic	3	4207.81549
TPD ~ SR	Linear	3	7509.71288
	Quadratic	4	5991.89076
	Cubic	**5**	**4789.68315**
	Logarithmic	3	5069.61519
Faith's PD ~ SR	Linear	3	18244.6293
	Quadratic	4	16357.5184
	Cubic	**5**	**15179.1848**
	Logarithmic	3	18500.1222
EvoH ~ SR	Linear	3	17515.196
	Quadratic	4	15376.4867
	Cubic	**5**	**14136.6174**
	Logarithmic	3	18502.7374

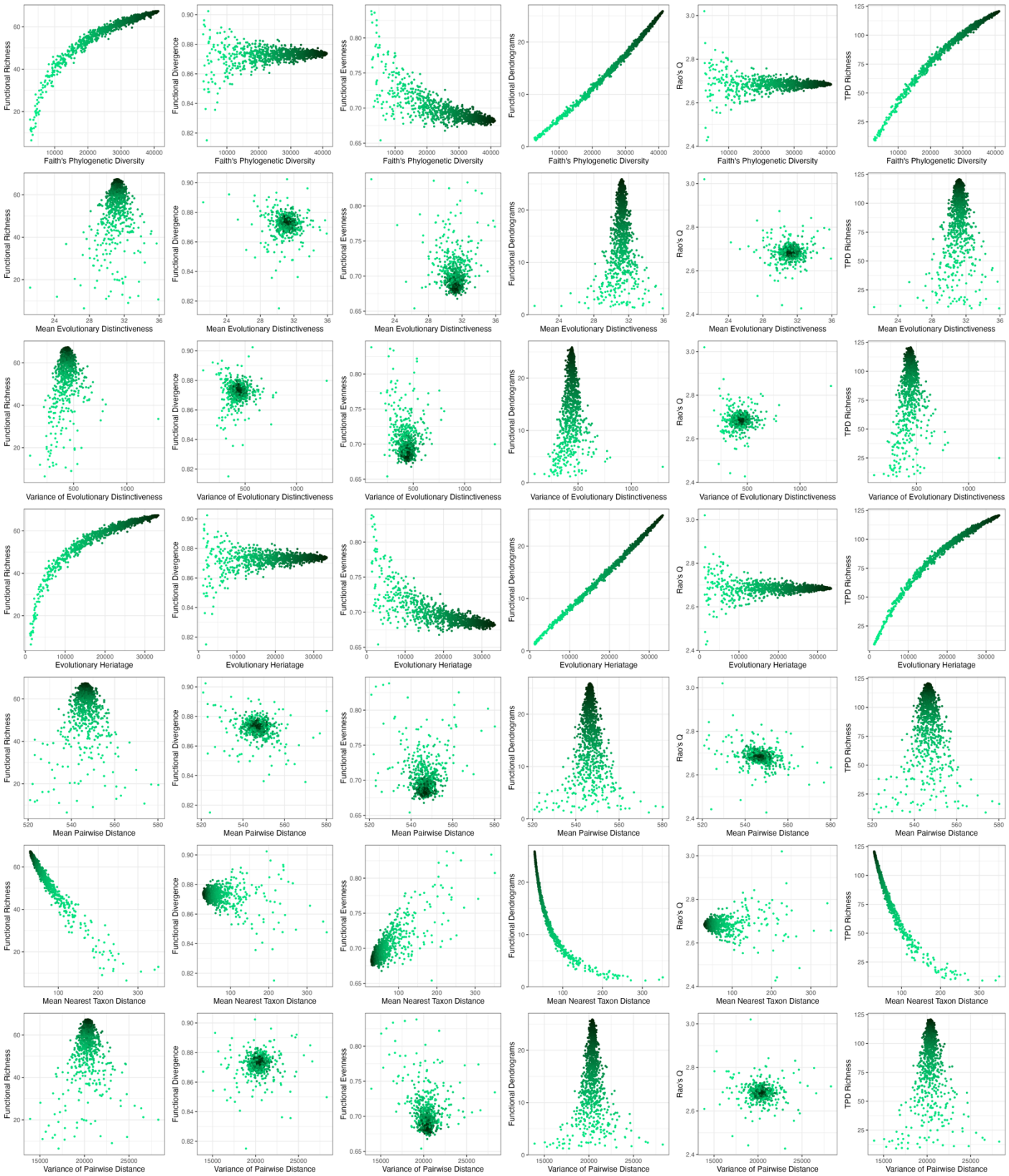


Fig. S3. Scatterplots to show the relationship between different phylogenetic and functional metrics. Colour represents species richness with light green tones indicating low species richness and dark green tones indicating high species richness.

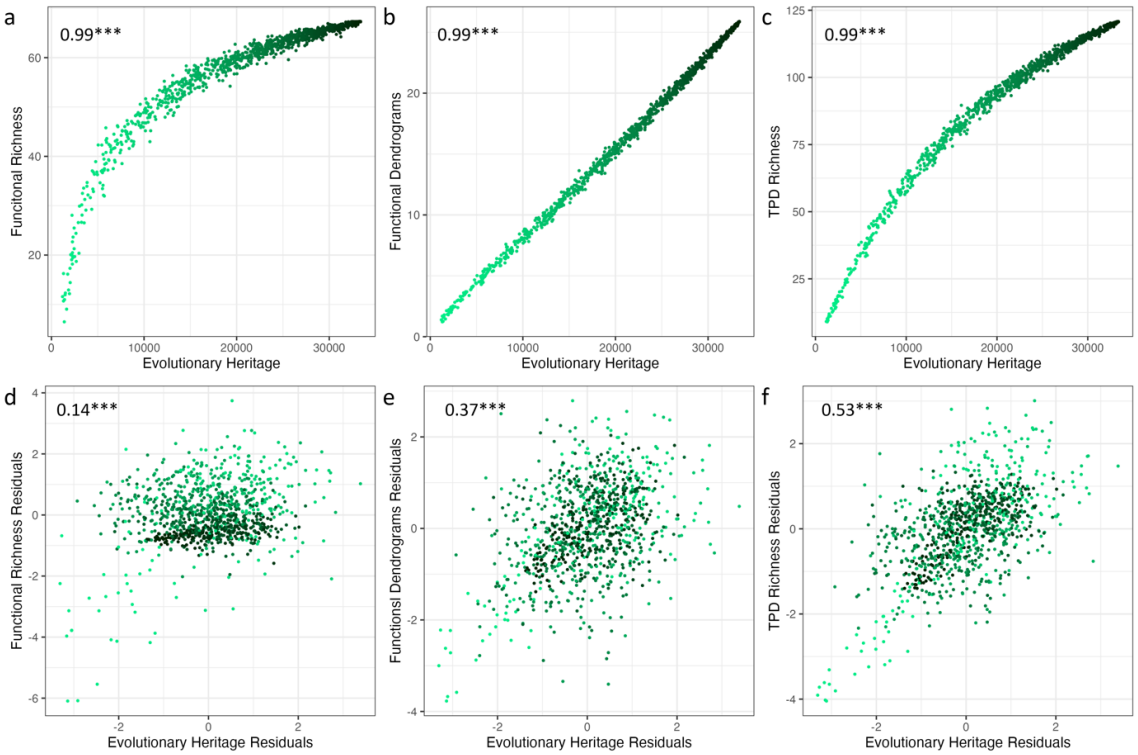


Fig. S4. Scatterplots to compare richness-based diversity metrics where PD and FD are measured with species richness not accounted for (a, b and c) and species richness independent measures of PD and FD (d, e and f). Spearman's coefficient values are shown in the top left corner (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Colour represents species richness with light green tones indicating low species richness and dark green tones indicating high species richness. Richness-based diversity measures are represented by evolutionary heritage for PD and functional richness, functional dendrograms and TPD richness for FD.

Chapter 3 – Prioritising Functionally Distinct and Globally Endangered (FuDGE) sharks for conservation action

3 – Abstract

Ecological differences between species are associated with their contribution to the functioning, stability and resilience of ecosystems. Measuring the ecological uniqueness of species will improve understanding of how species loss might impact ecosystem function and services. However, robust species-level methods for quantifying ecological differences have yet to be incorporated into conservation strategies. In this chapter, I describe a new approach to measure the unique contribution of species to overall FD and incorporate it into an actionable conservation metric. I propose the Functionally Distinct and Globally Endangered (FuDGE) prioritisation metric for directing conservation action to species whose extinction would result in significant losses of irreplaceable FD. I 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, and that 17-24% of extant shark trait space is at risk of extinction. I show that exploitation by humans threatens to disproportionately erode shark trait space, with 70% of trait space at risk from exploitation. The FuDGE metric can be used to guide the conservation of functionally irreplaceable species in the face of human impacts.

3 – 1 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 (Mace et al., 2012). Efforts to mitigate declines in biodiversity require strategic decision-making and often utilise established metrics of risk or priority, such as conservation status (IUCN Red List of Threatened Species), taxonomic diversity (Hoekstra et al., 2005), endemism (Mittermeier et al., 2003), climate vulnerability (Foden et al., 2019; IPCC, 2022) and evolutionary history (Isaac et al., 2007). However, relatively little progress has been made at incorporating the variation of functional traits of species, measured as FD (Cadotte et al., 2011; Violle et al., 2007), into conservation decision-making (Miatta et al., 2021). For example, Goal A of the United Nations CBD KMGBF focuses on maintaining, restoring and enhancing biodiversity to improve functions and services (CBD, 2022), yet the accompanying monitoring framework contains no means for tracking progress towards recovery of FD.

Measuring the FD of species assemblages can help to inform how species loss might impact ecosystem functions and services (de Bello et al., 2021a), 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 (Ali et al., 2023; Carmona et al., 2021). However, current prioritisation metrics that consider taxonomic or phylogenetic information alone do not adequately capture FD (Oliveira et al., 2020; Pollock et al., 2017).

Advances in metrics that prioritise species for conservation based on PD (the sum of phylogenetic branch lengths connecting a set of taxa (Faith, 1992)) have produced approaches that are based on the established conceptual framework of averting expected losses of the most imperilled biodiversity (Faith, 2008; Gumbs et al., 2023b; Jensen et al., 2016; Robuchon et al., 2021; Steel et al., 2007). For example, the EDGE2 protocol (Gumbs et al., 2023b), prioritises species based on the amount of threatened PD their conservation would secure. In contrast, proposed metrics to prioritise species for conservation based on FD (e.g. Hidasi-Neto et al., 2015; Pimiento et al., 2020) often lack fundamental conceptual and mathematical foundations (Gouhier and Pillai, 2020), with rare exceptions (Pavoine and Ricotta, 2023). However, growing focus on the maintenance of functionally diverse systems for conservation (Cadotte et al., 2011; Violle et al., 2007), the increasing availability of trait data across the tree of life (Mammola et al., 2021; Pollock et al., 2017), and established methods to quantify FD (Tucker et al., 2017) 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 (Stein et al., 2018) and functionally unique (Pimiento et al., 2020) vertebrate lineages and perform a range of ecological roles (including apex predators and mesopredators) across global marine ecosystems, and some estuarine and freshwater habitats(Dedman et al., 2024). However, sharks are one of the most imperilled vertebrate clades (30% of species threatened with extinction; Dulvy et al., 2021; IUCN Red List of Threatened Species),

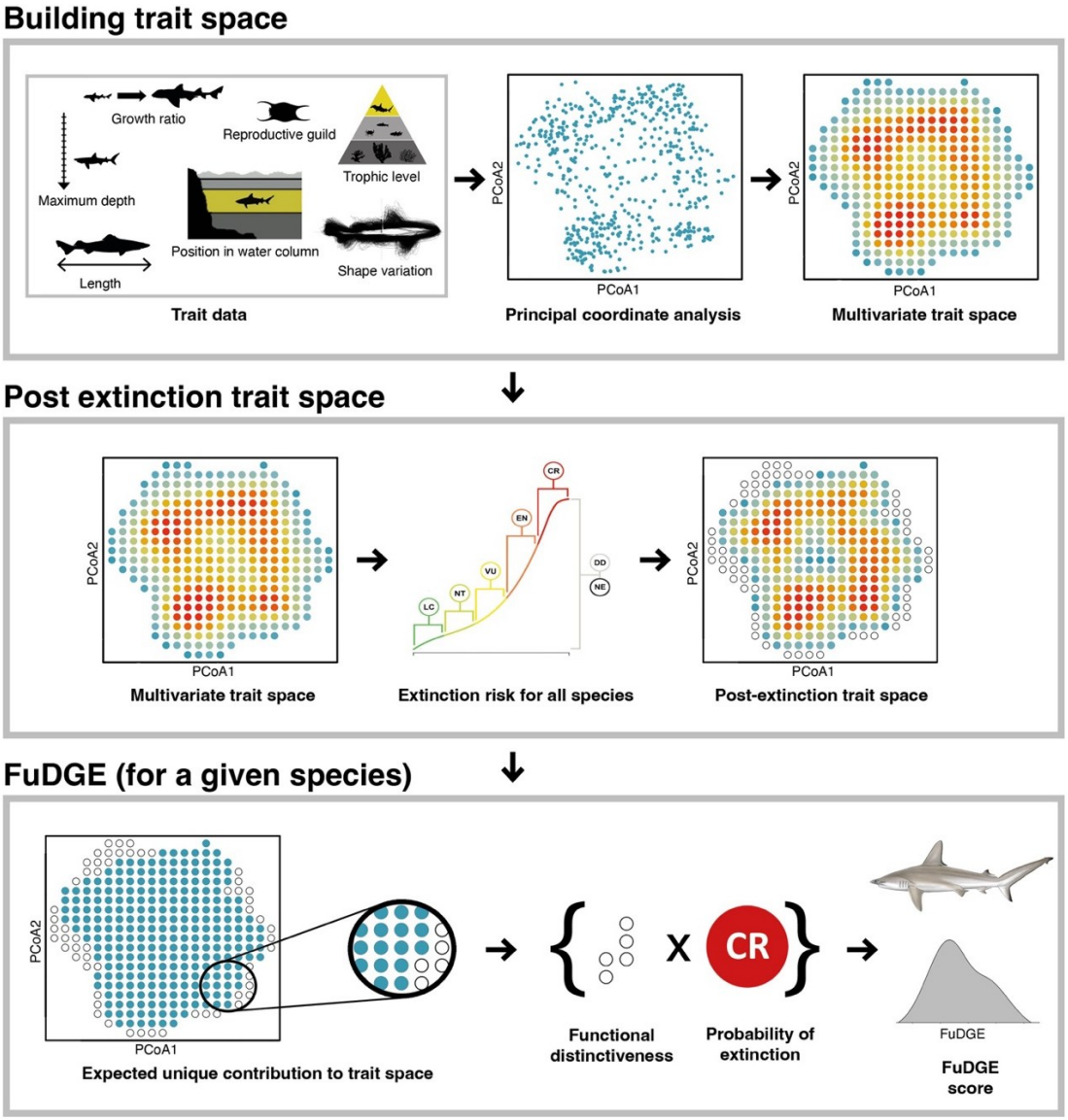
and many species are experiencing population declines due to overexploitation, habitat degradation and climate change (Almond et al., 2022). Overfishing is one of the primary threats faced by sharks (Cardeñosa et al., 2022) and species targeted by humans might be distinct in different biodiversity facets (Gumbs et al., 2023c; Molina-Venegas, 2021). These declines threaten the stability and health of aquatic ecosystems globally and require focused conservation action to prevent irreversible loss (Dulvy et al., 2017; Finucci et al., 2024).

In this chapter, I set out to develop a method that prioritises functionally irreplaceable and threatened species for conservation. I present the Functionally Distinct and Globally Endangered (FuDGE) metric, which quantifies the expected loss of species FD that can be averted through species-focused conservation action. I apply FuDGE to the world's sharks and explore the relationship between FuDGE and its phylogenetic equivalent, EDGE (Gumbs, Gray, Böhm, et al., 2023). I 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.

3 – 2 Methods

3 – 2.1 Functionally Distinct and Globally Endangered (FuDGE) calculations

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 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). For each species, FuDGE is the product of 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. 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.



3 – 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; Carmona et al., 2019). 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 create a continuous distribution of extinction probabilities, following Gumbs et al.(2023) where the median of each Red List category was defined as; Critically Endangered = 0.97, Endangered = 0.485, Vulnerable =0.2425, Near Threatened = 0.12125, and Least Concern = 0.060625. Species probability of extinction is randomly selected from the distribution of extinction probabilities defined by their IUCN Red List categories. Species that were not assessed or had IUCN Red List category listed as Data Deficient, were randomly sampled from the entire distribution of extinction probabilities. 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 score of a species is then calculated as the product of its functional distinctiveness and probability of extinction. Both components are calculated 1000 times to capture the distribution of outcomes from the probability of extinction. Shark illustration: Marc Dando.

3 – 2.1.1 Species coverage of trait space

One way to measure FD, the property I aim to maximise through the prioritisation scheme outlined in this chapter, 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, functional richness is given by;

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

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 I use in practice here, I 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 (Carmona et al., 2019) applied here 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 of the assumption that 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.

3 – 2.1.2 Irreplaceable species-specific trait space (functional distinctiveness)

To quantify the expected contribution of a given focal species to total FD in the future, I 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. My method for the functional distinctiveness is based on three steps and is performed on every species (summarised in Fig. 1).

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. I followed the Gumbs et al.(2023) weighting of IUCN Red List categories(IUCN, 2001) to estimate probability of extinction for each species. IUCN Red List categories were converted to represent probability of extinction based on a continuous distribution of extinction probabilities, where the median of each Red List category was defined as,

Critically Endangered (CR) = 0.97; Endangered (EN) = 0.485; Vulnerable (VU) = 0.2425; Near Threatened (NT) = 0.12125; Least Concern (LC) = 0.060625. Species that were not assessed or had IUCN Red List category listed as Data Deficient (DD), were randomly sampled from the entire distribution of extinction probabilities.

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.

3 – 2.1.3 Avertable loss (FuDGE)

To capture the avertable loss of irreplaceable FD I multiplied the functional distinctiveness of each species by its probability of extinction (GE) to quantify the expected loss of FD given the extinction risk of the species. I 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. I calculated 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 I opted 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 I did here is a much more practical way of quickly approximating to the same result as a precise evaluation of the formula. To facilitate comparability between functional distinctiveness and FuDGE scores calculated from different trait spaces, I present the scores as the percentage of total trait space.

Current functional distinctiveness and FuDGE values. Incorporating functional complementarity into the functional distinctiveness calculations will change the consequences of each species functional distinctiveness score, depending on their relation in trait space with other species, and those species extinction probability. To test the correlation between current functional distinctiveness and future functional distinctiveness, and ensure there is no overweighting of extinction probabilities, I also calculated functional distinctive that represent the current trait space, where no extinction scenarios have taken place in trait space (Fig. S1).

Comparing functional metrics. To investigate the variations between different metrics, I used Pearson's correlation to compare functional distinctiveness against other metrics that measure FD (Fig. S2). I investigated 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; Grenié et al., 2017). 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; Grenié et al., 2017). 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; Carmona et al., 2019).

3 – 2.2 Calculating FuDGE for sharks

3 – 2.2.1 Data collection

I collated published data for extinction risk, traits and evolutionary history of sharks (Selachimorpha). I limited this study to sharks, omitting other clades of Chondrichthyes (Batoidea and Holocephali), as I have added new data to the trait database I collated in chapter 2. Due to limited availability of comparable data for Batoidea and Holocephali, I decided to omit these species from this analysis. To taxonomically match species information from different datasets, I used nomenclature from FishBase (accessed 11/2023; Froese & Pauly, 2023), which included 557 species. All database manipulation and analyses were performed using R statistical software (v. 4.3.1; R Core Team, 2023).

Extinction risk data. I used the IUCN Red List of Threatened Species (v. 2023.1) to obtain information of species extinction risk. This includes assessment data for 540 species, including 467 data sufficient species (LC; NT; VU; EN; or CR) and 73 categorised as Data Deficient (DD). The remaining 17 species in my dataset are Not Evaluated (NE) on the Red List. To calculate a species probability of extinction I generated a continuous distribution of extinction probabilities following methods outlined by Gumbs et al.(2023), where the median of each Red List category was defined as, CR = 0.97; EN = 0.485; VU = 0.2425; NT = 0.12125; LC = 0.060625. Probability of extinction was randomly selected from the distribution of values within each species' Red List categorisation. Where species were categorised as DD or NE their extinction probability was randomly selected from the whole distribution of extinction risk values.

Evolutionary history data. I used the EDGE2 protocol (Gumbs et al., 2023b) 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 I 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.(2018) tree distribution of 10000 Chondrichthyes trees, where species absent from the phylogenies were inserted based on taxonomy using the same approach as outlined in chapter 2.

Trait data. I collated eight traits for my analysis (Table 1), obtained from FishBase (Froese and Pauly, 2023) and Sharks of the World: A Complete Guide (Ebert et al., 2021). I selected traits based on data availability and representation of functional guilds (Table 1). Traits were selected to capture a broad suite of traits that are important in describing species role within an ecosystem reflecting life history strategies, habitat use, trophic interactions and morphological variation (Henderson et al., 2024; Siders et al., 2022; Table 1). To measure body shape, I modified methods shown in Siders et al.(2022), which uses Elliptical Fourier analysis (EFA) to represent variation in shark body shape. I

collected 515 illustrated images from Sharks of the World: A Complete Guide (Ebert et al., 2021) to measure the variation in shark body shape using EFAs. These images were first converted into outlined silhouettes using photoshop (v. 23.5.5; Adobe Inc., 2023). Using the R package Momocs (v. 1.4.1; Bonhomme et al., 2014) each outline was scaled and centred on a matrix (Fig. S4) and EFA was performed on the outlines, using 16 harmonics (Fig. S5). 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 my analysis (Fig. S6), PC1 represents 43% variation and PC2 represents 19% variation. Visual inspection of PC1 and 2 showed that PC1 relates to elongation of the pectoral fin and caudal fin and PC2 highlights the sharks width and prominence of the dorsal fin.

3 – Table 1 | Species traits. Traits used to build trait space and the functional guild each trait represents.

Trait	Definition	Source	Unit	Data type	Number of species (% coverage)	Functional guild
Maximum Body Length	The maximum total length of an individual species (where the mean maximum values is taken if sex maximum length differs)(Froese and Pauly, 2000)	FishBase	cm	Continuous	535 (96.1%)	Related to body size, metabolism and impact on the food web (Henderson et al., 2024)
Maximum Depth	The maximum reported depth for juveniles and adults of the species (Froese and Pauly, 2000)	FishBase	m	Continuous	488 (87.6%)	Can reflect vertical mobility, swim performance and nutrient cycling (Andrzejaczek et al., 2022)
Trophic Level	Where the species operate in their respective foodwebs (Froese and Pauly, 2000)	FishBase	1 + mean trophic level of species food items	Continuous	278 (49.9%)	Can reflect trophic interactions and the position occupied on a food web (Henderson et al., 2024)
Body shape variation PC1	Principal component 1 of the PCA describing the elliptial fourier analysis of each species lateral sillouette (Siders et al., 2022)	Sharks of the world		Continuous	512 (91.9%)	Can reflect morphological variation, swim performance and predator-prey interactions (Sternes and Shimada, 2020)
Body shape variation PC2	Principal component 2 of the PCA describing the elliptial fourier analysis of each species lateral sillouette (Siders et al., 2022)	Sharks of the world		Continuous	512 (91.9%)	Can reflect morphological variation, swim performance and predator-prey interactions (Sternes and Shimada, 2020)
Growth Ratio	The relative increase in length of the species based on the length at birth and maximum length	Sharks of the world, FishBase	length (cm) / length at birth (cm)	Continuous	342 (61.4%)	Can reflect life history strategies (Cortés, 2004)
Reproductive Mode	Whether the species lays eggs (oviparous) or gives birth to live young (viviparous)	Sharks of the world, FishBase	oviparous, viviparous, aplacental viviparous, viviparous (with a yolk sac placenta)	Categorical	557 (100%)	Can reflect life history strategies (Cortés, 2004)
Habitat preference	The particular environment preferred by the species (Froese and Pauly, 2000)	FishBase	pelagic, benthopelagic, demersal, reef-associated, bathypelagic, bathydemersal	Categorical	469 (84.2%)	Can reflect hunting or foraging behaviour, nutrient cycling and microhabitat formation (Sorenson et al., 2014)

Imputing missing data. My compiled database contained 557 species. To complete missing values in the trait database, I imputed missing data using the missForest function in the missForest R package (v. 1.5; Stekhoven & Bühlmann, 2012). 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. To test the performance of the imputation, I used methods outlined in chapter 2 (section 2.2) to simulate unknown trait data and examine how imputation affected the estimation of FD.

3 – 2.2.2 Quantifying trait space

Distance matrix. Prior to quantifying a distance matrix, I log transformed, scaled and centred to mean = 0, SD = 1 continuous traits to ensure normal distribution and prevent overweighting. I calculated a dissimilarity distance matrix using the function gawdis (v. 0.1.5; de Bello et al., 2021). This approach prevents disproportionate weighting of categorical traits to produce multi-trait dissimilarity with more uniform contributions of different traits (de Bello et al., 2021a).

Principal coordinate analyses. Using the dudi.pco function in the ade4 package (v. 1.7.22; Dray & Dufour, 2007) I 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 which together represent 45.28% of total variation.

Multidimensional trait space. TPDs represent each species in functional trait space as a multivariate kernel density estimation. I approximated TPD values using the measured traits available in the analysis and an estimated variability using the TPD package (v. 1.1.0; Carmona et al., 2019). 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. I applied the methods stated above to calculate functional distinctiveness and FuDGE values for all sharks. Following the EDGE2 protocol (2023) and applying it to the FuDGE metric, I 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; Appendix A1).

3 – 2.3 Relationship between FuDGE and EDGE

I 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 FD and PD I 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) I 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. I plotted each dimension of trait space and

highlighted the three species and their congeners in trait space (Fig. S3).

3 – 2.4 FuDGE and exploited sharks

I identified exploited shark species using the IUCN Red List threats classification scheme (https://www.iucnredlist.org/resources/threat-classification-scheme; IUCN Red List of Threatened Species), where threat type was listed as Biological resource use Fishing & harvesting aquatic resources (5.4). I considered a species intentionally exploited when the species being assessed is the target, as codified 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).

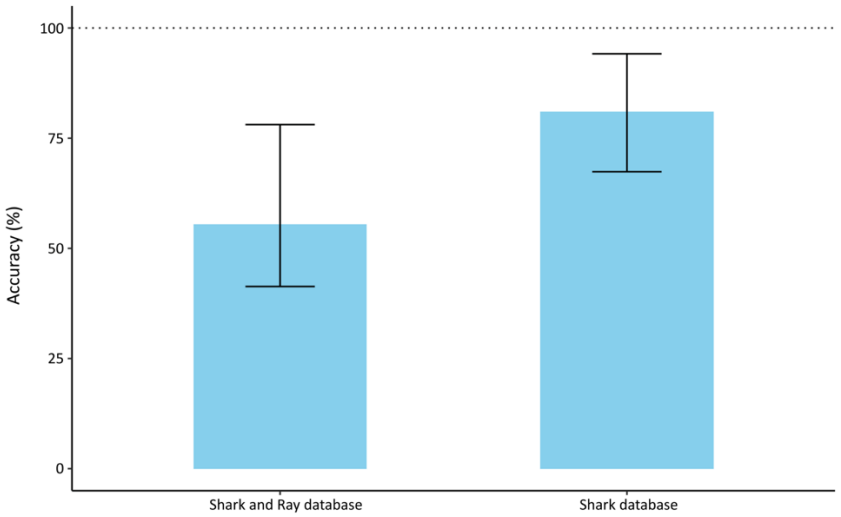
To explore the potential of different prioritisation strategies at safeguarding intentionally exploited species, I randomly selected 10%, 20%, 30%, 40% and 50% of all shark species, weighted by different prioritisation measures: evolutionary distinctiveness score; EDGE score; functional distinctiveness score; FuDGE score and also from an equally weighted distribution for comparison. I repeated this 1000 times for each approach and compared the number of intentionally exploited species captured by each approach for each sample size. I included EDGE and FuDGE in this analysis to investigate how effectively prioritisation strategies that aim to protect threatened PD and FD capture threatened and intentionally exploited species. To test if prioritisation strategies differed significantly at safeguarding intentionally exploited species I 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 I calculated the functional and evolutionary distinctiveness scores of species listed as intentionally exploited and species listed as unintentionally exploited and compared them using t-tests. To investigate the potential impact of human exploitation on shark FD and PD, I removed species categorised as i) intentionally exploited and ii) both intentionally and unintentionally exploited from trait space and the phylogenetic tree. I compared the loss of trait space and evolutionary history in exploited species to a randomly selected sample of species of the same number.

3 – 3 Results

3 – 3.1 Erosion of shark FD

Taxonomic coverage of the traits selected to quantify trait space was high overall (mean coverage = 81.6%, median = 89.8%; Table 1). 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 habitat preference having 100% coverage. Imputing my updated shark trait database had significantly more accuracy at estimating TPD richness compared to imputed data used in chapter 2 (Fig. 2; two-sample T-tests $p > 0.001$). The median accuracy for estimating TPD richness for the updated shark database was 81% (Fig. 2). The spearman's rank correlation between complete functional distinctiveness values and simulated imputed functional distinctiveness values was 0.78 (p

> 0.001).

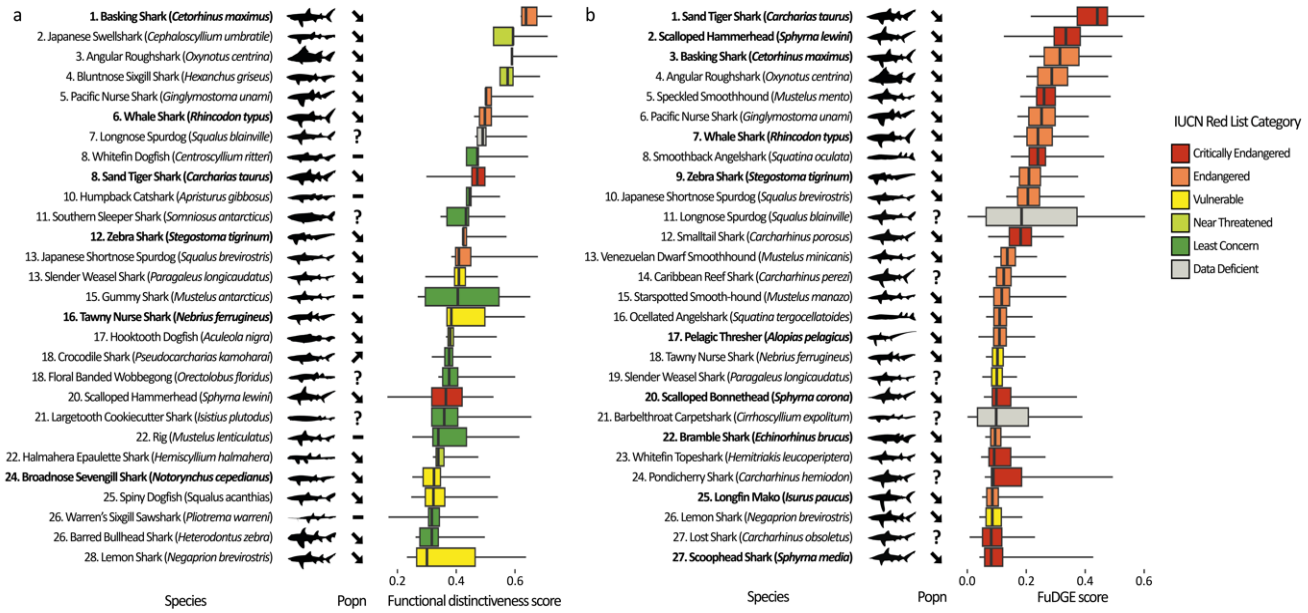


3 – Fig. 2 | Imputation accuracy. Estimations of TPD richness for simulated databases from chapter 2 (shark and ray database) and chapter 3 (shark database) where missing data was imputed using missForest compared to FD estimates calculated using the complete dataset (represented by the dotted line). Bars represent median values of 100 replicates where trait data was randomly removed from the complete dataset, error bars represent 95% confidence intervals.

To estimate the projected impact of extinction on shark trait space, I calculated the proportion of trait space that would be lost with the extinction of all 167 currently threatened species (VU, EN, CR on the IUCN Red List). I found that 17.18% of global shark trait space is at risk of extinction, potentially increasing to 23.58% if I were to also consider all DD and NE species as at risk of extinction.

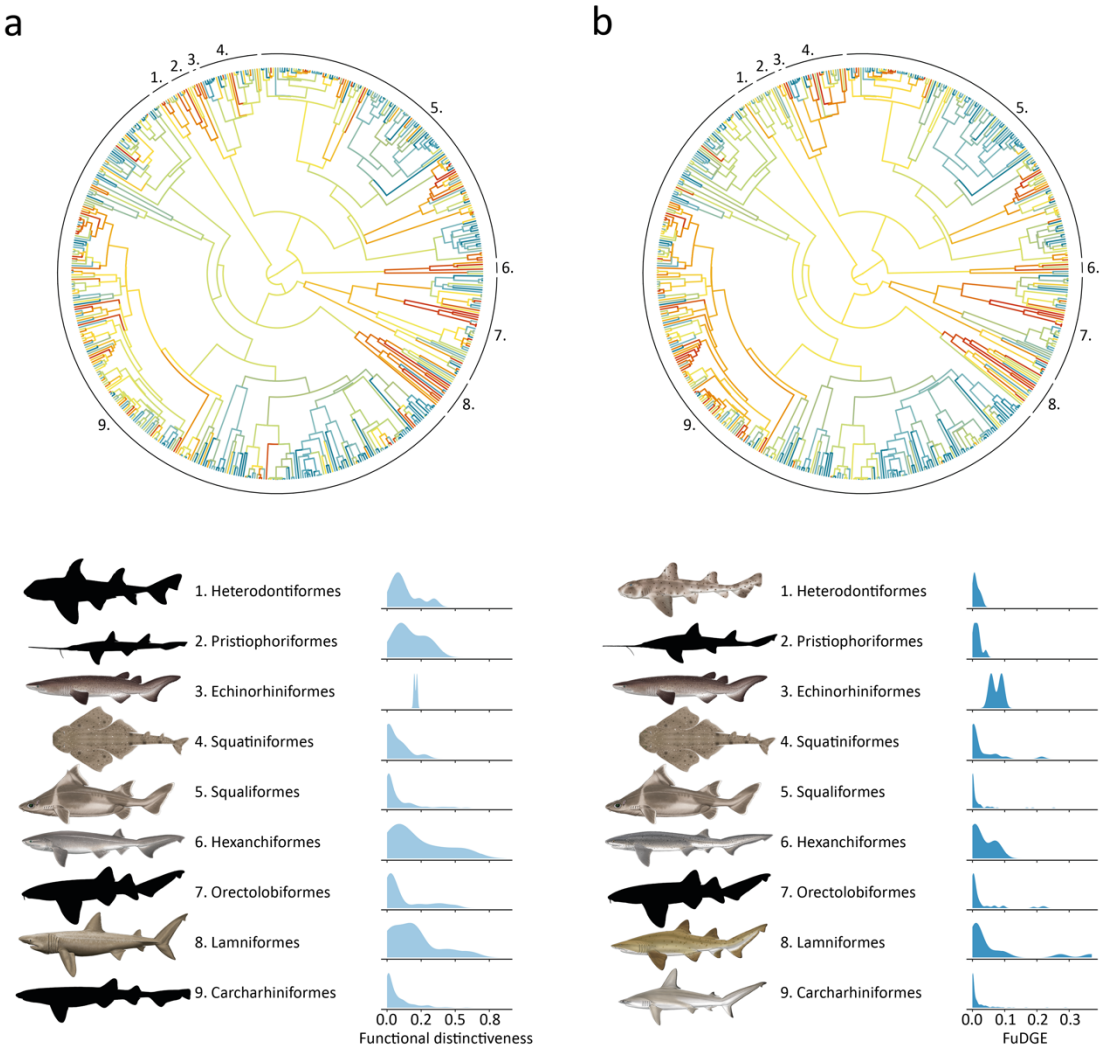
3 – 3.2 Shark functional distinctiveness and risk

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 most functionally distinct species (28 spp.) together occupy 10.85% of unique trait space (Fig. 3). Overall, 46% of the top 5% functionally distinct species are threatened with extinction, compared with 30% of all sharks being threatened with extinction (IUCN Red List of Threatened Species).



3 – Fig. 3 | 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). Shark silhouettes: Marc Dando.

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. 4a). 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. 4a). Correlations between functional distinctiveness and a measure of functional distinctiveness where the current full assemblage of species is used (no extinction scenarios occur) was significantly positive ($r = 0.96$, $p < 0.001$; Fig. S1). I compared my functional distinctiveness measure against other approaches to quantifying species-specific contributions to overall FD (Carmona et al., 2019; Violle et al., 2017), and found significant but only moderate positive relationships between them (Fig. S2).



3 – Fig. 4 | 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 1000 phylogenetic trees used in this study to calculate EDGE scores. Illustrations: Marc Dando.

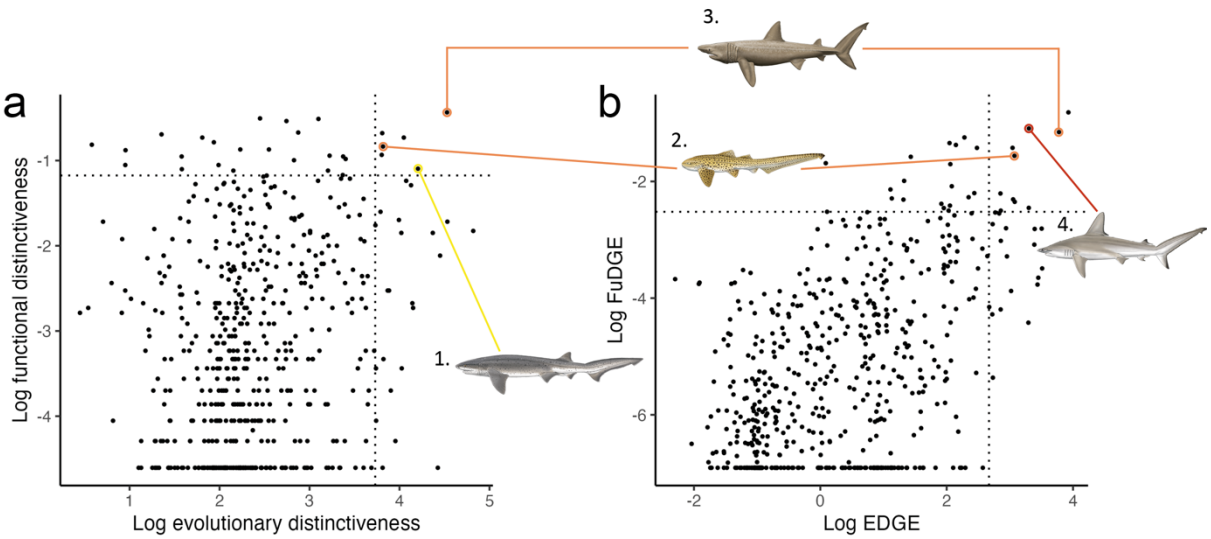
3 – 3.3 Priority FuDGE species

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. 4b). In total, 12 species were included in both the top 5% functionally distinct and FuDGE lists (Fig. 3). I identified 76 shark species as priority 'FuDGE' species, defined as threatened with 95% certainty that they are above median FuDGE (mirroring the approach to identifying priority 'EDGE species' (Gumbs et al., 2023b); full list in Appendix A1).

3 – 3.4 Relationship between FuDGE and EDGE

Functional distinctiveness and evolutionary distinctiveness had a weak but significant positive correlation (Pearson's correlation: r = 0.18, p < 0.001; Fig. 5a). 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. 3a and Fig. 5a). 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. 5a).

FuDGE and EDGE had a significant positive correlation (Pearson's correlation: r = 0.51, p < 0.001; Fig. 5b). Ten species were in the top 5% of both FuDGE and EDGE, and I classify these species as the most Extremely Distinct and Globally Endangered (ExDGE) shark species on Earth (species in bold in Fig. 3b). 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).



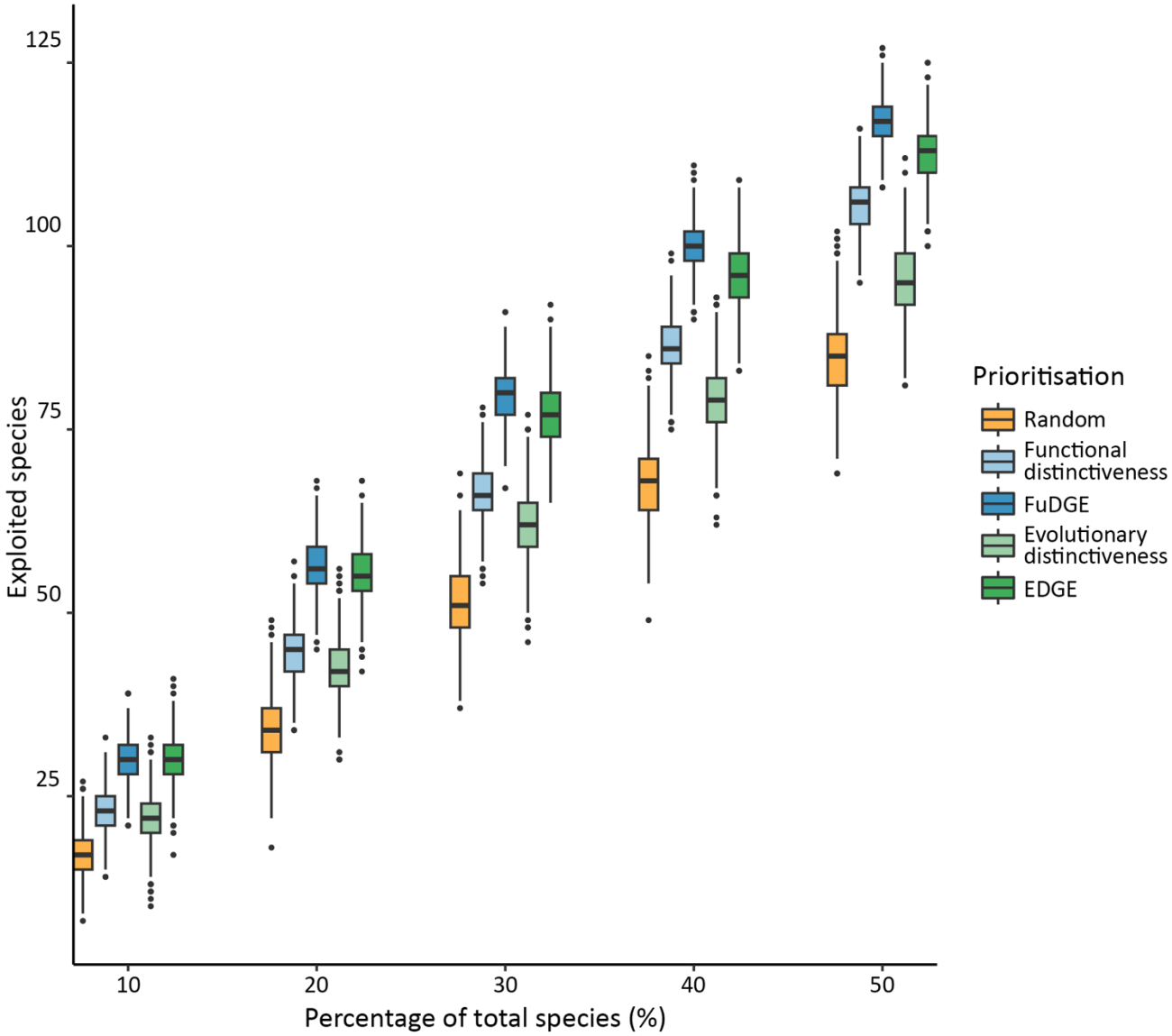
3 – Fig. 5 | Correlation between prioritisation metrics. Correlations between (a) evolutionary distinctiveness and functional distinctiveness and (b) Evolutionarily Distinct and Globally Endangered (EDGE) and Functionally Distinct and Globally Endangered (FuDGE) scores. Dotted lines represent the upper 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*). Illustrations: Marc Dando.

3 – 3.5 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 (IUCN Red List of Threatened Species). 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.

To determine whether different prioritisation strategies effectively highlight species targeted for exploitation, I 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. All prioritisation strategies performed significantly better than random at highlighting intentionally exploited species (Fig. 6; ANOVA with Tukey's test all $p < 0.001$ compared with random; all pairwise comparison results available in Table S1). Functional distinctiveness highlighted more intentionally exploited species than evolutionary distinctiveness at all sample sizes (Fig. 6; Table S1). At all sample sizes, species sets weighted by FuDGE highlighted significantly more intentionally exploited species than functional distinctiveness (Fig. 6; Table S1) and evolutionary distinctiveness (Fig. 6; Table S1), 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. 6; Table S1).

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 S2). I 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 I 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.



3 – Fig. 6 | 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.

3 – 4 Discussion

In this chapter I outline FuDGE, a novel approach for identifying species for conservation action, whose extinction would result in significant losses of irreplaceable FD. Given the wealth of evidence linking FD to the provision of functions and services, it is vital to prevent further erosion of functional trait space (Cadotte, 2017; Díaz et al., 2013; Violle et al., 2017). I show that over one-sixth of shark trait space is currently at risk of being lost. Using the

FuDGE framework, I identify 76 sharks that are globally threatened and have above-median FuDGE scores. My results show that 100% of the top 5% (28) FuDGE sharks and 78.6% of the top 5% (28) functionally distinct sharks have declining or unknown population trends, based on Red List data (IUCN Red List of Threatened Species). 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 (White et al., 2019).

By implementing a FD-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 (Boldrocchi et al., 2023).
The weak correlation between shark functional and evolutionary distinctiveness echoes recent studies that challenge the longstanding assumption that PD should be employed as a surrogate for FD (Cooke et al., 2020; Faith, 1992; Mazel et al., 2018; Vane-Wright et al., 1991). Instead, PD and FD are associated yet distinct dimensions of biodiversity, the conservation of which is of value both to ecosystems (Cadotte, 2017; Collen et al., 2011; Forest et al., 2007) and to human wellbeing (Gumbs et al., 2023c; Molina-Venegas, 2021). Indeed, this work further highlights the complex and non-linear relationship between major adaptive change and evolutionary time (Kemp, 2015; Rosindell et al., 2024; Tucker et al., 2018). 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. S3).

The stronger correlation between FuDGE and EDGE is driven by the incorporation of extinction risk in both metrics. I 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 (Molina-Venegas, 2021; Molina-Venegas et al., 2021) and birds (Gumbs et al., 2023c) indicate that functionally and evolutionarily distinct species are disproportionately utilised by humans. This 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, I 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 (Ripple et al., 2019, 2017), fishing (Ripple et al., 2019, 2017) and the pet trade (Toomes et al., 2022). Beyond targeted fishing and exploitation, incidental catch is also a problem for many marine species (Branch et al., 2013; Dulvy et al., 2021). When considering all species that are threatened by exploitation (intentional and unintentional), I show that 70.39% of global 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 (Isaac et al., 2007). EcoDGE (Hidasi-Neto et al., 2015) uses functional dendrograms to replace phylogenetic trees in the original EDGE calculation. FUSE (Pimiento et al., 2020) 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 (Gouhier and Pillai, 2020). However, the EDGE approach has evolved into a mechanistic tool that is based on the concept of expected loss (Gumbs et al., 2023b), where species are measured on their expected contribution to biodiversity and how much of this contribution is at risk of being lost through extinction. The FuDGE metric, which measures the expected contribution of species to overall trait space, embeds the conservation of FD in an expected loss framework.

My 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 can be used 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. These changes can be monitored over time to look at the shrinking of trait space and

reduction in probability of occupancy as extinctions occur. This method could be used to adopt an FD indicator to monitor the effective safeguarding of FD, akin to the PD indicator outlined in Gumbs, Chaudhary et al.(2023). Here I calculate FuDGE for sharks globally; however, the method outlined in this chapter can also be calculated at regional, national or community levels. These complementary levels of analysis could be used to identify species whose function within specific ecosystems or localities is expected to be distinct and at risk of being lost (Cadotte et al., 2013; Mazel et al., 2018).

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 lack of trait data availability increases across taxonomic groups (Froese and Pauly, 2023; Meiri, 2024; Mull et al., 2022; Oliveira et al., 2017; Oskyrko et al., 2024; Tobias et al., 2022), 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 I was 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 (Curnick et al., 2019) 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.

The FuDGE method outlined in this chapter demonstrates how we can effectively prioritise species to avert the greatest impending losses of FD. EDGE has been able to galvanise conservation action through prioritising highly evolutionarily distinct and threatened species for practical conservation (Gumbs et al., 2023b). I hope that FuDGE lists will inform conservation in a similar light to guide the effective prioritisation of imperilled FD. 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 (Blowes et al., 2019; Cooke et al., 2019b; Hillebrand et al., 2018), with local and global declines of species happening at an unprecedented rate (IPBES, 2019). The integration of species with distinct functional roles into conservation strategies is critical to maintain diverse, resilient ecosystems and support human wellbeing. I propose that FuDGE could provide a mechanistically justified approach to support these important goals.

3 – Supplementary material

Table S1. ANOVA pairwise comparisons between prioritisation strategies with Tukey's Honestly Significant Difference post hoc test.

Percentage of total species	Prioritisation	Difference in means	Lower bounds	Upper bounds	p
10%	FuDGE-EDGE	0.276	-0.1073561	0.6593561	0.28
	FuDGE-Functional distinctiveness	7.2	6.8166439	7.5833561	< 0.001
	FuDGE-Evolutionary distinctiveness	8.178	7.7946439	8.5613561	< 0.001
	EDGE-Evolutionary distinctiveness	7.902	7.5186439	8.2853561	< 0.001
	Functional distinctiveness-EDGE	-6.924	-7.3073561	-6.5406439	< 0.001
	Functional distinctiveness-Evolutionary	0.978	0.5946439	1.3613561	< 0.001
	Random-FuDGE	-13.151	-13.534356	-12.767644	< 0.001
	Random-EDGE	-12.875	-13.258356	-12.491644	< 0.001
	Random-Functional distinctiveness	-5.951	-6.3343561	-5.5676439	< 0.001
	Random-Evolutionary distinctiveness	-4.973	-5.3563561	-4.5896439	< 0.001
20%	FuDGE-EDGE	1.128	0.6489503	1.60705	< 0.001
	FuDGE-Functional distinctiveness	11.486	11.0069503	11.96505	< 0.001
	FuDGE-Evolutionary distinctiveness	13.82	13.3409503	14.29905	< 0.001
	EDGE-Evolutionary distinctiveness	12.692	12.2129503	13.17105	< 0.001
	Functional distinctiveness-EDGE	-10.358	-10.83705	-9.87895	< 0.001
	Functional distinctiveness-Evolutionary	2.334	1.8549503	2.81305	< 0.001
	Random-FuDGE	-22.386	-22.86505	-21.90695	< 0.001
	Random-EDGE	-21.258	-21.73705	-20.77895	< 0.001
	Random-Functional distinctiveness	-10.9	-11.37905	-10.42095	< 0.001
	Random-Evolutionary distinctiveness	-8.566	-9.0450497	-8.08695	< 0.001
30%	FuDGE-EDGE	2.775	2.252573	3.297427	< 0.001
	FuDGE-Functional distinctiveness	13.717	13.194573	14.239427	< 0.001
	FuDGE-Evolutionary distinctiveness	18.181	17.658573	18.703427	< 0.001
	EDGE-Evolutionary distinctiveness	15.406	14.883573	15.928427	< 0.001
	Functional distinctiveness-EDGE	-10.942	-11.464427	-10.419573	< 0.001
	Functional distinctiveness-Evolutionary	4.464	3.941573	4.986427	< 0.001
	Random-FuDGE	-28.544	-29.066427	-28.021573	< 0.001
	Random-EDGE	-25.769	-26.291427	-25.246573	< 0.001
	Random-Functional distinctiveness	-14.827	-15.349427	-14.304573	< 0.001
	Random-Evolutionary distinctiveness	-10.363	-10.885427	-9.840573	< 0.001
40%	FuDGE-EDGE	4.367	3.836569	4.897431	< 0.001
	FuDGE-Functional distinctiveness	14.033	13.502569	14.563431	< 0.001
	FuDGE-Evolutionary distinctiveness	21.186	20.655569	21.716431	< 0.001
	EDGE-Evolutionary distinctiveness	16.819	16.288569	17.349431	< 0.001
	Functional distinctiveness-EDGE	-9.666	-10.196431	-9.135569	< 0.001
	Functional distinctiveness-Evolutionary	7.153	6.622569	7.683431	< 0.001
	Random-FuDGE	-32.47	-33.000431	-31.939569	< 0.001
	Random-EDGE	-28.103	-28.633431	-27.572569	< 0.001
	Random-Functional distinctiveness	-18.437	-18.967431	-17.906569	< 0.001
	Random-Evolutionary distinctiveness	-11.284	-11.814431	-10.753569	< 0.001
50%	FuDGE-EDGE	4.642	4.117626	5.166374	< 0.001
	FuDGE-Functional distinctiveness	11.307	10.782626	11.831374	< 0.001
	FuDGE-Evolutionary distinctiveness	22.125	21.600626	22.649374	< 0.001
	EDGE-Evolutionary distinctiveness	17.483	16.958626	18.007374	< 0.001
	Functional distinctiveness-EDGE	-6.665	-7.189374	-6.140626	< 0.001
	Functional distinctiveness-Evolutionary	10.818	10.293626	11.342374	< 0.001
	Random-FuDGE	-32.273	-32.797374	-31.748626	< 0.001
	Random-EDGE	-27.631	-28.155374	-27.106626	< 0.001
	Random-Functional distinctiveness	-20.966	-21.490374	-20.441626	< 0.001
	Random-Evolutionary distinctiveness	-10.148	-10.672374	-9.623626	< 0.001

Table S2. Summary of t-test statistic hypothesis testing of FuDGE, EDGE functionally distinct and evolutionary distinct scores between intentionally and unintentionally exploited species.

	t	df	p
FuDGE	4.6444	203.09	< 0.001
EDGE	6.3515	189.21	< 0.001
Functional distinctiveness	3.0479	287.71	0.003
Evolutionary distinctiveness	4.2882	242.64	< 0.001

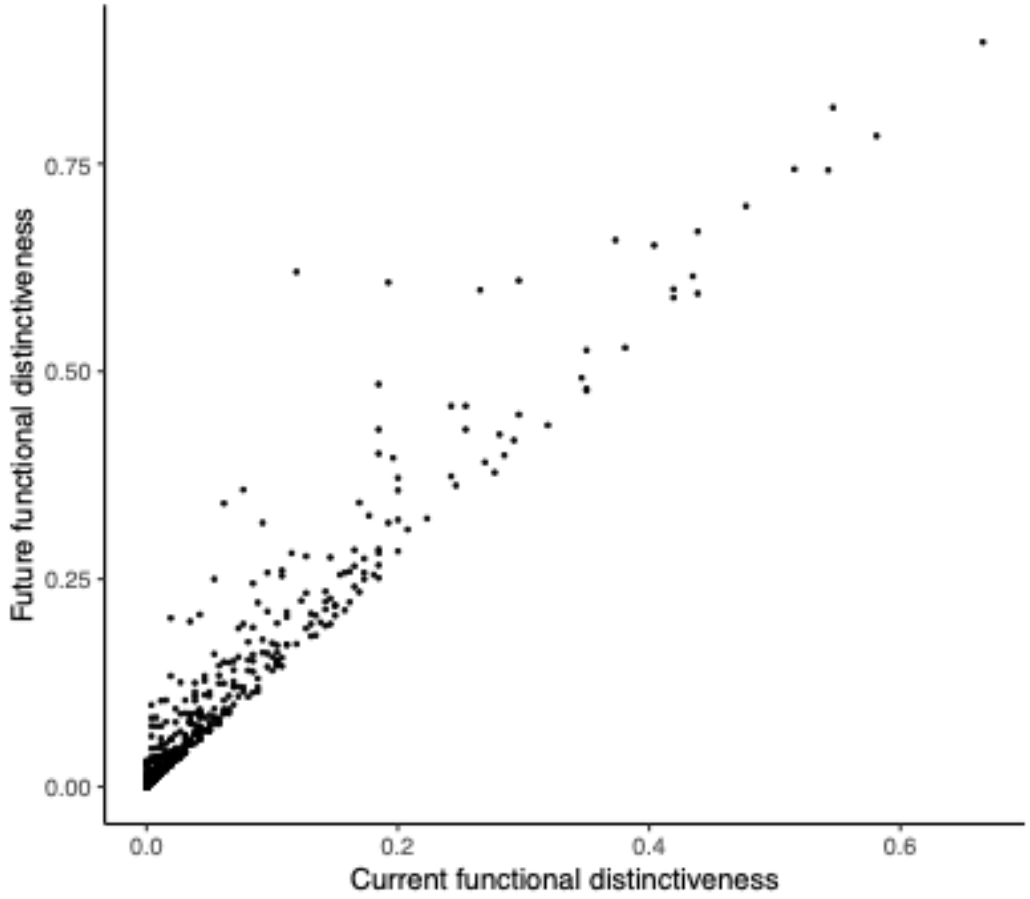


Fig. S1. Correlation between future and current functional distinctiveness. A scatterplot to compare the relationship between future functional distinctiveness (where functional complementarity is accounted for) and current functional distinctiveness (where all species are included in trait space when calculating functional distinctiveness). Correlations between future and current functional distinctiveness were significantly positive (Spearman's correlation: $r = 0.96$, $p < 0.001$).

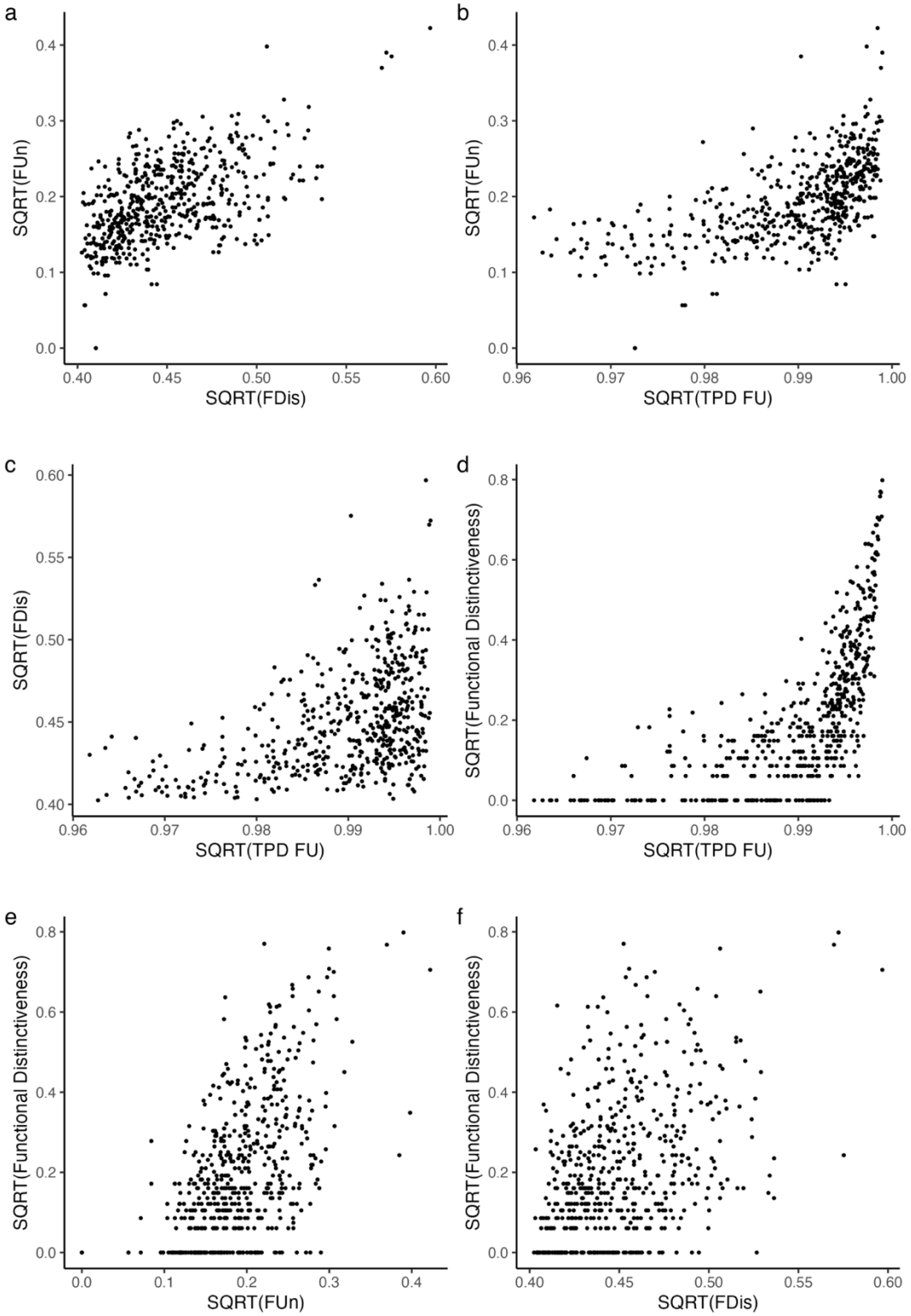


Fig. S2. Correlation between functional indices. Scatterplots to compare species-specific functional diversity indices between; a) Functional Uniqueness (FUn) and Functional Distinctiveness (FDis; Pearson's correlation: r = 0.56, p < 0.001), b) Functional Uniqueness and Trait Probability Density Functional Uniqueness (TPD FU; Pearson's correlation: r = 0.57, p < 0.001), c) FDis and TPD FU (Pearson's correlation: r = 0.47, p < 0.001), d) TPD functional distinctiveness and TPD FU (Pearson's correlation: r = 0.66, p < 0.001), e) TPD functional distinctiveness and FUn (Pearson's correlation: r = 0.55, p < 0.001) and f) TPD functional distinctiveness and FDis (Pearson's correlation: r = 0.43, p < 0.001).

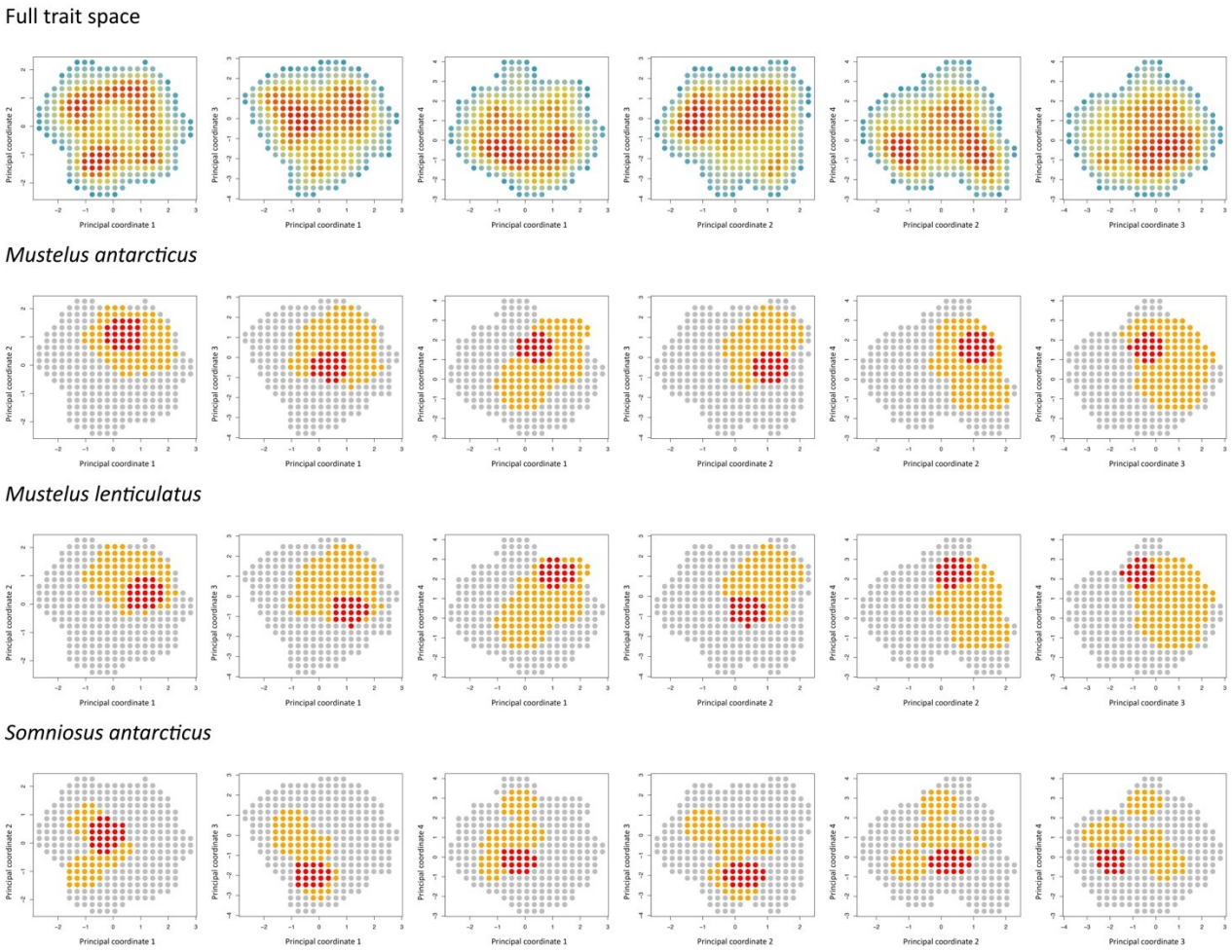


Fig. S3. Occupation of trait space for selected species and their congeners. Probability of occupancy of full trait space (a). Area of trait space occupied by all species in Mustelus genus (orange) and space occupied by Mustelus antarcticus (b) and Mustelus lenticulatus (c). Area of trait space occupied by all species in Somniosus genus (orange) and space occupied by Somniosus antarcticus (red; d).

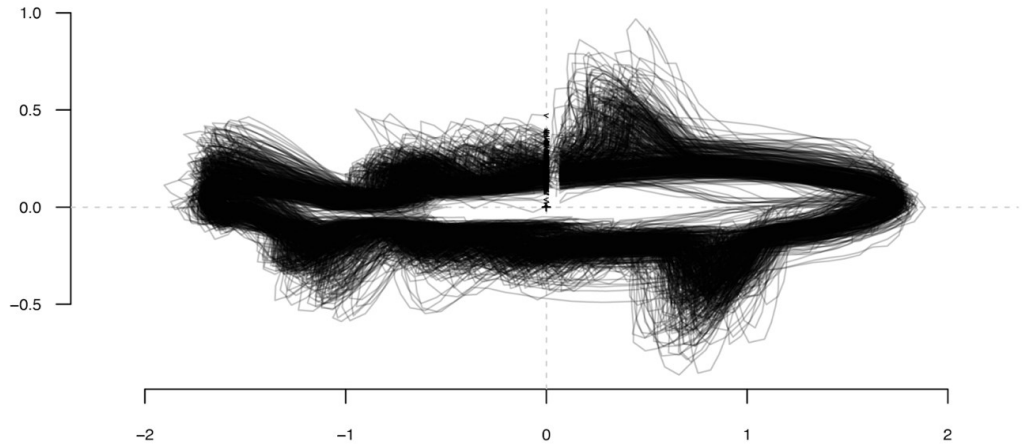


Fig. S4. Stacked shark outlines. Scaled and centred outlines to show the body shape silhouettes of 515 images of shark species collected from Sharks of the World: A Complete Guide(Ebert et al., 2021).

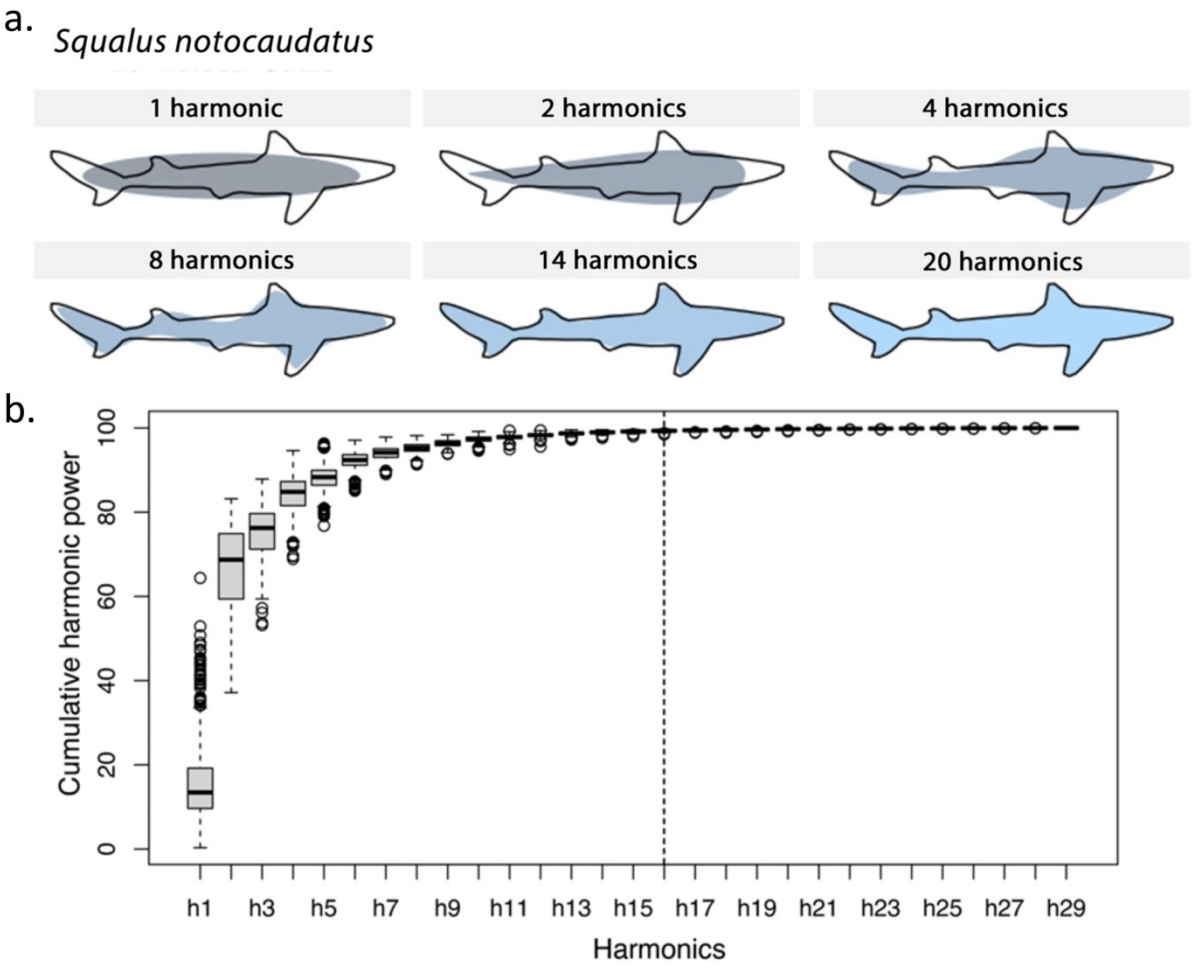


Fig. S5. Harmonic power required to fit shark outline. a) Number of harmonics required to gather cumulative harmonic power from the outlines of sharks following elliptical fourier analysis. b) Boxplots to show the harmonic power for the sum of harmonics (h1-h29) for the body shape elliptical fourier analysis. 16 harmonics were selected to gather 99% of cumulated harmonic power.

Chapter 4 – Tracking the expected erosion of the global functional spectrum of sharks and birds

4 – Abstract

As global biodiversity continues to decline, the KMGBF outlines goals to halt biodiversity loss, protect ecosystems, and sustain human well-being. Yet, empirical studies indicate that current species extinction estimations will lead to disproportionate losses in FD, eroding specific areas of functional space. Such loss of FD jeopardises the continued delivery of nature's contributions to people, given the established links between functional traits and ecosystem services. Achieving policy targets requires indicators that capture FD, yet current measures focus mainly on species numbers and conservation status without directly integrating FD. This study develops an indicator to estimate FD loss, based on species' IUCN Red List assessments, using trait-based probabilistic mapping for sharks and birds. These analyses reveal non-uniform FD erosion, with both sharks and birds displaying clustered vulnerabilities in trait space. The risk of FD loss in both sharks and birds increased over time, with observed extinction trends depleting FD more rapidly than random. This indicator's application across taxa with varying data quality illustrates its broader relevance; while birds benefit from comprehensive Red List Index (RLI) data, sharks lack equivalent data, necessitating an alternative temporal approach to tracking FD trends. My results underscore the need for conservation strategies that explicitly consider FD to protect essential ecological strategies globally.

4 – 1 Introduction

The United Nations CBD KMGBF sets ambitious targets to address biodiversity loss, and protect and restore ecosystems while ensuring that nature continues to support human well-being (CBD, 2022). Meeting these international targets requires robust indicators that can monitor the rate of biodiversity loss and assess the effectiveness of conservation actions. Yet there are no indicators that directly incorporate measures of FD (Díaz et al., 2020). For example, Goal B focuses on the sustainable use of ecosystems to benefit current and future generations, however accompanying indicators focus primarily on species, their number, population size and conservation status (CBD, 2022; Díaz and Malhi, 2022). Ignoring FD as a means of monitoring biodiversity impedes our ability to track the contribution of species to ecosystem processes in the face of environmental change.

Global biodiversity is declining at unprecedented rates and such changes destabilise ecosystems and alter the goods and services that ecological communities can provide (Díaz et al., 2020; Waldén et al., 2023). Given the well-established link between ecosystem services and FD (Cadotte et al., 2011; Díaz et al., 2013; IPBES, 2019), monitoring the diversity and distribution of the functional traits of species may play an important role in preserving nature's contributions to people (NCPs; IPBES, 2019; Mace et al., 2014). Indeed, certain trait combinations expressed by species have been associated with contributions to ecosystem processes (Díaz et al., 2016; Pigot et al., 2020; Schmera et al., 2022) and underpinning various NCPs for multiple taxa (Gumbs et al., 2023c; Molina-Venegas, 2021; Molina-Venegas et al., 2021). Moreover, species' functional traits can inform their ability to persist in an environment and adapt to future change (Díaz et al., 2013; Suding et al., 2008). As such, species that display traits with sensitivity to ongoing environmental change may be at greater risk of future extinction, though consistent relationships between traits and extinction risk are rare (however see Fritz & Purvis, 2010).

Empirical evidence increasingly suggests that observed species extinctions will cause disproportionate losses of FD compared to random extinction (Ali et al., 2023; Carmona et al., 2021; Cooke et al., 2019b; Oliveira et al., 2020; Toussaint et al., 2021). Studies that project future loss of threatened species have identified erosions to specific areas of functional space, suggesting that loss of FD is not unified or random (Ali et al., 2023; Carmona et al., 2021). Therefore, it is important to identify regions which are particularly vulnerable to current extinction risk. Since species do not equally contribute to the diversity of functional assemblages, their loss will affect the FD of a community in varying ways (Mammola et al., 2021). Understanding the impact of species extinction on the functional spectra of a community will provide a deeper understanding of the ecological impacts of biodiversity loss (Cooke et al., 2019b; Martínez-Núñez et al., 2023).

Recent analyses offer a refined description of how species declines will impact ecosystem functioning (Kohli and Jarzyna, 2021), illustrating how extinction risk varies according to each species' position within functional space (Ali et al., 2023; Carmona et al., 2021). Estimating the impact of projected extinctions on FD could offer valuable insights into the effectiveness of current conservation efforts in preserving and restoring ecosystem functionality. Additionally, monitoring these trends over time will track the efficiency and success of global conservation targets in protecting FD. The KMGBF already includes global-scale temporal indicators—such as the Red List

Index (RLI;Butchart et al., 2004), Living Planet Index (LPI;Loh et al., 2005), and the PD indicator (Gumbs et al., 2023a)—that measure progress towards international targets to reverse biodiversity decline (CBD, 2022). Integrating FD into this set of indicators would enhance our ability to monitor ecosystem functionality and its associated values.

To understand the potential functional impact of species extinctions, I first map species traits to a probabilistic global trait space for sharks and birds. I quantify the effects of potential future extinctions on global FD by calculating the proportional loss of occupancy of each point in trait space, based on species' IUCN Red List assessment. These analyses indicate that estimated FD erosion is not uniform in trait space, across sharks and birds, with both groups exhibiting trait clustering in certain regions of trait space. Using historical IUCN Red List assessments, I develop an indicator to monitor trends in estimated FD loss, which reveals an increase in expected loss of FD over time. I evaluate the functional impacts of extinctions on both birds and sharks to illustrate my indicator's applicability to taxa with differing data quality. Birds have highly reliable RLI data with frequent updates, enabling effective monitoring of trends in expected FD loss. For sharks, which lack RLI data, I divide historical IUCN Red List assessments into time intervals to identify global trends in shark FD loss. Simulated extinction scenarios demonstrate that current extinction trajectories are eroding FD more rapidly than random extinction patterns. These results emphasize the importance of conservation polices that consider FD loss to protect global ecological strategies.

4 – 2 Methods

4 – 2.1 Trait data

To calculate the FD indicator for sharks, I used trait data collated in chapter 3 (see 3 – 2.2.1). This data comprises 557 shark species and eight traits (Table 1). For birds, I collated 10 traits from AVONET (Tobias et al., 2022) and Myhrvold et al. (2015; Table 1), to represent functional guilds relating to body size, body shape, foraging strategy, reproduction and habitat preference for 11009 species (Table 1). To represent foraging strategy, body shape and body size, I obtained four morphological traits relating to body shape (tarsus length, wing length, length to first secondary and tail length) and four morphological traits relating to foraging strategy (beak culmen length, beak nares length, beak width and beak depth) from the AVONET dataset (Table 1; Tobias et al., 2022). Since avian morphological traits are often correlated due to an underlying association with body size (Pigot et al., 2020), I performed a two-step PCA, following steps outlined in Trisos et al. (2014), to extract meaningful trait information for body shape, body size and foraging strategy from the eight morphological traits collected from the AVONET dataset. In the first step, I conducted two separate PCAs: one for the body shape traits and one for the foraging strategy traits. In both PCAs, the first principal component (PC1) was strongly correlated with body size. Therefore, I used the second principal component (PC2) from each analysis to capture the variation in body shape and foraging strategy, respectively. Finally, I performed a third PCA on the PC1 scores from the body shape and foraging strategy PCAs to isolate the variation related to body size. The first principal component from this final PCA was used to represent body size. I then combined these traits relating to body size, body shape, foraging strategy with clutch size and habitat preference to construct a trait database for birds (Table 1). I taxonomically

matched all bird species using nomenclature from BirdLife (BirdLife International, 2024). To complete missing values in these trait databases, I imputed missing data using the missForest function (v. 1.5; Stekhoven & Bühlmann, 2012). This method uses a random forest trained on the observed values of the trait matrix to impute missing values and can be used to predict both continuous and categorical data (Stekhoven and Bühlmann, 2012b).

To build trait space I first calculated a distance dissimilarity matrix using the function gawdis (v. 0.1.5; de Bello et al., 2021), with continuous data first being logged, scaled and centred to ensure normal distribution. Gawdis can handle both continuous and categorical data and prevents disproportionate weighting of categorical data. I summarised the dissimilarity distance matrix using the dudi.pco function (v. 1.7.22; Dray & Dufour, 2007) to perform the Principal Coordinate Analyses (PCoA) and inspect the first two axes to examine properties of trait space and visualise where trait are expressed. With both sharks and birds, I built multivariate trait space by extracting the first four PCoAs, representing 45.87% and 44.97% variation respectively. Using the TPD package (v. 1.1.0; Carmona et al., 2019), I calculated trait probability densities (TPD) to represent each species in functional trait space as a multivariate kernel density estimation.

4 – Table 1 | Species traits. Traits used to build trait space and the functional guild each trait represents.

Clade	Trait	Unit	Data type	Functional guild	Number of species (% coverage)	Source
Birds	Beak culmen length (foraging strategy PCA)	mm	Continuous	body size/foraging strategies	11009 (100%)	Avonet
	Beak nares length (foraging strategy PCA)	mm	Continuous	body size/foraging strategies	11009 (100%)	Avonet
	Beak width (foraging strategy PCA)	mm	Continuous	body size/foraging strategies	11009 (100%)	Avonet
	Beak depth (foraging strategy PCA)	mm	Continuous	body size/foraging strategies	11009 (100%)	Avonet
	Tarsus length (body shape PCA)	mm	Continuous	body size/body shape	11009 (100%)	Avonet
	Wing length (body shape PCA)	mm	Continuous	body size/body shape	11009 (100%)	Avonet
	Length to first secondary (body shape PCA)	mm	Continuous	body size/body shape	11009 (100%)	Avonet
	Tail length (body shape PCA)	mm	Continuous	body size/body shape	11009 (100%)	Avonet
	Clutch size	number of eggs	Continuous	reproduction	6148 (55.8%)	Myhrvold et al. (2015)
	Habitat preference	forest, shrubland, woodland, rock, grassland, human modified wetland, marine, desert, riverine coastal	Categorical	habitat preference	11009 (100%)	Avonet
Sharks	Maximum Body Length	cm	Continuous	body size	535 (96.1%)	FishBase
	Maximum Depth	m	Continuous	vertical mobility	488 (87.6%)	FishBase
	Trophic Level	1 + mean trophic level of species food items	Continuous	diet/predator-prey relationship	278 (49.9%)	FishBase
	Body shape variation PC1		Continuous	body shape	512 (91.9%)	Sharks of the world
	Body shape variation PC2		Continuous	body shape	512 (91.9%)	Sharks of the world
	Growth Ratio	length (cm) / length at birth (cm)	Continuous	reproduction	342 (61.4%)	Sharks of the world, FishBase
	Reproductive Mode	oviparous, viviparous, aplacental viviparous, viviparous (with a yolk sac	Categorical	reproduction	557 (100%)	Sharks of the world,

		placenta)				FishBase
	Habitat preference	pelagic, benthopelagic, demersal, reef-associated, bathypelagic, bathydemersal	Categorical	habitat preference	469 (84.2%)	FishBase

4 – 2.2 Extinction risk data

I used the IUCN Red List of Threatened Species (v. 2023.1; IUCN) to measure the extinction risk of species. This includes assessment data for 540 shark species and 10975 bird species. For historical extinction risk data for birds, I used the data underpinning the Red List Index (RLI), which includes seven time points (1988, 1994, 2000, 2004, 2008, 2012, 2016; Henriques et al., 2020). Since there is no RLI data available for sharks I used extinction risk data from historical IUCN Red List assessments and IUCN Red List table 7 data to only include assessments with genuine category changes (i.e. excluding non genuine changes such as changes caused by taxonomic revision or previous lack of data; Bates et al., 2024). I split this data into two distinct time bins (1996-2014 and 2015-2021) for sharks to maximise the number of species that had more than one assessment. If species had more than one assessment in their time bin, I used the most recent assessment. Where species had Red List assessments listed as Data Deficient (DD) and those that did not have current or historical assessments I assign these species a Red List category based on varying probability. The probability of a Red List category being assigned is based on the observed distribution of Red List categories in the respective clade and time point to assume that species with unknown assessments will follow a similar pattern of extinction risk to those currently sampled. I randomly sampled these values 1000 times to get a distribution of assigned assessment values which reflect the uncertainty of these species' extinction risk. With the discrete Red List categories, I generated a continuous distribution of extinction probabilities following methods outlined by Gumbs et al. (2023), where the median of each Red List category was defined as, CR = 0.97; EN = 0.485; VU = 0.2425; NT = 0.12125; LC = 0.060625. I generated 1000 different extinction probability values for each species to capture a full range of extinction probabilities within their category.

4 – 2.3 Projecting extinction risk to global trait space

To understand the future impact of species extinctions on global trait space, I compare the estimated current and future occupancy of trait space, to predict the proportional loss of each voxel in trait space. Future occupancy of voxels in trait space is calculated as a function of current occupancy of species in trait space and extinction probabilities, following methods listed below. Each future projection is calculated 1000 times to reflect the distribution of species extinction predictions. I mapped these predictions onto the first two axes of trait space to visualise the impact of extinction on different areas of trait space and identify certain trait combinations that may be vulnerable to extinction. To compare the predicted loss of trait space, I calculated the voxel occupancy, based on extinction risk categories assessed at different time points. To understand how changes to species extinction risk categories at different time points have impacted future trait space, I compared future scenarios to get a value of relative change for each voxel.

4 – 2.4 FD indicator

To monitor the trends of projected erosion of FD in a given time frame, based on extinction predictions, I have developed the FD indicator. The FD indicator measures the proportion of functional trait space expected to be lost based on species extinction predictions at each time point. To estimate this, I calculated the probability that at least one species remains in a given voxel, after accounting for extinction probabilities, and divide this by the probability that at least one species currently occupies that voxel:

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

Where $x_{i,v}$ is the probability that species i is present in voxel v of trait space, E_i is the probability of extinction for species i and S is the set of all species. To express the total expected occupancy of trait space as a proportion I added the proportional expected occupancy for each voxel and divided this by the total number of voxels. To calculate the expected loss of FD I subtract the expected occupancy of trait space from one. This can be multiplied by 100 to be expressed as a percentage:

$$\left(1-\frac{\sum_{v\in V}\left(\frac{1-\prod_{i\in S}\left(1-x_{i,v}(1-E_i)\right)}{1-\prod_{i\in S}(1-x_{i,v})}\right)}{n_V}\right)\times 100$$

Where V is the set of all possible voxels of trait space and n_V is the total number of pixels in trait space. I incorporated standardised IUCN Red List extinction risk data for all species, where available, for multiple time points to generate trends in the status of FD, based on the established expected PD loss framework (Faith, 2018; Gumbs et al., 2023a).

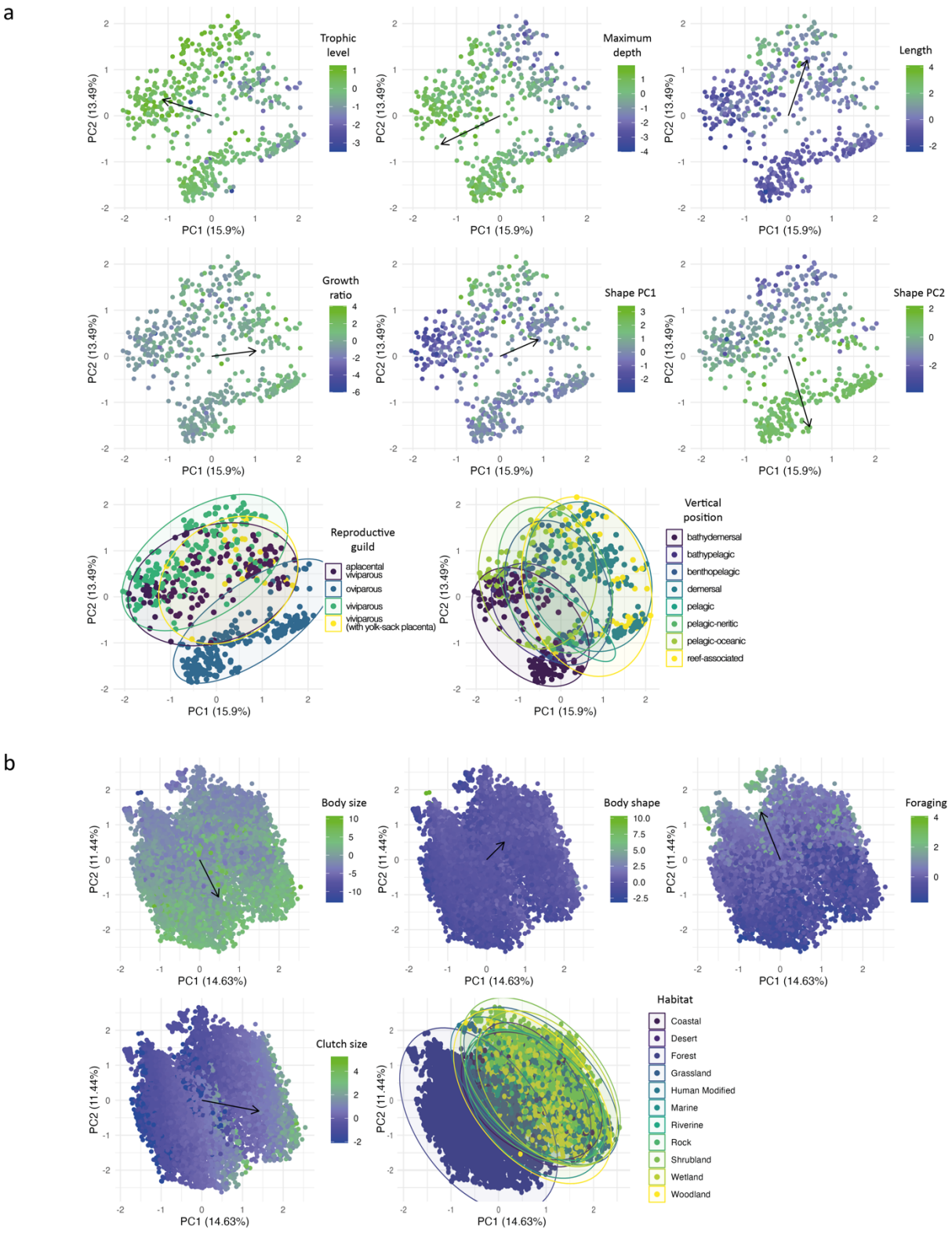
To assess whether the orientation of extinctions in trait space influence potential losses of FD, I recalculated the expected FD erosion at each time point under different extinction scenarios: Observed extinction scenarios, calculated using the given extinction probability for each species at each time point; Random extinction scenarios, where the expected FD erosion was recalculated at each time point by randomly redistributing extinction probabilities among species within trait space; High expected FD loss scenarios, calculated by assigning the highest extinction probabilities to species with the greatest functional distinctiveness, with probabilities decreasing as functional distinctiveness decreases; Low expected FD loss scenarios, determined by assigning extinction probabilities in ascending order, giving species with the lowest functional distinctiveness the highest extinction probabilities. To test if extinction scenarios differed significantly, I use ANOVA with Tukey's Honestly Significant Difference post hoc test to test the pairwise difference between

strategies.

4 – 3 Results

4 – 3.1 The structure of global shark and bird functional space

For both sharks and birds, I used the first four principal components (PCs) to describe trait space, which explain 45.87% and 44.97% of total variation respectively. Each subsequent axis explained less than 6.5% of total variation (Fig. S1) and significantly increased computational power. For shark global trait space, PC1 positively correlated with growth ratio and body shape1 and negatively correlated with maximum depth and trophic level (Fig. 1a, Table S1a). PC2 positively correlated with body length and growth ratio and negatively correlated with body shape2 (Fig. 1a, Table S1a). PC3 negatively correlated with growth ratio, body length and maximum depth (Table S1a). PC4 negatively correlated with body shape1 and trophic level (Table S1a). Visual inspection of PC1 and PC2 revealed clustering of species that lay eggs (oviparous) and bathydemersal species (Fig. 1a). For bird global trait space, principal component (PC) 1 positively correlated with clutch size (Fig. 1b, Table S1b). PC2 positively correlated with foraging strategy and negatively correlated with body size (Fig. 1b, Table S1b). PC3 negatively correlated with foraging strategy and body size (Table S1b). PC4 negatively correlated with body shape (Table S1b). Visual inspection of PC1 and PC2 revealed clustering of species that live in the forest, all other habitat types were clustered together in trait space (Fig. 1b).



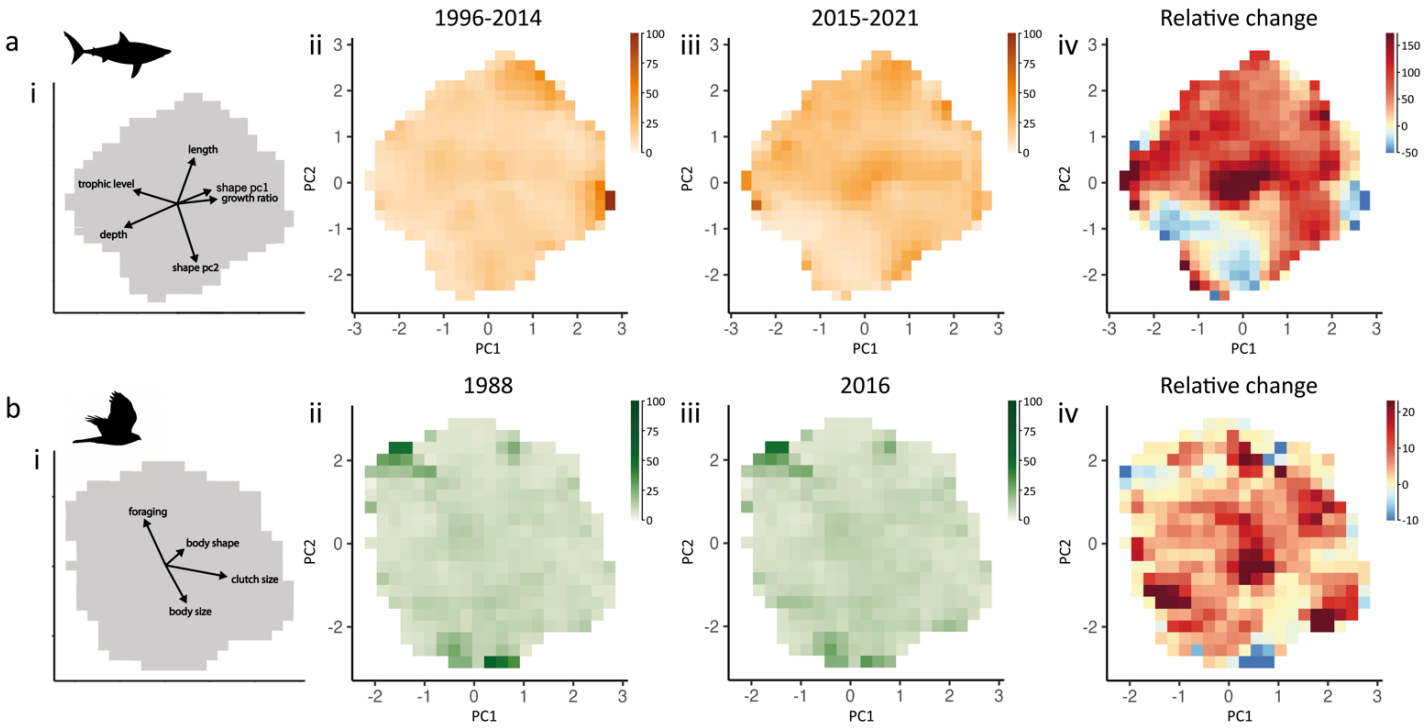
4 – Fig. 1 | Global trait space for sharks and birds. Projections of the distribution of (a) shark and (b) bird global trait space defined by the first two principal components (PC1 and PC2). Colours indicate trait value for continuous data and trait categories for categorical data. Arrows indicate the direction and weighting of traits (Table S1). Percentage values represent proportion of the total variation explained by each PC.

4 – 3.2 Projecting extinction risk to global trait space

Mapping extinction risk onto trait space revealed trait-based variation in the vulnerability to extinction. Visual inspection of projections from 1996-2014 extinction predictions in shark trait space indicated greater extinction risk in regions occupied by species with specific traits: shallow depth range combined with increased body length, and shallow depth range with lower trophic levels and a higher growth ratio (a greater disparity between birth size and adult size; Fig. 2 ai). Projections from 2015-2021 extinction predictions in shark trait space revealed greater risk of extinction to areas of trait space occupied by demersal or reef-associated species, that give birth to live young (viviparous) and have increased body length and low body shape2 values (broad width and prominent dorsal fin), as well as viviparous species that have low body shape1 values (rounded pectoral fins and lobed caudal fins; Fig. 2aii).

Comparing extinction risk projections from 1996-2014 to 2015-2021 revealed an increase in expected erosion across the majority of shark trait space (82% of voxels with an increase), with particularly increased erosion to the centre of trait space (Fig. 2aiv). The relative change in the expected erosion of voxels in trait space increased by a median of 58% from 1996-2014 to 2015-2021. Some trait combinations have reduced expected erosion from 1996-2014 to 2015-2021, these include smaller, bathydemersal species and species with shallow depth range with lower trophic levels and a higher growth ratio (Fig. 2aiv).

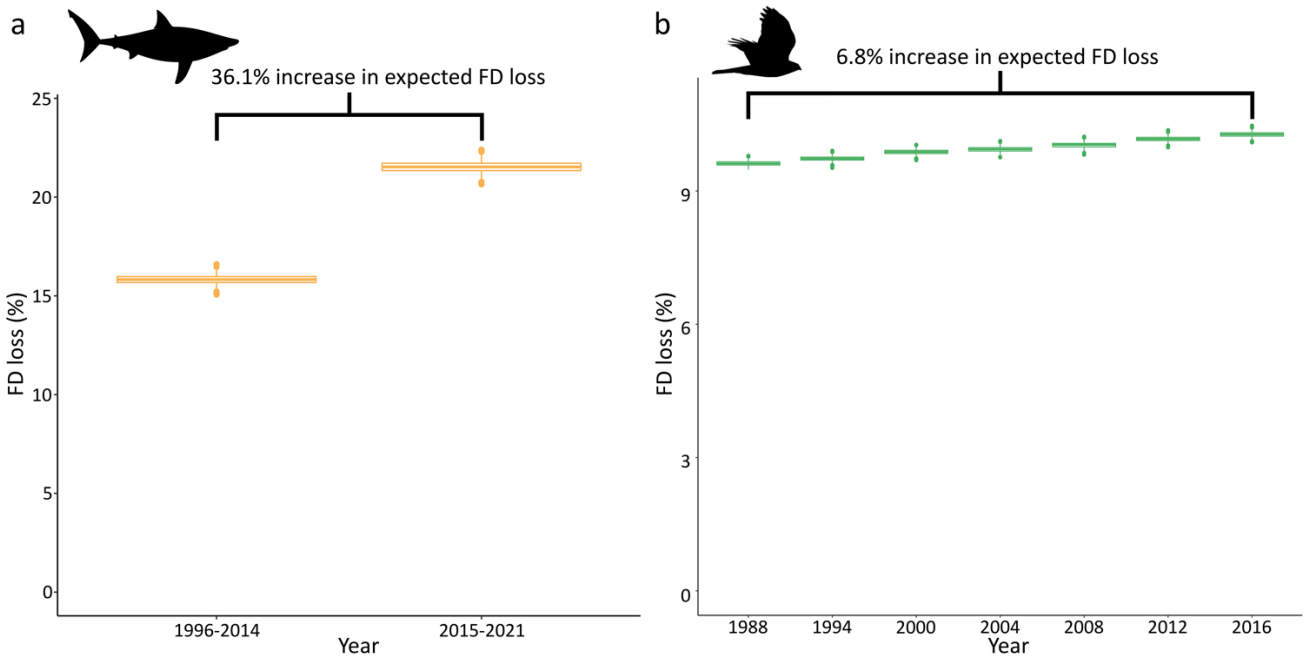
In bird trait space visual inspections of PC1 and PC2 revealed expected erosion of traits including species with extreme body size values (very high body size values and very low body size values), low clutch size, very high foraging strategy values (long narrow beak) and very low foraging strategy values (wider, shorter beak; Fig. 2bi-ii). The majority of bird trait space had increased predicted erosion from 1988 to 2016 (81% of voxels with an increase), particularly affecting species with large body size and low foraging strategy values. Changes in extinction risk projections from 1988 to 2016 show less expected erosion of trait space than sharks, with 4% median increase in the predicted erosion to voxels (Fig. 2baiv).



4 – Fig. 2 | Predicted erosion of trait space. (a) Shark trait space defined by the first two principal coordinate axes (PC1 and PC2) to show; (ai) the direction and weighting of the considered traits, (aii) projections of predicted loss based on historical IUCN Red List assessments (1996-2014), (aiii) projections of predicted loss based on the most recent IUCN Red List assessments (2015-2021). Light orange indicates low erosion and dark orange indicates high erosion of trait space. (aiv) The relative change for each voxel in trait space between the earliest and most recent assessment time points, blue tones indicate a decrease in expected FD loss between time points, red tones indicate an increase in expected FD loss between time points. (b) Bird trait space defined by the first two principal coordinate axes (PC1 and PC2) to show; (bi) the direction and weighting of the considered traits, (bii) projections of predicted loss based on historical IUCN Red List assessments (1988), (biii) projections of predicted loss based on the most recent IUCN Red List assessment from the Red List index (2016). Light green indicates low erosion and dark green indicates high erosion of trait space. (biv) The relative change for each voxel in trait space between the earliest and most recent assessment time points, blue tones indicate a decrease in expected FD loss between time points, red tones indicate an increase in expected FD loss between time points. Silhouettes were downloaded from phylopic (www.phylopic.org).

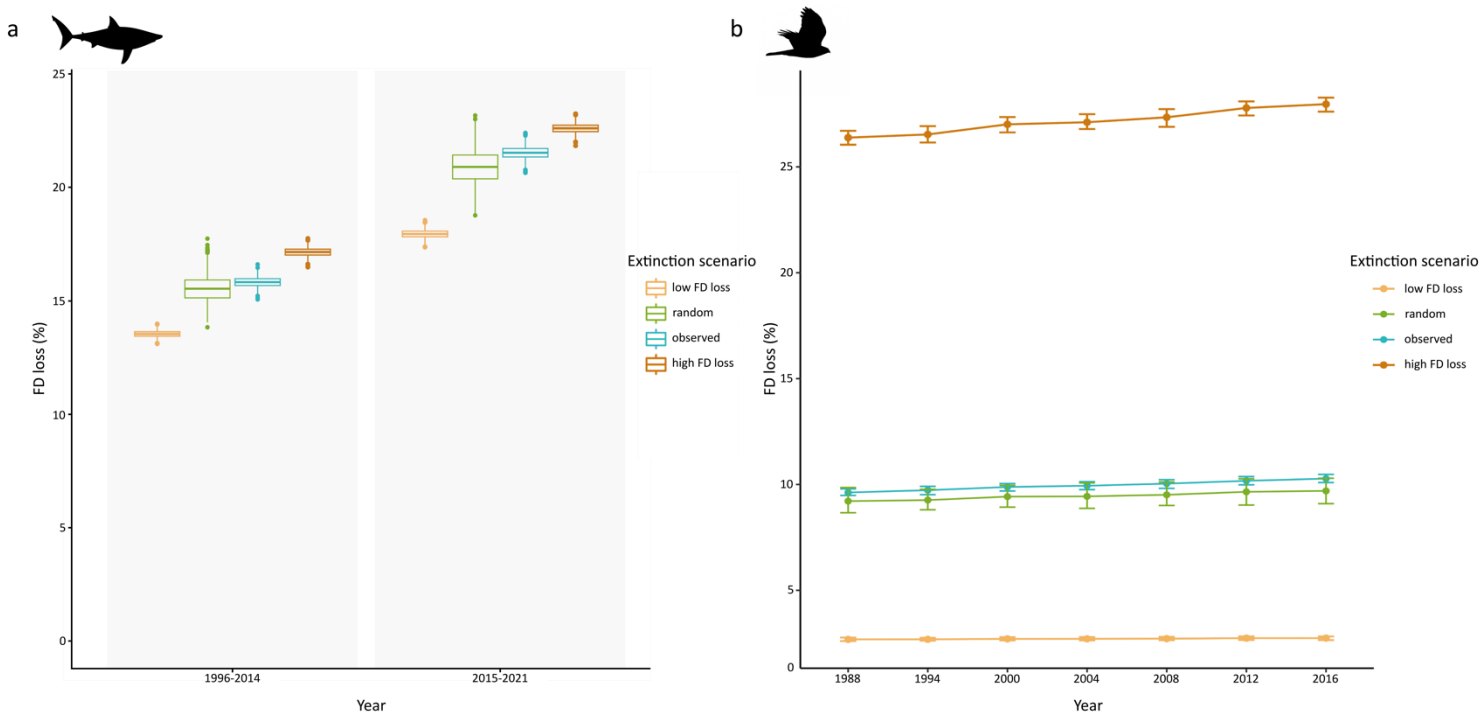
4 – 3.3 FD indicator

The overall expected loss of FD increased over time for both clades (Fig. 3a and 3b; paired T-test $p < 0.001$ for all time points; all comparison results available in Table S2). Sharks had the highest overall expected loss of FD with a median proportional loss of 21.5% in the 2015-2021 time bin (Fig. 3). This showed an increase from the 1996-2014 time bin where a median FD loss of 15.8% was predicted (Fig. 3a). Birds had an increase in expected loss of FD from a median proportional loss of 9.6% in 1996 to a median proportional loss of 10.3% in 2016 (Fig. 3b). The relative change of expected proportional loss from the earliest time point to the most recent was 36.1% median increase for sharks and 6.8% for birds (Fig. 3).



4 – Fig. 3 | Expected future loss of FD based on historical IUCN Red List assessments. Trends in the percentage of expected overall loss of FD for (a) shark and (b) bird trait space due to extinction, based on historical IUCN Red List assessments. Percentages above bracket show the percentage change in expected FD loss between the earliest and most recent time point. Boxplots represent the range, interquartile range and median values in the percentage of overall loss. Silhouettes were downloaded from phylopic (www.phylopic.org).

When I compared different extinction scenarios for both shark and bird trait space, all scenarios were significantly different ($p < 0.001$).The high FD loss scenario had significantly more expected FD loss than all the other scenarios for both sharks and birds, for all time points (Fig. 4a and 4b, ANOVA with Tukey's test all $p < 0.001$ compared with high FD loss; all pairwise comparison results available in Table S3a and S3b). Low FD loss had significantly less expected FD loss than all other scenarios in all time bins for both sharks and bird (Fig. 4a and 4b, ANOVA with Tukey's test all $p < 0.001$ compared with low FD loss; all pairwise comparison results available in Table S3a and S3b). The observed scenario had significantly more FD loss than random for both sharks and birds across all time points (Fig. 4a and 4b, $p < 0.001$ for all tests).



4 – Fig. 4 | Extinction scenarios. Expected FD loss for (a) sharks and (b) bird based on extinction predictions at different time points for four different scenarios: Observed (blue) - species extinction probabilities are assigned based on the Red List category listed at each given point in time, high FD loss (purple) - calculated by assigning the highest extinction probabilities to species with the greatest functional distinctiveness, low FD loss (red) – calculated by assigning extinction probabilities in ascending order, where species with the lowest functional distinctiveness have the highest extinction probabilities, and random (green) – calculated by randomly redistributing extinction probabilities across species. The frequency of extinction probabilities is kept constant, based on the frequency of the observed scenario at each time point, under all four scenarios. Boxplots (a) represent the range, interquartile range and median values in the percentage of overall loss, error bars and points (b) represent the range and median of overall loss. Silhouettes were downloaded from phylopic (www.phylopic.org).

4 – 4 Discussion

In this chapter I developed a biodiversity indicator that directly incorporates measures of trait variation to estimate the percentage of FD expected to be lost across trait space given changes in extinction risk over time. For both sharks and birds, I combined data on multiple functional traits with IUCN Red List assessments from different points in time to show the distribution of trait combinations expressed by each taxonomic group and how potential extinctions may erode their trait space. Current extinction trajectories illustrate erosions of larger, demersal or reef-associated sharks, that give birth to live young, leading to a functional shift towards smaller, egg-laying species. In birds, trajectories show increased vulnerability to extreme trait characteristics such as size and beak shape, suggesting functional shifts to more average sizes and foraging strategies. Monitoring trends in the expected erosion of FD over time revealed that estimated extinction based on IUCN Red List assessments is eroding FD at a greater rate than random extinction scenarios for all time points.

My analyses show that there are clear areas of global trait space that are more vulnerable to future extinctions for both sharks and birds. Vulnerable areas of extinction are not explicitly on the periphery of trait space, with expected erosions occurring in the centre of trait space for both taxa. Notably, monitoring trends in expected FD loss over time revealed large increases in erosion of central areas of trait space. These results demonstrate how extinctions can reorganise the internal structure of trait space. Such changes can occur in core areas of trait space that are occupied by a small number of species, which could lead to the loss of unique trait combinations and ecological strategies, creating internal holes in the functional structure (Blonder, 2016; Carmona et al., 2021). Alternatively, erosion of internal areas in trait space that have high redundancy (i.e. areas occupied by species that perform similar roles in an ecosystem), could lead to reductions in ecosystem resilience and stability (Cooke et al., 2019a; Laliberté et al., 2010; Maure et al., 2018). Although assemblages with high functional redundancy will ensure certain processes can continue even when species are lost from the assemblage, large erosions to these areas of trait space will diminish redundancy and functional resilience in response to environmental pressures (Oliver et al., 2015). These findings emphasise the importance of targeted measures that address both central and peripheral regions of trait space (Carmona et al., 2021).

Standard measures of FD (e.g. convex hull functional richness) assume uniform occupancy within the boundaries of trait space, therefore only captures loss of trait space at the periphery (Oliveira et al., 2020). A number of studies have investigated the impact of extinctions on FD, focusing on the total loss of FD (Cooke et al., 2019b; Oliveira et al., 2020; Pimiento et al., 2020; Toussaint et al., 2021). Yet, this does not fully reflect the impact of extinction on the global functional spectra; considering densities of occupancy and their subsequent erosions offers a more comprehensive and nuanced summary of FD decline. Carmona et al. (2021) explored the internal erosion of trait space by comparing the current functional spectra with the spectra after possible extinctions. However, following extinction simulations the reduction in occupancy is buffered when areas of trait space display high degrees of aggregation, downplaying potential erosions to trait space. Here I have addressed these limitations by calculating the proportional loss of each voxel in trait space, to highlight the erosions of individual areas. Calculating the proportional loss of each point identifies potential erosions of space that are still somewhat occupied by species and prevents buffering of loss by highly occupied areas of trait space.

I assessed the functional impacts of extinctions on both birds and sharks to demonstrate the application of my indicator on taxa with different qualities of data. Birds have perhaps the gold standard of RLI data with regular updates facilitating the monitoring of trends of expected FD loss. Since sharks do not have RLI data I have split historical IUCN Red List assessments into time bins to identify trends in global shark FD loss and highlight the importance of expanding taxonomic representation when monitoring trends in biodiversity loss. Despite the differences in the quality of these data, temporal trajectories show that the expected FD loss is worsening over time for both sharks and birds. Nonetheless, the most recent time points reveal that sharks are predicted to lose

more than double the proportion of FD than birds. Additionally, comparing the relative changes in expected loss of FD over time showed that sharks have over five times more increase in expected loss than birds. Both taxonomic groups reveal declining trends in future FD loss, yet sharks show a more severe expected loss of FD, despite being significantly less studied and reported (Hughes et al., 2021).

Birds have been used in several global studies of FD because they are well surveyed and have the most comprehensive trait datasets currently available of all vertebrate groups (Hughes et al., 2021). Additionally, birds are widely used as indicators of biodiversity and ecosystem health to inform and improve current management practices (Fraixedas et al., 2020). However, the impacts of biodiversity loss on birds may not map directly onto other taxonomic groups or trophic levels (Schulze et al., 2004; Toussaint et al., 2021). Further studies are needed across different systems to assess the impact of biodiversity decline in different regions and taxonomic groups. I use sharks to demonstrate how courser global datasets can be used to assess the functional implications of biodiversity loss at a global scale (Schleuning et al., 2023).

Although overall trends show declines in predicted FD loss, this does not imply that conservation efforts have been ineffective. When comparing relative changes in between the earliest and most recent trajectories, some areas of trait space show a reduction in expected FD loss. For example, within shark species, areas of trait space associated with small, bathydemersal species with high depth ranges showed a reduction in expected FD loss. This shift could suggest that certain conservation measures have reduced species extinction risk, thereby mitigating expected functional loss in specific trait areas. The exploitation of deep-sea ecosystems increased significantly after the 1970s, following the establishment of Exclusive Economic Zones, which limited foreign fishing near coastal areas (Cochran et al., 2019). Use of alternative fishing areas such as the deep sea led to developments in industrial scale trawling technologies (Morato et al., 2006). Since trawling nets are highly indiscriminate and destructive of surrounding ecosystems, deep-sea habitats are particularly vulnerable to fishing impacts (Norse et al., 2012). In response to these threats, the FAO introduced the *International Guidelines for the Management of Deep-sea Fisheries in the High Seas* in 2008 (FAO, 2009). These guidelines have led to significant improvements in bottom fishery management and environmental protection, supporting stock recovery (Thompson and Reid, 2024). Tracking these trends over time reveals how conservation efforts may have helped reduce the expected loss in FD.

This study focuses on global-scale assessments, yet the impact of species decline will vary significantly at local scales (Toussaint et al., 2021). Examining the functional spectra of species assemblages at a community level will give a more realistic view of functional structures and trait variation in local ecosystems. Different ecosystems may occupy unique portions of global trait space, with less overlap and aggregation of species clustering in the same areas (Carmona et al., 2021; Pavoine and Ricotta, 2023). Consequently, species extinctions are likely to have a greater impact on the structure and volume of trait space at local levels. Future work should aim to forecast changes to FD at finer spatial scales, enabling a deeper understanding of the regional and local impacts of biodiversity loss on ecosystem function. Community level estimations of FD loss could reveal regional vulnerabilities and areas where distinct functional roles are most at risk to inform local conservation priorities. Additionally, incorporating a national-level FD indicator could support

countries in tracking their progress towards biodiversity goals, such as those outlined in the KMGBF (CBD, 2022). Since many conservation policies are defined at a regional level, local scale analyses may be the most impactful for implementing practical conservation measures in response to global change (Anderle et al., 2024; Pavoine and Ricotta, 2024). Finally, because countries contain distinct ecosystems, local species often represent unique trait combinations that may be common globally but are essential at the local level. This distinctiveness underscores the importance of capturing local ecological roles, as these may be overlooked in global assessments.

Monitoring FD is important to predict ecological outcomes in the context of species extinctions (Ali et al., 2023; Carmona et al., 2021; Toussaint et al., 2021). These approaches are becoming increasingly urgent, with mounting evidence of stressors such as climate change, land use change and overexploitation affecting ecological integrity at a global scale (Green et al., 2022; Jaureguiberry et al., 2022). Here I have demonstrated how FD can be used to monitor biodiversity and the future variation of functional roles within ecosystems. Indicators that measure the state of global FD could be used to monitor progress towards international targets to restore biodiversity and ecosystem function. Ecosystem function is a key component of goals outlined in the KMGBF, for example Goal A outlines that "the integrity, connectivity and resilience of all ecosystems are maintained, enhanced, or restored" and Goal B outlines that "nature's contributions to people, including ecosystem functions and services, are valued, maintained and enhanced" (CBD, 2022). Despite clear evidence of the link between FD and ecosystem functions (Cardinale et al., 2012; Gagic et al., 2015; Petchey et al., 2004; Scherer-Lorenzen, 2008; Tilman et al., 1997) and studies demonstrating that FD is not adequately captured through other measures of biodiversity (Oliveira et al., 2020; Veron et al., 2021), there are no indicators that directly incorporate measures of FD in the KMGBF. Without direct measures of FD, species and regions prioritised for conservation may fail to avert losses of large areas of the global functional spectra. In this chapter I address this by developing an FD indicator that aligns with the GBF PD indicator methodology (Gumbs et al., 2023a) to monitor trends in FD loss and enable comparable reporting between the two different biodiversity facets.

4 – Supplementary Material

Table S1. PCoA loadings for (a) sharks and (b) birds.

a)

	PC1	PC2	PC3	PC4
length	0.21493953	0.60239208	-0.5805673	-0.2581405
trophic.level	-0.5630165	0.17427206	0.02537413	-0.4530755
max.depth	-0.6760982	-0.3092706	-0.4553597	0.10285902
growth.ratio	0.50841548	0.05881848	-0.5922693	-0.0838575
shape.pc1	0.43661251	0.17985719	-0.2121416	-0.6534218
shape.pc2	0.24224546	-0.7649396	0.1212227	0.01733297

b)

	PC1	PC2	PC3	PC4
body.shape	0.22818606	0.25210215	0.10952008	-0.7541466
foraging	-0.2319756	0.6804744	-0.5045837	-0.1215547
body.size	0.23729987	-0.5323819	-0.7188186	-0.1984663
clutch.size	0.70193161	-0.154447	0.30368849	-0.2225868

Table S2. Summary of paired T-test hypothesis testing for projected extinction predictions between time points for sharks and birds.

	Time points	Difference in means	t	df	p
Sharks	1996.2014 - 2015.2021	-5.71	-501.47	999	p < 0.001
Birds	1988 - 1994	-0.11	-44.24	999	p < 0.001
	1994 - 2000	-0.15	-62.41	999	p < 0.001
	2000 - 2004	-0.06	-24.04	999	p < 0.001
	2004 - 2008	-0.09	-36.20	999	p < 0.001
	2008 - 2012	-0.14	-54.70	999	p < 0.001
	2012 - 2016	-0.10	-38.81	999	p < 0.001

Table S3. ANOVA pairwise comparisons between extinction scenarios with Tukey's Honestly Significant Difference post hoc test.

a)

Year	Extinction scenario	Difference in means	Lower bounds	Upper bounds	p
1996-2014	observed - high FD loss	-16.76722	-16.779462	-16.754977	<0.001
	observed - low FD loss	6.9390799	6.9268375	6.9513223	<0.001
	observed - random	0.4020739	0.4143164	0.3898315	<0.001
	high FD loss - low FD loss	23.7062993	23.7185417	23.6940569	<0.001
	high FD loss - random	17.1692934	17.1815358	17.157051	<0.001
	low FD loss - random	-6.5370059	-6.5247635	-6.5492483	<0.001
2015-2021	observed - high FD loss	-16.801359	-16.813709	-16.789009	<0.001
	observed - low FD loss	7.0427686	7.0304186	7.0551185	<0.001
	observed - random	0.4686785	0.4810285	0.4563286	<0.001
	high FD loss - low FD loss	23.8441279	23.8564779	23.831778	<0.001
	high FD loss - random	17.2700379	17.2823878	17.2576879	<0.001
	low FD loss - random	-6.57409	-6.5617401	-6.58644	<0.001

b)

Year	Extinction scenario	Difference in means	Lower bounds	Upper bounds	p
2000	observed - high FD loss	-17.125801	-17.138328	-17.113273	<0.001
	observed - low FD loss	7.1718835	7.159356	7.1844108	<0.001
	observed - random	0.4533648	0.465892	0.4408376	<0.001
	high FD loss - low FD loss	24.2976841	24.310211	24.2851569	<0.001
	high FD loss - random	17.5791654	17.591693	17.5666382	<0.001
	low FD loss - random	6.7185187	6.705991	6.7310459	<0.001
2004	observed - high FD loss	-17.167377	-17.180137	-17.154617	<0.001
	observed - low FD loss	7.2309847	7.2182245	7.2437449	<0.001
	observed - random	0.4985874	0.5113475	0.4858272	<0.001
	high FD loss - low FD loss	24.3983618	24.411122	24.3856017	<0.001
	high FD loss - random	17.6659645	17.6787247	17.6532043	<0.001
	low FD loss - random	-6.7323973	-6.7196372	-6.7451575	<0.001
2008	observed - high FD loss	-17.303431	-17.31601	-17.290852	<0.001
	observed - low FD loss	7.3168449	7.304266	7.3294238	<0.001
	observed - random	0.5299368	0.5425157	0.5173579	<0.001
	high FD loss - low FD loss	24.620276	24.6328549	24.6076972	<0.001
	high FD loss - random	17.8333679	17.8459468	17.8207891	<0.001
	low FD loss - random	-6.7869081	-6.7743292	-6.799487	<0.001
2012	observed - high FD loss	-17.612126	-17.624635	-17.599617	<0.001
	observed - low FD loss	7.4319866	7.4194773	7.4444959	<0.001
	observed - random	0.5208082	0.5333175	0.5082989	<0.001
	high FD loss - low FD loss	25.0441123	25.0566216	25.031603	<0.001
	high FD loss - random	18.132934	18.1454433	18.1204247	<0.001
	low FD loss - random	-6.9111783	-6.898669	-6.9236876	<0.001
2016	observed - high FD loss	-17.689442	-17.702474	-17.676411	<0.001
	observed - low FD loss	7.5292227	7.5161909	7.5422546	<0.001
	observed - random	0.5796593	0.5926912	0.5666275	<0.001
	high FD loss - low FD loss	25.218665	25.2316969	25.2056332	<0.001
	high FD loss - random	18.2691016	18.2821335	18.2560698	<0.001
	low FD loss - random	-6.9495634	-6.9365315	-6.9625952	<0.001

Chapter 5 – Discussion

Numerous studies have examined the impact of human activities on biodiversity, with one consistent conclusion; human actions are having a detrimental effect on natural systems worldwide (IPBES, 2019). Despite global mobilisation to address biodiversity loss, species extinction continues at rates estimated to be thousands of times higher than the pre-human background rate (Ceballos et al., 2020, 2015). These rapid declines in biodiversity threaten the persistence of natural habitats as well as nature's capacity to provide beneficial services critical to maintaining the quality of human life (Díaz et al., 2019). It is now well established that biodiversity has multiple facets each providing unique information and value (Cadotte and Tucker, 2018; Pollock et al., 2017; Purvis and Hector, 2000). As such, the impact of species extinction on biodiversity facets, such as PD or FD, is not uniform (Oliveira et al., 2020; Veron et al., 2021). In this thesis, I explore the PD and FD of global taxonomic groups to provide novel insights into the current and future state of biodiversity. I have compiled chondrichthyan and avian datasets from books (Ebert et al., 2021) and published databases (Froese and Pauly, 2023; Myhrvold et al., 2015; Tobias et al., 2022) to investigate how changing patterns of diversity are expressed in different biodiversity facets. These findings underscore the urgency of conserving functionally and phylogenetically irreplaceable species in the face of global change.

5 – 1 Linking facets of biodiversity

In recent years there has been a shift from measuring biodiversity based on a species taxonomic identity to considering species' evolutionary history and variation of traits (Cardoso et al., 2024; McGill et al., 2006; Pavoine and Bonsall, 2011). Under the assumption that PD may be able to capture a wider variety of form and function, it has been increasingly considered as a proxy for ecosystem function, as the extensive trait data required to measure FD is often unavailable (Faith et al., 2010; Forest et al., 2007; Redding and Mooers, 2015; Srivastava et al., 2012). Advances in global datasets of phylogenetic relationships (Jetz et al., 2012; Soares et al., 2023; Stein et al., 2018) and trait data (Froese and Pauly, 2023; Kattge et al., 2020; Tobias et al., 2022) for numerous taxonomic groups has provided a solid basis to assess how these aspects of biodiversity are related, sparking recent debates about how well PD can capture FD (Mazel et al., 2018; Owen et al., 2019). Yet, there is still uncertainty about the relationship between PD and FD (Mazel et al., 2018; Owen et al., 2019),

particularly when there is a large variety of indices to measure both PD and FD. In chapter 2, I found that PD and FD in sharks, ray and chimaeras does not always align, suggesting that these biodiversity facets are complementary rather than interchangeable.

The correlation between PD and FD was strongest when diversity metrics were richness-based but the correlation between PD and FD decreased when they were decoupled from species richness. This aligns with previous work suggesting that species richness alone may be an insufficient proxy for capturing more nuanced diversity aspects (Cadotte et al., 2011; Díaz et al., 2013; Gagic et al., 2015). Additionally, this study shows that there is no 'silver bullet' measure for biodiversity; when PD and FD deviate from species richness, they do so in distinct ways. By comparing various PD and FD metrics, I found that the strongest correlation came from Faith's PD and TPD richness, even after controlling for species richness. This may be because TPD richness was the only metric in this analysis that incorporated intraspecific variation in species traits. Since PD captures the full extent of all species trait variation (see chapter 1), the inclusion of intraspecific variation in TPDs may provide a broader reflection of the total variation of species traits than metrics that rely on a single point to represent trait diversity.

These results suggest that conservation efforts relying solely on species richness could overlook critical components of biodiversity, such as unique functional roles that are not well represented in taxonomic metrics. For example, some species may be evolutionarily distinct but functionally redundant or vice versa. I expand on this assumption in chapter 3, where I show that species-specific measures of PD and FD have a weak relationship. This highlighted functionally irreplaceable species that would not be captured under PD prioritisation frameworks such as EDGE. The weak correlation between shark functional distinctiveness and evolutionary distinctiveness echoes recent studies that challenge the longstanding assumption that PD should be employed as a surrogate for FD Chapter 3 reveals a weak correlation between evolutionary and functional distinctiveness in sharks, however this has also been demonstrated in other taxonomic groups (Cooke et al., 2020; Veron et al., 2021). This mirrors findings in chapter 2 that show weak correlations between different PD and FD metrics.

5 – 2 Prioritising FD for conservation

PD reflects evolutionary history, capturing the tempo and mode of divergence across the Tree of Life (Isaac et al., 2007). As a measure of living variation, PD is linked to the maintenance of future options for humanity, offering a reservoir of potential genetic, biochemical, and ecological innovations that may prove invaluable in adapting to unforeseen challenges (Faith, 1992; Faith, 2015). As such, PD is widely recognised as a valuable measure for conservation efforts (Gumbs et al., 2023a). In contrast, FD captures the variation of species traits, reflecting potential to enhance ecosystem function and resilience (de Bello et al., 2021c). Despite this, FD is yet to be a well-established conservation measure akin to PD.

To address this, chapter 3 introduces a framework that prioritises functionally irreplaceable and threatened species for conservation. This expands on previous prioritisation methods (Gumbs et al., 2023b; Hidasi-Neto et al., 2015; Isaac et al., 2007; Pavoine and Ricotta, 2024; Pimiento et al., 2020)

by quantifying species FD whose loss can be averted through species-focused conservation action. New developments from this thesis include: (i) using TPD kernels to incorporate intraspecific variation in species traits; (ii) considering the extinction risk of closely related species when calculating functional distinctiveness to predict how much FD individual species are likely to represent in the future; (iii) incorporating uncertainty in the estimated future trait space; (iv) incorporating uncertainties in extinction risk, which includes data deficient species or species not assessed by the IUCN Red List. The application of this framework to sharks reveals 76 species with above median functional distinctiveness and that are also threatened with extinction. These findings can inform policy by identifying high-priority species whose protection could maximize conservation outcomes for FD.

In chapter 4, I extended this framework by creating a probabilistic trait space for sharks and birds to simulate potential losses of FD under ongoing extinction predictions. I reveal vulnerable areas of trait space and identify potential changing patterns of shark and bird diversity. This aligns with recent analyses on biodiversity loss, highlighting that the erosion of FD is not a random process but one that may disproportionately impact certain ecological strategies (Carmona et al., 2021; Cooke et al., 2019b; Toussaint et al., 2021). The FD indicator developed for both clades demonstrates a growing expected FD loss. The framework for the FD indicator aligns with the GBF PD indicator methodology (Gumbs et al., 2023a) to enable comparable reporting between the two.

5 – 3 Trait data and its role in FD analyses

Prioritising conservation based on FD requires extensive trait data covering a majority of the species being measured, along with an understanding of traits that will represent functional interactions within an ecosystem (Mammola et al., 2021). Many FD studies preferentially use continuous data to capture fine-scale variations between species (de Bello et al., 2021b; Kohli and Jarzyna, 2021). In chapter 3, I extend my trait database, using EFAs to represent body shape as continuous data in sharks and catalogue finer resolution changes in species' body shape. The AVONET dataset, which includes continuous measurements of morphological traits for all living bird species, has become a widely used resource for studying bird FD (Tobias et al., 2022). Since its publication, numerous studies have relied on this dataset to explore bird FD, using morphological traits as indicators of species' ecological roles (Cardoso et al., 2024; Pigot et al., 2020). However, defining functional space based solely on morphology overlooks important functions such as reproductive ability, lifespan, and habitat preference. As a result, this approach may not fully capture the range of ecological roles species contribute to an ecosystem, thus limiting the conclusions a study can make about the implication for ecosystem processes and functions. In chapter 4, I use bird trait data from different sources to describe functional space beyond morphometrics and capture a broader suite of trait combinations.

Knowledge gaps and limited data on traits can constrain FD studies, often restricting them to specific taxonomic groups and geographic areas (Oliveira et al., 2020). As a result, many studies focus on plants and birds, which have well-documented functional traits (Kattge et al., 2020; Tobias et al., 2022). This narrow focus may lead to conclusions about FD that are not broadly applicable, as they are based on isolated groups. To broaden the taxonomic scope, this thesis centres on sharks, using

traits that may reflect their roles in ecosystem function. While finer trait detail can give more nuanced FD representations (Oliveira et al., 2020; Tucker et al., 2018), we lack the time to collect a "perfect dataset" given the urgency of current conservation needs. This thesis illustrates how limited trait data can still be used to approximate FD for important yet data limited clades.

5 – 4 Measuring biodiversity in the marine realm

Compared to terrestrial biodiversity, which reaches its peak in the wet tropics for most taxa (Hillebrand, 2004), biodiversity patterns in the ocean display a greater variability (Grady et al., 2019; Lotze, 2021). Recent work by Jaureguiberry et al. (2022) revealed that the dominant drivers of biodiversity loss in the ocean are exploitation and climate change. This contrasts with terrestrial and freshwater systems, where land-use change is the leading cause of biodiversity decline (Jaureguiberry et al., 2022; Sala et al., 2000). With the global human population likely to exceed 9 billion by 2050 (United Nations, 2022), exploitation of ocean resources will continue to increase (Duarte et al., 2020). On top of this, average global temperatures continue to rise (Rogelj et al., 2016), impacting many marine species' biological processes and compromising ecosystem productivity, threatening the future of multiple marine ecosystems (Duarte et al., 2020). To effectively protect marine habitats worldwide, biodiversity conservation efforts must address how these pressures impact the composition and distribution of various biodiversity components.

Although research to understand biodiversity and the impact of its decline in the ocean is gaining momentum, there is an urgent need for solutions to combat decline (UNESCO-IOC, 2021). A central goal of this thesis was to provide measurable values to represent imperilled FD, with the aim of informing future policy and strategies to protect marine biodiversity. Using sharks as a focal group, I illustrate in chapters 3 and 4 usable measures for marine species that contribute to closing the knowledge gap between marine and terrestrial biodiversity conservation.

With the push towards a blue economy, marine environments offer many benefits to society including aquaculture, blue carbon storage and energy production (Jolly, 2016). However, the rapid acceleration of marine activities and maritime industrial development are exacerbating already established threats to marine biodiversity (Duarte et al., 2020). At least one-third of fish stocks are overfished and the Australian beach protection program recorded a 90% decline in catch rates of large coastal sharks since the 1960s, despite the number of nets remaining relatively constant (Dedman et al., 2024; Roff et al., 2018). Overexploitation is one of the primary threats faced by sharks (Cardeñosa et al., 2022), in chapter 3 I show that exploited species are often more evolutionarily and functionally distinct. Pruning the evolutionary and functional variation of an ecosystem may reduce its capacity to recover and adapt in a changing environment (de Bello et al., 2021c; Forest et al., 2015).

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 (Gumbs et al., 2023c; Molina-Venegas, 2021; Molina-Venegas et al., 2021). A number of real-world examples demonstrate marine species' ability to recover when anthropogenic pressures are removed or reduced. For example, during both World War I and World War II decreased fishing pressures led to

a rise in fish stocks (Duarte et al., 2020). Additionally, improvements to ecosystem health in the Black Sea and Adriatic Sea was observed, due to a reduction in the use of fertilizers following the collapse of the Soviet Union (Mozetič et al., 2010; Oguz and Velikova, 2010). More recently, restricted human activity during the COVID-19 pandemic resulted in increases in reef fish density and abundance as well as higher hatch rates of sea turtles (Mallik et al., 2022).

With the recent adoption of the KMGBF (CBD, 2022) and the High Seas Treaty (UN General Assembly, 2023), there is increased motive for the protection of marine habitats towards the goal of conserving 30% of the ocean by 2030 (Kittinger et al., 2024). Although some management strategies have already been implemented, including the expansion of MPAs and other effective area-based conservation measures (OECMs), these interventions are still relatively new and their full benefits yet to be realised (Duarte et al., 2020). Indicators that monitor the state of recovery will be essential to ensure resources are targeted in the most efficient way.

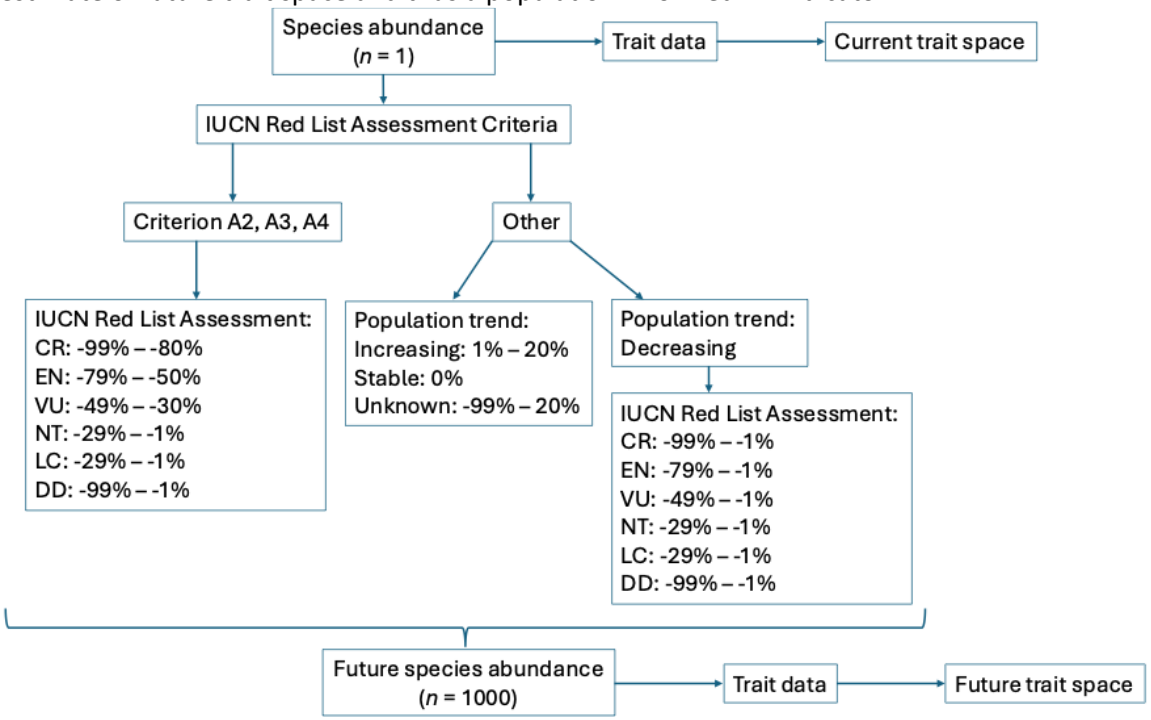
5 – 5 Limitations and future directions

In chapter 4 I demonstrated the utility of an FD indicator that measures the erosion of trait space by estimating the proportional reduction in the probability of occupancy of each voxel, based on the extinction probability of each species occupying the voxel. However, a similar method could also be applied to measure overall loss of FD. Akin to previous work that has estimated future projections of FD (Ali et al., 2023; Carmona et al., 2021; Cooke et al., 2019b; Oliveira et al., 2020), the FD indicator framework could be applied instead to use extinction scenarios to estimate future trait space. In chapter 3 I have outlined how IUCN Red List data can be used to estimate future trait space with extinction scenarios. The overall loss of FD would be the proportional change in total volume of trait space following extinction scenarios. With historical IUCN Red List assessments, the overall loss of FD could be taken at different time points to calculate trends in FD loss over time.

I developed the FD indicator framework focusing on species loss, based on extinction risk. However, integrating population data could provide a more accurate, real-time reflection of functional shifts incorporating both growth and decline in species abundance. Declines in population sizes—even without complete extinction—can erode FD by diminishing the abundance and influence of certain functional traits within ecosystems. Calculating a population-informed FD indicator would require information on species population trends and species abundance data (Box 1). Much of this information is available for birds at a global scale (Box 1; Callaghan et al., 2021; IUCN). Additionally, this framework can be adapted for local applications or tailored to specific populations, provided trait and population data are accessible.

Box 1| Preliminary work calculating a population-informed FD indicator

An example of how to calculate a population-informed FD indicator, using bird trait data (collated in chapter 4), global abundance estimates (Callaghan et al., 2021) and IUCN Red List species assessment information (IUCN); first, an abundance-weighted TPD is calculated based on species trait data and abundance estimates, providing an estimate of current trait space. Future species abundances can then be calculated by estimating a rate of population change based on information given in the IUCN Red List Assessment Criteria (IUCN, 2001). For species assessed under criterion A2, A3, or A4, population decline rates are estimated by conservation status: CR species are projected to decline by 80-99%, EN by 50-79%, VU by 30-49%, NT/LC by 1-29%, and NE/DD by 1-99%. For species not assessed under these criteria, population change rates can be estimated based on their population trend information given in the IUCN Red List Assessment Criteria. Species where population trend is listed as increasing are expected to grow between 1-20%, this range is based on the distribution of population increases observed in the eBird status and trends data (Fink et al., 2023). Species with population trends listed as stable will see no changes to their abundance estimates. Species with a decreasing population trend are estimated to decline based on conservation status (CR: 1% - 99%, EN: 1% - 79%, VU: 1% - 49%, NT/LC: 1 - 29%, NE/DD: 1% - 99%), where the maximum decline rate is estimated based on criterion A2-4 population reduction categories but the minimum decline rate is 1 to reflect that since these species are not assessed under criterion A their reduction rate is unknown. To incorporate uncertainty, each population change rate is randomly selected from these ranges 1000 times for each species, generating a distribution of future abundance estimates. These estimates are then used to calculate an abundance-weighted TPD, providing a projected estimate of future trait space and thus a population-informed FD indicator.



Box Fig. 1| A flow chart demonstrating the key components for calculating a population-based FD indicator.

A critical priority is to understand how extinctions and population declines impact local communities. Extinctions are likely to have the greatest impact on ecosystem function at the

community level. Local communities are where many ecosystem services are primarily delivered, and species' extinctions or reductions in abundance often have more pronounced effects in these settings. Using local population data to track trends in future predictions of trait space will provide more nuanced feedback of functional shifts within ecosystems in response to local pressures. This enhances the relevance of FD measures for conservation planning and policy at both national and global levels, as it aligns closely with the practical benefits observed in local communities. Additionally, tracking trends in predicted FD loss at a local scale will highlight potential areas where conservation action is and isn't working providing feedback for practitioners to critically analyse different approaches to conservation and apply the most efficient methods.

In chapter 3, I have demonstrated the global application of FuDGE, aligning with the majority of studies that assess functional distinctiveness at a global scale (Cooke et al., 2020; Veron et al., 2021). However, local scale analyses may have more impact, as sorting species into their geographic assemblages will reflect more realistic interactions between species and highlight locally important species. Some species may be functionally redundant at a global level but have a distinct functional role within a local ecosystem. With many species already assessed on National Red Lists (National Red List, 2024), these assessments could be applied to give a more locally representative measure of a species extinction risk. Local FuDGE lists could also incentivise countries to protect species representing unique ecological roles within their borders, fostering a sense of ownership of locally distinct species. Since most conservation policies are developed at a local scale, directing local-level conservation action is likely to have the greatest influence for prioritising imperilled FD. This targeted approach aligns well with local conservation priorities, enhancing the impact of efforts to protect species and their irreplaceable ecological roles.

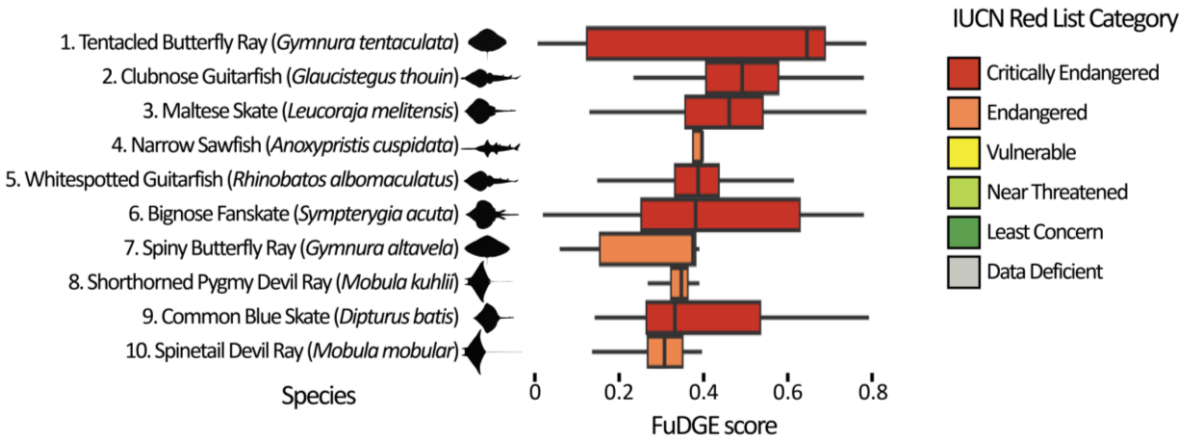
Many conclusions in this thesis rely on the assumption that FD effectively represents ecological function. While this assumption is well-founded through experiments to explain the biodiversity-ecosystem functioning relationship (e.g. Lavorel et al., 1997; Tilman et al., 1997) the traits selected to represent FD are vital to explain how traits affect ecosystem processes. In FD studies, traits are generally selected based on their links to ecological roles and their availability within the taxonomic group of interest (Cadotte and Tucker, 2018). Many traits used to represent ecological roles are often specific to particular taxonomic groups and may not be applicable across clades; for example, wingspan is relevant for birds and insects but cannot characterise plants (de Bello et al., 2021b). As a result, FD is typically measured within a single clade, limiting comparisons of FD across taxonomic groups and providing limited insight into interactions between different clades within an ecosystem. To enable direct comparisons across taxonomic groups, would require the use of broad, universally applicable traits to create a unified trait space (see Cooke et al., 2019; Pimiento et al., 2023). However, this approach may dilute trait specificity and generalise many ecological strategies. Traits may function in subtly different ways. Applying broad scale traits to species to integrate multiple taxonomic groups, may overlook the hidden and potentially significant idiosyncrasies in functionality that can be identified in finer scale trait combinations (Kohli and Jarzyna, 2021). It is generally favourable to split species by clade and include more detailed trait information (Carmona et al., 2021; Toussaint et al., 2021). In this thesis, I do not delve into the broader issue of using multiple taxonomic groups versus incorporating finer-scale trait combinations. However, in chapter 3, I address cross-clade comparability within the FuDGE framework by calculating each species'

proportional contribution to the trait space. This approach provides a basis for comparing how much different species contribute to their assemblage's overall FD, potentially enabling comparisons across clades. Yet, as I only measured FuDGE in a single clade, this feature of the FuDGE metric remains untested.

In chapter 3, sharks serve as a case study to illustrate the FuDGE framework. While these analyses highlight the functional contributions of sharks within marine ecosystems, conclusions drawn from sharks alone cannot be generalised across all clades, as different groups occupy unique functional niches (Chacón-Labella et al., 2023; Gonçalves-Souza et al., 2023). Expanding the taxonomic scope of FuDGE is therefore essential to capture a more comprehensive picture of FD and to pinpoint species across taxa whose extinction would result in irreplaceable functional losses. The availability of global datasets of species traits for an increasing number of taxonomic groups provides opportunities for widening the taxonomic scope of FD measures. Broadly applicable frameworks, such as the FUDGE framework outline in chapter 3, facilitate the expansion of taxonomic coverage of species prioritised for conservation, based on their functional contributions. To illustrate the use of FuDGE in other taxonomic groups, I have developed a FuDGE list of rays, using the same methods as outlined in chapter 3 (Box 2).

Box 2| FuDGE list of rays

To calculate a FuDGE list for rays, I use trait data from chapter 2 together with additional body shape data collected using the EFA methods outline in chapter 3 (section 2.2.1) and extinction risk data from the IUCN Red List of Threatened Species (v. 2023.1). Following the methods outlined in chapter 3, I calculate FuDGE scores for 766 species of rays (FuDGE list available in Appendix A2).



Box Fig. 2| The top 10 highest ranked FuDGE ray species. Boxplots represent the range, interquartile range and median of FuDGE scores calculated over 1000 iterations. Box colours represent IUCN Red List categories (red = Critically Endangered, orange = Endangered, yellow = Vulnerable, light green = Near Threatened, green = Least Concern, grey = Data Deficient). Silhouettes: Marc Dando.

5 – 6 Conclusion

As new challenges emerge from climate change, human population growth, and escalating pollution (IPBES, 2019), biodiversity is subjected to pressures at an unprecedented scale. Historical shortfalls

in conservation efforts highlight the urgent need for focused and coordinated action to prevent further biodiversity loss (Díaz et al., 2020). Understanding the consequences of extinction is essential to prevent erosion of evolutionary and ecological biodiversity dimensions. Effective conservation of threatened biodiversity demands accurate and robust prioritisation of imperilled species, as well as the identification of key regions for strategic interventions across the globe. This thesis set out to enhance our understanding of global biodiversity and the ecological consequences of biodiversity loss. First, I investigate the correlation between PD and FD, showing that richness-based dimensions of biodiversity have strong correlations that are primarily driven by species richness. This analysis reveals nuances between PD and FD metrics beyond those explained by species richness alone, highlighting the importance of prioritising FD directly, as PD alone cannot fully capture subtle differences between the two metrics. Second, I introduce a species-specific measure that prioritises imperilled FD for conservation, which allows me to assess the conservation priorities of the world's sharks. This assessment underscores an urgent need to protect threatened species that represent distinct functional roles, particularly those exploited for resources. Finally, I develop a framework to quantify expected FD losses under current extinction trajectories. I hope that the research presented here can support effective conservation prioritisation and guide practical conservation actions. Such strategic prioritisation is vital to prevent unprecedented loss of biodiversity.

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Appendices

Appendix A1. FuDGE list of sharks

A1.1 Above median FuDGE species (see chapter 3)

Species	Red List Category	Functional Distinctiveness	FuDGE
Sand Tiger Shark (Carcharias taurus)	CR	0.472	0.441
Scalloped Hammerhead (Sphyrna lewini)	CR	0.365	0.335
Basking Shark (Cetorhinus maximus)	EN	0.637	0.314
Angular Roughshark (Oxynotus centrina)	EN	0.590	0.287
Speckled Smoothhound (Mustelus mento)	CR	0.276	0.260
Pacific Nurse Shark (Ginglymostoma unami)	EN	0.501	0.252
Whale Shark (Rhincodon typus)	EN	0.497	0.240
Smoothback Angelshark (Squatina oculata)	CR	0.258	0.239
Zebra Shark (Stegostoma tigrinum)	EN	0.424	0.209
Japanese Shortnose Spurdog (Squalus brevirostris)	EN	0.409	0.205
Smalltail Shark (Carcharhinus porosus)	CR	0.195	0.181
Venezuelan Dwarf Smoothhound (Mustelus minicanis)	EN	0.273	0.136
Caribbean Reef Shark (Carcharhinus perezi)	EN	0.228	0.124
Starspotted Smooth-hound (Mustelus manazo)	EN	0.221	0.117
Ocellated Angelshark (Squatina tergocellatoides)	EN	0.228	0.110
Pelagic Thresher (Alopias pelagicus)	EN	0.225	0.109
Tawny Nurse Shark (Nebrius ferrugineus)	VU	0.383	0.102
Slender Weasel Shark (Paragaleus longicaudatus)	VU	0.409	0.100
Scalloped Bonnethead (Sphyrna corona)	CR	0.099	0.099
Bramble Shark (Echinorhinus brucus)	EN	0.192	0.094
Whitefin Topeshark (Hemitriakis leucoperiptera)	CR	0.096	0.091
Pondicherry Shark (Carcharhinus hemiodon)	CR	0.096	0.088
Longfin Mako (Isurus paucus)	EN	0.147	0.085
Lemon Shark (Negaprion brevirostris)	VU	0.300	0.085
Lost Shark (Carcharhinus obsoletus)	CR	0.090	0.081
Spiny Dogfish (Squalus acanthias)	VU	0.322	0.079

Broadnose Sevengill Shark (Notorynchus cepedianus)	VU	0.324	0.078
Argentine Angelshark (Squatina argentina)	CR	0.081	0.077
Japanese Angelshark (Squatina japonica)	CR	0.077	0.077
Oceanic Whitetip Shark (Carcharhinus longimanus)	CR	0.083	0.075
Atlantic Nurse Shark (Ginglymostoma cirratum)	VU	0.287	0.071
Nursehound (Scyliorhinus stellaris)	VU	0.276	0.070
Shortspine Spurdog (Squalus mitsukurii)	EN	0.136	0.067
Snaggletooth Shark (Hemipristis elongata)	VU	0.265	0.064
Longsnout Dogfish (Deania quadrispinosa)	VU	0.269	0.062
Sharptooth Smoothhound (Mustelus dorsalis)	VU	0.254	0.061
Whitetip Reef Shark (Triaenodon obesus)	VU	0.236	0.054
Knifetooth Dogfish (Scymnodon ringens)	VU	0.210	0.052
Broadfin Shark (Lamiopsis temminckii)	EN	0.099	0.051
Michael's Epaulette Shark (Hemiscyllium michaeli)	VU	0.206	0.050
Bonnethead Shark (Sphyrna tiburo)	EN	0.099	0.050
Little Gulper Shark (Centrophorus uyato)	EN	0.092	0.049
Smalleye Hammerhead (Sphyrna tudes)	CR	0.055	0.048
Narrownose Smoothhound (Mustelus schmitti)	CR	0.048	0.048
Indonesian Houndshark (Hemitriakis indroyonoi)	EN	0.099	0.047
Angelshark (Squatina squatina)	CR	0.052	0.045
Striped Smoothhound (Mustelus fasciatus)	CR	0.048	0.044
Taiwan Spurdog (Squalus formosus)	EN	0.085	0.043
Blackspotted Smoothhound (Mustelus punctulatus)	VU	0.181	0.042
Winghead Shark (Eusphyra blochii)	EN	0.088	0.042
Brazilian Sharpnose Shark (Rhizoprionodon lalandii)	VU	0.166	0.041
Flapnose Houndshark (Scylliogaleus quecketti)	VU	0.177	0.041
Night Shark (Carcharhinus signatus)	EN	0.077	0.037
Barbeled Houndshark (Leptocharias smithii)	VU	0.147	0.036
Blacknose Shark (Carcharhinus acronotus)	EN	0.066	0.033
Smooth Hammerhead (Sphyrna zygaena)	VU	0.136	0.033
Milk Shark (Rhizoprionodon acutus)	VU	0.125	0.032

Whitetip Weasel Shark (Paragaleus leucolomatus)	VU	0.118	0.032
Banded Houndshark (Triakis scyllium)	EN	0.055	0.029
Dusky Shark (Carcharhinus obscurus)	EN	0.055	0.029
Sickelfin Weasel Shark (Hemigaleus microstoma)	VU	0.114	0.029
Roughskin Dogfish (Centroscymnus owstonii)	VU	0.147	0.027
Grey Reef Shark (Carcharhinus amblyrhynchos)	EN	0.059	0.027
Pigeye Shark (Carcharhinus amboinensis)	VU	0.151	0.026
Lizard Catshark (Schroederichthys saurisqualus)	VU	0.099	0.026
Greeneye Spurdog (Squalus chloroculus)	EN	0.052	0.025
Caribbean Sharpnose Shark (Rhizoprionodon porosus)	VU	0.096	0.024
Whitefin Smoothhound (Mustelus widodoi)	VU	0.077	0.020
Greenland Shark (Somniosus microcephalus)	VU	0.077	0.019
Porbeagle (Lamna nasus)	VU	0.070	0.017
Kitefin Shark (Dalatias licha)	VU	0.070	0.017
Indonesian Whaler Shark (Carcharhinus tjutjot)	VU	0.059	0.016
Graceful Catshark (Proscyllium habereri)	VU	0.070	0.016
Philippine Spurdog (Squalus montalbani)	VU	0.063	0.015
Andaman Smoothhound (Mustelus andamanensis)	VU	0.052	0.015
Bull Shark (Carcharhinus leucas)	VU	0.044	0.012

A1.2 Top 75th percentile FuDGE species (see chapter 3)

Species	Red List Category	Functional Distinctiveness	FuDGE
Sand Tiger Shark (Carcharias taurus)	CR	0.472	0.441
Scalloped Hammerhead (Sphyrna lewini)	CR	0.365	0.335
Basking Shark (Cetorhinus maximus)	EN	0.637	0.314
Angular Roughshark (Oxynotus centrina)	EN	0.590	0.287
Speckled Smoothhound (Mustelus mento)	CR	0.276	0.260
Pacific Nurse Shark (Ginglymostoma unami)	EN	0.501	0.252
Whale Shark (Rhincodon typus)	EN	0.497	0.240
Smoothback Angelshark (Squatina oculata)	CR	0.258	0.239
Zebra Shark (Stegostoma tigrinum)	EN	0.424	0.209

Japanese Shortnose Spurdog (Squalus brevirostris)	EN	0.409	0.205
Smalltail Shark (Carcharhinus porosus)	CR	0.195	0.181
Venezuelan Dwarf Smoothhound (Mustelus minicanis)	EN	0.273	0.136
Caribbean Reef Shark (Carcharhinus perezi)	EN	0.228	0.124
Starspotted Smooth-hound (Mustelus manazo)	EN	0.221	0.117
Ocellated Angelshark (Squatina tergocellatoides)	EN	0.228	0.110
Pelagic Thresher (Alopias pelagicus)	EN	0.225	0.109
Tawny Nurse Shark (Nebrius ferrugineus)	VU	0.383	0.102
Slender Weasel Shark (Paragaleus longicaudatus)	VU	0.409	0.100
Bramble Shark (Echinorhinus brucus)	EN	0.192	0.094
Longfin Mako (Isurus paucus)	EN	0.147	0.085
Lemon Shark (Negaprion brevirostris)	VU	0.300	0.085
Spiny Dogfish (Squalus acanthias)	VU	0.322	0.079
Broadnose Sevengill Shark (Notorynchus cepedianus)	VU	0.324	0.078
Atlantic Nurse Shark (Ginglymostoma cirratum)	VU	0.287	0.071
Nursehound (Scyliorhinus stellaris)	VU	0.276	0.070
Snaggletooth Shark (Hemipristis elongata)	VU	0.265	0.064
Longsnout Dogfish (Deania quadrispinosa)	VU	0.269	0.062
Sharptooth Smoothhound (Mustelus dorsalis)	VU	0.254	0.061
Whitetip Reef Shark (Triaenodon obesus)	VU	0.236	0.054
Knifetooth Dogfish (Scymnodon ringens)	VU	0.210	0.052
Michael's Epaulette Shark (Hemiscyllium michaeli)	VU	0.206	0.050
Blackspotted Smoothhound (Mustelus punctulatus)	VU	0.181	0.042
Brazilian Sharpnose Shark (Rhizoprionodon lalandii)	VU	0.166	0.041
Whitetip Weasel Shark (Paragaleus leucolomatus)	VU	0.118	0.032

A1.3 Top 95th percentile FuDGE species (see chapter 3)

Species	Red List Category	Functional Distinctiveness	FuDGE
Basking Shark (Cetorhinus maximus)	EN	0.637	0.314
Angular Roughshark (Oxynotus centrina)	EN	0.590	0.287
Pacific Nurse Shark (Ginglymostoma unami)	EN	0.501	0.252
Whale Shark (Rhincodon typus)	EN	0.497	0.240
Zebra Shark (Stegostoma tigrinum)	EN	0.424	0.209
Japanese Shortnose Spurdog (Squalus brevirostris)	EN	0.409	0.205
Tawny Nurse Shark (Nebrius ferrugineus)	VU	0.383	0.102
Slender Weasel Shark (Paragaleus longicaudatus)	VU	0.409	0.100

Appendix A2. FuDGE list of Rays

A2.1 Above median FuDGE species (see chapter 5 box 2)

Species	Red List Category	Functional Distinctiveness	FuDGE
Tentacled Butterfly Ray (Gymnura tentaculata)	CR	0.665	0.645
Clubnose Guitarfish (Glaucostegus thouin)	CR	0.507	0.491
Maltese Skate (Leucoraja melitensis)	CR	0.475	0.461
Narrow Sawfish (Anoxypristis cuspidata)	EN	0.817	0.396
Whitespotted Guitarfish (Rhinobatos albomaculatus)	CR	0.399	0.387
Bignose Fanskate (Sympterygia acuta)	CR	0.393	0.381
Spiny Butterfly Ray (Gymnura altavela)	EN	0.773	0.375
Shorthorned Pygmy Devil Ray (Mobula kuhlii)	EN	0.716	0.347
Common Blue Skate (Dipturus batis)	CR	0.342	0.332
Spinetail Devil Ray (Mobula mobular)	EN	0.633	0.307
Ocellate Eagle Ray (Aetomylaeus milvus)	EN	0.614	0.298
Duckbill Eagle Ray (Aetomylaeus bovinus)	CR	0.304	0.295
Shortnose Eagle Ray (Myliobatis ridens)	CR	0.304	0.295
Whitespotted Wedgefish (Rhynchobatus djiddensis)	CR	0.291	0.283
Lusitanian Cownose Ray (Rhinoptera marginata)	CR	0.285	0.276
Zonetail Butterfly Ray (Gymnura zonura)	EN	0.557	0.270

Sicklefin Devil Ray (Mobula tarapacana)	EN	0.557	0.270
Spotback Skate (Atlantoraja castelnaui)	CR	0.272	0.264
Oceanic Manta Ray (Mobula birostris)	EN	0.529	0.256
Roughback Whipray (Fluvitrygon kittipongi)	EN	0.519	0.252
Korean Skate (Hongeo koreanus)	CR	0.253	0.246
Flapper Skate (Dipturus intermedius)	CR	0.234	0.227
Longnose Skate (Dentiraja confusa)	CR	0.222	0.215
Coach Whipray (Himantura uarnak)	EN	0.431	0.209
Raya Amazonica (Potamotrygon tigrina)	EN	0.424	0.206
Giant Freshwater Whipray (Urogymnus polylepis)	EN	0.412	0.200
Smalltooth Sawfish (Pristis pectinata)	CR	0.203	0.197
Roughskin Skate (Dipturus trachyderma)	EN	0.399	0.193
Graytail Skate (Bathyraja griseocauda)	EN	0.399	0.193
Mottled Skate (Beringraja pulchra)	EN	0.399	0.193
Longhorned Mobula (Mobula eregoodootenkee)	EN	0.399	0.193
Atlantic Pygmy Devil Ray (Mobula hypostoma)	EN	0.393	0.190
Longtail Butterfly Ray (Gymnura poecilura)	VU	0.735	0.178
Common Eagle Ray (Myliobatis aquila)	CR	0.177	0.172
Blotched Fantail Ray (Taeniurops meyeni)	VU	0.678	0.164
Naru Eagle Ray (Aetobatus narutobiei)	VU	0.659	0.160
Xingu Freshwater Stingray (Potamotrygon leopoldi)	VU	0.602	0.146
Oman Cownose Ray (Rhinoptera jayakari)	EN	0.291	0.141
Tubemouth Whipray (Urogymnus lobistoma)	EN	0.291	0.141
Mottled Eagle Ray (Aetomylaeus maculatus)	EN	0.285	0.138
White-edge Whipray (Fluvitrygon signifer)	EN	0.279	0.135
Eyespot Skate (Atlantoraja cyclophora)	EN	0.272	0.132
Javan Whipray (Brevitrygon javaensis)	EN	0.272	0.132
Halavi Guitarfish (Glaucostegus halavi)	CR	0.133	0.129
Indian Sharpnose Ray (Telatrygon crozieri)	EN	0.247	0.120
Mangrove Whipray (Urogymnus granulatus)	VU	0.481	0.117
Diamond Stingray (Hypanus dipterurus)	VU	0.478	0.116

Maugean Skate (Dipturus maugeanus)	EN	0.234	0.114
Sharpnose Whipray (Maculabatis macrura)	EN	0.234	0.114
Whitespotted Eagle Ray (Aetobatus narinari)	EN	0.228	0.111
Japanese Sleeper Ray (Narke japonica)	VU	0.456	0.111
Java Stingaree (Urolophus javanicus)	CR	0.114	0.111
Smalltooth Stingray (Hypanus rudis)	CR	0.114	0.111
Ornate Eagle Ray (Aetomylaeus vespertilio)	EN	0.222	0.107
Aden Torpedo (Torpedo adenensis)	EN	0.222	0.107
Marbled Torpedo Ray (Torpedo marmorata)	VU	0.437	0.106
Munk's Pygmy Devil Ray (Mobula munkiana)	VU	0.437	0.106
Groovebelly Stingray (Dasyatis hypostigma)	EN	0.215	0.104
Mekong Stingray (Hemitrygon laosensis)	EN	0.215	0.104
Narrow Cowtail Ray (Pastinachus gracilicaudus)	EN	0.215	0.104
Hyuga Fanray (Platyrhina hyugaensis)	VU	0.418	0.101
Whitedotted Skate (Bathyraja albomaculata)	VU	0.418	0.101
Southern Eagle Ray (Myliobatis goodei)	VU	0.415	0.101
Brazilian Cownose Ray (Rhinoptera brasiliensis)	VU	0.412	0.100
Sandy Skate (Leucoraja circularis)	EN	0.203	0.098
American Cownose Ray (Rhinoptera bonasus)	VU	0.402	0.098
Dwarf Whipray (Brevitrygon heterura)	VU	0.399	0.097
Yellowback Stingaree (Urolophus sufflavus)	VU	0.399	0.097
La Plata Skate (Atlantoraja platana)	EN	0.196	0.095
Honeycomb Whipray (Himantura undulata)	EN	0.196	0.095
Rio Skate (Rioraja agassizii)	VU	0.393	0.095
African Wedgefish (Rhynchobatus luebberti)	CR	0.095	0.092
Reef Manta Ray (Mobula alfredi)	VU	0.380	0.092
Marbled Whipray (Fluvitrygon oxyrhynchus)	EN	0.190	0.092
Panther Torpedo (Torpedo panthera)	EN	0.190	0.092
Indonesian Sharpnose Ray (Telatrygon biasa)	VU	0.367	0.089
Rosette Torpedo (Torpedo bauchotae)	EN	0.184	0.089
Common Stingray (Dasyatis pastinaca)	VU	0.342	0.083

Bleeker's Whipray (Pateobatis bleekeri)	EN	0.171	0.083
Javanese Cownose Ray (Rhinoptera javanica)	EN	0.171	0.083
Winter Skate (Leucoraja ocellata)	EN	0.171	0.083
Japanese Eagle Ray (Myliobatis tobijei)	VU	0.336	0.081
Brown Numbfish (Narcine timlei)	VU	0.336	0.081
Undulate Skate (Raja undulata)	EN	0.165	0.080
Thorny Skate (Amblyraja radiata)	VU	0.323	0.078
Thintail Skate (Dipturus leptocauda)	VU	0.323	0.078
Polkadot Skate (Dipturus chinensis)	VU	0.317	0.077
Porcupine Ray (Urogymnus asperrimus)	VU	0.317	0.077
Sandyback Stingaree (Urolophus bucculentus)	VU	0.317	0.077
Yellow-spotted Fanray (Platyrhina tangi)	VU	0.310	0.075
Greenback Stingaree (Urolophus viridis)	VU	0.310	0.075
Rabbitfish (Chimaera monstrosa)	VU	0.304	0.074
Whitenose Whipray (Pateobatis uarnacoides)	EN	0.152	0.074
Coastal Stingaree (Urolophus orarius)	EN	0.152	0.074
Round Whipray (Maculabatis pastinacoides)	EN	0.152	0.074
Thickbody Skate (Amblyraja frerichsi)	VU	0.304	0.074
Reticulate Round Ray (Urotrygon reticulata)	CR	0.076	0.074
Brown Stingray (Bathytoshia lata)	VU	0.298	0.072
Ocellate Torpedo (Torpedo torpedo)	VU	0.298	0.072
White Skate (Rostroraja alba)	EN	0.146	0.071
Freckled Guitarfish (Pseudobatos lentiginosus)	VU	0.291	0.071
Finless Sleeper ray (Temera hardwickii)	VU	0.291	0.071
Southern Banded Guitarfish (Zapteryx xyster)	VU	0.291	0.071
Browneye Skate (Okamejei schmidti)	VU	0.288	0.070
Pacific Eagle Ray (Aetobatus laticeps)	VU	0.285	0.069
Longhead Eagle Ray (Aetobatus flagellum)	EN	0.139	0.068
Izu Stingray (Hemitrygon izuensis)	VU	0.279	0.068
Chilean Eagle Ray (Myliobatis chilensis)	VU	0.266	0.064
Spotted Shovelnose Ray (Aptychotrema timorensis)	VU	0.260	0.063

Madagascar Skate (Dipturus crosnieri)	VU	0.260	0.063
Yellow Spotted Skate (Okamejei hollandi)	VU	0.260	0.063
Spotted Eagle Ray (Aetobatus ocellatus)	VU	0.253	0.061
Cortez Numbfish (Narcine entemedor)	VU	0.234	0.057
American Elephantfish (Callorhinchus callorynchus)	VU	0.228	0.055
Onefin Skate (Gurgesiella dorsalifera)	VU	0.228	0.055
Borneo Sand Skate (Okamejei cairae)	VU	0.228	0.055
Melbourne Skate (Spiniraja whitleyi)	VU	0.228	0.055
Daisy Whipray (Fontitrygon margarita)	VU	0.222	0.054
Shagreen Skate (Leucoraja fullonica)	VU	0.222	0.054
Peruvian Eagle Ray (Myliobatis peruvianus)	VU	0.222	0.054
West African Torpedo (Torpedo mackayana)	EN	0.108	0.052
Smalleye Round Ray (Urotrygon microphthalmum)	CR	0.051	0.049
Krefft's Blind Numbfish (Benthobatis kreffti)	VU	0.196	0.048
Sharpnose Ray (Telatrygon acutirostra)	VU	0.177	0.043
Bennett's Stingray (Hemitrygon bennettii)	VU	0.171	0.041
Pale-edge Sharpnose Ray (Telatrygon zugei)	VU	0.171	0.041
Borneo Guitarfish (Rhinobatos borneensis)	EN	0.082	0.040
Longtail Stingray (Hypanus longus)	VU	0.165	0.040
Spadenose Guitarfish (Pseudobatos buthi)	VU	0.165	0.040
Blackfish Stingray (Hemitrygon navarrae)	VU	0.165	0.040
Leopard Whipray (Himantura leoparda)	VU	0.165	0.040
Colombian Dwarf Numbfish (Diplobatis colombiensis)	VU	0.152	0.037
Bullnose Eagle Ray (Myliobatis freminvillei)	VU	0.146	0.035
Sharpspine Skate (Okamejei acutispina)	VU	0.146	0.035
Boeseman's Skate (Okamejei boesemani)	VU	0.127	0.031
Whitespotted Whipray (Maculabatis gerrardi)	EN	0.063	0.031
Broad Cowtail Ray (Pastinachus ater)	VU	0.120	0.029
Banded Eagle Ray (Aetomylaeus nichofii)	VU	0.114	0.028
Longnose Eagle Ray (Myliobatis longirostris)	VU	0.108	0.026

Fake Round Ray (Urotrygon simulatrix)	VU	0.108	0.026
Roughtail Stingray (Bathytoshia centroura)	VU	0.095	0.023
Bigeye Skate (Okamejei meerdervoortii)	VU	0.095	0.023
Japanese Butterfly Ray (Gymnura japonica)	VU	0.063	0.015