



Trait-based approaches reveal that deep reef ecosystems in the Western Indian Ocean are functionally distinct

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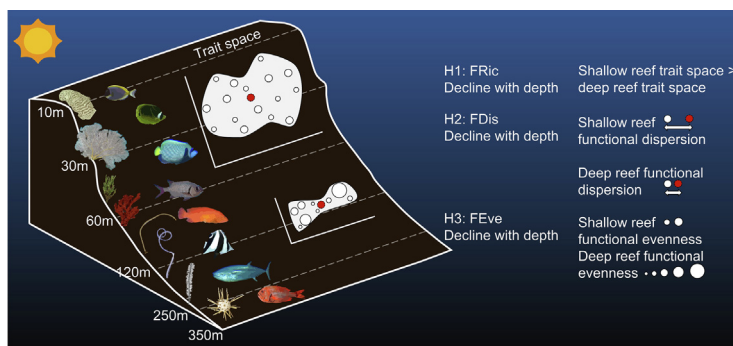
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HIGHLIGHTS

- Limited reef data >30 m hinders their appreciation and awareness.
- We found unique suites of reef taxa (fishes and benthos) and traits across 10–350 m.
- Functional metrics painted a complex, depth-dependent picture of reef functioning.
- Deep-reef taxa were functionally important and of conservation concern.
- Results show the need to explicitly consider deep reefs in conservation plans.

GRAPHICAL ABSTRACT



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ABSTRACT

Tropical deep reefs (>30 m) are biologically and ecologically unique ecosystems with a higher geographic reach to shallow (<30 m) reefs. Yet they are poorly understood and rarely considered in conservation practices. Here, we characterise benthic and fish communities across a depth gradient (10–350 m) in remote coral atolls in Seychelles, Western Indian Ocean. Using taxonomic and trait-based approaches we present the taxonomic and functional composition of shallow and deep reef communities, with distinct communities and traits dominating different depths. Depth-related changes in community metrics (taxa richness, abundance and biomass) and functional diversity metrics (richness, dispersion, and evenness) indicate complex relationships across different biological components (fish, benthos) that differ between shallow and deep reefs. These in turn translate into different patterns of reef resilience against disturbance or species invasions with depth. Notably, deep reefs host on average fewer and less abundant taxa but with higher functional contribution and originality scores, some of which are of conservation concern. Overall, the results highlight the unique nature of deep reefs that requires their explicit consideration in conservation and management activities.

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1. Introduction

Mesophotic coral ecosystems (MCEs, >30–150 m) and rariphotic reef habitats (~150–300 m), are widespread in tropical and subtropical regions (Baldwin et al., 2018; Pyle and Copus, 2019). Hereafter they are referred to as 'deep reefs' to distinguish from deep-sea or cold-water coral reefs that exist exclusively in aphotic environments below 200 m (Roberts et al., 2006). Previous studies have focused on the taxonomic composition and diversity patterns of deep reef communities and highlighted that they harbour unique biodiversity (Pyle and Copus, 2019) and need targeted conservation efforts (Rocha et al., 2018; Stefanoudis et al., 2022). However, there has been little focus on their functional diversity (i.e. diversity of ecological roles performed by species within an ecosystem) and their links to ecosystem functioning and derived ecosystem services. Although deep reefs are suggested to provide essential goods and services including food security, nutrient cycling, and habitat for threatened species, most existing information is not quantitative and some has been extrapolated from shallow coral ecosystems (Holstein et al., 2019). Since ecosystem functions and services are central in supporting marine conservation, management planning and policy-making (Van der Biest et al., 2020), it is important to move from a descriptive documentation of deep-reef fauna and flora to a more mechanistic understanding of those ecosystems.

Trait-based approaches help bridge the gap between biodiversity and ecosystem functions. Traits are individually measurable variables that reflect species forms, functions, diets, physiologies and life histories, and together are used to characterise a community. Increasingly available species trait data, and the development of analytical methods to estimate trait diversity and variation (Laliberté and Legendre, 2010; Blonder et al., 2018), have led to a plethora of trait-based studies that have sought to better understand community assembly rules (Wieczynski et al., 2019), ecosystem resilience to disturbance (McLean et al., 2019), as well as to guide global conservation efforts (Pimiento et al., 2020). While trait-based ecology has been used to describe tropical shallow-reef fish (D'agata et al., 2014; McLean et al., 2021) and benthic communities (Darling et al., 2012; Madin et al., 2016; McWilliam et al., 2018), few studies have focused on deep-reef fish (Velasco-Lozano et al., 2020; Medeiros et al., 2021), and to our knowledge, there are none for deep-reef benthos, the latter most likely due to lack of publicly available comprehensive trait information in the same manner as for reef fish (e.g. FishBase).

Here, we use traits to infer functional composition and diversity patterns of tropical reef fish and benthic communities across a depth gradient (10–350 m). We assess the degree of functional interconnectedness of reefs through a trait-based analytical approach.

In particular, we hypothesise that (Fig. 1a):

- i) Functional richness (relating to the size of the trait space encompassing all unique trait combinations in a community) of fish and benthic communities will be positively correlated with taxonomic richness (Clarke and Warwick, 1999; Schumm et al., 2019). Hence, it will decrease with depth, mirroring depth-dependent taxonomic richness patterns observed in other warm-water coral reef ecosystems (Pyle and Copus, 2019).
- ii) Functional dispersion (relating to the extent to which unique trait combinations differ from the community mean) will decrease with depth given less environmental variability and thus fewer available ecological niches (Costello et al., 2018). Therefore, species from deep reefs are more likely to have low functional originality and trait combinations that are similar to each other, leading to greater trait redundancy. Consequently, deep reefs will be more resilient to perturbations that might affect a particular taxon, since a different taxon is likely to be able to perform the same role. However, this will not be the case if the disturbance affects all taxa indiscriminately.
- iii) Functional evenness (relating to the regularity in distribution of unique trait combinations in a community) will decrease with depth, with fewer taxa and with more extreme traits dominating communities, successfully adapted to the specific environmental conditions prevalent in

deeper waters (i.e. less light and food availability, higher pressure). This phenomenon, known as habitat filtering (Cornwell et al., 2006), has been reported from environmentally extreme ecosystems such as caves (Gibert and Deharveng, 2002), and deep-sea hydrothermal vents and cold seeps (Tunncliffe and Cordes, 2020). This would make deep reefs more prone to species invasions since some niches will remain underutilised.

For definition and ecological relevance of all above-mentioned metrics see Fig. 1b.

2. Materials and methods

2.1. Study site and data collection

Seven sites across six coral atolls were investigated around Seychelles Outer Islands, four in the Amirantes Group (Poivre, D'Arros/St. Joseph, Desroches and Alphonse), and three in the Aldabra Group (Aldabra North, Aldabra West, Astove) (Fig. S1) during the *First Descent: Seychelles* expedition, onboard the *R/V Ocean Zephyr* (5 March–18 April 2019). Horizontal transect surveys were conducted across discrete depth bands (~10, 30, 60, 120, 250, 350 m) by SCUBA divers, submersibles and remotely operated vehicles (ROVs), each equipped with stereo-video systems (two cameras and lights). In total, 106 and 108 transects were conducted for demersal fish and benthic communities, respectively. Summary characteristics of transect surveys are available in Table 1, with detail per transect survey in Data S1, while detailed information on survey design and equipment specifications can be found in Supporting Information Methods.

Environmental factors and physicochemical properties of the water column such as temperature, salinity, dissolved oxygen concentration, *in situ* fluorescence, were measured using a CTD profiler equipped with sensors (Supporting Information Methods). In addition, nine metrics characterising seabed terrain structure at the location of the transect (e.g. slope, orientation, curvature and terrain complexity) were also calculated (see Supporting Information Methods).

2.2. Data processing

Stereo-video footage from all camera systems was calibrated and synchronised using a 3D calibration cube and CAL software v3.30 (SeaGIS Pty Ltd., Australia).

2.2.1. Fish

Fish identity and total length was determined and reported using EventMeasure v5.43 (SeaGIS Pty Ltd., Australia), with the minimum fish length that could reliably be detected set at ~1.5 cm (Supporting Information Methods). Fish length measurements were converted into biomass using Eq. (1):

$$W = a \times L^b \quad (1)$$

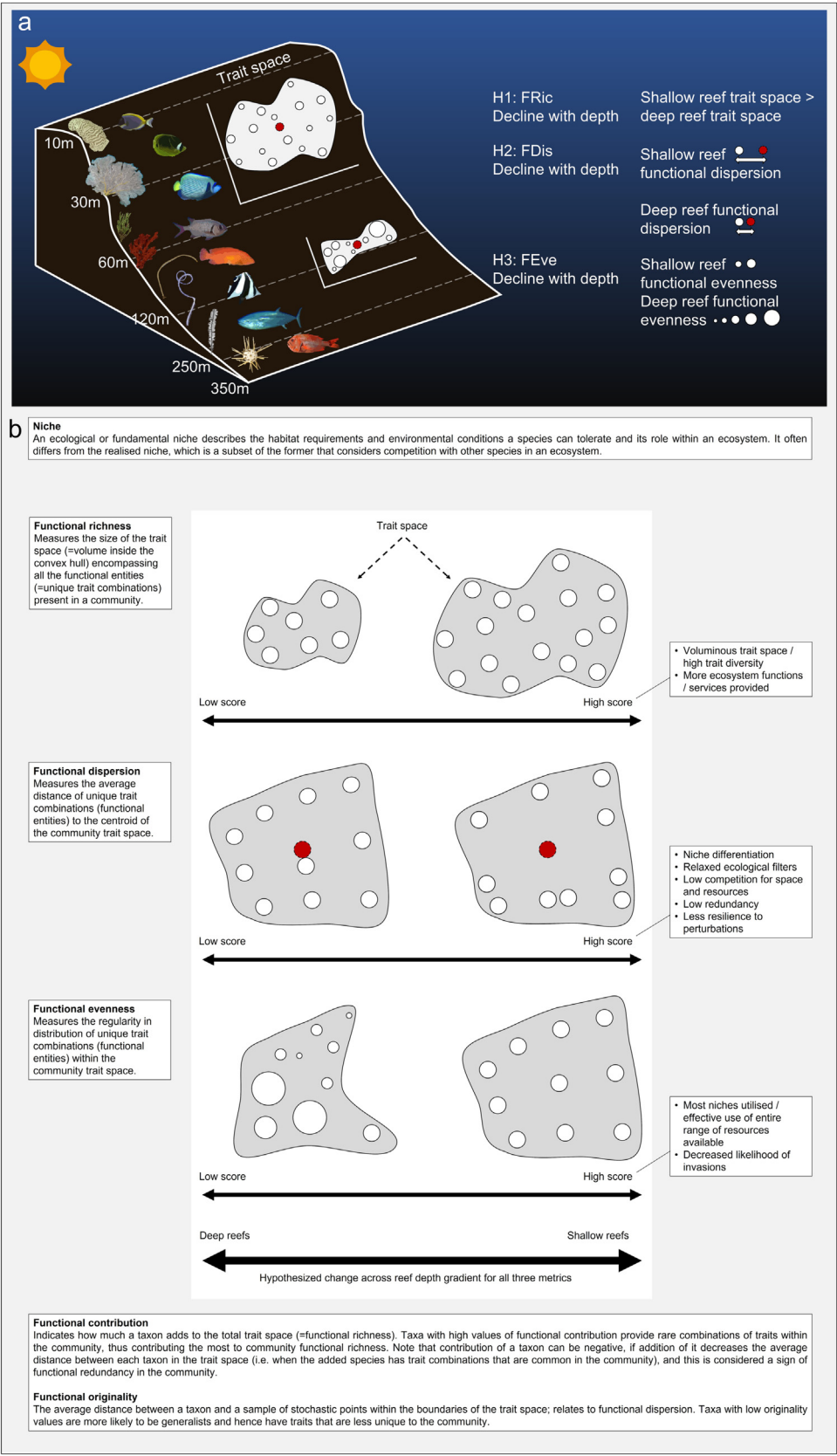
where L represents the fish length in centimetres, W the weight in grams, and a and b are species-specific conversion constants from FishBase (<http://www.fishbase.org>).

2.2.2. Benthos

For benthos, video was translated into still images, by taking frames at set intervals to avoid spatial overlap (Supporting Information Methods). After images were scaled in EventMeasure they were imported into TransectMeasure v3.31 (SeaGIS Pty Ltd., Australia), where virtual dynamically sized quadrats were generated in order to maximise the investigated area per image (Supporting Information Methods). Random points (20 per m²) were overlaid within the superimposed quadrats for percentage cover estimates of benthos and substratum (TransectMeasure).

Quantification of epibenthos was carried out for a total of 3941 quality-controlled images (Supporting Information Methods). Most taxa were placed into putative morphotypes (i.e. morphologically similar individuals)

that often corresponded to genus or family-level classifications, (Supporting Information Methods), reflecting standard practice in image-based marine benthic surveys (Howell et al., 2019). Photographic evidence and short



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descriptions of all morphotypes observed in this study are available in Fassbender et al. (2021). All individuals were enumerated except for forms that were too problematic to count reliably given that they often overlap with other organisms (e.g., encrusting algae and sponges) or they form subsurface networks with only parts being visible above the substratum (e.g., thalli of seaweeds), in which case presence was noted instead (Data S2).

2.2.3. Substratum

Substratum composition of each annotated image was identified to: bedrock, boulders (defined as rocks greater than or equal to 25 cm), rhodolith beds (defined as unattached accretions of non-geniculate coral-line algae), coral rubble, mats (bacterial), pebbles and gravel (rock fragments up to 25 cm), sediment (including mud and sand whose size is too small to be determined via imagery), sediment veneer (which applies to bedrock beneath a thin sediment layer as indicated by the presence of sessile biota). Substratum cover per type was expressed as a mean per transect.

2.3. Data analysis

2.3.1. Taxonomic diversity and composition

Changes in abundance, biomass and taxon richness with depth (fixed factor) were compared using a Kruskal-Wallis test on raw data since they all followed a non-normal distribution (Shapiro-Wilk, $p > 0.05$) even after transformations, followed by Mann-Whitneys pairwise comparisons applied with a Bonferroni correction. Fish abundance and biomass were standardised per 500 m², while benthic abundance was standardised per m².

Changes in fish or benthic community composition were visualized using principal coordinates ordination analysis (PCoA) on Bray–Curtis similarity matrices of the following datasets: (i–ii) square-root transformed fish abundance and biomass data, respectively, to reduce the effect of common taxa (note: using presence-absence fish data produced identical results, hence, they will not be shown here), (iii) presence-absence data for the entire benthic community, to include taxa that were not possible to enumerate (note: using the Jaccard similarity index produced identical results, hence, the Bray-Curtis-based analyses were kept), (iv) square-root transformed abundance data for a subset of numerated habitat-forming benthic taxa (Data S2 in supporting information). These were followed by permutational analysis of variance (PERMANOVA) (fixed factor: depth; 9999 permutations; type III partial sums of squares, unrestricted permutation of raw data) to identify significant differences between communities, and subsequently, permutational analysis of multivariate dispersions (PERMDISP) (distances to centroids; 9999 permutations) to test if any the PERMANOVA differences were due to differences in dispersions. Note, that we did not find any significant differences in community composition and gear type (e.g. submersibles vs. ROV transects at 30 m at the same site; PERMANOVA $p > 0.05$ for all benthic and fish datasets; Table S1) in line with results reported elsewhere (Schramm et al., 2020; Jessop et al., 2022), hence, this factor was omitted from the analyses. We also did not find any consistent community patterns across sites (see PERMANOVA pairwise comparisons in Table S2), hence, these results will not be discussed here. Moreover, we further assessed community composition variation across depth by estimating taxonomic beta diversity using Jaccard's

dissimilarity index on presence-absence data of fish and benthos, respectively, via the function *beta.muli* of package 'BAT' v. 2.5.0 in R (Cardoso et al., 2015). Beta diversity between any two depth strata was calculated as the average among all pairwise comparisons of transects at those depths, and was further partitioned into its two components, beta replacement and beta richness (Legendre, 2014). Beta replacement or turnover is explained by replacement of taxa alone, while beta richness is explained by taxa loss/gain (richness differences) alone (Legendre, 2014).

Kruskal-Wallis and Mann-Whitney post hoc tests were performed in SPSS v24 (IBM Corp., Armonk, NY), and multivariate statistical analyses (PCO, PERMANOVA, PERMDISP) were carried out in PRIMER 7 and the add-on package PERMANOVA+ (Primer-E, Plymouth, UK).

2.3.2. Traits

We compiled 9 traits (4 categorical: trophic group, minimum population doubling time as a proxy for resilience, position in the water column, vertical home range; 5 continuous: maximum length, maturity length, age at first maturity, mortality, trophic level) for 275 fish species (for which abundance data were available), and 7 traits (6 categorical: compactness, vertical home range, mobility, surface complexity, top heaviness, trophic group; 1 continuous: maximum length) for the 150 benthic morphotypes that could be enumerated, which were chosen to describe natural history and ecology, population dynamics, habitat preference, habitat provision and resilience (Data S3). Information was collected at the lowest possible taxonomic level and inferred, when needed, from data available from other species in the genus, or from higher taxonomic levels (this was necessary more often for benthic morphotypes where trait information is less readily available than for fishes). While we recognise that these traits only represent a subset of the true multidimensional species niche, they are; widely accepted proxies of fish (Samoilys et al., 2019; McLean et al., 2021) or benthic functions (Teixidó et al., 2018; Boyé et al., 2019) and have been used to assess ecosystem functioning (Morais et al., 2020). Full details on modalities of selected traits, sources of information and relevance to ecological functions are included in Data S3.

2.3.3. Trait space and functional metrics

Multidimensional trait spaces were created separately for fish and benthic community data by applying PCoA to a Gower similarity matrix of the species \times traits table. First continuous trait variables were rescaled by subtracting mean and dividing by standard deviation (pooling the data for all species), so as to moderate their effect on the resulting trait space (Blonder et al., 2018). In addition, any highly correlated traits (Pearson correlation $r > 0.8$) were removed prior to running the PCoA (fish maturity length and age at first maturity; highly correlated with fish maximum length and natural mortality rate, respectively). The first five axes cumulatively explained 70 % and 84 % of total variance for the fish and benthic trait space, respectively and effectively capture community variation while maintaining initial Gower dissimilarity (Maire et al., 2015). Using species abundances and the five trait axes, hypervolumes (= geometrical representation of trait space) for both fish and benthos were constructed with the convex hull generation procedure (method = 'box', chosen bandwidth 10 and 2 times of the default settings for fish and benthic datasets, respectively) using the package 'hypervolume' v.2.0.1.2 (Blonder et al., 2018) in R v.4.0.5.

Fig. 1. Hypotheses, ecological concepts and functional metrics used in this study. (a) Visual representation of shallow and deep reef communities across depth, along with hypothesised changes to their trait space. White circles represent unique combinations of traits or functional entities (defined as groups of species sharing the same trait values; sensu Mouillot et al., 2014) in the community trait space, whose size is proportionate to their abundance in the community. Arrows used to indicate the average distance between trait combinations (functional entities) and the trait space centroid (red circle). The number and size of trait combinations (circles) for each trait space was randomly chosen to help illustrate the hypotheses. FRic = Functional richness, FDis = Functional dispersion, FEve = Functional evenness. (b) Brief explanation of ecological concepts and functional metrics used in this study. Functional richness, dispersion and evenness are community-level metrics, while functional contribution and originality are taxon-level metrics. White circles represent unique trait combinations (functional entities) in the community trait space, whose size is proportionate to their abundance in the community, and red circles represent the centroid of the community in the trait space. Definitions adapted from Mammola et al. (2021) and based on probabilistic hypervolumes as a framework for estimating functional diversity and illustrating trait space. For functional richness, dispersion and evenness ecologically relevant characteristics descriptive of high scores are also given.

Table 1

Summary of transect survey characteristics. N = number; ROV = Remotely-operated vehicle; SUB = submersibles. For detailed information see Data S1 and Supporting Information Methods.

Survey method	Depth (m)	N of fish surveys	N of benthic surveys	Transect duration (min)	Transect length (m)	Distance between replicate transects
SCUBA	10	14	14	8	100	20 m
Mini-ROV	10	3	4	10	100	
	30	3	3			
SUB	30	17	17	25	250	5 min of navigation
	60	22	22			
	120	21	21			
	250	21	21			
ROV	30	3	3	25	250	
	250	1	2			
	350	1	1			
Total		106	108			

Subsequently, several functional metrics were estimated to summarise specific features of variation within the generated trait space. Community-level metrics functional richness, functional dispersion, and functional evenness (Box 1) were estimated via functions *kernel.alpha*, *kernel.dispersion*, and *kernel.evenness*, and taxon-level metrics functional contribution and functional originality (Box 1) via functions *kernel.contribution* and *kernel.originality* of package 'BAT' v. 2.5.0 in R (Cardoso et al., 2015). Furthermore, dissimilarity in trait composition across depth was assessed by estimating functional beta diversity and its components replacement and richness (Carvalho and Cardoso, 2020; Mammola and Cardoso, 2020) using the function *kernel.beta* of package 'BAT', and following the same workflow as for estimating taxonomic beta diversity. Additionally, community weighted means (CWM) for each trait were also estimated using the package 'FD' (Laliberté et al., 2014) in R, in order to assess changes in specific traits across depth. For continuous traits, community weighted means provides the average trait score for all taxa in a community weighted by their abundance; for categorical traits the metric provides abundance of each trait level in a community.

All metrics changes across depth were compared using a Kruskal-Wallis test followed by Mann-Whitneys against the global average (i.e. taking into account all depths) applied with a Bonferroni correction in R. Similar to the taxonomy-based metrics, no trends across sites were observed, hence, they will not reported here.

2.3.4. RLQ and fourth-corner analysis

To analyse trait–environment relationships, the RLQ and the fourth-corner methods were applied (Dray et al., 2014) using the package 'ade4' (Dray and Dufour, 2007) in R. These two complementary approaches combine an environment-sites matrix (R), a species-occurrence or species-abundance matrix (L), and a species-trait matrix (Q). RLQ is a multivariate analysis performing ordination tests between the three datasets (R, L and Q) and the resulting ordination plane visualises the associations between traits and environmental variables, while the fourth-corner analysis statistically tests the significance of pairwise relationships between traits and environmental variables.

Here, the RLQ and fourth-corner routines were performed twice, once with water chemistry and substratum as the environmental dataset, and another using only terrain variables as environmental data, since they were available for a subset of transect surveys.

3. Results

3.1. Taxonomic diversity and composition

A total of 279 fish species and 178 benthic morphotypes (150 + 28 morphotypes of algae and sponges that were non-countable) were recorded across a depth range of 9–351 m.

Fish abundance and biomass, and benthic abundance decreased with depth (Kruskal-Wallis, $p < 0.001$ in all cases, Fig. 2a, b, d). Further, both fish species richness and benthic morphotype richness decreased with depth (Kruskal-Wallis, $p < 0.001$ in both cases, Fig. 2c, e). Pairwise comparisons between depth bands are included in Fig. 2a–e. Depth was also the major driver for community composition, with distinct fish and benthic communities identified at ~10, 30, 60, 120, 250–350 m, irrespective of type of dataset used (Fig. 2f–i; PERMANOVA, $p = 0.0001$ in all cases). Further pairwise comparisons indicated that communities across each depth band were significantly distinct from each other (PERMANOVA, $p = 0.0001$ to 0.0002 in all cases). Only in the case of benthic communities dispersion also varied significantly across depth, (PERMDISP, $p = 0.0001$ for both abundance and presence-absence data) indicating that both changes in composition and dispersion played a role in the significant depth-related patterns identified with PERMANOVA. Finally, taxonomic composition dissimilarity as measured by Jaccard's dissimilarity index was consistently high (>0.6 and >0.8 , with 1 indicating total dissimilarity) between all depth bands for both fish and benthos (Fig. S2), further indicating community changes with depth. Those changes were in most cases because of species replacement with the exception of fish communities at 250 m where low richness was more important.

3.2. Trait space and functional diversity metrics

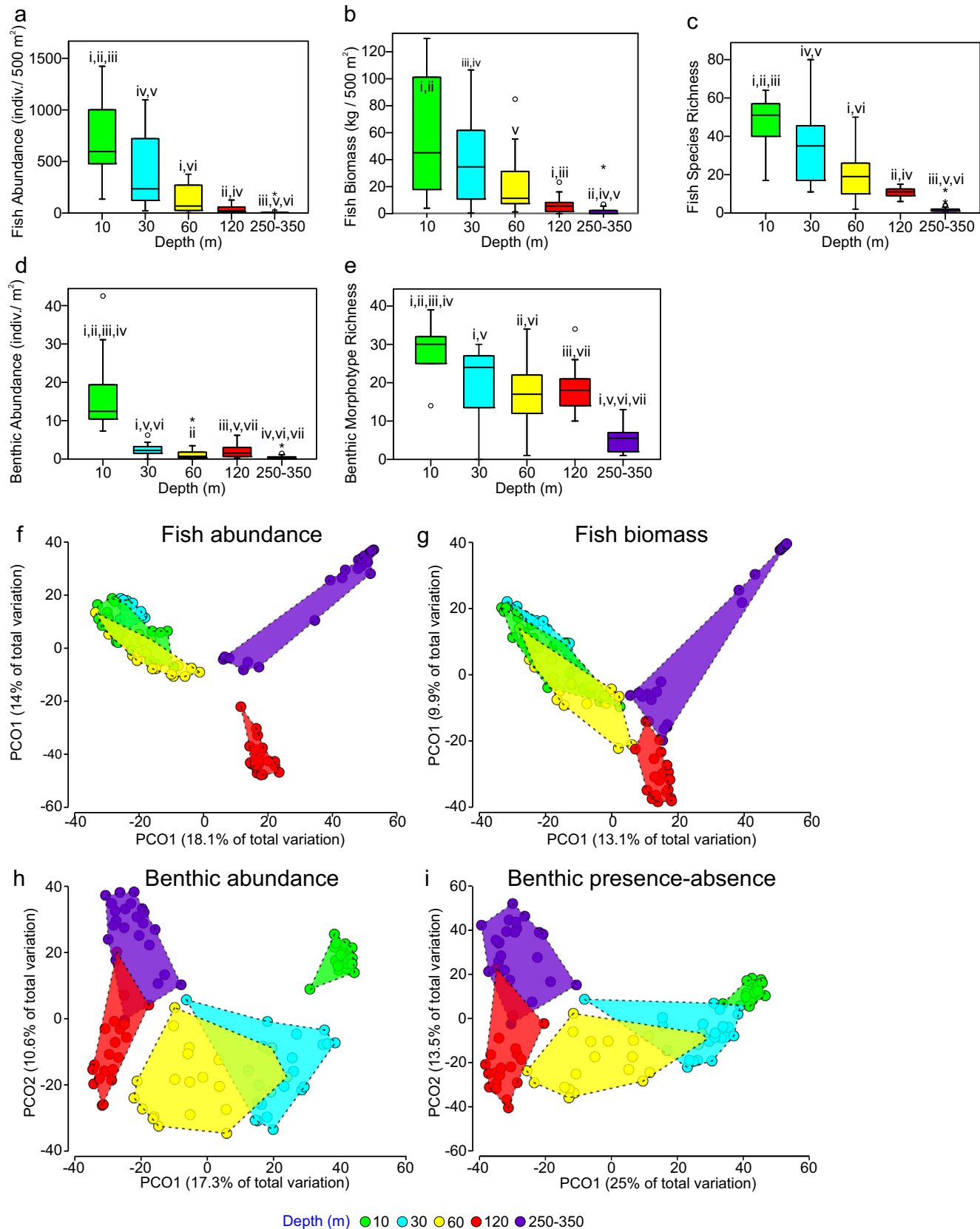
Fish and benthic trait spaces represented as 5-dimensional hypervolume plots are shown in Fig. S3. Properties of each trait space did not change consistently over depth: functional richness declined with depth for both fish and benthos (Fig. 3a, f), functional dispersion declined with depth for fish (Fig. 3b) but not for benthos (Fig. 3g), while there was no clear trend for functional evenness across depth for both fish and benthos (Fig. 3c, h). Furthermore, there were several positive correlations between taxonomic-based and functional-based diversity metrics, most notably between species/morphotype richness and functional richness (Pearson's correlation coefficient, $\rho = 0.87$ and 0.84 for fish and benthos, respectively) (Fig. 4).

Functional beta diversity comparisons between depths indicated moderate trait composition dissimilarity for fish (Jaccard dissimilarity index between 0.2 and 0.6), and comparatively higher levels for benthos (Jaccard index mostly >0.6) (Fig. S4). Those dissimilarities were mostly driven by differences in species richness in the case of fish, while morphotype replacement was more important for benthos.

Focusing at taxon-level functional metrics, average functional contribution per taxon, which indicates how much a taxon adds to the total trait space in a specific depth (Fig. 1), was comparable across depths (Fig. 3d, i). One exception were fish species at 250–350 m that had negative contribution values (Fig. 3d), which indicates functional redundancy (Fig. 1b) while the opposite was the case for benthos at 10 m. Average functional originality per taxon was higher at 10 m and 250–350 m and lower at 60 m for fish (Fig. 3e) indicating taxa with less unique traits (generalists) at 60 m and vice versa, while for benthic taxa, originality increased from the shallow to the deeper reefs indicating an increase of specialist taxa with depth (Fig. 3j). Finally, focusing on the average functional contribution and originality per taxon across all studied depths, the greatest contributors were consistently taxa occurring on deep reefs, between 60 and 350 m (Fig. 5; Data S4).

3.3. Trait composition patterns with depth

There was a decreasing contribution of low-trophic-level fish with depth (Fig. S5c), with browsing, corallivorous, detritivorous, grazing, excavating and scraping trophic groups being largely restricted to 10 m and occasionally 30 m (Fig. S5p–u, zb). In addition, benthic communities at 10–30 m depth were dominated by benthic primary producers/suspension feeding morphotypes (Fig. S6u), mostly of the Order Scleractinia (Data S3) with mainly a compact morphology (Fig. S6j) (e.g. massive colonies of *Porites*). Benthic organism size was significantly higher at 30–60 m due to dominance of large (up to ~3 m high) *Annella* sea fans at those depths



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(Fig. S6f). Finally, reefs at 10–30 m were home to more organisms with small (<30 and 30–59 m) home ranges (Fig. S5h; S6a–c) compared to deeper reefs.

Reefs between 60 and 350 m, contained more taxa with larger bathymetric home ranges (>60 m) (Figs. S5j–l, S6c–e) than shallower reefs, as well as more mobile benthic taxa (Fig. S6g). Moreover, they contained proportionally more fast-reproducing fish species such as anthiades (*Pseudanthias* spp.) (Data S2, S3), and occasionally more piscivorous and omnivorous fish (Fig. S5x, y, za) many of which are commercially important (e.g. groupers - *Cephalopholis* and *Epinephelus* spp., two species were exclusively found between 10 and 30 m versus nine species found between 60 and 350 m; Data S2). Finally, more top-heavy benthos (i.e. body biomass concentrated at the upper part of the organism) was present in 60–350 m, including several species of Plexauridae and Paragorgiidae sea fans and branching black corals (Data S2, S3).

3.4. Trait–environment relationships

None of the abiotic variables collected or estimated in this study, (water chemistry, substratum or terrain-related variables), were significantly associated with any fish trait modalities (Fig. S7). There were, however, many significant associations between benthic trait modalities and abiotic variables (Fig. S8). Specifically, dissolved oxygen concentration and coral rubble were positively associated with traits such as very low (<30 m) home range, primary producers and high compactness, such as massive scleractinian colonies of *Dipsastraea*, *Favites* and *Porites* that often dominated degraded reefs ≤ 30 m. On the contrary, structural complexity (i.e. VRM), orientation, and sediment veneers, the latter more likely to be characteristic of reefs ≥ 60 m, were associated with top-heavy taxa (e.g. sea fans or branching whip corals), suspension and deposit feeders, mobile taxa (e.g. sea stars and sea urchins) and/or those with larger home ranges (≥ 60 m).

4. Discussion

Despite deep reefs having a higher geographic areal extent than their shallower counterparts (Montgomery et al., 2019), key information on deep reef biodiversity and functioning is largely missing, in part making them a low conservation priority worldwide (Turner et al., 2019; de Oliveira Soares et al., 2020), including the Seychelles and the wider Western Indian Ocean region (Stefanoudis et al., 2022). This is despite the fact that deep reefs are affected by many of the disturbances present in shallow reefs including thermal stress, cyclones, overfishing and invasive species (Bongaerts et al., 2013; Frade et al., 2018; Smith et al., 2019; Eyal et al., 2022). Here, we provide baseline information on the biodiversity, trait composition and functioning of Seychelles' deep reefs, representing a region that has particularly poorly-described deep reefs (Pyle and Copus, 2019).

4.1. Taxonomic diversity patterns across depth

Our taxon-based analysis revealed distinct fish and benthic communities at 10 m, 30 m, 60 m, 120 m and 250–350 m, showcasing the unique biological nature of deep reefs in the WIO region (Osuka et al., 2021) and supporting this as a global pattern (Rocha et al., 2018). We found depth-related decreases in community metrics with depth (abundance, biomass, richness), similar to that previously reported for tropical reef fish (Pyle et al., 2019; Stefanoudis et al., 2019a; Swanborn et al., 2022b) and benthos (Stefanoudis et al., 2019b; Swanborn et al., 2022a).

4.2. Reef characteristics across depth based on dominant traits

Reefs at 10–30 m contained higher abundance and biomass of fish and benthos than at deeper depths (Fig. 2a, b, d). Most of the scleractinian coral colonies were compact, (Fig. S6j); this form is less susceptible to thermal stress, such as during the 2014–2017 global bleaching event (Cerutti et al., 2020), and thus provide continued reef matrix stability. Notably, shallow reefs contained more lower-trophic-level fish than deeper reefs (Fig. S5c, u, zb). These are generally of lesser value to fisheries but important for coral reef health as they control coral-algal dynamics (Samoilys et al., 2019). Many of them are also coral-dependent, hence, any future disturbance of reefs also puts these fish communities at risk (Graham et al., 2015).

Deep reefs at 60–350 m had greater diversity of traits, compared to shallower reefs, that are indicative of less disturbed and potentially more resilient environments. For example, more species of the commercially important groupers were present below 30 m, and while some of them might reside there due to habitat preference (Osuka et al., 2022), the fact that many are known to also occur in shallow reefs, but were not seen there, indicates potentially lower levels of fishing pressure at deep reefs. In fact, due to their remoteness, all studied coral atolls have low levels of commercial fishing in deeper waters, with recreational fishing largely occurring in the top 50 m. Subsistence fishing occurs in the shallows, but has minimal impact due to the small resident populations (average of 100 per island). In addition, below 30 m more fish species with fast reproduction rates were present (Fig. S5g), there were also more mobile benthic taxa (Fig. S6g), and overall more taxa with larger bathymetric ranges (Figs. S5j–l, S6c–e), all of which suggest the ability to recover faster from disturbance events through repopulation or avoiding disturbance altogether via vertical migration. This inferred resilience is likely to be higher for fish rather than for benthos, considering that only 18 % of recorded benthic taxa are mobile (Data S3), and fewer benthic taxa have large home ranges (56 % of recorded fish taxa vs. 32 % of benthic taxa). However, the above finding comes with an important caveat. The overall lower levels of richness and abundance at depth, especially in the case of fish at 250–350 m (Fig. 2a–c), means that even a small loss of species could lead to the disappearance of whole traits – and thus possible ecosystem functions – from the community. Moreover, deep reefs at 60–350 m comprised more top-heavy benthic taxa such as sea fans, which enhance habitat complexity and provide habitat and shelter for a variety of invertebrates and fish (Boland and Parrish, 2005).

Finally, while we detected some significant trait–environment associations for benthos, mostly corresponding to the contrasting abiotic conditions prevalent in shallow and deep reefs, respectively, we did not find any for fish. The latter could be due to the mobile nature, and hence, large home ranges of fish that exceed the size of the survey areas covered here, which might have compromised detection of accurate trait–environment relationships (Kendall et al., 2011).

4.3. Reef trait diversity patterns across depth

We found that, compared to reefs at 10–30 m, deeper reefs at 60–350 m had lower functional richness (Fig. 3a, f), meaning that they supported fewer traits. This confirms our first hypothesis of decreasing functional richness with depth. The positive correlation between taxonomic and functional richness reported here, which has previously been shown for shallower reef-fish communities up to 50 m (Stuart-Smith et al., 2013; Parravicini et al., 2014), indicates that ecosystem protection would preserve trait diversity, and thus,

Fig. 2. Taxonomic diversity and composition changes across depth, as identified by Kruskal-Wallis (a–e) and Principal Component Ordination analysis (f–i). (a) total fish abundance against depth, (b) total fish biomass against depth, (c) fish species richness against depth, (d) benthic abundance against depth, (e) Benthic morphotype richness against depth. Boxes (a–e) indicate median, and the 25th and 75th quantiles, whiskers are 1.5 times the interquartile. Columns sharing the same roman numeral indicate statistically significant differences ($p \leq 0.05$) based on Mann-Whitney pairwise tests applied with a Bonferroni correction. (f–i) Principal coordinates analysis ordination on sqrt-transformed fish abundance (f), fish biomass (g), benthic abundance (h) and benthic presence-absence (i), using Bray-Curtis similarity resemblance matrix. Axes describe percentage variation in terms of total fish community structure. Dotted lines indicate statistically distinct clusters (PERMANOVA pairwise comparisons against all other depths, $p \leq 0.05$).

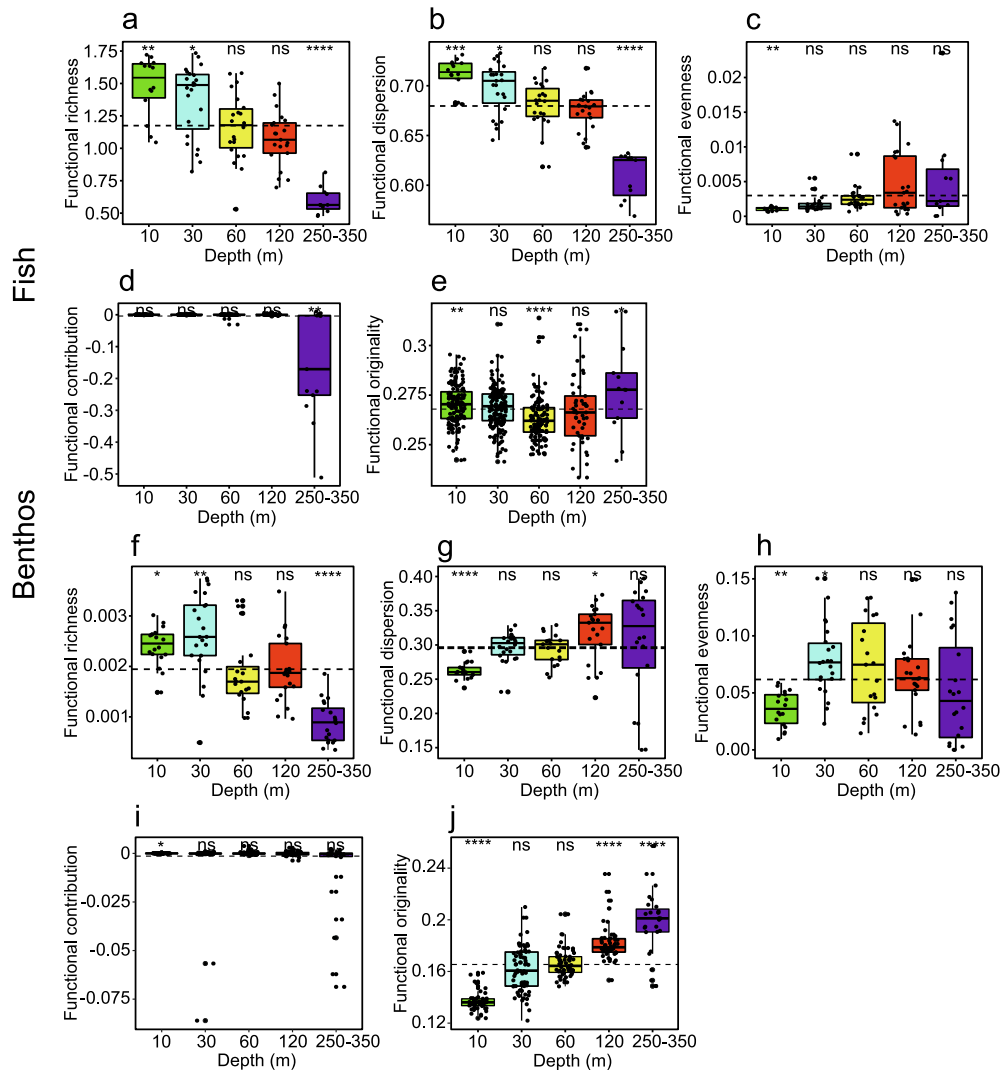


Fig. 3. Functional diversity changes across depth. Boxplots showing functional richness, dispersion, evenness, contribution and originality of fish (c–g) and benthic (h–j) communities. Boxes indicate median, and the 25th and 75th quantiles, whiskers are 1.5 times the interquartile. Dotted line represents the global average across all depths. Asterisks indicate significant differences against the ‘global’ (all depths combined) community average as identified by pairwise Mann-Whitney comparisons at the 0.05 (*), 0.01 (**), 0.001 (***) and 0.0001 (****) level, respectively; ns = not significant.

potentially ecosystem functions. However the link between specific traits and ecosystem functions is, in most cases, theoretical (Bellwood et al., 2019), so establishing those relationships in the future will be key to target those traits that lead to favourable reef ecosystem states.

Compared to shallow reefs, reef communities between 60–350 m were less dispersed in the case of fish (Fig. 3b), with species having traits that are more similar to each other, but more dispersed in the case of benthos (Fig. 3g). This indicates that deep-reef fish communities are likely more resilient to species-specific disturbances (e.g. fisheries targeting particular species). However, if the disturbance affects all taxa indiscriminately (e.g. bottom trawling; thermal stress), this would not follow. This observation partly confirms the second hypothesis of decreasing functional dispersion, and thus potential increasing resilience of fish communities with depth. This finding is also supported by the negative functional contribution values of fish at 250–350 m indicative of trait redundancy (Mammola et al., 2021). However, since taxon richness is in general much lower on deep reefs (Fig. 2c, e); (Pyle et al., 2019; Stefanoudis et al., 2019b) the loss of even a few taxa, that tend to have a proportionally higher functional originality (Fig. 3e), might lead to the loss of whole traits from the community, ultimately casting doubts over the resilience of deep-reef fish communities to disturbance.

Finally, fish and benthic community traits at 60–350 m were overall more even compared to those at 10–30 m indicating fewer dominant traits at deeper depths (Fig. 3c, h). Ecologically, this means that deep reefs could be less prone to species invasions since fewer niches remain underutilised compared to shallower communities. This mostly contradicts the third hypothesis that predicted a less even trait space with increased depth, where some taxa and traits were suggested to be more dominant compared to others as a result of habitat filtering (Cornwell et al., 2006), as has been reported from other environmentally extreme ecosystems including caves (Gibert and Deharveng, 2002), hydrothermal vents and cold seeps (Tunnicliffe and Cordes, 2020). It is possible that limited energy availability at depth (Carney, 2005), which is evidenced by the reduction of photosynthetically active radiation and fluorescence at depth across our study locations (Woodall and Rivers, 2019), has prevented taxa to competitively exclude other taxa, and hence, for particular traits to dominate, eventually leading to a homogenous trait space.

Comparisons with other trait-based studies from tropical reefs are difficult since most primarily focus on depths <50 m or focus on different facets of functional diversity (Darling et al., 2012; Stuart-Smith et al., 2013; Denis et al., 2017; McWilliam et al., 2018; McLean et al., 2021). Nevertheless, high functional richness coupled with low redundancy was also reported for Seychelles' Inner Islands shallow-reef fish communities (McLean et al.,

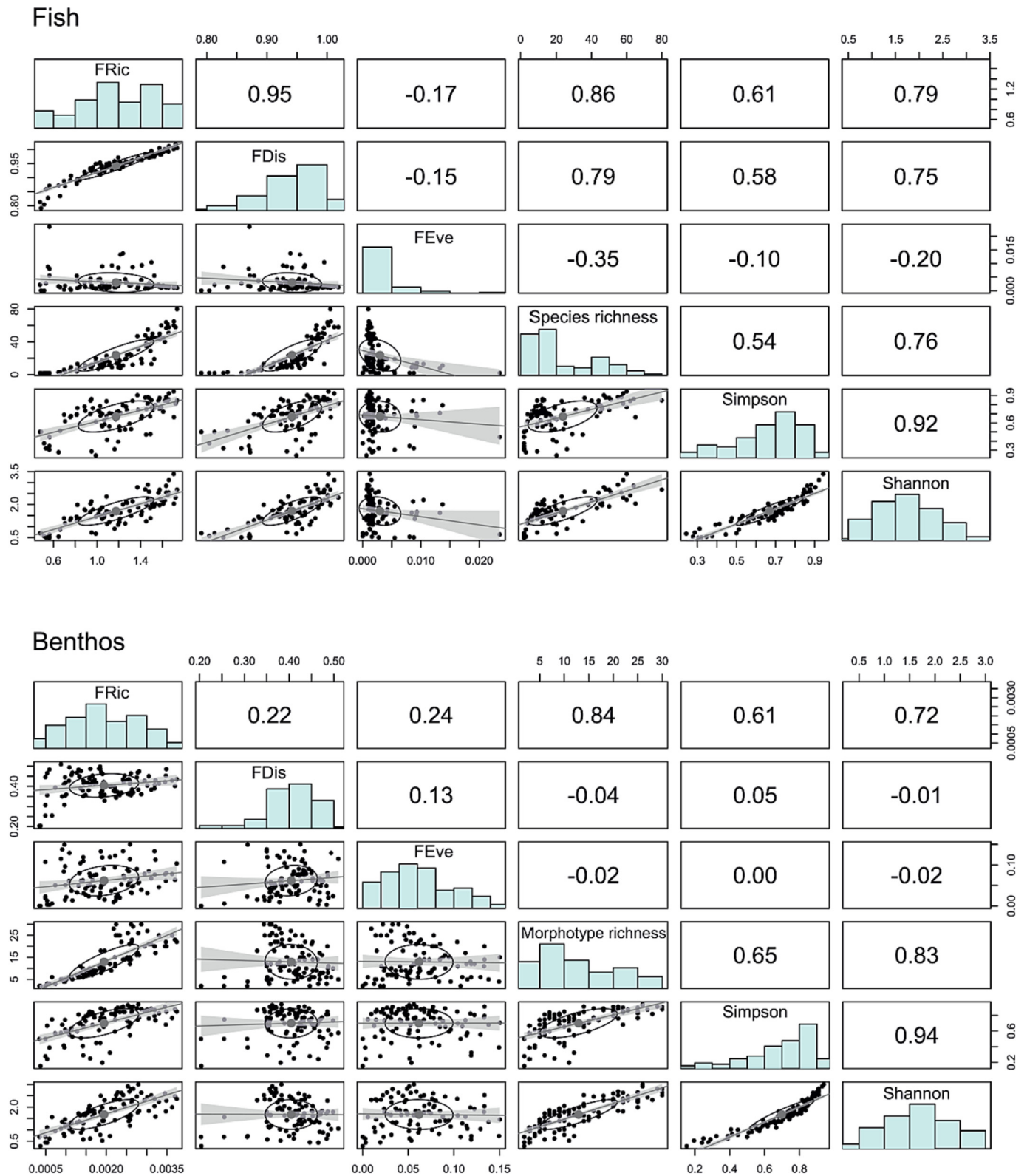


Fig. 4. Person's correlations between functional-based and taxonomic-based diversity metrics for fish (upper plots) and benthos (lower plots), respectively. FRic = Functional richness, FDis = Functional dispersion, FEve = Functional evenness.

2019), while low functional redundancy has been found for shallow tropical reef-fish communities in the eastern Atlantic (Bosch et al., 2021).

Although our results indicate specific patterns in the functional traits of communities across depths, additional studies on deep reefs need to be undertaken to elucidate any general patterns.

4.4. Deep reef conservation value

In the case of limited available resources for marine management, more effort might be diverted towards conserving those species that are functionally original and contribute most to the functional richness of an ecosystem

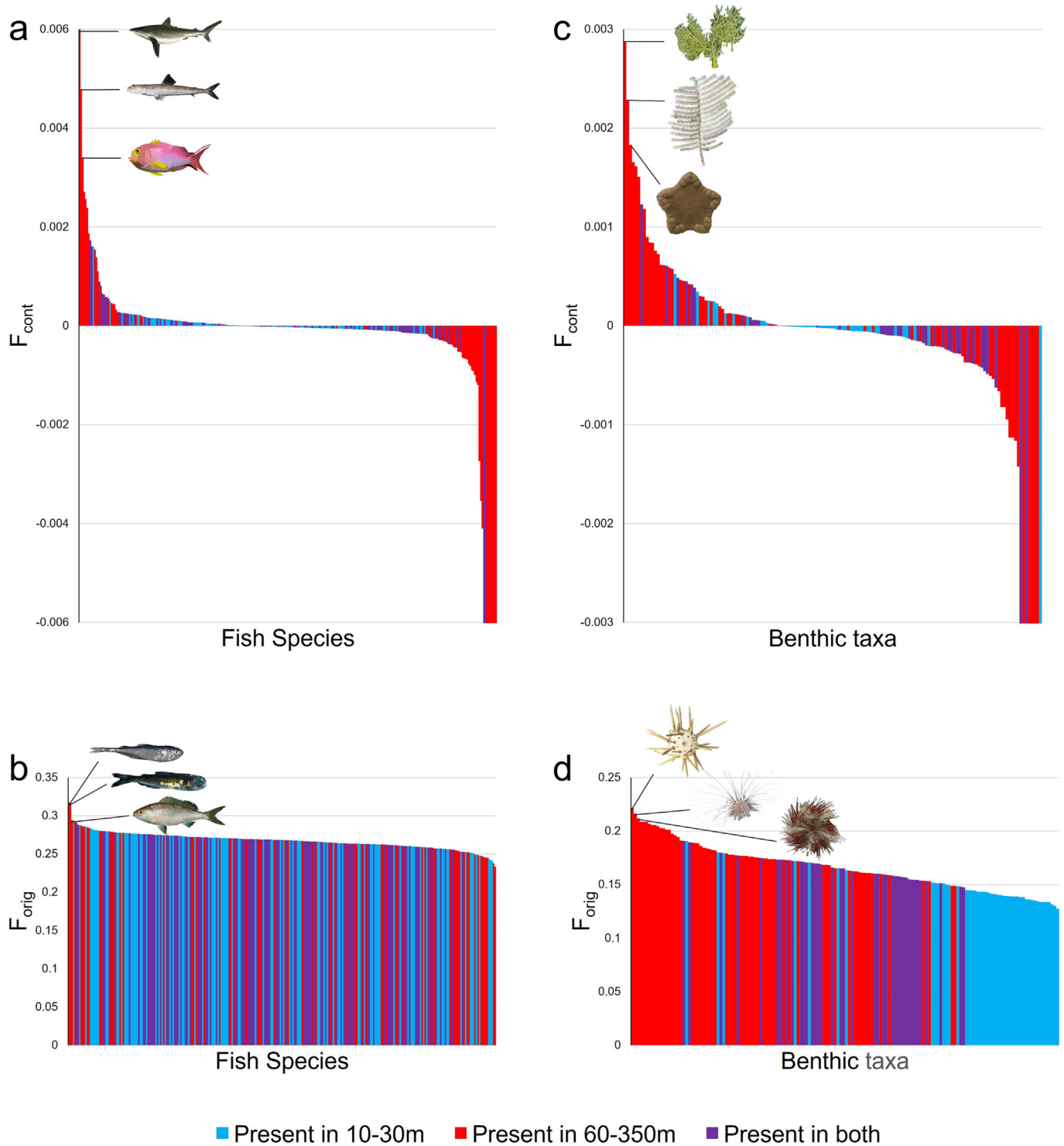


Fig. 5. Taxon contribution to functional richness (i.e. functional contribution; F_{cont}) and dispersion (i.e. functional originality; F_{orig}) across fish and benthos. Bars represent mean values for each taxon across all transects they have been observed. (a) F_{cont} for Fish, Top species: *Carcharhinus albimarginatus*, *Synodus* sp., *Meganthias* sp. (b) F_{orig} for Fish, Top species: *Centrobranchius nigroocellatus*, *Myctophum* sp., *Pristipomoides* sp. (c) F_{cont} for Benthos, Top morphotypes: Plexauridae sp. 11, *Bathypathes* sp., *Sphaeriodiscus*. (d) F_{orig} for Benthos, Top morphotypes: Cidaroida sp. 2, Aspidodiadematidae sp., *Micropygia* spp. Note that 23 fish and 8 benthic taxa had functional contribution values that exceeded the lowest limit of the y axis in (A) and (C) and are therefore not illustrated.

(Pimiento et al., 2020). In the present study, taxa that were found exclusively in reefs below 30 m consistently topped functional contribution and originality metrics both in the case of fish and benthos (Fig. 5), highlighting the importance of deep reefs from a trait-based perspective. Many of those top benthic taxa were sea fans that provide habitat and shelter for numerous organisms (Boland and Parrish, 2005), which

indicates the value of excluding seabed disruption activities that might damage such top-heavy taxa. Furthermore, several taxa found inhabiting deep reefs in this study are of conservation concern (vulnerable or near-threatened - IUCN), including species of shark (*Alopias pelagicus*, *Carcharhinus albimarginatus*, *Galeocerdo cuvier*), sunfish (*Mola mola*) and grouper (*Epinephelus fuscoguttatus*) (Data S2; Woodall and Rivers,

2019), further indicating the value of deep reefs from a conservation perspective.

5. Conclusions

By combining taxonomic and trait-based analyses we were able to provide a nuanced assessment of the ecology and ecosystem functioning of shallow and deep reef habitats. The unique trait composition and diversity patterns of shallow and deep reef communities, which also occasionally differed between fish and benthos, indicated that there is a complex picture when it comes to reef resilience against disturbance or species invasions. These findings highlight that depending on the desired conservation outcomes there might be a need to explicitly consider deep reefs in marine management and planning activities.

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CRediT authorship contribution statement

L.C.W. and P.V.S. conceived and designed the study, directed and oversaw fieldwork data collection, the latter with the help of K.S.-N., S.T. and N.F. L.C.W. served as the chief scientist on the First Descent: Seychelles Expedition. P.V.S., N.F. and S.W. annotated the collected video and imagery for biological and substratum data. Final taxonomic identifications were overseen by P.V.S., N.F. and K.S.-N. for benthos, and P.V.S. and M.S. for fish. J.H. collected and processed the water-chemistry data. D.S. collected and processed the seabed structure data. P.V.S. collected the trait data. All authors co-decided the direction of the manuscript and analyses during several online meetings. P.V.S. carried out the statistical analysis and prepared the tables and figures. The manuscript was drafted by P.V.S. with the assistance of L.C.W. All authors reviewed the manuscript and gave final approval for publication.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Material.

Declaration of competing interest

Authors declare that they have no competing interests.

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