

Global patterns of marine megafauna functional diversity

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Scientific Abstract

Marine megafauna (i.e. large-bodied marine animals with a body mass of >45 kg) perform important ecological roles in the oceans, yet their contributions to the stability and resilience of ecosystems are undermined by ongoing population decay due to intensified anthropogenic activities. Given the limited resources available to invest in conservation programs and the increasing numbers of threatened species due to fast-paced rate of biodiversity loss, recent efforts have been made into identifying species and areas of high conservation priority for protecting their ecological functionality. While species diversity has often been considered in guiding conservation actions, such recent interest in preserving species' ecological contributions has advocated for integrating functional diversity in conservation planning. In this study, I assessed the global patterns of the functional and taxonomic diversity (i.e. functional richness and species richness, respectively) of marine megafauna to identify areas of exceptional functional importance. Accordingly, I identified the degree of congruence between locations of high species and functional richness by means of hotspots overlap analysis and applied a novel conservation index, FUSE (Functionally Unique, Specialized, and Endangered) to identify areas of conservation prioritization according to species' contributions to functional diversity and their endangerment status. Hotspots of functional richness overlapped only marginally with those of species richness (by 34.5%). The South-West Pacific resulted as a major hotspot of exceptionally high functional richness, while the Caspian Sea and Gulf of Mexico were identified as areas of potential conservation priority harbouring species with high-ranking FUSE scores. Furthermore, the South-West Pacific was also an aggregation centre of high-ranking FUSE species. Overall, this study showed that setting conservation priority areas based on metrics of species diversity alone would be insufficient for safeguarding the ecological contributions of marine megafauna to the ecosystem, and that larger protection areas should be considered.

Lay Summary

Marine megafauna (i.e. large-bodied marine animals with a body mass of >45 kg) perform important ecological roles in the oceans. The intensified defaunation and exploitation of natural habitats have led to an exceptionally rapid decline in their abundances over the last century, undermining the persistence of their ecological roles, thus triggering important repercussions on the productivity, structure, and stability of the ecosystems. Given the limited resources available to invest in conservation programs and the increasing numbers of threatened species, recent efforts have been made into identifying species and areas of high conservation priority for protecting their ecological functionality. Particularly, area-based conservation strategies, such as biodiversity hotspots, have been advocated as key tools for reversing trends of biodiversity loss and protecting species and ecosystem functioning. While species diversity has often been considered in guiding such conservation strategies, the recent interest in preserving species' ecological contributions has advocated for integrating functional diversity in conservation planning. Assessing functional diversity allows to estimate the functional contributions of individual species and communities to ecosystems and develop appropriate approaches to protecting biodiversity by identifying those species assemblages whose functional integrity is most vulnerable to taxonomic loss. In this study, I assessed the global patterns of the functional and taxonomic diversity (i.e. functional richness and species richness, respectively) of marine megafauna to identify areas of exceptional functional importance. Accordingly, I identified the degree of congruence between locations of high species and functional richness by means of hotspots overlap analysis and applied a novel conservation index, FUSE (Functionally Unique, Specialized, and Endangered) to identify areas of conservation prioritization according to species' contributions to functional diversity and their endangerment status. Hotspots of functional richness overlapped only marginally with those of species richness (by 34.5%). The South-West Pacific resulted as a major hotspot of exceptionally high functional richness, while the Caspian Sea and Gulf of Mexico were identified as areas of potential conservation priority harbouring species with high-ranking FUSE scores. Furthermore, the South-West Pacific was also an aggregation centre of high-ranking FUSE species. The fact that the South-West Pacific also resulted as an aggregation center of marine megafaunal species of conservation priority, as well as an hotspot of exceptional functional richness, stresses the functional importance of the species assemblages inhabiting this region and therefore the need to be the target of conservation actions for safeguarding the future of marine megafaunal diversity. Overall, this study showed that setting conservation priority areas based on metrics of species diversity alone would be insufficient for safeguarding the ecological contributions of marine megafauna to the ecosystem, and that larger protection areas should be considered.

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Data Curation	CP, AC
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Supervision	CP, JG
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Visualization	AC
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Student Name: Arianna Chiti

Student Number: 2 [REDACTED]

Project title: Global patterns of marine megafauna functional diversity

Category	Item	Description	Cost
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Conference	Conference fee	CPEG 2021 – Reduced Rate Registration	€ 60
Total			€ 640

I hereby certify that the above information is true and correct to the best of my knowledge.

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Ethics Approval

Project Ethics Assessment Confirmation|Cadarnhad o Asesiad Moeseg Prosiect



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Friday, 5 February 2021 at 13:46

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This is an automated confirmation email for the following project. The Ethics Assessment status of this project is: APPROVED

Applicant Name: Arianna Chiti

Project Title: Global patterns of marine megafauna functional diversity

Project Start Date: 25.01.2021

Project Duration: 8 months

Approval No: SU-Ethics-Student-050221/3746

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Neges awtomataidd yw hon ar gyfer y prosiect canlynol. Statws Asesiad Moeseg y prosiect hwn yw: APPROVED

Enw'r Ymgeisydd: Arianna Chiti

Teitl y Prosiect: Global patterns of marine megafauna functional diversity

Dyddiad Dechrau'r Prosiect: 25.01.2021

Hyd y Prosiect: 8 months

Rhif y Gymeradwyaeth: SU-Ethics-Student-050221/3746

SYLWER: Nid yw'r hysbysiad hwn o gymeradwyaeth foesebol yn cynnwys agweddau sy'n ymwneud ag lechyd a Diogelwch. Dylech gwblhau unrhyw asesiadau risg perthnasol cyn dechrau eich prosiect.

Health & Safety and Risk Assessment



HEALTH & SAFETY
IECHYD A DIOGELWCH

Risk Assessment			
College/ PSU	College of Science	Assessment Date	
Location	Home-based	Assessor	
Activity	Desk-based MRes Project	Review Date (if applicable)	
Associated documents	•		

Part 1: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Display Screen Equipment	Student	Inappropriate working station set-up	Use of equipments in good working order; adjust screen at eye level, appropriate distance and brightness for the user; use of separate keyboard and mouse on a flat desk; limit use of portable devices (e.g. laptops) for short periods of time; frequently change posture and taking regular breaks from the workstation (every hour).	3	1	3	No				
Homeworking	Student	Unbalanced distribution of working and free time over the duration of	Planning work on a weekly basis and	3	1	3	No				

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
		the student's project	taking breaks throughout the day; exercising regularly and staying in contact with the line manager and research team members on a biweekly basis.								

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No

Appendix 1. Risk Matrix

		Consequences				
		1 Insignificant No injuries/ minimal financial loss	2 Minor First aid treatment/ medium financial loss	3 Moderate Medical treatment/high financial loss	4 Major Hospitalised/ large financial loss	5 Catastrophic Death/ Massive Financial Loss
Likelihood	5 Almost Certain Often occurs/ once a week	5 Moderate	10 High	15 High	20 Catastrophic	25 Catastrophic
	4 Likely Could easily happen/ once a week	4 Moderate	8 Moderate	12 High	16 Catastrophic	20 Catastrophic
	3 Possible Could happen/ happen once a year	3 Low	6 Moderate	9 Moderate	12 High	15 High
	2 Unlikely Hasn't yet happened but could happen	2 Low	4 Moderate	6 Moderate	8 High	10 High
	1 Rare Concievable but 1/100 year event	1 Low	2 Low	3 Low	4 Moderate	5 Moderate

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Abbreviations

SR: Species Richness.

FRic: Functional Richness.

FUn: Functional Uniqueness

FSp: Functional Specialization

IUCN: International Union for the Conservation of Nature.

EDGE: Evolutionary Distinct and Globally Endangered.

FUSE: Functionally Unique, Specialized, and Endangered.

Introduction

Marine megafauna comprises all large-bodied marine animals (with a body mass of >45 kg; Estes *et al.* 2016), including 334 species among marine mammals (i.e. 119 species of cetaceans, pinnipeds, sirenians, sea otters, polar bears) fishes (i.e. 202 species of chondrichthyes and osteichthyes), marine reptiles (i.e. 7 species of sea turtles), molluscs (i.e. 5 species of cephalopods and bivalves), and one species of seabird (i.e. the Emperor penguin). Altogether, these species perform important ecological roles in the oceans: they regulate trophic dynamics both as consumers of large amounts of biomass and as prey (Roman *et al.* 2014); disperse nutrients across ecosystems (Roman *et al.* 2014; McCauley *et al.* 2015); provide biogenic habitats by means of their feeding strategies, locomotion, and detritus (Roman *et al.* 2014; McCauley *et al.* 2015). Additionally, marine megafauna includes charismatic species of long-standing cultural, social, and economic importance (Mazzoldi *et al.* 2019; Malinauskaite *et al.* 2021).

The intensification of anthropogenic pressures over the last century has resulted in dramatic declines in abundance of marine megafauna (Estes *et al.* 2016; Pimiento *et al.* 2020), driving some species to local extinctions (i.e. restricted species' geographical occurrences - e.g. large pelagic fish; Worm & Tittensor, 2011) and others to ecological extinction (i.e. decreased global abundance to insufficient levels for species to have significant ecological impacts on the marine ecosystem – e.g. in kelp forests, coral reefs, and estuaries; Jackson *et al.*, 2001). Such marine defaunation has had significant repercussions on community structure and the overall functioning of marine systems (Tavares *et al.* 2019), revealing that the ongoing population decay undermines not only the diversity of marine megafauna species but also that of their ecological contributions to the stability and resilience of ecosystems.

Species' ecological contributions are dictated by their functional traits (Lefcheck & Duffy 2015). These are morphological, physiological, behavioral characteristics (e.g. body size, thermoregulation, feeding strategies) that determine how species perform in the ecosystem and respond to the environment (Diaz & Cabido 2001). Quantifying the diversity of functional traits in a species assemblage (i.e. functional diversity) allows to appreciate the ecological properties of the community and its impact on ecosystem processes (Gagic *et al.* 2015; Lefcheck & Duffy 2015; Duffy *et al.* 2016). To describe the functional diversity of a

community, species are located in a functional trait space, whose axes represent traits (Mouillot *et al.* 2013). Within this trait space, the total variety of the community's functional abilities can be quantified by assessing the range of trait modalities that the given community presents – i.e. functional richness (Villéger *et al.* 2008).

By differentiating species of a given community according to their trait combinations, functional diversity accounts for the fact that species may overlap in their traits (that is, they are functionally redundant; Diaz & Cabido, 2001). Functional redundancy is an important aspect of biodiversity, as a greater number of ecologically similar species buffers against taxonomic loss (and thus loss of species' ecological contributions) over time and space, so that ecosystem functioning is maintained (Walker 1992; Yachi & Loreau 1999; Loreau 2004).

Furthermore, functional diversity allows to assess how individual species contribute to the diversity of traits in a given community and identify those that perform unique or highly specialized ecological functions that add to and support diversity. Species expressing unique trait combinations (i.e. functionally unique) perform functions that are vulnerable to taxonomic loss because they cannot be compensated or replaced by other species (Mouillot *et al.* 2013; Griffin *et al.* 2020; Pimiento *et al.* 2020); species with extreme trait combinations (i.e. functionally specialized) importantly define the range of trait diversity of the community (Mouillot *et al.* 2013; Griffin *et al.* 2020; Pimiento *et al.* 2020). Hence, assessing functional diversity allows to estimate the functional contributions of individual species and communities to ecosystems and develop appropriate approaches to protecting biodiversity by identifying those species assemblages whose functional integrity is most vulnerable to taxonomic loss.

While species diversity has often been considered in assessing ecosystem integrity and guiding conservation efforts, a recent interest in preserving species' ecological contributions has advocated for integrating functional diversity in conservation planning (Devictor *et al.* 2010; Cadotte *et al.* 2011). Biodiversity hotspots – i.e. areas representing exceptional concentration of biodiversity under exceptional levels of threats (Myers *et al.* 2000) – have been considered as cost-effective strategies to target conservation investments to areas encompassing great species richness, endemism, and hosting species with high vulnerability to extinction (Brooks *et al.* 2006; Jenkins *et al.* 2013). However, such areas have been traditionally prioritized according to their representation of taxonomic diversity, thus overlooking species' contributions to ecosystem functioning (Reiss *et al.* 2009; Cardinale *et*

al. 2012). Spatial mismatch between attributes of biodiversity has been previously documented in multiple natural systems, both terrestrial (Devictor *et al.* 2010), and aquatic (marine (Albouy *et al.* 2017) and freshwater (Strecker *et al.* 2011)), and studies have demonstrated that taxonomic-only approaches to conservation planning leave functionally diverse areas unprotected (Parravicini *et al.* 2014; Brum *et al.* 2017). Integrating assessment of spatial patterns of functional diversity with species diversity is therefore needed to (i) assess to what extent areas prioritized for species diversity capture functional diversity, and (ii) identify single-faceted biodiversity hotspots (i.e. areas only rich in species or functional diversity) for preserving not only the persistence of species but also their ecological functionality.

Given the limited resources available to invest in conservation programs and the increasing numbers of threatened species due to fast-paced rate of biodiversity loss, recent efforts have been made into devising tools to identify species of high conservation priority based on their individual contributions to biodiversity facets and their extinction risk (Isaac *et al.* 2007; Hidasi-Neto *et al.* 2015). The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species has proven to be a valuable tool for conservation planning (Rodrigues *et al.* 2006) by assessing species' endangerment status and providing their current geographical distributions. While this information has been previously combined with species' evolutionary distinctiveness to identify species that are "evolutionary distinct and globally endangered" (EDGE; Isaac *et al.* 2007) and map conservation priority sites encompassing unique evolutionary history (Stein *et al.* 2018), the functional roles of threatened species have started to be considered in conservation prioritization setting only recently. A novel prioritization index, the FUSE index (Functionally Unique, Specialized, and Endangered) has been proposed, which quantifies species' individual contributions to functional diversity and combines it with their extinction risk (Griffin *et al.* 2020; Pimiento *et al.* 2020). To prevent the loss of vulnerable species that play important roles in maintaining ecosystems stable and resilient, effective conservation actions demand for knowledge of such species' spatial distribution so to identify areas of highest priority for preserving their ecological functionality.

As one-third of marine megafauna species is threatened due to intensive anthropogenic pressures (Estes *et al.* 2016; Pimiento *et al.* 2020), and a recent study has warned that their

ecological functioning in the ecosystem may be significantly degraded if the current trajectories of population declines are not counteracted (Pimiento *et al.* 2020), assessing the global distribution of their biodiversity attributes and identifying the locations where conservation efforts should be prioritized is therefore crucial to protect their currently threatened ecological contributions to the ecosystem.

In this study, I specifically aimed to:

- (i) assess the spatial distribution of marine megafauna biodiversity in terms of species and functional richness;
- (ii) examine the spatial relationship between functional and species richness and the extent of spatial overlap between their respective hotspots;
- (iii) assess the geographic patterns of the FUSE index and the components of this metric (functional uniqueness, functional specialization, and endangerment);
- (iv) identify hotspots of exceptional functional richness of marine megafauna and hotspots harbouring the greatest richness of the most functionally important and endangered species (i.e. high-FUSE species).

To achieve these goals, I assessed the geographic distributions of taxonomic and functional diversity of marine megafauna in 1° x 1° grids. The spatial patterns of hotspots of species and functional richness were further explored to identify hotspots of exceptional functional diversity. Then, metrics of functional diversity and species' geographic distributions were further combined with IUCN status to compile the FUSE index and locate areas of conservation priority.

Methods

This study's analyses were performed in the R environment (R Core Team 2020).

Functional traits, threat status and spatial data

The main ecological characteristics of marine megafaunal species were outlined using a set of 10 functional traits (i.e. maximum body mass, thermoregulation, terrestriality, habitat zone, vertical position, migration, feeding mechanism, diet, breeding site, and group

size/sociality), while their imperilment was expressed according to their IUCN Red List status. The functional traits and the threat status of these species were gathered from Pimiento *et al.* (2020).

Species' geographic distributions were available from the IUCN Red List of Threatened Species (IUCN 2021; last accessed in March 2021) for 295 of the 334 species of marine megafauna. The IUCN database provides range maps (in the format of shapefiles), which outline polygon areas enclosing all known extant, possibly extant, possibly extinct, and extinct occurrences for each species. As such, these maps assume species are uniformly distributed within their extent of occurrences (IUCN 2021). This study focused only on records of species' extant and possibly extant occurrences. To assess the spatial patterns of marine megafaunal functional diversity, a grid cell presence-absence matrix was generated using a resolution of 1° of longitude by 1° of latitude. To do so, I used the “lets.presab” function from the letsR package (Vilela & Villalobos 2015).

Functional space

The global marine megafauna functional space was built based on the 295 species from which spatial data was available (see above). First, a trait distance matrix was created to assess the functional dissimilarity between species based on their trait combinations. Species' dissimilarities were measured as pairwise functional distances using a generalization of Gower's distance (Pavoine *et al.* 2009), which treats different types of functional traits (coded as continuous, ordinal, nominal, and binary variables) and weighs each function equally (Maire *et al.* 2015). This matrix was generated with the function “dist.ktab” from the ade4 package (Dray & Dufour 2007) and laid the basis for building the trait space (Mouillot *et al.* 2013), where species dissimilarity was decomposed along axes representing traits and extracted from a Principal Coordinate Analysis (PCoA) using the function “pcoa” from the package ade4 (Dray & Dufour 2007). **Table S1** lists what traits each of the PCoA axes was most correlated to. To find the dimensionality of the functional space that best described the functional properties of the species assemblage (i.e. the functional space that faithfully represented species' initial functional trait values and correctly positioned species between each other), I calculated the mean squared deviation between species' distances originally measured in the dissimilarity matrix and their distances in the functional space (Maire *et al.* 2015). The mean squared deviation index (mSD) was estimated for each possible dimensionality of the functional space (from 2 dimensions - the

minimum number of traits required to build a functional space – to 10 dimensions - the total number of traits considered in the study): an eight-dimensional functional space resulted to best represent the marine megafaunal functional composition (mSD= 0.002).

However, the final functional space was built with 4 dimensions, which were selected based on the elbow inflection point for the mSD index (**Figure S1**). The elbow method – a common method used in dimensionality analyses (Nguyen & Holmes 2019; Mouillot *et al.* 2021) allowed to identify the number of PCoA axes representing the most parsimonious balance between maximising the space's quality (in terms of representativeness) and minimizing its dimensions (the quality difference between an 8-dimensional and 4-dimensional functional trait was 0.003).

Assemblage-based metrics

For each grid cell, I computed species richness (SR; number of species) and functional richness (FRic; proportion of the space volume occupied (Villéger *et al.* 2008), where the total space is that of the global functional space; see above). Because FRic could only be expressed for those communities with at least one more species than the number of PCoA axes of the functional space (Villéger *et al.* 2008), the functional diversity analysis was conducted only on those cells with 5 or more species (N = 39,867 out of the original N = 52,114). Four species of marine megafauna only occurred in the discarded cells (*Acipenser transmontanus*, *Arius gigas*, *Atractosteus spatula*, *Rita rita*), which were excluded from the analysis.

Additionally, I quantified functional uniqueness (FUn; the mean distance of each species to its five nearest neighbors (Pimiento *et al.* 2020)) and functional specialization (FSp; the Euclidean distance of each species to the centroid of the functional space (Mouillot *et al.* 2013; Griffin *et al.* 2020; Pimiento *et al.* 2020). These were both estimated at the species level first and then expressed as the mean score per grid cell based on the individual scores of the species occurring per cell.

Similarly, I assessed the extinction risk per species and averaged scores per grid cell according to species' occurrences. Species' extinction risks were calculated as probabilities extrapolated from the IUCN Red List categories of species' imperilment as in Davis *et al.* (2018) (**Table 1**). Finally, all species assemblage-level metrics were mapped.

Table 1. Extinction probabilities extrapolated from IUCN Red List categories from Davis *et al.* (2018). Probabilities are reported for two extinction timescales. IUCN Red List acronyms: LC = least concern; NT = near threatened; VU = vulnerable; EN = endangered; CR = critically endangered.

IUCN Category	Extinction Probabilities	
	50 years	100 years
CR	0.969	0.999
EN	0.428	0.672
VU	0.051	0.100
NT	0.007	0.014
LC	0.001	0.002

FUSE index

The FUSE index was estimated at the species level as follows:

$$\text{FUSE} = \text{FUGE} + \text{FSGE}$$

where

$$\text{FUGE} = \ln(1 + \text{FUn} * \text{GE})$$

and

$$\text{FSGE} = \ln(1 + \text{FSp} * \text{GE})$$

Species' FUn and FSp were standardized (between 0 and 1) and global endangerment (GE) expressed as species' extinction risk. While IUCN threat categories don't assume differences in the extinction risk between ranks, extinction probabilities account for the non-linearity of the extinction risk between them (Mooers *et al.* 2008; Davis *et al.* 2018) and were therefore considered more appropriate for estimating the FUSE index (Griffin *et al.* 2020). This study compiled the FUSE index under two extinction scenarios, assessing species' ranking order according to extinction probabilities in 50-years-time and 100-years-time.

High-FUSE species were identified as those with index scores falling within the highest quartile of FUSE scores' distribution (hereafter referred to as top 25% FUSE species). To assess the spatial distribution of the FUSE index, I mapped the mean FUSE score per grid cell based on the individual scores of the species occurring per cell.

Hotspots

First, I assessed the spatial relationship between SR and FRic by computing their coefficient of correlation. To account for spatial autocorrelation in both variables and the consequential likelihood of inflating Type-I statistical error rates (Legendre & Legendre 1998), the correlation significance was assessed by using Dutilleul's correction of degrees of freedom implemented in the function "modified.ttest" from the SpatialPack package (Osorio *et al.* 2016). Since SR can intrinsically affect FRic (because of sampling effect, FRic is expected to increase with more species in the community; Vileger *et al.*

2008), geographical patterns of FRic were disentangled from the spatial gradient of SR by mapping the residuals of the linear regression of FRic on SR, so to identify locations where FRic deviated from expectations (i.e. from the line of best fit). This model did not account for spatial dependence between samples (i.e. grid cells) for capturing the underlying biogeographical processes governing diversity and its distribution.

Hotspot cells were defined as the 2.5% of the richest cells for FRic and SR (David *et al.* 2005; Albouy *et al.* 2017). The spatial congruence between FRic and SR was calculated as the proportional overlap between FRic and SR hotspots as O_o/O_{max} , where O_o was the observed number of overlapping cells and O_{max} was the maximum number of cells that could overlap, calculated as the smaller of the pair of hotspot sets (Prendergast *et al.* 1993).

Hotspot cells harboring the greatest number of high-FUSE species were identified by estimating the richness of the top 25% FUSE species per grid cell and considering the richest 2.5% of these cells. The spatial congruence between richness hotspots of all marine megafauna species and those of the top 25% FUSE species was further assessed according to the proportional overlap outlined above.

Complementary analysis

Because realm-crossing traits (e.g. movements between marine and terrestrial/freshwater habitats) and association with coastal habitats are over-represented by certain taxa (Pimiento *et al.* 2020), the functional diversity and spatial analyses were replicated with a subset of traits that consisted exclusively of marine modalities to assess species' functional contributions to marine-only ecosystems. To do so, the functional space was built excluding

traits of terrestriality, migration, and breeding site. For marine-only traits, the best functional space was also built with 4 dimensions (**Figure S1** and **Table S1**).

Results

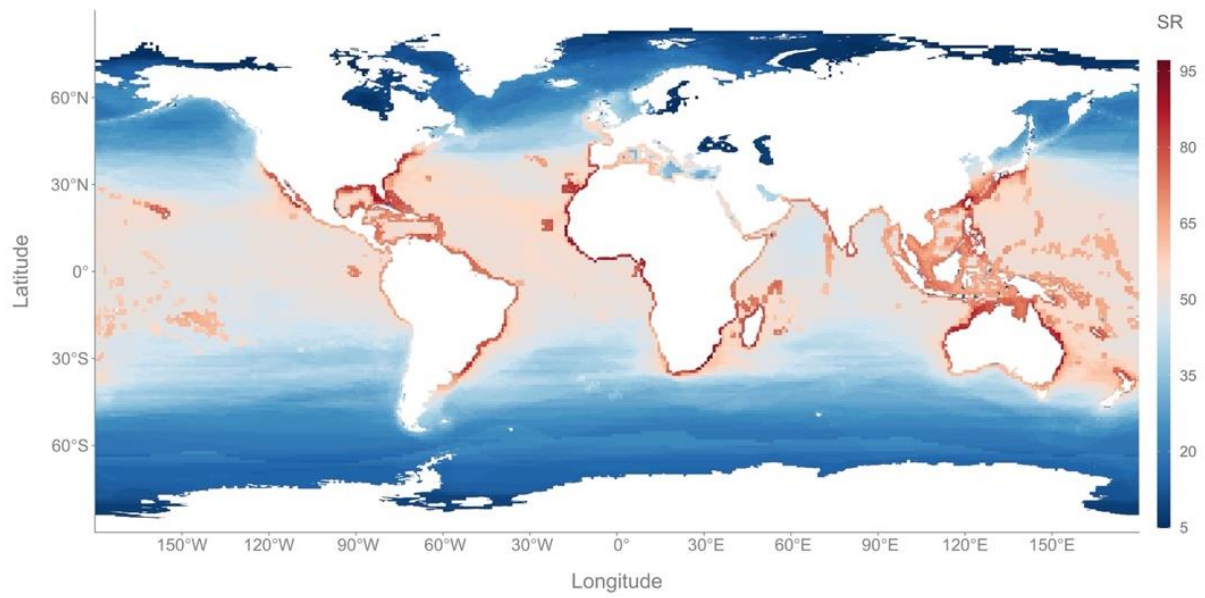
Spatial distribution of species and functional richness

I found a latitudinal gradient in SR along coastal and oceanic waters (**Figure 1(a)**). Regions of high species diversity ranged between 40 degrees North and South to the equator: these peaks (holding more than 73 species per cell, representing between 22 and 29% of all marine megafauna) were distributed along the Atlantic continental shelves, South-East Africa, the Eastern Indian subcontinent, Japan, China, the South-West Pacific, Australia, New Zealand, the Hawaii, Galapagos, and the Pacific coast of USA and Mexico. Polar waters recorded the lowest species diversity (harboring between 5 and 31 species per grid cell, which represent up to 9.3% of the marine megafaunal assemblage), together with the Black and Caspian Seas, as well as Hudson Bay, Canada.

High FRic was restricted along continental shelves, with more localized peaks (where species assemblages occupied more than 30% of the functional space) along the Pacific coasts of North, Central, and South America, the Atlantic waters of Northern USA and British Isles, West-central and South-eastern Africa, and the Indo-Australian Archipelago (**Figure 1(b)**). Lower FRic (accounting for less than 10% of the functional space) stretched from the poles to the open water of North and South Atlantic, Pacific, and Indian Oceans.

When only marine functional traits were considered in the analysis, FRic concentrated in both coastal and oceanic waters between 30 degrees North and South to the equator and peaked in the South-West Indian and South-West Pacific oceans (**Figure S2**).

(a)



(b)

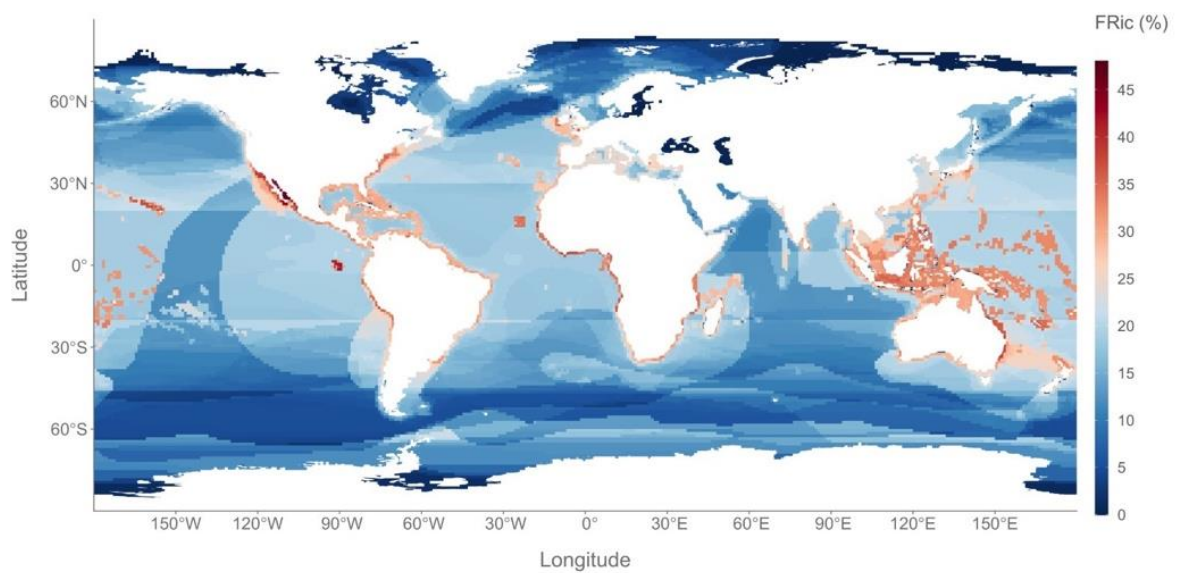


Figure 1. Global map of (a) species richness (SR) and (b) functional richness (FRic) for marine megafauna. SR is expressed as the number of species present per $1^\circ \times 1^\circ$ grid cell; FRic is measured as the volume of the functional space occupied by the species assemblage of each grid cell and expressed as a percentage.

Spatial relationship between species and functional richness and their hotspots

FRic and SR were positively and significantly correlated (based on all traits: $r = 0.846$, p -value < 0.001 ; based on marine-only traits: $r = 0.936$, p -value < 0.001). They showed a linear relationship, although variability of FRic increased along the SR gradient (**Figure 2**).

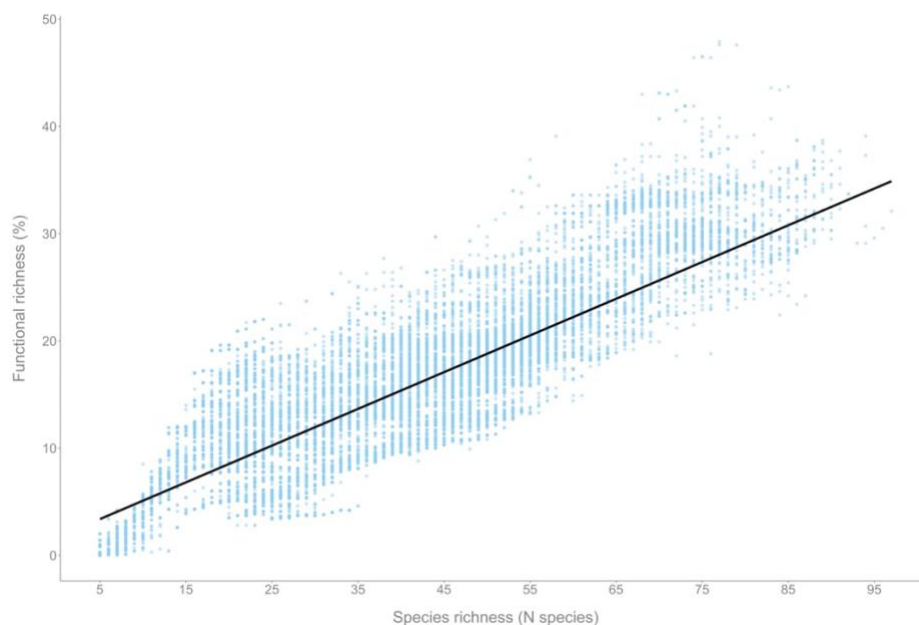


Figure 2. Relationship between species richness and functional richness (expressed as percentage) of marine megafauna. Each point represents data for a single $1^\circ \times 1^\circ$ grid cell. The figure displays the line of best fit computed by the linear model in black (slope \pm SE = 0.342 ± 0.001 , $F_{1, 39865} = 0.00001$). The linear model did not account for spatial autocorrelation of the data. The large sample size due to the lack of correction for dependence among observations resulted in very small confidence intervals overlapping the line of best fit.

When the residuals of the linear relationship between FRic and SR were mapped, areas showing a positive deviance of FRic from the expected values (i.e. the line of best fit) ranged from as far North as the Bering and Greenland Seas to the Southern Ocean (**Figure 3**). Although waters at high latitudes (North Pacific, North Atlantic, and Southern Oceans) hosted the least diverse megafaunal assemblages (**Figure 1(a)**), their faunal composition was responsible for occupying between 5 to 15% more volume of the functional space than what would be expected based on their species richness. Positive deviation of FRic from expectations also extended to more species-rich coastal regions of the Pacific Ocean at tropical and equatorial latitudes. Overall, Baja California, the Galapagos Islands, and the

British Isles showed the greatest deviation, with species occupying up to 20% more volume of the functional space. Regions of negative FRic deviance (harboring species assemblages that occupied up to 10% less volume of the functional space than expected) concentrated in pelagic waters of the Indian, Pacific, North and South Atlantic oceans, as well as at polar latitudes.

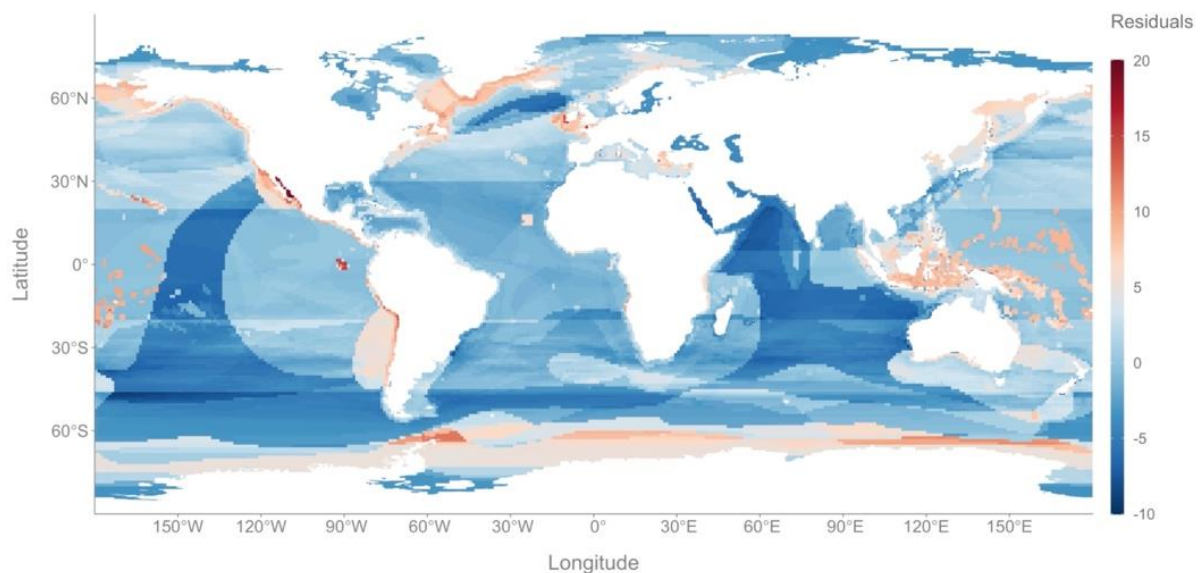


Figure 3. Global map of residuals from the linear regression of functional richness (FRic) on species richness (SR).

The spatial hotspot congruence analysis revealed that FRic and SR hotspots including 2.5% of their richest cells overlapped by 34.5% (**Figure 4**). These multifaceted hotspots (i.e. congruent hotspot cells between SR and FRic) were not uniformly distributed but rather scattered along the coasts of United States (Hawaiian archipelago included), Mexico, the Galapagos Islands, Venezuela, Brazil, from Mauritania to Angola and from South Africa to Kenya, Japan, the Philippines, Malaysia, Indonesia, Papua New Guinea, Australia, New Caledonia, and New Zealand.

The remaining hotspot cells were idiosyncratic to individual components of biodiversity: SR hotspots extensively stretched along the coasts of the Atlantic Ocean, Eastern Africa,

Western Indian subcontinent, Japan, and West Australia; FRic hotspots mainly concentrated in the waters of the South-West Pacific but also spread along the coasts of California, Central America, Peru, Chile, Tanzania, Polynesia, Greece, and off the British Isles.

Notably, coastal regions of Baja California and the Galapagos, for which we recorded the greatest deviance between observed and predicted FRic values, also resulted as hotspots for both variables, while the coastal waters of the British Isles remained single-faceted FRic hotspots. Hotspots of SR and FRic based on marine-only traits overlapped by 49%: multifaceted hotspots extended to the Gulf of Mexico, along the Atlantic coast of North Africa up to the Iberian Peninsula, and to both South-West and South-East Indian Ocean; the South-West Pacific remained a major single-metric hotspot for FRic but no FRic hotspots were found either on the Pacific coast of the American continents or off the British Isles (**Figure S3**).

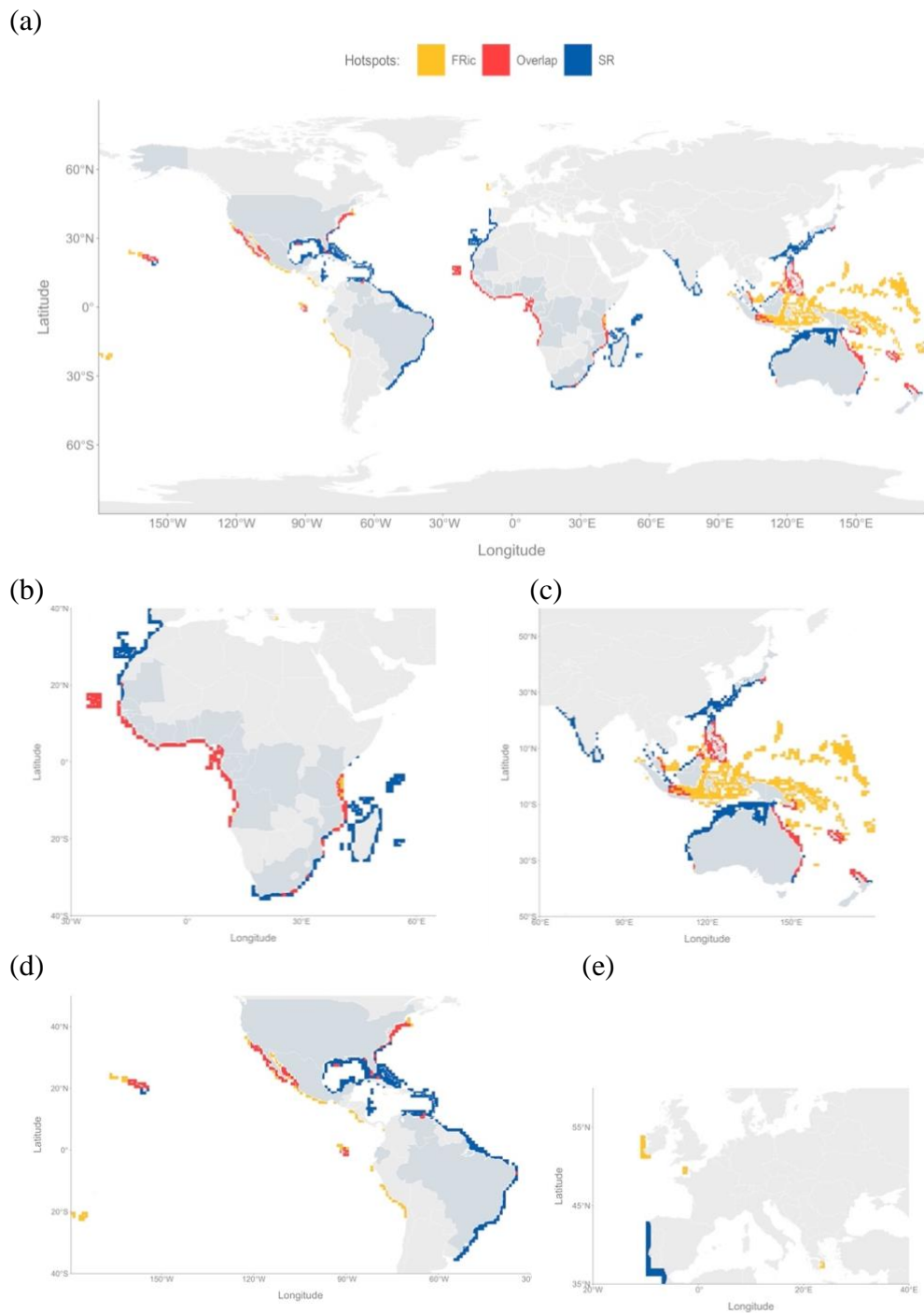


Figure 4. Map of the hotspots congruence and incongruence between functional richness (FRic) and species richness (SR) of marine megafauna. Map (a) displays the global distribution of hotspots, while the remaining maps enlarge the hotspots distribution along the coasts of (b) Africa, (c) Asia, (d) Americas, and (e) Europe. Hotspots for each variable were defined as the richest 2.5% cells. Red cells indicate multifaceted hotspots (i.e. congruent hotspot cells between SR and FRic) and the countries of their jurisdiction shaded in dark grey. Blue and yellow cells are single-faceted hotspots of SR and FRic, respectively.

Spatial patterns of FUn, FSp, extinction probabilities, and the FUSE index

Mean FUn per grid cell was highest at polar and northern temperate latitudes (North Pacific, North Atlantic, and Mediterranean Sea; mean FUn > 0.30).

Mean FSp per grid cell was consistently high across the oceans, with the Southern and Arctic Oceans, Hudson Bay and Caspian Sea holding the greatest mean FSp per grid cell (mean FSp > 0.50; **Figure 5(b)**).

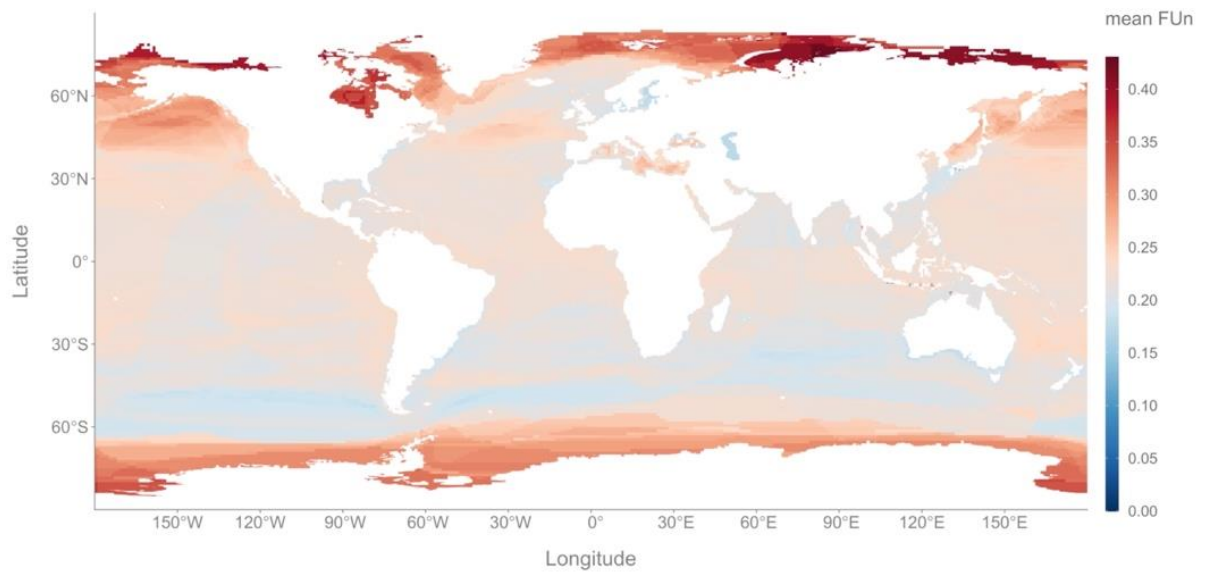
While mean FUn displayed similar spatial distributions under both trait sets (**Figure S6(b)**), mean FSp computed with marine-only traits was also high across oceans (peaking in the Southern Ocean, South Pacific, and North Atlantic from up to Svalbard and the Barents Sea) but dropped at very high arctic latitudes (above 70 degrees North the equator; **Figure S7(b)**).

The spatial patterns of species' extinction probabilities per grid cell resulted highest in the Caspian Sea and Gulf of Mexico: (**Figure 5(c)**): the faunal assemblage in the Caspian Sea had on average 70% chance of going extinct in the next 50 years, whereas those of the remaining water bodies showed a mean extinction probability of 20%.

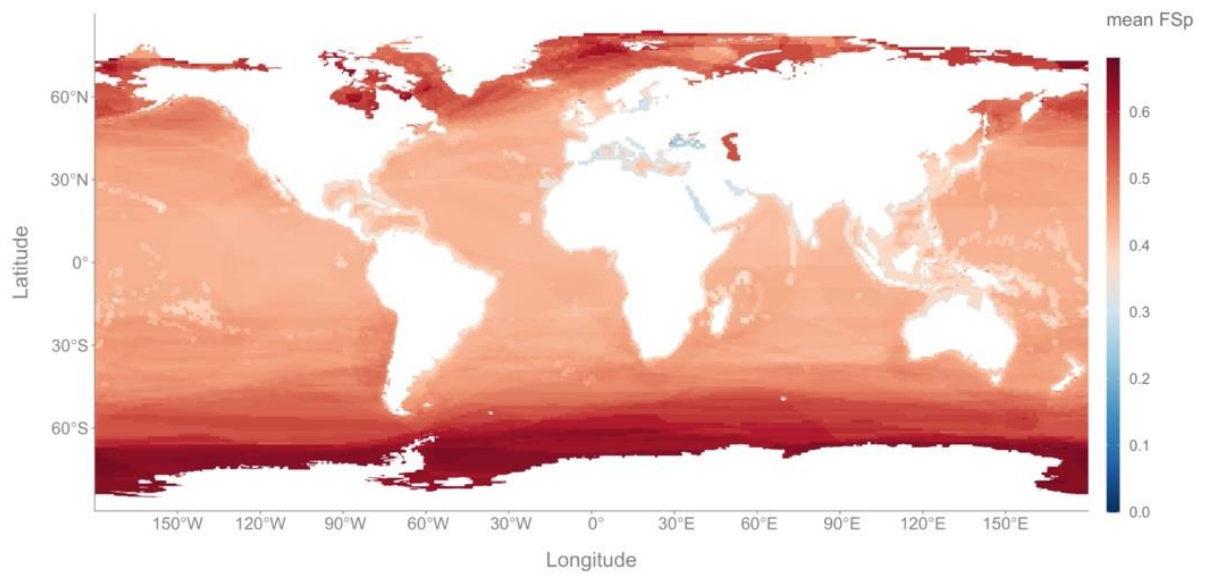
The overall patterns of mean FUSE per cell based on 50-years-time extinction probabilities mirrored those of species' extinction probabilities: scores peaked in the Caspian Sea and in a small region of the Gulf of Mexico (mean FUSE index per cell = 0.38, **Figure 5(d)**), while they remained homogeneously low elsewhere (ranging between 0 and 0.10).

FUSE index computed with marine-only traits displayed similar patterns, although regions in the North Atlantic, North and South-East Pacific, and South-East Indian oceans showed a higher average FUSE scores per cell (**Figure S5**). Despite a rearrangement of species' order, the distribution of mean FUSE index based on 100-years extinction probabilities remained constant (**Figure S4**).

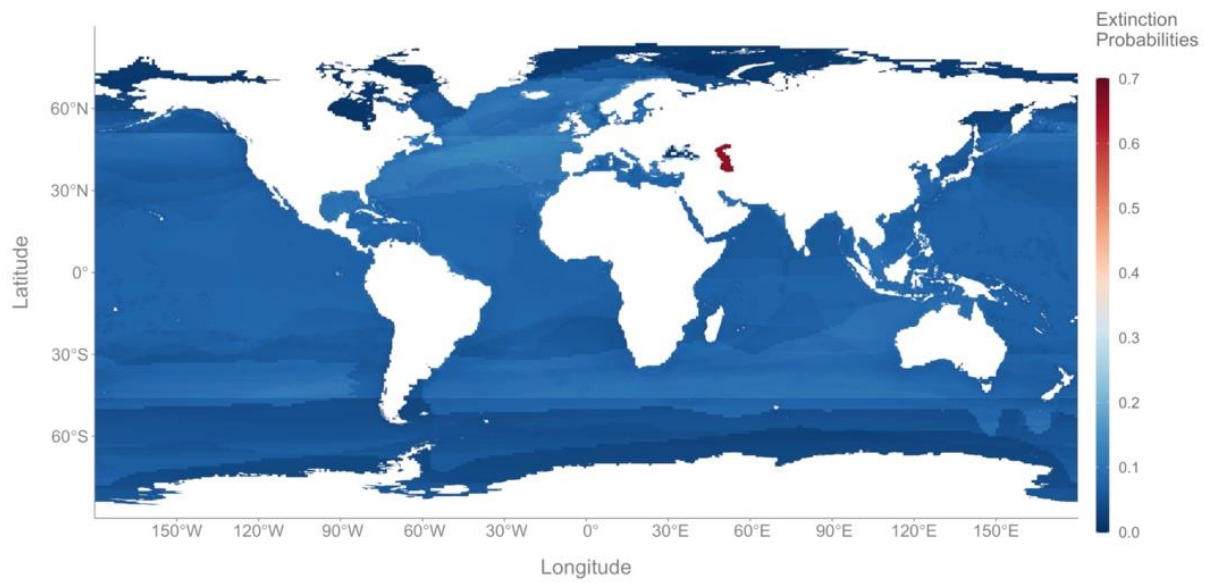
(a)



(b)



(c)



(d)

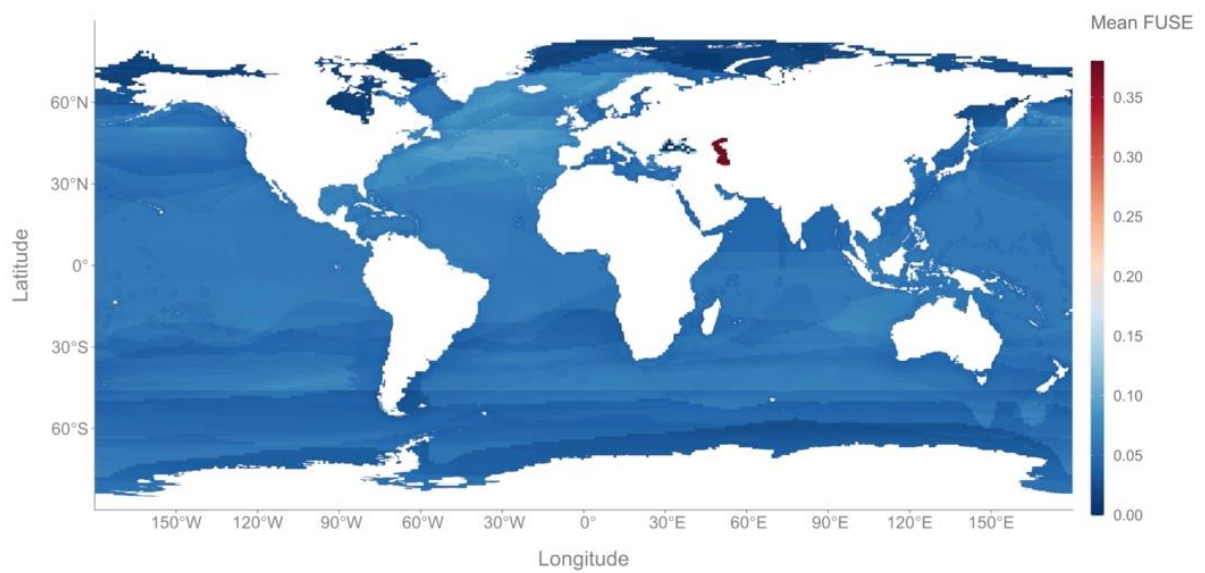


Figure 5. Global map of mean FUSE and its components: (a) Functional uniqueness (FUn), (b) functional specialization (FSp), (c) extinction probabilities, (d) FUSE index. FUSE index and all other metrics are expressed as the mean of the species-level scores present per cell.

Spatial patterns of the top 25% FUSE species and their richness hotspots

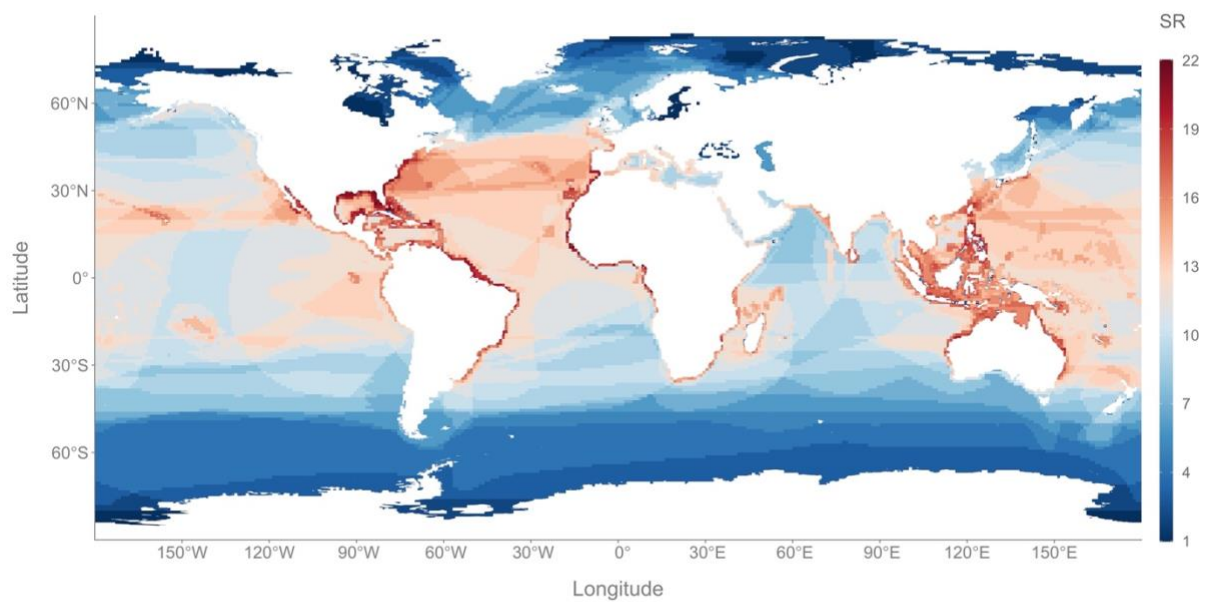
The coastal waters from mid temperate to tropical latitudes harbored the greatest numbers of top 25% FUSE species (**Figure 6(a)**). These patterns reflected the spatial distribution of marine megafaunal SR (**Figure 1(a)**) but diverged from that observed for the average FUSE index per grid cell (**Figure 5(a)**): while the coasts of Gulf of Mexico also showed richness in numbers of high-FUSE species, the species-poor region of the Caspian Sea (**Figure 1(a)**) harbored the lowest number of species of conservation priority (**Figure 6(a)**).

The congruence between patterns of richness of all marine megafauna species and that of top 25% FUSE species was further confirmed by their hotspots overlap. Locations richest in species of marine megafauna and high-FUSE species overlapped by 59% along the continental shelves of Baja California, Hawaii, Galapagos Islands, the Atlantic coasts of the American continent and from the Iberian Peninsula to Angola, South and South-east Africa, North-west India, Sri Lanka, Japan, China, Taiwan, the Philippines, Australia, and South-west Pacific (**Figure 6(b)**).

Distributions of the remaining hotspots mostly diverged off the coast of Northern USA, along the Pacific coast of Central and South America, in the Azores, in the Bay of Biscay, and the Indo-Pacific triangle, where the major richness hotspots of top 25% FUSE species were found (**Figure 6(b)**). Since the top 25% FUSE species subset based on either 50 or 100-years extinction scenarios remained the same, conservation priority locations remained unvaried under the two timescales.

When the hotspots overlap analysis was repeated with marine-only traits, the top 25% FUSE species subset slightly varied according to the timescale of species' extinction probabilities: richness hotspots were congruent by 62% under 50 years-time extinction scenario and increased up to 70% under 100 years-time extinction probabilities.

(a)



(b)

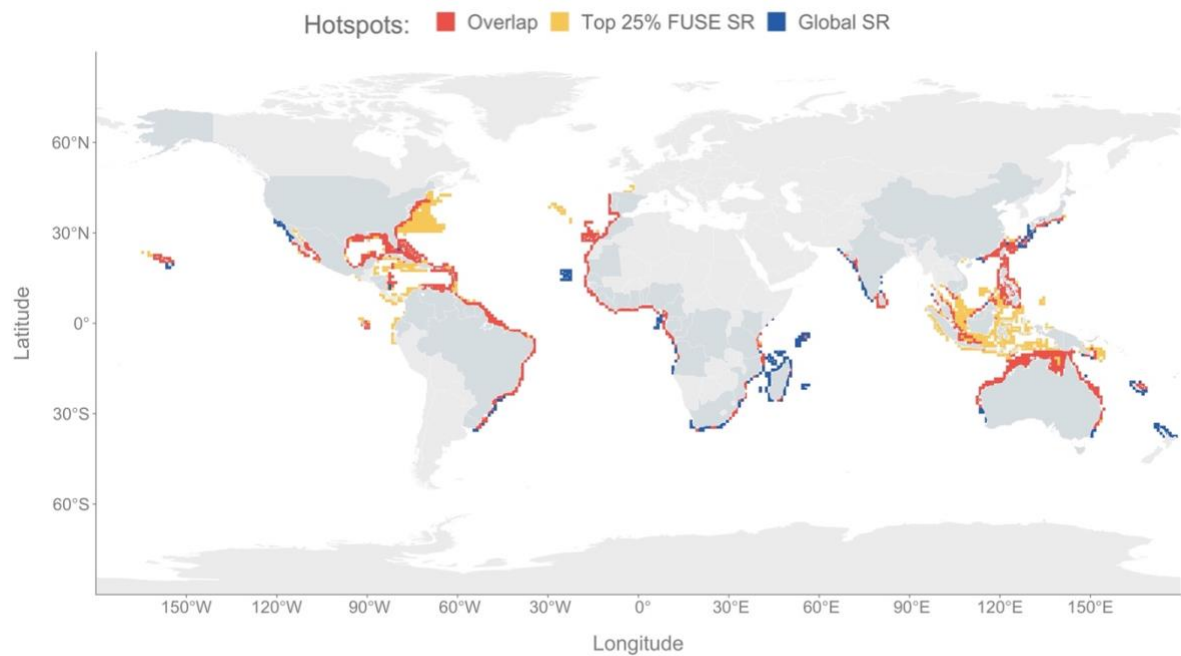


Figure 6. Spatial patterns of top 25% FUSE species: (a) global map of top 25% FUSE SR expressed as the number of species present per 1° x 1° grid cell; (b) map of the hotspot congruence and incongruence between marine megafaunal SR and top 25% FUSE SR. Red cells indicate multifaceted hotspots (i.e. congruent hotspot cells between marine megafaunal SR and top 25% FUSE SR) and the countries of their jurisdiction are shaded in dark grey. Blue and yellow cells are single-faceted hotspots of marine megafaunal SR and top 25% FUSE SR, respectively.

Discussion

The results showed that the species richness of marine megafauna followed a common latitudinal gradient from polar to tropical latitudes, concentrating along continental shelves, where the functional richness was also highest (**Figure 1**). Interestingly, patterns of high functional richness extended to oceanic waters when marine-only traits were considered (**Figure S2**), suggesting a broader geographical distribution of megafaunal assemblages performing highly diverse functional roles related to marine systems only.

The similar spatial repartition of functional and species richness was confirmed by their positive, linear relationship (**Figure 2**). However, local variation in their relationship was recorded at polar, temperate, tropical, and equatorial latitudes (**Figure 3**). The hotspots overlap analysis resulted in a marginal congruence between SR and FRic hotspots and highlighted the South-West Pacific as a major hotspot idiosyncratic to FRic (**Figure 4**). Spatial assessment of the FUSE index showed the Caspian Sea and Southern Gulf of Mexico as the locations of highest conservation priority (**Figure 5(d)**). These only partially corresponded to areas harboring the greatest richness of high conservation priority species: the top 25% FUSE species tended to aggregate in species-rich, coastal waters of the Gulf of Mexico, Caribbean Sea, Atlantic, Pacific, and Indian Oceans (**Figure 6(b)**).

Previous theoretical and empirical studies investigating the relationship between species and functional diversity across natural systems have described a variety of shapes (ranging from linear to asymptotic curves; Díaz & Cabido 2001; Naeem & Wright 2003; Mayfield *et al.* 2005; Micheli & Halpern 2005; Halpern & Floeter 2008) and strength (from strongly to weakly positive; Lucifora *et al.* 2011; Parravicini *et al.* 2014; Albouy *et al.* 2017). Although the nature of this relationship appears to be very context-dependent (it is influenced by the functional redundancy of the natural systems under investigation, the number and identity of functional traits evaluated, and the metric chosen to describe functional diversity; Cadotte *et al.* 2011), the association between species and functional richness found in this study (Figure 2) is one of the strongest and linear observed across taxonomic groups, suggesting a high degree of trait complementarity among species of marine megafauna and an overall low functional redundancy. While theoretical and empirical results show that the former confers greater variation in species responses to environmental changes, thus maintaining ecosystem functioning in the long-term (Díaz & Cabido 2001), the latter has been predicted to

undermine the functional stability of ecosystems in case of species loss (Fonseca & Ganade 2001; Rosenfeld 2002; Guillemot *et al.* 2011). However, there was variability around this linear trend. The megafaunal assemblages of Baja California, the Galapagos Islands, the British Isles, and polar regions were highlighted as unexpectedly functionally rich areas relative to the number of species present (**Figure 3**). Most worryingly, the megafaunal communities at polar latitudes were also found to host the greatest functional uniqueness and specialization across the globe, which, combined with their low species diversity, warns about their low functional redundancy. In case of species extinctions, these ecosystems may face severe functional loss. A recent study forecasting the impacts of marine megafaunal species extinctions on functional diversity has, in fact, identified polar regions as particularly vulnerable to the loss of specialized and unique species, predicting reductions of functional richness (up to 49% in the Southern Ocean, and 70% in the Arctic Ocean) and increases in functional uniqueness (between 9% in the Southern Atlantic and 33% in the Southern Ocean), respectively (Pimiento *et al.* 2020). Conversely, megafaunal communities in the Indian, Pacific, North and South Atlantic oceans showed smaller ranges of functional trait diversity according to their species richness (**Figure 3**). Although such trend would be indicative of higher functional redundancy (i.e. with more species supporting similar functions), these systems may not be functionally stable and remain vulnerable to changes in species composition, as empirical evidence suggests that species may over-represent only few trait combinations (i.e. redundancy may be trait-biased) and leave others without functional insurance (Halpern & Floeter, 2008; Mouillot *et al.* 2014; Parravicini *et al.* 2014). The functional redundancy patterns observed in this study therefore stress the importance that preserving species richness of marine megafaunal assemblages may have in maintaining the multiple functions they perform in the ecosystem.

This study showed that setting conservation priority areas based on hotspots of species diversity alone would be insufficient for safeguarding the ecological contributions of marine megafauna to the ecosystem, and that larger protection areas should be considered.

The linear relationship between SR and FRic would suggest a similar spatial repartition of their high values, thus that their hotspots would largely overlap. However, the scatter of FRic around the gradient of SR resulted in these two metrics overlapping only marginally (**Figure 4**). The South-West Pacific was highlighted as a major hotspot of functional but not of species richness of marine megafauna. This region has been previously identified as a global

biodiversity hotspot (Roberts *et al.* 2002; Tittensor *et al.* 2010) and a conservation priority area for its high species richness, endemism, and number of threatened species (Asaad *et al.* 2018). It has also been described as a center of coral reef fish (Mouillot *et al.* 2014; Parravicini *et al.* 2014) and sharks' (Lucifora *et al.* 2011) functional diversity. However, studies have shown that the functional integrity of these systems are highly vulnerable to anthropogenic stressors, such as fishing (D'agata *et al.* 2016). Chondrichthyan species, in particular, are severely threatened by fisheries' bycatch and destructive practices (Stevens *et al.* 2005), and extinction projections have predicted that the range of functions they perform may be critically reduced in the near future (Pimiento *et al.* 2020). 2000 Marine Protected Areas (MPAs) have been designed and implemented to maintain and protect this diversity-rich region (White *et al.* 2014) but they have been found to under-represent ecological diversity and lack enforcement (Weeks *et al.* 2014; White *et al.* 2014). The limited functional redundancy of marine megafauna observed in this study, together with the documented functional vulnerability of the South-West Pacific to anthropogenic activities, urge to target conservation actions to this region. Additionally, the overall concentration of both FRic and SR hotspots along coastlines, where the greatest cumulative impact of anthropogenic activities has been recorded (Halpern & Floeter 2008), additionally alerts to the exposure of the richest and most diverse coastal communities to severe threats in lack of adequate protection.

Marine megafaunal assemblages inhabiting the coast of the Gulf of Mexico and the Caspian Sea consisted, on average, of species with high conservation priorities according to FUSE index (**Figure 5(d)**). The Caspian Sea harbours valuable commercial species of sturgeons that have undergone severe declines due to overfishing and illegal catch (Pourkazemi 2006). It is also inhabited by a key predator of the Caspian ecosystem, the Caspian seal (*Pusa caspica*), whose population abundance has heavily decreased in response to bycatch, poaching, and loss of breeding habitat due to extractive activities and global warming (Harkonen *et al.* 2012). The coastal system in the Gulf of Mexico is inhabited by species equally threatened by anthropogenic activities. Sea turtles and sawfish are particularly exposed to extractive activities, vessel strikes, pollution, and bycatch (Dulvy *et al.* 2014; Lamont & Johnson 2021) that concentrate in the neritic and estuarine habitats of these species. Notably, these species' use of benthic habitats in the coastal shelf and movements across the marine and terrestrial realms have been predicted to be particularly vulnerable to extinction (Pimiento *et al.* 2020). Given the overall functional importance and degree of endangerment of the species

assemblages found at these locations, prioritizing conservation investments to these regions would greatly benefit all the local megafaunal species.

While priority hotspots based on their representation of the top 25% FUSE species (i.e. species of highest conservation priority according to their functional importance and endangerment status) were identified along the coasts of the Gulf of Mexico, none was found in the Caspian Sea. More than half of the regions harboring the greatest richness of high conservation priority species were found in the most species-rich waters, indicating that conservation actions targeting areas of highest marine megafaunal species richness would also moderately protect species of functional importance (**Figure 6(b)**). The fact that the South-West Pacific also resulted as an aggregation center of marine megafaunal species of conservation priority, as well as a FRic hotspot, stresses the functional importance of the species assemblages inhabiting this region and therefore the need to be the target of conservation actions for safeguarding the future of marine megafaunal diversity. However, the diverging spatial patterns observed between areas harboring high mean FUSE species assemblages and areas with the greatest richness of top 25% FUSE species were dictated by the criteria used to define species of highest conservation priority: the top 25% FUSE species of this study amounted to 73 species, while the Caspian Sea only harbor 9 species of marine megafauna in total. For this reason, despite harboring species ranked high in the FUSE index on average, the megafaunal community of the Caspian Sea did not classify as the richest in number of high-FUSE species.

The high concentration of functional uniqueness and specialization in polar regions suggests that megafaunal assemblages inhabiting high latitudes perform specialized and very unique functional roles that lack replacement in case of species loss (**Figure 5(a)-(b)**). These regions were not identified as conservation priorities (according to spatial patterns of FUSE index) because they were characterized by low mean extinction probabilities (**Figure 5(c)**). However, the IUCN threat status used to extrapolate the extinction probabilities applied in this study may not be fully reflective of the current conservation status of polar species. IUCN species' imperilment is determined by assessing populations size, geographical range, and probability of extinction every four years (or more; Butchart et al. 2007). As the Arctic and Antarctic regions have been warming at unprecedented rates (Comiso *et al.* 2017; Turner *et al.* 2017), studies have documented that reductions in the

extent and seasonal duration of sea ice have already resulted in population declines and contraction of geographical ranges for several polar species (Forcada *et al.* 2006; Korczak-Abshire *et al.* 2012; Sundqvist *et al.* 2012; Bromaghin *et al.* 2015). In light of these fast-paced population declines, it is possible that the frequency of species assessment may not be sensitive enough to detect that polar systems are deteriorating in species' abundances and therefore fail to reflect their imperilment.

The spatial patterns of FUSE index were based on scores computed according to global endangerment status of each species. In consideration that the conservation status of species may vary between global and regional scale, this research could be further advanced by integrating regional assessments of species' imperilment into FUSE index to capture regional variations in each species' extinction risk and target conservation actions to those assemblages that are regionally threatened.

Overall, these results are based on the analysis of functional diversity from an incomplete set of marine megafauna species: 39 species, between fishes and molluscs, were not included because the IUCN database did not provide spatial data for them. These species, corresponding to 12% of marine megafauna species, present a set of both realm-crossing and marine-only traits, and their geographical occurrences are spread across all oceans. Given such wide geographical distribution and trait diversity, having omitted this set of species from the analysis is unlikely to have critically biased the measures of functional diversity presented in this study. However, future studies could source and integrate spatial information of these species from alternative databases, such as AquaMaps (Kaschner *et al.* 2021). Although strong spatial agreement for the distribution of well-studied species has been found between IUCN and AquaMaps databases (O'Hara *et al.* 2017), data integration requires cautious decision. While spatial data from IUCN relies on experts' opinion on species' geographical distributions (IUCN 2021), data from AquaMaps derives from model predictions generated independently from IUCN (Kaschner *et al.* 2021), potentially leading to different spatial results (O'Hara *et al.* 2017). Inspecting the extent of spatial overlap between the available range maps for marine megafauna from both databases could inform the best approach to move forward.

Conclusion

Despite it is widely acknowledged that functional trait approaches are more informative of the links between species communities and ecosystem stability and resilience than measures of taxonomic diversity alone (Reiss *et al.* 2009; Cardinale *et al.* 2012), functional diversity has only recently started to be integrated in conservation priority setting (Devictor *et al.* 2010; Cadotte *et al.* 2011; Parravicini *et al.* 2014; Albouy *et al.* 2017). However, the rapid declines in species abundances witnessed over the last century and the evidence for their far-reaching ecological consequence urgently demand for conservation approaches that prioritize the preservation of both species diversity and their functional contributions to ecosystems (Cadotte *et al.* 2011).

This study explored patterns of biodiversity of marine megafauna by integrating the spatial assessment of species diversity with that of functional diversity, providing important insights into the spatial relationship between these two biodiversity attributes and the locations where conservation efforts should be prioritized. The low functional redundancy of marine megafauna resulting from the linear relationship between species and functional richness is indicative of a high degree of functional complementarity among species and warns about the importance to preserve species numbers in order to conserve the diversity of ecological roles they perform in the ecosystem. Examining how functional richness relate with species richness is also crucial to capture the variability of their association and identify individual systems that may be on the verge functional collapse. The hotspot overlap analysis exemplified how spatial conservation planning solely based on taxonomic richness could neglect such systems by ignoring localities that are less speciose but functionally important, as it was the case for the South-West Pacific. Integrative approaches to conservation that adopt complementary prioritization criteria (e.g. species contributions to functional diversity and their endangerment status) are even more needed in consideration of the limited resources to invest into conservation. Applying the FUSE index to marine megafauna and exploring its spatial patterns revealed the Caspian Sea and the Gulf of Mexico as potential targets for conservation planning. Additionally, the South-West Pacific resulted as an aggregation centre of conservation priority species according to the FUSE index, further highlighting the functional importance embodied by this region. Future research could consider combining these spatial estimates of conservation priority with measures of protection efforts (e.g. the presence of protected areas within conservation priority regions),

as well as exposure to anthropogenic threats to further identify where conservation actions are most urgently needed to halt degradation of marine megafaunal biodiversity.

Appendix I

Table S1. Axes of the functional space of marine megafauna. The axes A1 to A4 represent the PCoA coordinates of the reduced four-dimensional space. The values in black report the correlation (r-squared scores) between the functional traits and the coordinates of the space. In grey are the scores based on the functional space built on marine-only megafaunal species pool. Highlighted r-squared scores indicate the traits explaining the highest variation per each axis.

Traits	A1	A2	A3	A4
Weight	0.080	0.000	0.144	0.074
	0.142	0.054	0.150	0.011
Thermoregulation	0.216	0.384	0.003	0.017
	0.428	0.227	0.000	0.000
Terrestriality	0.469	0.027	0.028	0.046
	na	na	na	na
Migration	0.077	0.163	0.024	0.001
	na	na	na	na
Feeding	0.084	0.007	0.437	0.137
	0.207	0.200	0.334	0.082
Habitat	0.061	0.031	0.051	0.009
	0.032	0.058	0.008	0.174
Breeding	0.055	0.533	0.048	0.026
	na	na	na	na
Vertical position	0.383	0.002	0.117	0.359
	0.548	0.080	0.187	0.094

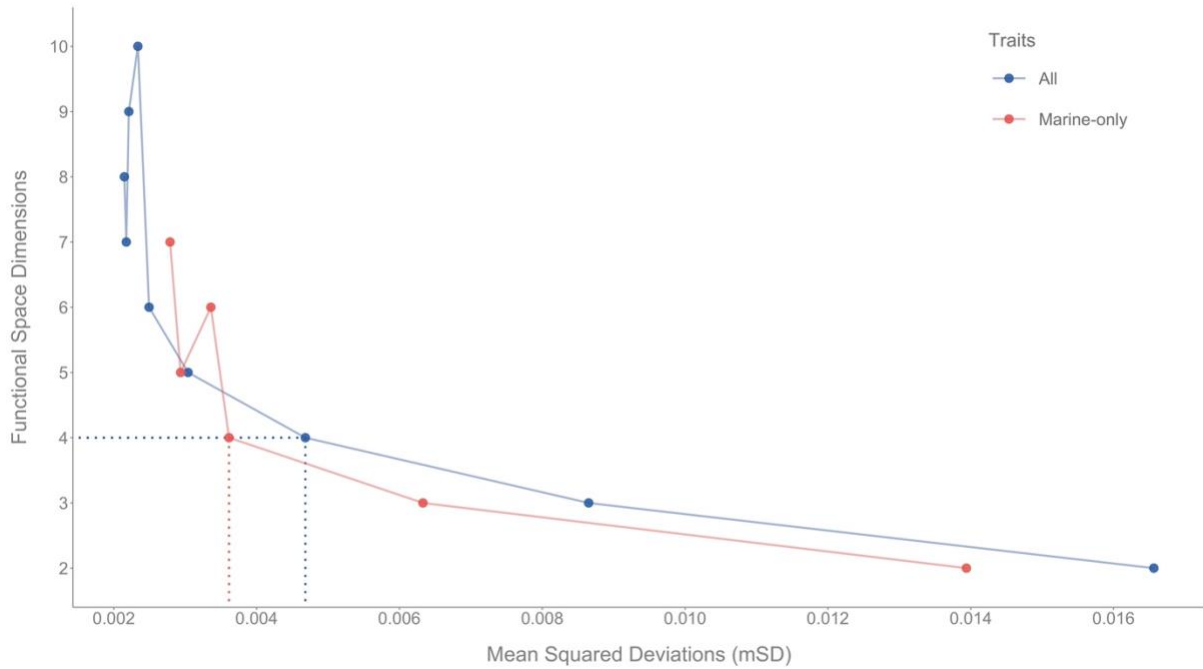


Figure S1. Quality of multidimensional functional spaces. Mean squared deviation (mSD) scores are shown per each dimensionality of the functional space based on the total (blue) and marine-only (red) traits. Quality of the functional space decreases with increasing mSD scores. Dimensions refer to the number of PCoA axes forming the functional space. mSD scores represent the deviation between the initial species distances and their distances in the functional space. Dashed lines indicate the most parsimonious dimensionality chosen for building the functional space based on the total (blue) and marine-only (red) megafaunal species pool.

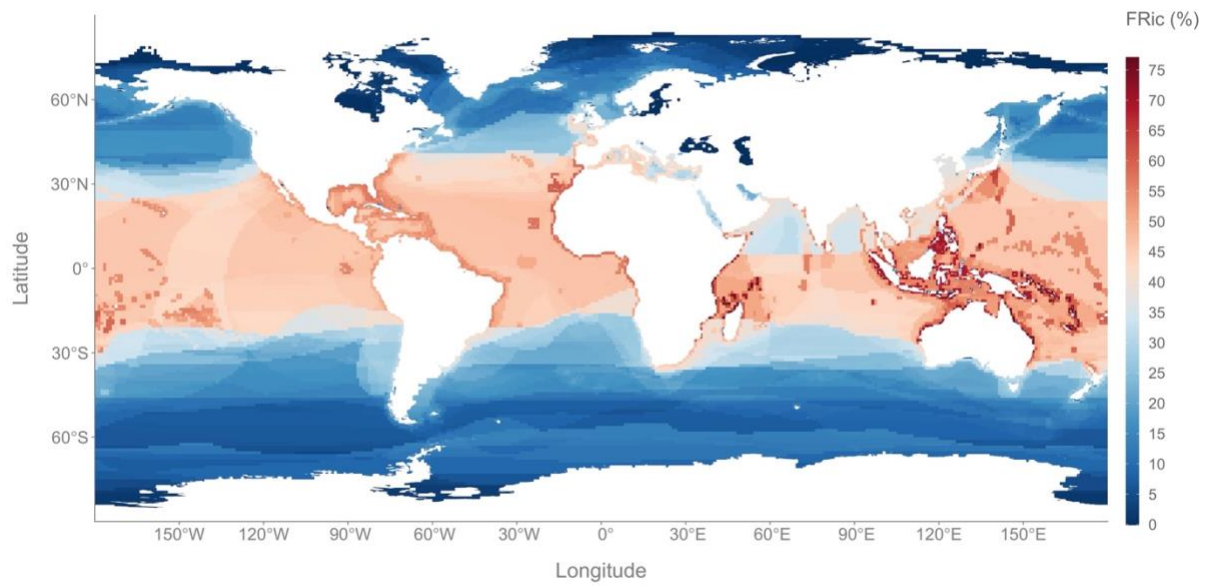


Figure S2. Global map of functional richness (FRic) of marine megafauna based on marine-only traits. FRic is measured as the volume of the functional space occupied by the species assemblage of each 1° x 1° grid cell and expressed as a percentage.

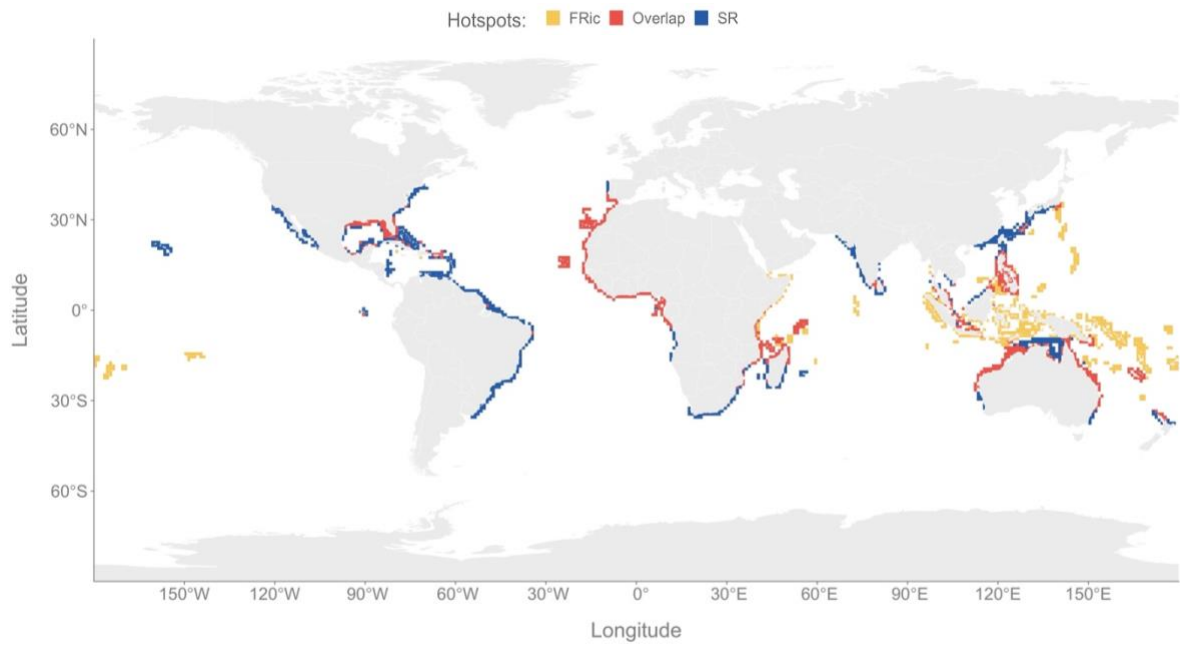
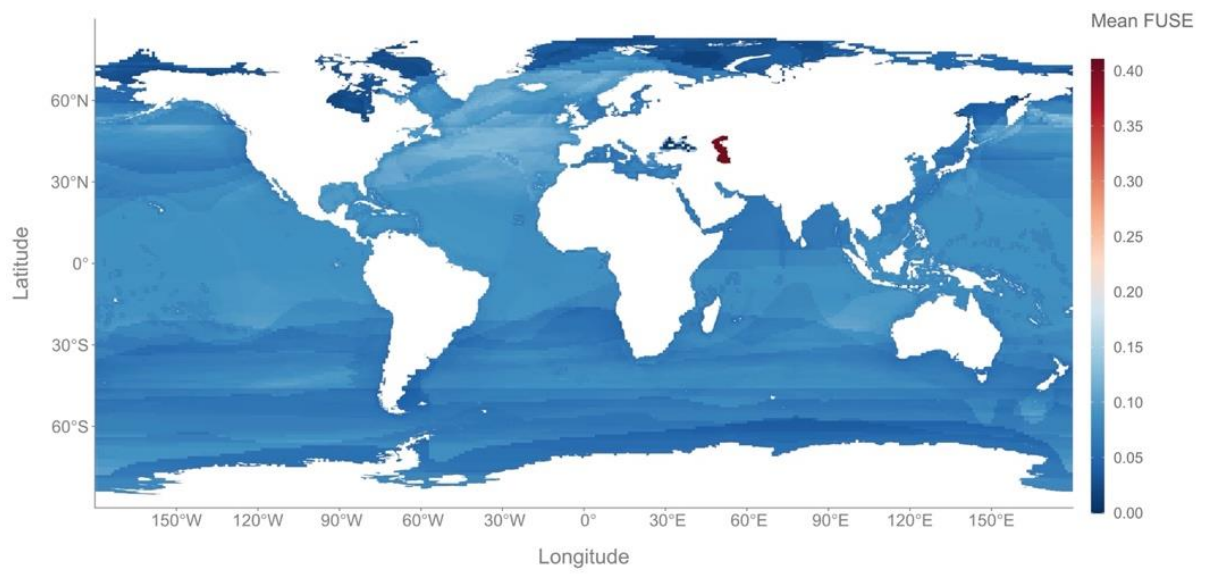


Figure S3. Map of the hotspots congruence and incongruence between species richness (SR) and functional richness (FRic) computed on marine-only traits. Hotspots for each variable were defined as the richest 2.5% cells. Red cells indicate multifaceted hotspots (i.e. congruent hotspot cells between SR and FRic) and the countries of their jurisdiction shaded in dark grey. Blue and yellow cells are single-faceted hotspots of SR and FRic, respectively.

(a)



(b)

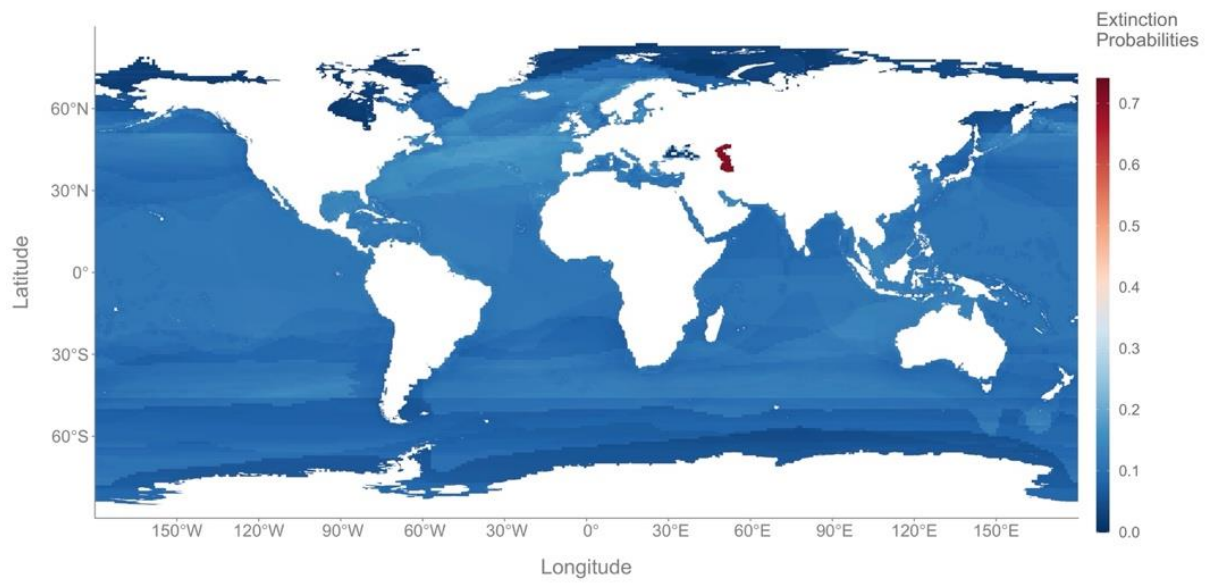
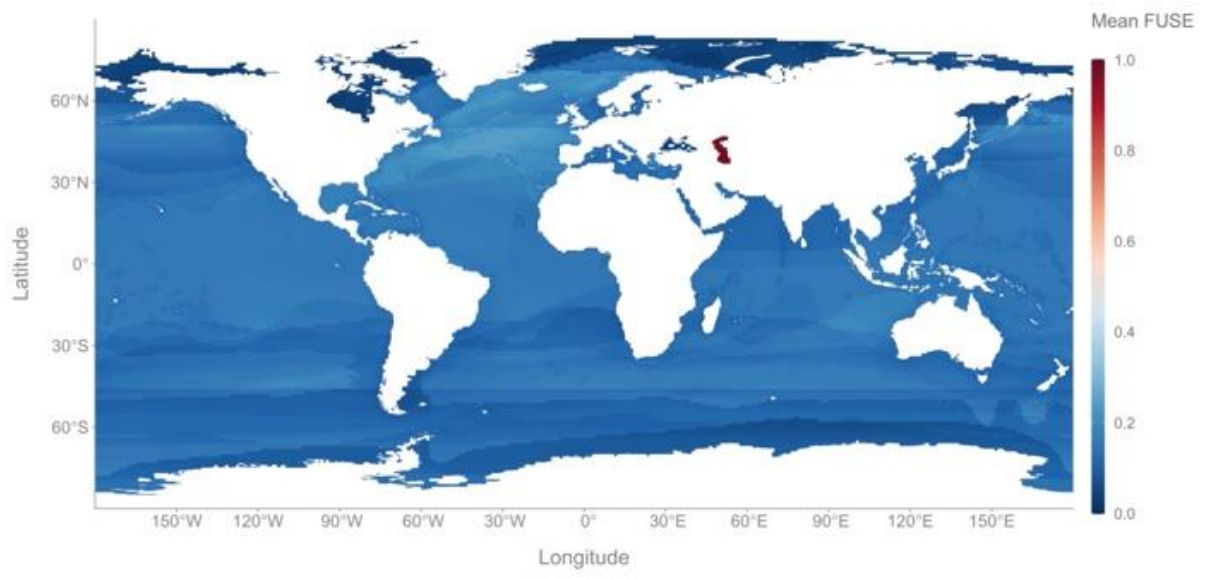
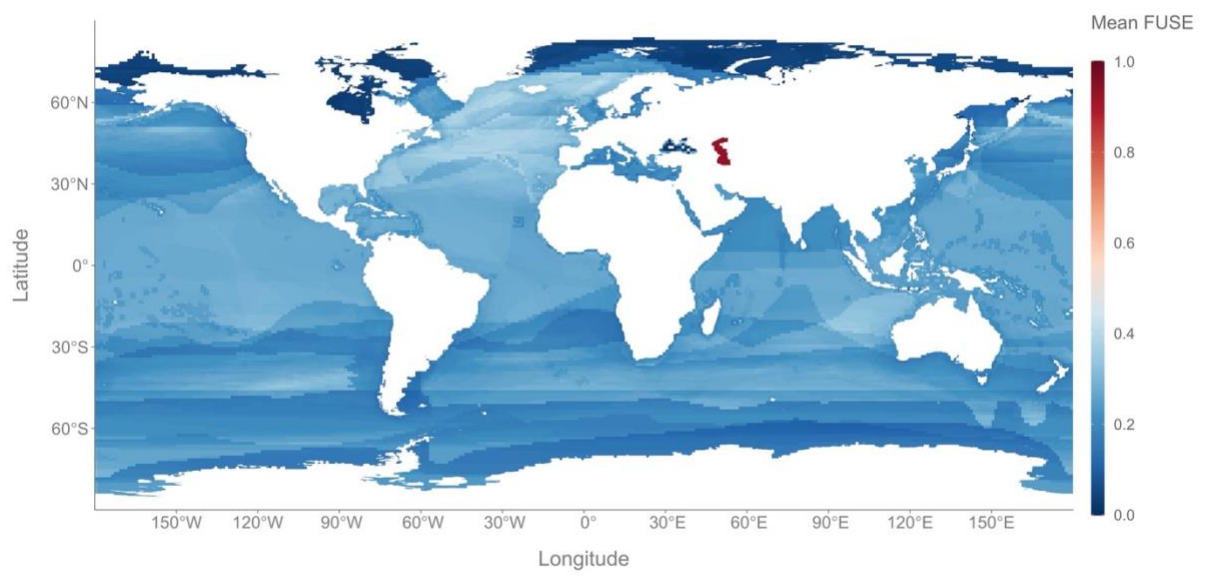


Figure S4. Global map of (a) FUSE index and (b) extinction probabilities based on 100 years-timescale.

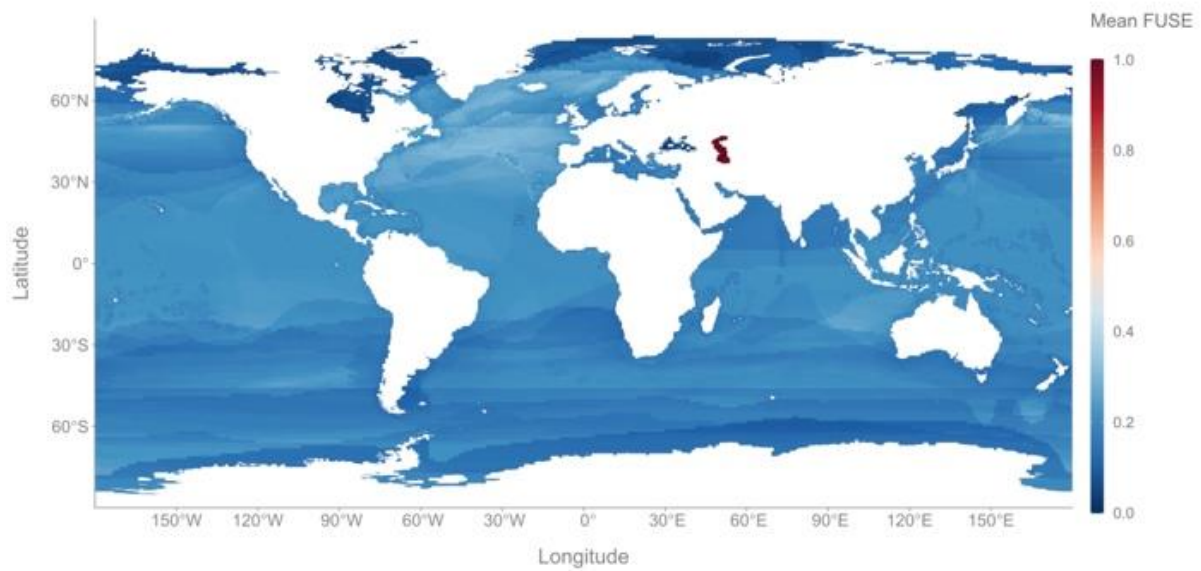
(a)



(b)



(c)



(d)

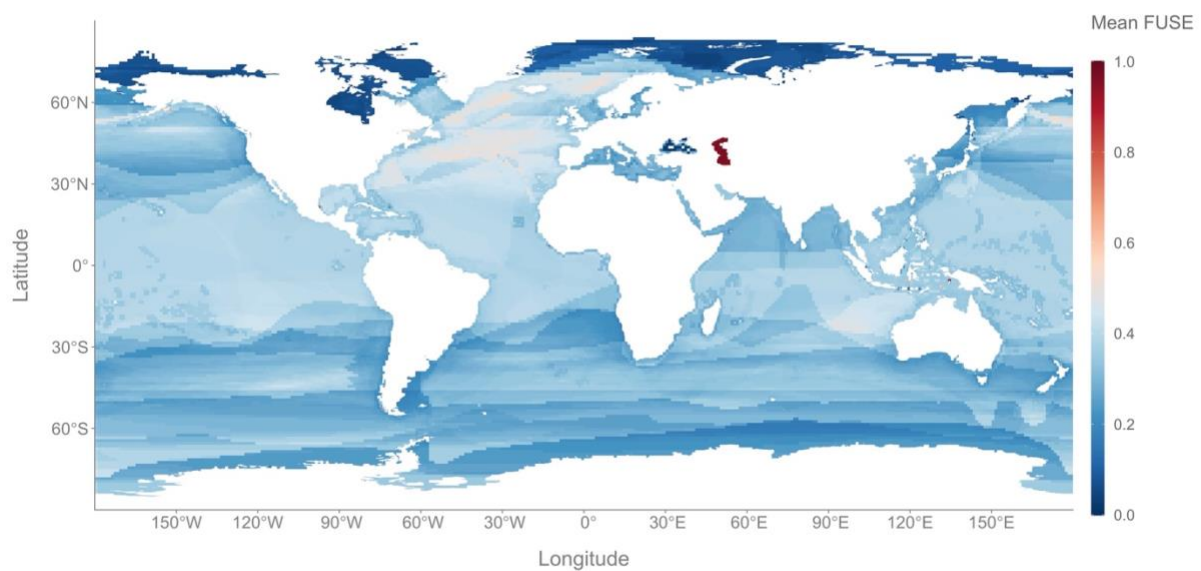
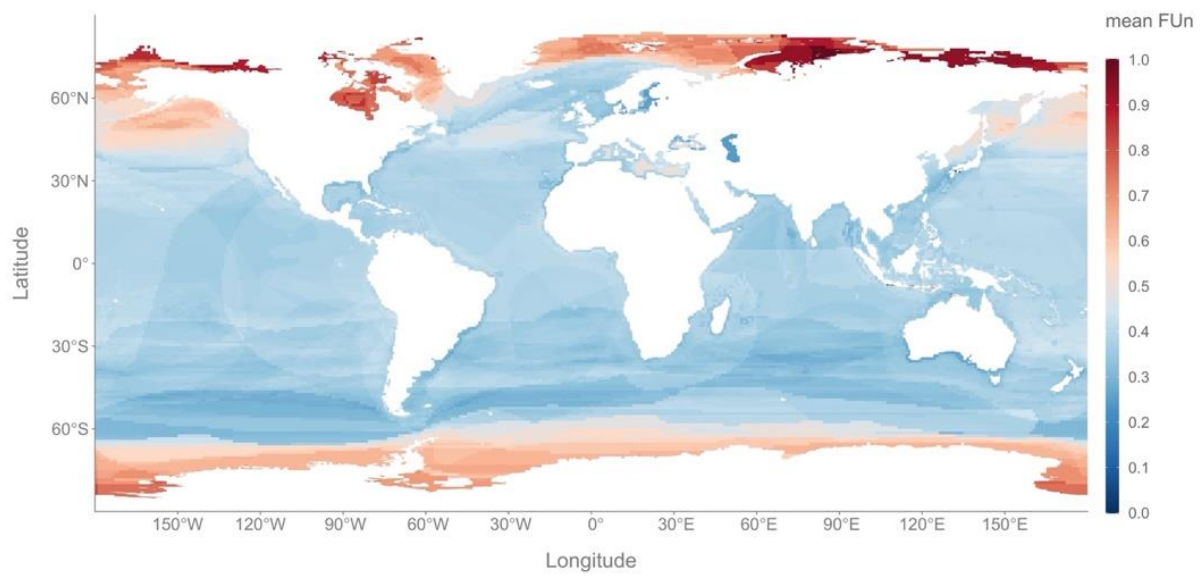


Figure S5. Comparison of maps of mean FUSE index based on the functional space built with all traits (*a* and *c*) and marine-only traits (*b* and *d*). (*a*) and (*b*) are based on 50 years-time extinction probabilities; (*c*) and (*d*) are based on 100 years-time extinction probabilities. Values of all the maps were re-scaled (between 0 and 1) for enabling comparison of spatial patterns.

(a)



(b)

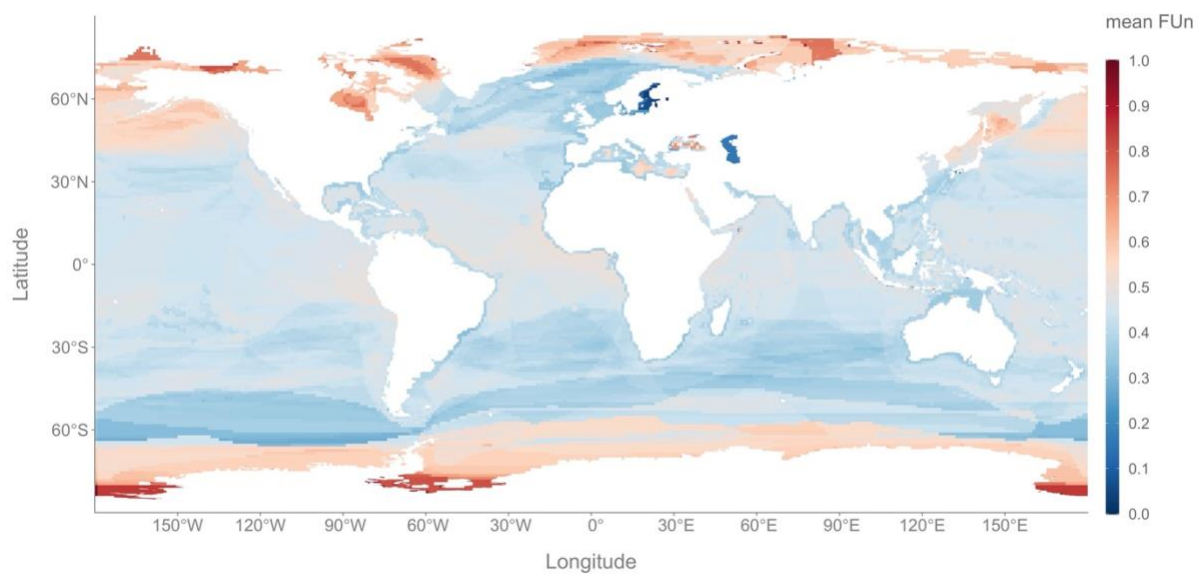
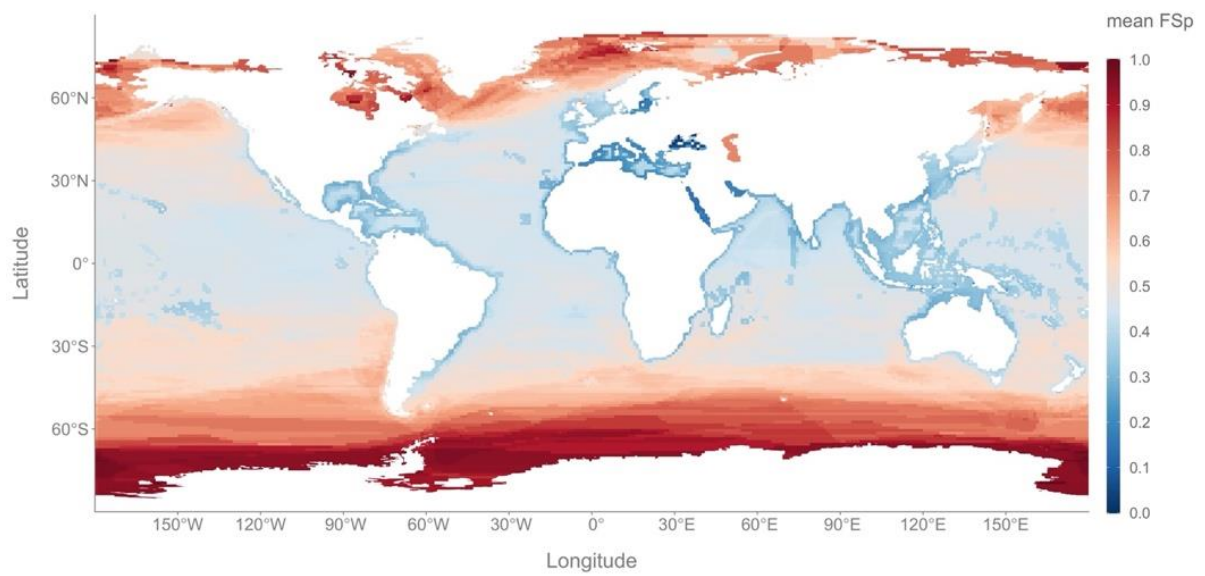


Figure S6. Comparison of maps of mean functional uniqueness (FU) per grid cell based on (a) the complete set of traits and (b) the subset of marine-only traits. Values of all the maps were re-scaled (between 0 and 1) for enabling comparison of spatial patterns.

(a)



(b)

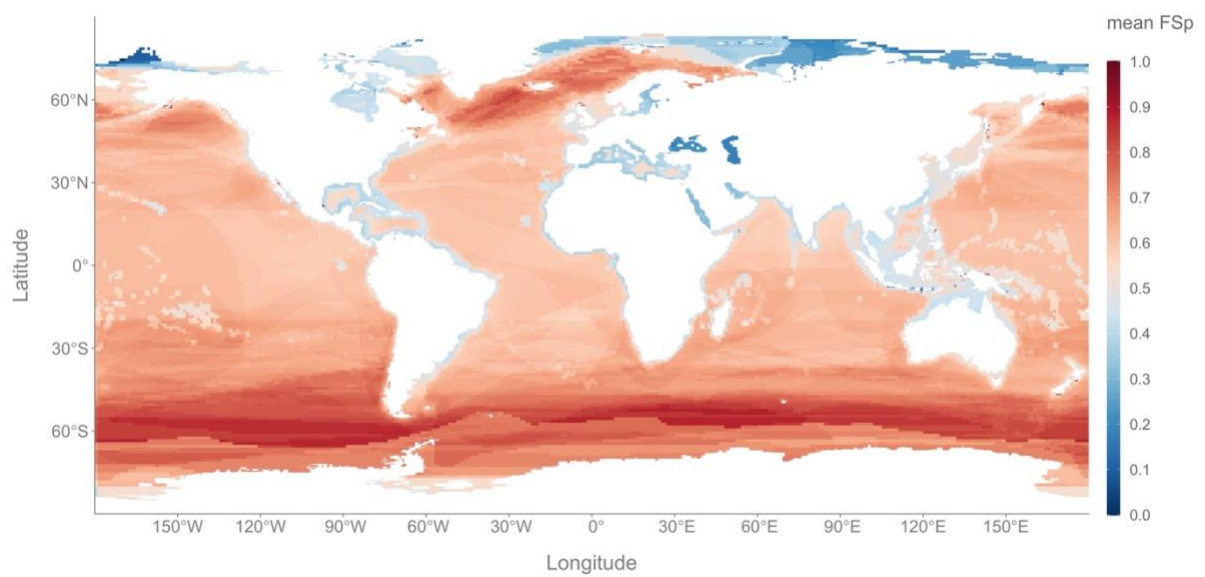


Figure S7. Comparison of maps of mean functional specialization (FSp) per grid cell based on (a) the complete set of traits and (b) the subset of marine-only traits. Values of all the maps were re-scaled (between 0 and 1) for enabling comparison of spatial patterns.

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