FUN Azores: a FUNctional trait database for the meio-, macro-, and megafauna from the Azores Marine Park (Mid-Atlantic Ridge)

Neus Campanyà-Llovet[1,2]*, Amanda E. Bates[3], Daphne Cuvelier[1,2], Eva Giacomello[1], Diana Catarino[1], Andrew J. Gooday[4,5], Björn Berning[6,7], Blanca Figuerola[8], Manuel A. E. Malaquias[9], Carlos J. Moura[1], Joana R. Xavier[10,11], Tracey T. Sutton[12], Laurence Fauconnet[1,2], Sofia P. Ramalho[13], Bárbara de Moura Neves[14], Gui M. Machado[1], Tammy Horton[4], Andrey V. Gebruk[15], Kirill Minin[15], Joël Bried[1,16], Tina Molodtsova[15], Mónica A. Silva[1,2], Anna Dilman[15], Antonina Kremenetskaia[15], Eudriano F. S. Costa[2], Jameson Clarke[3], Helen R. Martins[1], Christopher K. Pham[1,2], Marina Carreiro-Silva[1,2] and Ana Colaço[1,2]

[1]Institute of Marine Sciences — OKEANOS, University of the Azores, Horta, Portugal, [2]IMAR — Instituto do Mar, Departamento de Oceanografia e Pescas, University of the Azores, Horta, Portugal, [3]Ocean Ecosystem Change and Conservation, University of Victoria, Victoria, VIC, Canada, [4]National Oceanography Centre, Southampton, United Kingdom, [5]Life Sciences Department, Natural History Museum, London, United Kingdom, [6]Oberösterreichische Landes-Kultur GmbH, Geowissenschafltiche Sammlungen, Leonding, Austria, [7]CIBIO — Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Ponta Delgada, Portugal, [8]Institute of Marine Sciences (ICM-CSIC), Barcelona, Spain, [9]Department of Natural History, University Museum of Bergen, University of Bergen, Bergen, Norway, [10]CIIMAR — Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Matosinhos, Portugal, [11]Department of Biological Sciences, University of Bergen, Bergen, Norway, [12]Guy Harvey Oceanographic Research Center, Department of Marine and Environmental Sciences, Nova Southeastern University, Dania Beach, FL, United States, [13]CESAM — Centre for Environmental and Marine Studies and Biology Department, University of Aveiro, Aveiro, Portugal, [14]Department of Fisheries and Oceans Canada, St. John's, NL, Canada, [15]Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia, [16]Veterinary Practitioner, Biarritz, France

Trait-based approaches that complement taxonomy-based studies have increased in popularity among the scientific community over the last decades. The collection of biological and ecological characteristics of species (i.e., traits) provides insight into species and ecosystem vulnerability to environmental and anthropogenic changes, as well as ecosystem functioning. Here, we present the FUN Azores trait database, describe our approach, evaluate its scope, compare it to other marine trait databases, and explore the spatial distribution of its traits with "functional maps." While most of the available trait databases to date contain essential information to understand the functional diversity of a taxonomic or functional group, our ecosystem-based approach provides a comprehensive assessment of diverse fauna (i.e., meio-, macro-, and megafauna) from benthic and pelagic environments in the Azores Marine Park; including ridges, seamounts, hydrothermal vents, and the overlying water column. We used a collaborative approach involving 30 researchers with different expertise to develop the FUN Azores database, which contains compiled data on 14 traits representing morphological, behavioral, and life history characteristics for 1,210 species across 10 phyla. The "functional maps" show a distinct distribution of the two most common size classes, suggesting different communities with different functionalities. The following traits had the best scoring coverage (i.e., >95% of

the species scored): maximum body size, body form, skeleton material, feeding structure, motility, environmental position, substratum affinity, distribution, and depth range; while traits related to species behavior (e.g., sociability or aggregation tendencies) and life history (e.g., developmental mechanism) had lower scoring coverage, highlighting the need for further research to fill these knowledge gaps. We found a larger number of species in the benthic compared to the pelagic environment and differing species composition between areas within the Azores Marine Park resulting from varying biodiversity, ecosystem types, sampling effort, and methodologies used. The FUN Azores database will foster and facilitate trait-based approaches in the area, develop a framework for expansion of cross-ecosystem and cross-taxa trait databases elsewhere, and improve our ecological understanding of the Azores Marine Park and its conservation requirements.

1. Introduction

A trait is a well-defined, measurable characteristic of a species representing its morphology, physiology, phenology, life history, or behavior, as well as its performance in an ecosystem (McGill et al., 2006; Violle, 2007; Cadotte et al., 2011). Functional traits describe species influence on ecosystem function (i.e., effect traits) or species response to environmental change (i.e., response traits; Díaz et al., 2013). Offering an alternative essential unit to community analyses, traits can be used to answer new ecological questions on global change science, resource management, and conservation. Traits have been referred to as "common currency" across taxa and ultimately ecosystem types and serve as a bridge between species diversity and ecosystem function and services (McGill et al., 2006; Violle et al., 2014; Gómez-Gras et al., 2021; Martini et al., 2021). These advantages explain an increasing tendency over the last decades to use trait-based approaches in ecological studies and to compile trait databases.

Trait-based approaches are an important component of conservation, which complement species diversity measures. For instance, Stuart-Smith et al. (2013) revealed diversity hotspots among shallow-water reef fishes using functional diversity indices based on traits. Moreover, monitoring the recovery of a number of reef communities following protection allowed to detect positive effects when the assessment included trait-based approaches and no effects when focusing solely on species diversity metrics (Coleman et al., 2015). Other studies based on trait vulnerability to environmental change have also predicted the risk of reduction in key ecosystem functions (e.g., habitat provisioning: Gómez-Gras et al., 2021).

The application of trait-based approaches to address key ecological questions and aid the prioritization processes for management and conservation, has prompted the publication of an increasing number of trait databases, which, in the marine environment, can be habitat-specific (e.g., deep-sea hydrothermal vents – sFDVent: Chapman et al., 2019), region-specific (The Arctic Traits database: Degen and Faulwetter, 2019; FishMed: Albouy et al., 2015; a trait collection of marine fish species from North Atlantic

and Northeast Pacific continental shelf seas: Beukhof et al., 2019; and SAMT – South Australian Macrobenthic Traits: Lam-Gordillo et al., 2020), trait-specific (e.g., macrofaunal densities and biomass – BenBioDen: Stratmann et al., 2020), or taxon-specific (Polytraits: Faulwetter et al., 2014; The Coral Traits Database: Madin et al., 2016, 2017; and copepods: Brun et al., 2017). The selection of relevant traits from the extensive list of those that can be measured, as well as the collecting of trait information based on appropriate expertise, are often time-consuming tasks that benefit from a collaborative approach (Costello et al., 2015; Chapman et al., 2019). In our study, we contribute to the list of shallow-water and deep-sea trait databases with the FUN Azores database, a collaborative effort, which functionally characterizes ridge, seamount, hydrothermal vent ecosystems from the Azores Marine Park, also known as the Marine Park of the Azores. Following the definition of Marine Protected Areas by the IUCN (1988; i.e., "Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical, and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment") the Azores Marine Park (Calado et al., 2011), and therefore, the FUN Azores database, includes benthic, benthopelagic, and pelagic species.

The unique environmental conditions found on ridges, seamounts, and hydrothermal vents (e.g., abrupt topography, current acceleration, upwellings and tide amplification, and overall increased food and nutrient supply) may result in hotspots of marine diversity (Morato and Pauly, 2004; Morato et al., 2010). In fact, seamounts and ridges act as feeding grounds for top predators, including large fish, marine birds, and cetaceans (Morato et al., 2008; Tobeña et al., 2016), and support high densities and biomasses of benthic suspension and filter feeders, such as corals and sponges, that provide habitat for many demersal fish populations (Porteiro et al., 2013). Unique species occur at hydrothermal vents, where chemosynthetically derived primary production supports high biomasses of mostly benthic invertebrates and some fishes (Van Dover et al., 2018; Boschen-Rose and Colaço, 2021).

Paradoxically, the same uniqueness that promotes biodiversity on ridges, seamounts, and hydrothermal vents makes these systems

vulnerable to anthropogenic activities. The abundant and biomass-rich fish populations support fisheries, and their unique geology makes them one of the few underwater systems suitable for mineral extraction, although this is still in an exploratory phase (Drazen et al., 2020). Exploitation activities are occurring in the context of global climate change where increasing CO_2 emissions result mostly in varying temperatures, dissolved oxygen concentrations, and pH and carbonate saturation values (Sweetman et al., 2017). Increasing temperatures are expected to reduce body size of organisms, shift species distributions, and increase their metabolism, while likely deoxygenation effects include a decrease in abundance and biomass of larger organisms (i.e., macrofauna and megafauna; Sweetman et al., 2017). Ocean acidification may reduce the abundance and diversity of calcifying species, particularly species depositing more soluble $CaCO_3$ mineral phases such as aragonite and high-Mg calcite (Figuerola et al., 2021, 2023), while increasing their metabolic demands (Sweetman et al., 2017). Altogether, these factors result in ridges, seamounts, and hydrothermal vents being some of the most resource-rich and vulnerable ecosystems in the marine environment, which, given their remoteness and lack of fundamental biological knowledge, require special attention.

The FUN Azores trait database is based on a collaborative effort involving 30 researchers with different expertise and includes a broad range of taxa from benthic and pelagic environments to provide an ecosystem-based overview of the functional diversity associated with the ridges, seamounts, and hydrothermal vents within the Azores Marine Park, including benthic ecosystem and its overlying water column. Here, we present the step-by-step process of species and trait collection, with a description of the collaborative approach used in the species-scoring process. We finally describe and highlight the usefulness of the FUN Azores trait database for promoting trait-based approaches in the area by presenting species and trait coverage, their spatial distribution with "functional maps," and discuss the database strengths and limitations.

2. Materials and methods

2.1. Geographic coverage: the Azores Marine Park

The Azores Marine Park is one of the largest networks of Marine Protected Areas (MPAs) within the EU and is unique in integrating Areas Beyond National Jurisdiction (Calado et al., 2011; Maestro et al., 2020). This network of 15 MPAs covers a total area of 111,393 km², encompassing 13 MPAs that include ridges, seamount and hydrothermal vent ecosystems. One of these, MPA 10 – MARNA, is largely unexplored and therefore only the remaining 12 MPAs are considered in our study (Figure 1; Supplementary Table S1; UNEP-WCMC, 2022). Their resource-rich nature has incentivized commercial fishing, resulting in early signs of intensive exploitation in the 1980s, leading to, during the 2000s, investment in marine science (i.e., increased number of projects), monitoring of MPAs, and the implementation of protective measures for certain habitats (i.e., sponge aggregations, hydrothermal vent fields, and deep-sea coral gardens and reefs) and species (e.g., the long-lived and late-maturing orange roughy *Hoplostethus atlanticus*; Abecasis et al., 2015).

2.2. Species records

We compiled a list of species occurring on ridges, seamounts, and hydrothermal vents within the Azores Marine Park and its overlying water column, including organisms belonging to a range of taxonomic groups. For the purposes of demonstrating key results of this study, marine species/taxa were classified into the following groups: Actinopterygii (gigaclass), Anthozoa (class), Aves (class), Bryozoa (phylum), Decapoda (order), Echinodermata (phylum), Chondrichthyes (i.e., class Elasmobranchii and class Holocephalii), Foraminifera (phylum), Hydrozoa and Scyphozoa (class), Malacostraca (class, excluding the order Decapoda), Mammalia (class), Mollusca (phylum), Ostracoda (class), Porifera (phylum), Reptilia (class), Thecostraca (class), and vermiformes (phyla Annelida and Nematoda). We sourced species records from the European Marine Observation Data Network (EMODnet; https://emodnet.ec.europa.eu/en), which includes a variety of public datasets, and we complemented this list with published studies (Supplementary Material 1). We verified the taxonomic status of each entry using the World Register of Marine Species Traits (2022), WoRMS Editorial Board (2022) and validated their occurrences within the Azores Marine Park using the OBIS Ocean Biodiversity Information System (2022). Duplicates were removed to obtain a final list of accepted and validated taxa (Supplementary Figure S1). We included taxa at the species level or genera if no representative species was already present and if the scoring could be conducted with sufficient accuracy (i.e., >75% species from that genus in the area have similar trait scores, acknowledging a low certainty score for the trait modalities scored in this way – see section 2.4).

2.3. Selection of traits

We selected traits that match the following criteria: (1) increase our understanding of a species performance in its ecosystem (e.g., Maximum Body Size), (2) characterize the capacity of a species to adapt to change (e.g., Distribution), (3) characterize the ability of an organism to resist perturbation and environmental change (e.g., Skeleton Material), (4) are transferable across groups of taxa, and (5) are present in existing databases to ensure cross-ecosystem compatibility in terminology and definitions. In Table 1, we provide the selected traits and modalities within each trait category, their definition, and the rationale for trait inclusion.

2.4. Trait scoring

We scored traits based on the characteristics of the adult stage of each species, apart from the Developmental Mechanism trait, and according to global knowledge of the species characteristics (e.g., the scoring of the trait Maximum Body Size represent a potential maximum for a species across its range, rather than corresponding necessarily to the maximum size found in the Azores Marine Park). The resulting database, therefore, reflects "fundamental functional niches" (i.e., the potential functional space occupied by a particular species), from which we can infer potential responses to environmental heterogeneity and human-induced perturbations and, in turn, potential effects on overall ecosystem
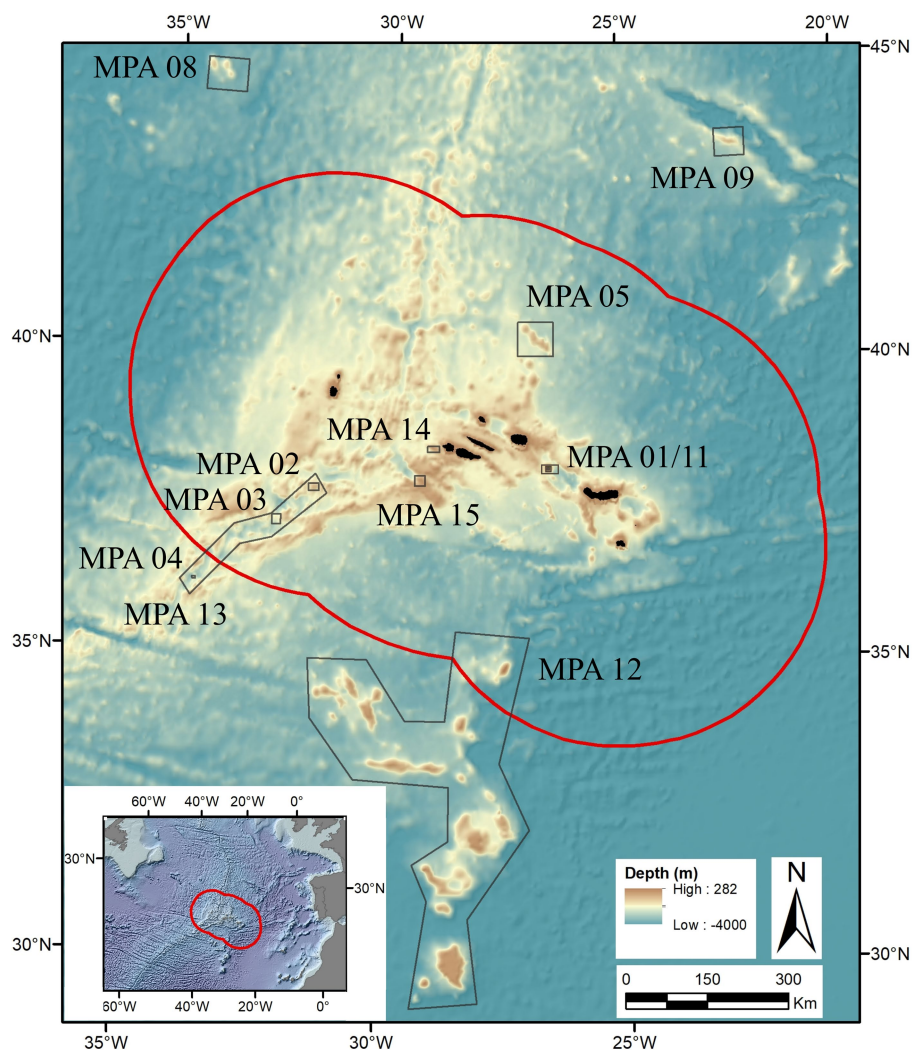
FIGURE 1
The 12 Marine Protected Areas (MPAs) from the Azores Marine Park included in the FUN Azores trait database.

functioning. This approach may, however, result in lower predictability at highly localized spatial scales (e.g., for specific seamount areas; Cordlandwehr et al., 2013). We designed a flexible database that allows for multiple modalities for each trait (e.g., a single species can be scored both as a "Carnivore" and "Scavenger" in the Feeding mode trait) and for future updates as knowledge about the species included increases. This flexibility in trait scoring, together with the broad classification of trait modalities, encompasses the associated variability at the individual level resulting from localized abiotic and biotic interactions. Our study focuses on categorical and ordinal traits, despite continuous traits resulting in a higher quality of functional spaces (Maire et al., 2015), highlighting knowledge gaps in continuous traits for deep-sea species that result from sampling constrains (i.e., costs and accessibility).

We collected trait information from available databases, literature searches and expert knowledge (Supplementary Figure S2). Taxonomic classification was taken from the World Register of Marine Species (WoRMS; see footnote 1), species distribution from Ocean Biogeographic Information System (OBIS; see footnote 2),

and depth ranges, life history, habitat, trophic ecology, species associations, morphology, and motility from other databases: FishBase (2022), SeaLifeBase (2022) TraitBank from the Encyclopedia of Life (2022), Marine Species Identification Portal (2022), and Biologic Traits Information Catalogue (BIOTIC[1]). We standardized the information extracted from the various databases to the stipulated definitions of FUN Azores (see Table 1). We filled in missing information with literature searches and inference from related species or from higher taxonomic levels (i.e., we selected the evolutionary closest taxon from which an observed trait value is available). Because this inference assumes that niche conservatism (i.e., tendency of a species to retain ancestral ecological characteristics; Wiens and Graham, 2005) prevails over niche partitioning (i.e., process by which competing species use the environmental resources in different ways, thereby permiting coexistence), we classified this type of scoring with low certainty as

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1   www.marlin.ac.uk/biotic/biotic.php

TABLE 1 List of species traits and modalities included in the FUN Azores database applicable to adult marine species from the Azores Marine Park.

MORPHOLOGY	
MAXIMUM BODY SIZE (cm)	
Typical maximum size reached by an individual or colony of the species. Can be height in rather upright animals (e.g., corals), body width or diameter in rather round animals (e.g., crabs) or body length in elongated animals (e.g., worms). The length of appendages, such as antennae, fins, wings, or tentacles is excluded. Therefore, as an example, in birds we record "max body size" not "max wingspan" and in corals the "max height" of the colony not of the individual polyp. Where sexes differ in maximum body-size then the default would be the largest adult body length.	
Very small	Order of mm (0.1–0.99 cm).
Small	Order of a few cm (1–9 cm).
Medium	Order of 10 s of cm (10–99 cm).
Large	Order of a few meters (100–999 cm).
Very large	More than 10 m (>1,000 cm).
Rationale: body size is directly and/or indirectly related to trophic position, where top predators tend to be larger than species with a low trophic level (Romero-Romero et al., 2016). Species abundance negatively correlates to its size (Peters and Wassenberg, 1983; Cohen et al., 2003) whereas metabolic rates positively correlate to an organism size (Brown et al., 2004). Finally, for species with an active dispersion method, the largest can move further than the smallest species (Jenkins et al., 2007).	
BODY FORM	
Growth shape of the essential unit of the species (individual or colony).	
Laterally compressed	Functionally flattened from side to side (e.g., amphipods, some fishes).
Dorsoventrally compressed	Functionally flattened from top to bottom creating a flat or encrusting profile (e.g., star fishes, encrusting sponges, flat fishes).
Globular	Spherical structure that can be solid (e.g., sea urchins, sponges), or the result of 3-dimensional growth (e.g., some arborescent, massive and foliose corals and bryozoans).
Upright	Growing as a straight structure perpendicular to sea bottom (e.g., coral, basket star, sponge).
Elongated	Length substantially larger than the depth or height from the individual or colony (e.g., worm and eels).
Rationale: body form suggests vulnerability to mechanical disturbances and relates to potential roles that the species can play in an ecosystem (i.e., habitat-forming). Species with an upright, globular, elongated, and laterally compressed body form are more exposed than dorsoventrally compressed taxa, which makes them an easier target for certain physical disturbances (e.g., fishing) but also a potential habitat for other organisms.	
SKELETON MATERIAL	
Elemental composition of supporting the structures of an organism.	
Aragonite	One of the most common forms of calcium carbonate occurring in nature (e.g., mollusc shells, scleractinean skeletons, and some serpulid tubes, cephalopods statoliths, fish otoliths, a few foraminifera).
Calcite	One of the most common forms of calcium carbonate occurring in nature (e.g., foraminifera shells, sponge spicules, brachiopods and echinoderm skeletons, some serpulids, most bryozoans and some bivalves).
Amorphous calcium carbonate	One of the most unstable forms of calcium carbonate occurring in nature (e.g., sea urchins, corals, molluscs, and foraminifera).
Calcium carbonate	One of the most common materials of skeleton structure in animals (e.g., corals and molluscs).
Chitin	One of the most abundant polysaccharides in nature (e.g., arthropods exoskeleton, radula, cephalopod beaks).
Silica	Oxide of silicon commonly found in nature (e.g., diatom skeleton and spicules of hexactinellid sponges).
Bone mineral	Light-weighted but resistant structure found in most vertebrates (e.g., fishes).
Cartilage	Resilient and smooth elastic tissue that supports some vertebrates (e.g., sharks and rays).

(Continued)

TABLE 1 (Continued)

MORPHOLOGY	
None	No skeleton structure.
Rationale: relevant to assess the impact of changes in ocean chemistry such as pH and carbonate saturation states (Ocean Acidification; Costello et al., 2015) as well as proxy for palatability (Degen and Faulwetter, 2019) and carbon sink in species with calcium carbonate (i.e., aragonite and calcite) skeletons (Rossi, 2013).	
FEEDING STRUCTURE	
Part of the body of an organism used to capture food.	
Tentacles, palps, pseudopodia, unarmed pharynx.	Soft tissue/organ.
Jaws, teeth (including armed pharynx), beak, claws.	Crushing/pincers.
Filtering mesh.	Net/Mesh (e.g., sponges, whale plates).
Rationale: the feeding structures of species vary according to the diversity of feeding types. Some feeding structures allow capture of various prey types and therefore plasticity and more generalist diet (e.g., baleen whales and whale sharks filter on zooplankton but can also engulf fish aggregations).	

BEHAVIOUR	
MOTILITY	
Capacity and degree of displacement of the adult stages of a species.	
Sessile-none	Non-motile; permanently attached at the base (e.g., corals, sponges, bryozoans, barnacles).
Discretely motile-low	Movement is restricted (e.g., some anemones, drifting plankton).
Motile	Movement is unrestricted (free movement, e.g., fishes, cetaceans, reptilians, cephalopods, decapods).
Rationale: capacity of an organism to explore areas with optimal conditions (e.g., presence of food) and to avoid unfavourable conditions (e.g., fishing grounds or presence of predators).	
ENVIRONMENTAL POSITION	
Location of the animal relative to the seafloor.	
Endobenthic	Benthic animals which live within the seabed (e.g., some polychaetes and bivalves).
Epibenthic	Living on the surface of the seabed (e.g., sea urchins).
Benthopelagic	Living and feeding near the bottom as well as in mid-waters or near the surface.
Pelagic	Inhabiting the open waters of the sea or ocean, excluding the bottom layers (e.g., sharks, cetaceans) and/or having their main impact on the water column (e.g., seabirds).
Rationale: relates to the area of influence of a species and varying threats they may face. Furthermore, benthopelagic species constitute a link between the two main compartments (i.e., benthic and pelagic environments).	
SUBSTRATUM AFFINITY	
Type of substrate where the species is commonly found.	
Soft	Sand and mud (e.g., most polychaetes, bivalves, sea pens).
Hard	Rock and gravel (e.g., corals, sponges).
Biological	Biological (epizoic or epiphytic-e.g., basket stars on corals, remoras on whale sharks or manta rays, copepods parasitic on fishes).
Water column	Vertical expanse of water stretching between sea surface and tens of meters above the seafloor, regardless of depth.
Rationale: preferred habitat of a species (Costello et al., 2015) that may supply physical support and nutrients (Faulwetter et al., 2014).	
DISTRIBUTION	
Spatial range where the species can be found.	
Ocean	Species distribution range extends to an entire ocean or beyond (e.g., Atlantic Ocean or North Atlantic Ocean).
Region	Species distribution range restricted to a particular region within an ocean (e.g., the Northeast Pacific or the Central Indian Ridge).

(Continued)

TABLE 1 (Continued)

BEHAVIOUR	
Ridge/Seamount	Species distribution range restricted to a particular ridge/seamount.
Rationale: key feature of a species geographic range (Costello et al., 2015). Related to the dispersal capability of a species, although sampling efforts should be considered before reaching any conclusion. It also represents plasticity in environmental conditions and opportunity to feed on various food sources (Keppeler and Winemiller, 2020).	
DEPTH RANGE (m)	
Species distribution relative to water depth.	
Neritic or shallow	0–50 m.
Shelf or epipelagic	50–200 m.
Upper bathyal or mesopelagic	200–1.000 m.
Middle bathyal or middle bathypelagic	1.000–2.000 m.
Lower bathyal or lower bathypelagic	2.000–3.500 m.
Abyssal or abyssopelagic	3.500–6.000 m.
Hadal or hadopelagic	>6.000 m.
Rationale: key feature of a species geographic range (Costello et al., 2015), which also denotes plasticity in environmental conditions and opportunity to feed on various food sources (Keppeler and Winemiller, 2020).	
FEEDING MODE	
Mechanism of food uptake.	
Filter feeder/Suspension feeder	Filtration of the suspended particulate organic matter in the water through a mesh either by actively pumping water (e.g., most Porifera) or by locating themselves perpendicular to existing currents (e.g., Pennatulacea).
Surface/subsurface deposit feeder	Collection of fragmented particulate organic matter from the sediment with tentacles, palps and other soft structures (e.g., some holothurians and sea stars).
Predator	Capture of living organisms through various hunting techniques: actively foraging for preys (e.g., some elasmobranchs), adopting a sit-and-wait predatory strategy (e.g., some angler fishes) or capturing drifting zooplankton within the water column (e.g., some anemones and corals).
Scavenger/opportunistic	Consumption of dead organic material (e.g., giant isopod, most amphipods, some echinoderms).
Symbiont contribution	Dietary components (all or a portion of them) provided by symbiotic partnerships with certain microorganisms (e.g., *Rimicaris exoculata*).
Parasite/commensal	Dietary components take from the host it parasitises (e.g., parasitic copepods on fishes).
Rationale: describes a functional role of a species in an ecosystem (Costello et al., 2015). Reflects the dependence of a species on a particular feature of the local environment (e.g., light, chemical elements, chemosynthetic symbionts, detritus, and prey; Chapman et al., 2019). Can indicate carbon transfer from pelagic to benthic realms (i.e., suspension feeders) and from benthic to pelagic realms (i.e., predators; Degen and Faulwetter, 2019).	
TROPHIC POSITION	
Rank of an animal in relation to the base of the food web (i.e., primary producers, autotrophs).	
Primary consumer	Species that feeds mostly on primary producers including parasite (e.g., sea urchins).
Secondary consumer	Species that feeds mostly on primary consumer and/or other carnivores including parasites (e.g., planktivorous fishes).
Omnivore: carnivore and Primary consumer	Species that feeds mostly on more than one trophic level including plants/marine snow/detritus and animals (e.g., some corals).
Tertiary consumer	Species that feeds mostly on secondary consumers including parasites (e.g., seabirds).
Quaternary consumer	Species that feeds mostly on tertiary consumers and has no predator including parasites (e.g., some sharks).
Carnivore	Species that feeds mostly on animals, with undetermined position on the food web resulting from lack of information on this particular species.
Parasite	Species that feeds mostly on another species in a process that does not involve death but damage and underperformance on the host organism.

(Continued)

TABLE 1 (Continued)

BEHAVIOUR	
Rationale: describes a functional role of a species in an ecosystem (Costello et al., 2015). Related to energy flow through the food web, what are the energy demands of a species and what is the energy that it makes available for higher trophic levels (Chapman et al., 2019; Degen and Faulwetter, 2019). The number of trophic levels a species can occupy also relates to its generalist or specialist feeding mode and therefore plasticity in front of environmental change affecting the species food resources.	
SOCIABILITY	
Degree to which individuals of the same species tend to cluster and can be found in groups or on their own.	
Gregarious	Individuals of the considered species are always found in groups.
Facultative gregarious	Individuals of that species tend to be found on their own but will aggregate for a particular reason (e.g., feeding, reproduction, moulting in crustaceans).
Solitary	Individuals of that species are always found on their own or at most in pairs for reproduction.
Rationale: the function and role a species plays in an ecosystem is magnified by a gregarious behaviour when compared to solitary species.	

LIFE HISTORY	
DEVELOPMENTAL MECHANISM	
Process by which the fertilized egg becomes an adult.	
Direct	Eggs develop into miniature adults.
Planktonic larvae or non-adult dispersal stages	The egg develops into a larva or a non-adult dispersal stage that is released into the water column without specification of the source of energy.
Lecithotrophic larvae	Released larva has yolk sac and no capacity to feed from the organic matter present in the surrounding environment.
Planktotrophic larvae	Released larvae grow and feed in the water column, using external food sources.
Rationale: related to the degree of dispersal a species can attain, its fecundity and degree of parental care. Direct development is generally associated with low dispersal capabilities, low fecundity, and high parental care whereas species with planktotrophic larvae are associated with high dispersal capabilities, high fecundity and low parental care, and therefore, high mortality rates.	
REPRODUCTIVE TYPE	
The way species reproduce, including information about where fertilization occurs and whether propagules are released or not.	
Asexual	Reproduction without exchange of genetic material. Individuals are derived from a single parent.
Sexual – external	Separate sexes with external fertilization (e.g., fishes).
Sexual – internal	Separate sexes with internal fertilization (e.g., cetaceans).
Sexual – brooding	Separate sexes with brooding of the eggs (e.g., some crustaceans).
Sexual	Separate sexes with no specification where fertilization occurs.
Rationale: relates to the ability of recovery after a substantial reduction of population numbers (Costello et al., 2015).	

Traits are grouped into three broad categories: Morphology, Behaviour, and Life history. We provide definitions with examples and the relevance of each trait from an ecosystem perspective (i.e., their role as "effect" or "response" traits).

a quality measure (see paragraph below). Additionally, we consulted a total of 30 experts in different taxonomic groups to validate and complement the extracted data based on their knowledge, supported by available literature and observational data. The consultation process consisted of an agreement to the terms and conditions, provision of the database set of the appropriate taxonomic speciality, together with instructions on how to fill in the database in an excel file, and a follow-up virtual or in-person meeting to clarify the scoring system and modify the database structure accordingly if needed.

For each trait we scored, we mentioned the respective trait modality for the species, the source of information (i.e., a specific reference, an online database, and/or "Expert knowledge"), and we defined a certainty score that classified the level of confidence in the annotation. The certainty modalities are: 0-No knowledge from the trait, 1-Inferred trait, 2-Expert knowledge and observation and/or data published once, 3-Expert knowledge and observation and/or published more than once. The certainty classification represents a quality control while the traceability of information allows researchers to re-use the data with the appropriate context for specific research questions.

We error-checked initial versions of the database following a series of steps to ensure completeness and consistency of the scored data: (1) removal of duplicate entries and synonymized names, (2) confirmation of blank entries (i.e., missing information) and low certainty scores, (3) ensuring nomenclature uniformization using drop-down menus to enter the data, and (4) ensuring the biological plausibility of trait combinations (e.g., a "sessile" species cannot be found in the "water column").

2.5. Data analyses

We mapped the distribution of the modal functional entities across all MPAs (i.e., "functional maps") with ArcGIS Desktop (version 10.8.1.14362). We plotted the kernel density based on georeferenced records from EMODnet. For that purpose, we used the "Kernel density" tool in the Spatial Analyst ArcToolbox to calculate DENSITY with the GEODESIC method and an output cell size of 0.01.

We ran rarefaction curves with the function rarefy () {vegan} in R programing software (v.4.2.1) to compare biodiversity and sampling efforts among areas and environmental domains (i.e., Benthic, Benthopelagic, and Pelagic). The rarefaction curves that we present are based only on the data extracted from EMODnet repositories where we could find both species records and numbers of records for each species (i.e., EMODnet and literature species records).

3. Results and discussion

The FUN Azores trait database compiles relevant information to understand the functional ecology of the Azores Marine Park using an ecosystem-based approach that includes species from shallow waters to the deep sea and open ocean. This is the second contribution to deep-sea trait databases following Chapman et al. (2019) and the first one to include both chemosynthetic and non-chemosynthetic seamount and ridge ecosystems, with a broad taxonomic coverage from a wide range of organism sizes (i.e., millimeters to meters) and representing benthic and pelagic environments. Our final list contained 1,210 species distributed among 10 phyla and 14 traits classified either into morphological, behavioral, or life history categories. The data collection approach used in the construction of the FUN Azores database follows the methodology used in Chapman et al. (2019), who developed a protocol for including expert knowledge to score traits.

3.1. Cross-ecosystem and cross-taxa compatibility

A key aspect of trait-based ecology is the use of a "common currency" (i.e., traits; Violle et al., 2014; Martini et al., 2021) that is independent of geographic region and species, facilitating comparisons across ecosystems (e.g., communities from different seamounts or chemosynthetic and heterotrophic environments) and taxa (i.e., phylogenetically distant taxa such as cetaceans and corals). To contextualize the FUN Azores database, the traits included are comparable to biological characteristics found in existing marine trait databases (Table 2) in terms of their ecological relevance and the accessibility of the information. However, comparisons become difficult with freshwater and terrestrial databases that include at least double the number of traits and have a larger proportion of numerical traits (Serra et al., 2016; Fraser, 2020), highlighting the large differences in knowledge availability between these environments.

Costello et al. (2015) identified the following 10 traits as those considered most relevant by marine ecologists: Taxonomic classification, Environment, Geography, Depth, Substratum, Mobility,

Skeleton, Diet, Body size, and Reproduction. These are all included in the FUN Azores database. Given the broader approach of FUN Azores (i.e., highly unrelated taxonomic groups and a combination of pelagic and benthic species) when compared to databases that focus on a particular taxonomic group (i.e., Polytraits: Faulwetter et al., 2014; marine copepods: Brun et al., 2017; and corals: Madin et al., 2016, 2017) or environmental compartment (i.e., benthos in the Arctic Trait Database: Degen and Faulwetter, 2019; and macrobenthos in Australia: Lam-Gordillo et al., 2020), the modalities for the same traits can differ among databases resulting in a broader classification in the FUN Azores. For example, where the FUN Azores includes three categories to describe fish morphology (i.e., "Elongated," "Dorsoventrally compressed," and "Laterally compressed"), fish databases will include more detailed information (e.g., "Deep," "Short," "Elongated," "Fusiform"; Albouy et al., 2015), thereby increasing cross-taxon comparisons at the expense of resolution.

3.2. Trait coverage

Traits included in the FUN Azores trait database cover a wide variety of functions within an ecosystem. Some of them represent multiple ecosystem functions such as Maximum Body Size, which reflects both carbon storage and food web structure, or represent specific functions in the ecosystem, such as Developmental Mechanism, which reflects the dispersal capabilities of the early life-history stages of the species. Traits that are commonly found in the original description of a species and/or in lists of species records are scored for most taxa in FUN Azores and with a high certainty score (i.e., Maximum Body Size, Body Form, Motility, Environmental Position, Distribution, and Depth Range).

The modal functional entity within the database is a small to medium-sized species (i.e., from a few to tens of centimeters) that corresponds to the description of carnivorous epibenthic Actinopterygii inhabiting the upper bathyal (i.e., 200–1,000 m) with non-adult dispersal and sexual reproduction (Supplementary Table S2). The "functional maps" (i.e., spatial distribution of the modal functional entities; Figure 2) reveals important characteristics of the database and of the different functions across MPAs. For example, there is a noticeable heterogeneity in the distribution of the two main size classes, where small organisms in the size range 1 to 9.99 cm are more prevalent in the south (MPA12) and organisms in the size range 10 to 99.9 cm are more prevalent in the center of the area of study (MPAs 14 – Condor Bank and 15 – Princesa Alice Bank), which suggests a different community with different functionalities. Other traits have a more homogenous representation of the main modality over all MPAs, resulting from their broad spatial coverage and representation in a large number of species (i.e., "Epibenthic," "Oceanic," "Upper bathyal," "Solitary"), or because the trait modality has a broad scope in order to accommodate uncertainties and lack of specific information (i.e., "Carnivore," "Planktonic or non-adult dispersal," and "Sexual" reproduction). A significant number of trait modalities match their spatial distribution (i.e., "Laterally compressed," "Bone mineral" and "Aragonite," "Jaws, teeth, plates, bills or beaks" as feeding structure, "Motile" and "Predators"). These define the vast majority of Actinopterygii and highlight the importance of this taxonomic group within the FUN Azores database. The overall distribution of the modal functional entities highlights their presence

TABLE 2 Equivalences of the species traits used in the FUN Azores database and other relevant marine databases (i.e., Marine Species Traits, sFDVents, Polytraits, and Arctic trait database).

FUN Azores	Marine Species Traits	sFDvent	Polytraits	Arctic trait database
Morphological traits				
Max. Body Size (cm)	Body Size	Estimated maximum body size (mm)	Body size (max)	Size (mm)
Body Form	Body Shape	Not included	Not included	Body Form
Skeleton Material	Supporting structure and enclosure (composition)	Not included	Not included	Skeleton
Feeding Structure	Not included	Not included	Feeding Structure	Not included
Behavioral traits				
Motility	Mobility	Relative Adult Mobility	Mobility of adult	Adult Movement/Mobility
Environmental Position	Environmental Position	Not included	Environmental position	Environmental Position
Substratum Affinity		Substratum	Habitat Type; Substrate type	Substratum Affinity/Living Habit
Distribution		Not included	Not included	Not included
Depth Range		Depth Range (m)	Depth Zonation	Depth Range
Feeding Mode	Feeding type	Not included	Feeding Type	Feeding Habit
Trophic Position		Trophic Mode	Not included	Trophic Level
Sociability	Sociability	Gregariousness	Sociability	Sociability
Life history traits				
Developmental Mechanism	Development	Not Included	Larval Development/Larval feeding type	Larval Development
Reproductive Type	Asexual reproduction and brooding	Not Included	Fertilization type/Mode of Reproduction/Parental care – brood protection	Reproduction

We include traits from database that share a similar concept with the traits presented in the FUN Azores trait database, regardless of trait modalities and trait denomination.
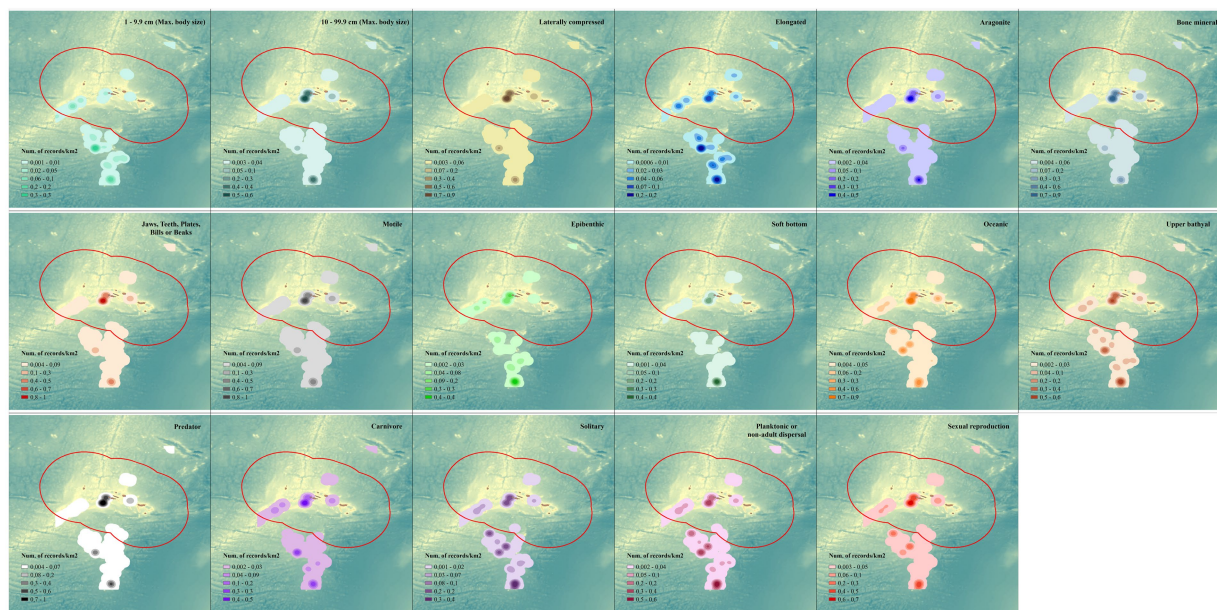

FIGURE 2
Kernel distribution of the modal functional entities of the FUN Azores database within each MPA of the Azores Marine Park.

in three areas with different spatial extents (i.e., MPA 14 – Condor Bank, MPA 15 – Princesa Alice Bank, MPA 12 – Meteor Ridge), again highlighting the larger knowledge base in those areas as well as the good representation of both species and functions.

Most of the available trait information was scored for species from the phylum Chordata (i.e., marine Mammalia, marine Aves, marine Reptilia, Actinopterygii, and Chondrichthyes), whereas little information exists for invertebrates (e.g., Ostracoda, vermiformes, Echinoderms; Supplementary Table S2 and Supplementary Figure S3). The specificity of the information required to score "Trophic position," usually determined from either gut contents or biochemical analyses, complicated the scoring of this trait when compared to other measurable morphological traits such as "Feeding structure," particularly for invertebrates. Furthermore, information relevant to behavioral and life history traits such as "Sociability" and "Larval development," which requires detailed observations or even experimentation in the laboratory, lacked information or had low certainty scores.

Conservation efforts based on trait-based approaches frequently use only a few traits (e.g., Maximum Body Size, Motility, Distribution, and Feeding Mode; Coleman et al., 2015), which are all well-represented in the FUN Azores database (Supplementary Table S2 and Supplementary Figure S3) and represent various components of the overall functional diversity. However, our extensive review of functional diversity has also highlighted knowledge gaps for the Azores Marine Park that are important for managing Marine Protected Area networks. For example, there is a critical gap in our knowledge of traits relevant to ecosystem recovery after perturbation, disturbance, or a change in the environment (i.e., reproductive type, larval development, Supplementary Figure S3; and growth rates and life span, which are not included in the database because of scarcity of the data). There is also a general lack of information for those invertebrates that link the pelagic chordates with the benthos (e.g., copepods, which are the diet of mesopelagic fishes that undertake vertical migrations, or the habitat provisioning of certain sessile invertebrates – corals, sponges, bryozoans, etc. – for fishes and their early stages in life; Porteiro et al., 2013; Drazen et al., 2020). These data are essential for effective ecosystem-based management.

3.3. Taxonomic coverage and sampling effort

The most species-rich taxonomic groups were the Actinopterygii ($n = 316$; >25%) and Mollusca ($n = 164$; 13.5%), followed by Foraminifera ($n = 120$; 9.9%), Hydrozoa ($n = 107$; 8.8%), Anthozoa ($n = 90$; 7.5%), and non-decapod Malacostraca ($n = 75$; 6.2%).

Particularities of each MPA of the Azores Marine Park contributed to the final taxonomic coverage of the FUN Azores trait database (i.e., species composition, surface area covered, sampling effort and methodology; Supplementary Figure S4). As a result, the number of species reported in the seamount complex found in MPA 12 (Meteor Ridge – South of the Azores) by far exceeds that of the less sampled Sedlo seamount (MPA 05). Condor (MPA 14) is one of the most studied seamounts of the Azores Marine Park and is represented by a larger number of species in the FUN Azores trait database than the less visited, but with similar surface area, Altair (MPA 08) and Antialtair (MPA 09) seamounts. Most of the taxonomic groups known from Condor belong to the megafaunal size spectrum (e.g., fishes, corals, cetaceans, birds, cephalopods, sponges) and have been

documented by intensive visual, video and longline fisheries surveys (Giacomello and Menezes, 2011; Porteiro et al., 2013; Silva et al., 2013). In contrast, on the Meteor Ridge to the south of the Azores (MPA 12) we have a larger representation of infauna (e.g., some foraminifera and vermiforme taxa) than on any other seamounts, as a result of the collection of numerous sediment samples during various research expeditions (Surugiu et al., 2008; Carvalho et al., 2020; Hoffman et al., 2020). Similarly, there is a low representation of Actinopterygii in MPA12 compared to all other MPAs. Perhaps the most unique fauna is that found in MPA 13, which includes hydrothermal vent species that are not found in other MPAs. These contrasts in taxonomic coverage are evident in both benthic and pelagic environments (Supplementary Figure S4).

The pelagic environment appears to be better sampled than the benthos (Supplementary Figure S5). In most cases we can attain almost complete taxonomic coverage of pelagic species, a statement that is far from true for the benthic and benthopelagic environments, where the lower sampling effort and undersampling of habitat variability result in rarefaction curves hardly reaching an asymptote with increasing number of records from the EMODnet database. In fact, with similar sampling efforts (i.e., same Num. ind.) the benthic environment has a higher number of species in most MPAs.

4. Future research directions

We emphasize the need for collaborative initiatives and the use of data inferences to improve the completeness of databases, and a transition from categorical to ordinal and numerical traits in this and future trait databases. We expect an iterative process with future versions of FUN Azores incorporating new knowledge, thereby increasing its taxonomic range and hopefully introducing a temporal dimension, a key element that is already being included in terrestrial plant databases (Kattge et al., 2020). We particularly emphasize the need for increased observation, experimentation, and modeling in the following three areas: (1) life history traits (e.g., developmental mechanism and larval dispersal), (2) variability in sampling methodologies and, therefore, targeted species, in each of the Azores Marine Park MPAs, and (3) the benthic environment, which in the Azores Marine Park is undersampled while also being the most species-rich.

The knowledge acquired will help to enhance the effective management of one of the largest Marine Protected Area networks in Europe.

Data availability statement

The original contributions presented in the study are published in a database repository following the FAIR principles (i.e., Findable, Accessible, Interoperable, and Reusable; Wilkinson et al. 2016). This data can be found here: PANGAEA, https://doi.org/10.1594/PANGAEA.955357. Further inquiries can be directed to the corresponding author.

Author contributions

Order of authorship is as follows: (a) first author (NC-L); (b) core FUN Azores scoring by the number of species contributed to;

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1050268/full#supplementary-material

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