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# **Coral Reefs**

## **Mesophotic reefs are not refugia for neither taxonomic nor functional diversity of reef fishes**

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*Keywords*: Coral reef, functional traits, beta diversity, video surveys, Western Indian Ocean

*Data availability*: All code and data will be provided on <https://github.com/LoiseauN/Bubot>

On behalf of all authors, the corresponding author states that there is no conflict of interest.

## ABSTRACT

Mesophotic reefs, defined as reefs between 30 m - 150m, have been less investigated than their shallower counterparts. Yet, more protected from human activities and bleaching events, they could be refuge zones allowing the resilience of shallow reefs. However, it is currently unknown if their role as refugia for species diversity also extends to functional diversity and thus potentially ecosystem functioning. Using an extensive video field surveys from Mayotte Island in the Western Indian Ocean, we analyzed how taxonomic diversity and functional diversity of coral reef fishes changed along a depth gradient from 10 to 100 m. We found that shallow and mesophotic reefs host different species, but that these dissimilar assemblages share similar richness combinations of traits values. However, when accounting for biomass of species, it appears that functional structure of assemblages differs along the depth gradient, with, for instance, herbivorous fishes being very scarce in deep reefs while large-bodied carnivorous are more abundant. Therefore, surveys of mesophotic fishes should assess not only species, but also trait composition, abundance and biomass. Overall, our results support the claim that extending marine protected areas to mesophotic reefs is required to maximize the protection of both species and functional diversities to eventually maintain coral reef ecosystem functioning and associated services across the broader seascape.

*Keywords: Coral reef, functional traits, beta diversity, video surveys, Western Indian Ocean*

## INTRODUCTION

Coral reefs cover close to 300,000 km<sup>2</sup>, which is just under 0.1% of the oceans' surface area (Spalding et al. 2001). Despite this restricted cover, coral reefs are one of the world's most diverse and productive ecosystems, supporting prodigious biodiversity and providing important ecosystem services to many millions of people. In fact, over 4,000 species of teleost fishes are associated with coral reefs (Sale 2013). Fishes are central to reef ecosystems, providing essential ecological functions such as biomass production, regulation of foodwebs, nutrient cycling and sand formation among others (Villéger et al. 2017; Brandl et al. 2019). Fishes also provide food security to hundreds of millions of people (Sala et al. 2021). However, coral reef fishes are severely affected by overexploitation, habitat loss and climate change, especially through marine heatwaves (Eddy et al. 2021). In response to this “coral reef crisis,” studies around the world have examined the social, institutional, and environmental conditions that influence fish biodiversity and ecosystem functions (Cinner et al. 2016, 2020). However, most of these studies focused on shallow (< 30m) reef communities (Rocha et al. 2018). As a result, the distribution, abundance and function of fish assemblages that occupy the deeper range of reefs are less known compared to shallow reefs. In other words, variation of the large diversity of biological traits (e.g. size, diet, mobility, behavior; (Villéger et al. 2017), and their participation in core processes (Brandl et al. 2019) along depth gradients remains largely unknown (see however Cure et al. 2021 and Carrington et al. 2021). Yet, unraveling the distribution of fishes and of their traits across depth is critical for effective ecosystem-based fisheries management (Lindfield et al. 2016).

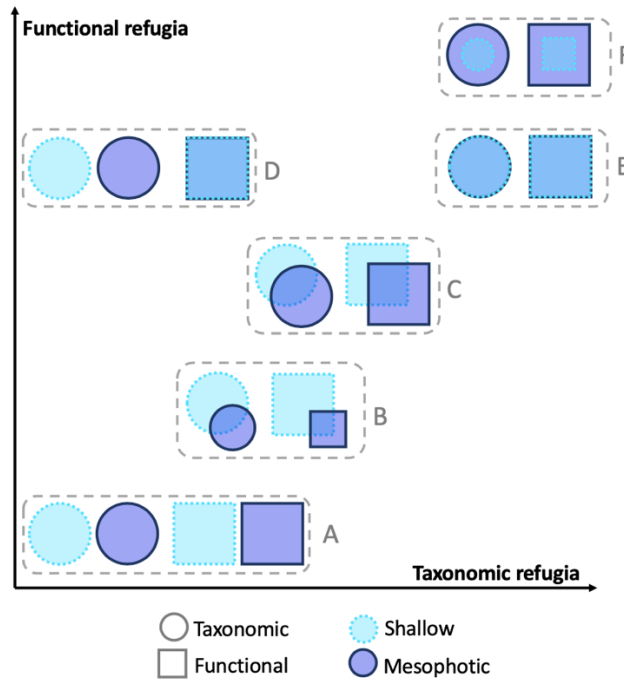
Mesophotic coral ecosystems occur in the deeper parts of the ocean's photic zone, with depth ranging from 30 to 150 m (Eyal et al. 2021), experience reduced temperatures and light, and may be protected from localized anthropogenic stressors such as pollution and fishing. This suggests that cooler conditions in deeper coral reefs could buffer the impacts of the strongest

stressors affecting fishes in shallow water. The deep reef refugia hypothesis emerged from genetic connectivity research (Lesser et al. 2009; Bongaerts et al. 2010; Assis et al. 2016) and was reinforced by the fact that many coral reef species occur across a wide depth range (Rocha et al. 2018; Medeiros et al. 2021). However, the increasing frequency and severity of marine heatwaves (Oliver et al. 2018; Venegas et al. 2019), and accumulating reports of impacts reaching mesophotic depths (Jackson et al. 2001), cast doubt on the ability of depth refuges to provide protection to fish communities over the long-term (Rocha et al. 2018).

A refugium is defined as an “habitat where some components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions” (sensu, Keppel et al. 2012). The role of refugia to protect species from extinction has been assessed worldwide for different taxa (Pellissier et al. 2014; Brown et al. 2020). However, biodiversity is multifaceted and includes other components in addition to the number of species. A largely unexplored dimension of the role of refugia is their effects on functional diversity, despite the importance of functional diversity for community and ecosystem functioning. In other words, the ability of refugia to fully encapsulate diversity has been poorly investigated, especially as it relates to their capacity to reduce the loss of ecological function (Ordóñez and Svenning 2015). This is particularly true for mesophotic reefs. Indeed, despite the hypothesis suggesting that mesophotic reefs could be refugia for reef biodiversity (Jankowski et al. 2015; Lindfield et al. 2016; Coleman et al. 2018; Rocha et al. 2018; Stefanoudis et al. 2019), there is still a critical lack of evaluation of their role as refugia for species and trait diversity of fishes (Carrington et al. 2021; Cure et al. 2021).

Thus, considering the multifaceted definition of biodiversity, the mesophotic reef refugia hypothesis could follow several expectations, depending on similarity in species and trait diversity between shallow and mesophotic reefs (Figure 1): (1) Enriched full refugia: mesophotic reefs host the same species and trait composition as shallow reefs, plus host unique species and traits not observed in shallow reefs; (2) Full refugia: mesophotic reefs host the same species and traits composition than shallow reef while maintaining the same biomass distribution among species; (3) Functional refugia: mesophotic reefs host different species than shallow reefs but these distinct species have the same trait values; (4) Not refugia: mesophotic and shallow reefs host distinct species and traits composition.

Here, we tested the potential refugia role of mesophotic ecosystems for multiple facets of fish diversity using a video-based survey in coral reefs from Mayotte (an island in the Western Indian Ocean), along a depth gradient from 7.8 to 99.7 m. More specifically, we analyzed how taxonomic and functional diversity and composition of coral reef fishes changed along the depth gradient.



	Taxonomic		Functional	
	$\Delta$ Richness	Dissimilarity	$\Delta$ Richness	Dissimilarity
<b>A</b>	0	1	0	1
<b>B</b>	< 0	$\approx 0.5$	< 0	$\approx 0.5$
<b>C</b>	0	$\approx 0.5$	0	$\approx 0.5$
<b>D</b>	0	1	0	0
<b>E</b>	0	0	0	0
<b>F</b>	> 0	$\approx 0$	> 0	$\approx 0$

Figure 1: A multifaceted approach to test whether deep reefs are refugia for taxonomic (circle) and functional (square) facets of biodiversity. The size of a circle or square represents the taxonomic or functional richness of an assemblage while overlapping represents similarity in species or functional composition between assemblages from mesophotic and shallow reefs. The associated table shows the expected value of four diversity metrics for each scenario.  $\Delta$ Richness is the difference in richness between mesophotic and shallow and dissimilarity is the proportion of richness not shared by shallow and mesophotic reefs. A: No refugia, mesophotic and shallow reefs host highly distinct species and trait combinations. B & C: Partial refugia, shallow and mesophotic reefs share a subset of species and traits but also a proportion of unique species and traits, in B, shallow reefs host more species and trait combinations than mesophotic reef. D: Functional refugia, mesophotic reef host dissimilar species communities from shallow reefs, but similar traits composition. E: Full refugia, mesophotic reefs host the same composition of species and hence of traits as shallow reefs. F: Enriched full refugia, mesophotic reefs host all the species and trait combinations present in shallow reefs, plus host unique species which have unique traits (absent in shallow reefs).

## MATERIALS AND METHODS

## Underwater video surveys of coral reef fishes

Mayotte is a volcanic island (360 km<sup>2</sup>) in the northern Mozambique Channel and is surrounded by one of the world's largest lagoons (area of ~1500 km<sup>2</sup> surface). The coral reefs of Mayotte hosts more than 700 fish species (Wickel et al. 2014), but recent and rapid human development (annual growth rate higher than 4%, Marie et al. 2018) is driving fast-paced change across the coral reef communities.

The choice of study sites was made using two complementary tools: observation of the habitat using rosette cameras and a 3D reconstruction of the site using data collected by the boat's sounder. The rosette camera system consisted of four cameras oriented in four different directions. This system was manually lowered to the bottom over the point of interest using a rope and the videos were viewed afterwards. For the 3D reconstruction, latitude, longitude and depth coordinates were recorded every second using a GPS plotter sonar (Lowrance, HDS10). These traces were then used to reconstruct the 3D profile of the substrate using the *raster* (Hijmans et al. 2015), *gstat* (Pebesma and Heuvelink 2016) and *sp* (Bivand et al. 2008) R packages (Figure 2). Using this information, we selected six sites along the west coral reef barrier of the island with as much similarity as possible in coral cover and complexity within each four different depths, ranging from 7.8 to 99.7 m deep (Figure 2).

Fish communities were surveyed using a non-baited remote underwater stereovideo system, which is a cost-effective technique for surveying reef fish across a range of depths and habitats and beyond the limits of regular scientific diving (Mallet and Pelletier 2014). We chose non-baited video systems to avoid over-representation of piscivore species. The stereovideo system consisted of two digital cameras (GoPro Hero 4+ and Hero 3+) inside 150m-rated housings mounted on an aluminum bar, 80 cm apart and each oriented 8° inward using 3D printed mounts to maximize pictures overlap 5 m away (Letessier et al. 2015). Four PVC legs (length 60 cm), each weighted with 1 kg, were attached under the bar to make a quadripod system. The recording was made using the cameras' medium view setting (84° of horizontal field of view in water) and at full HD definition (1080p) with a frame rate of 30 fps. Calibration of the system was performed using a 2x2x1 m black cubic frame with white dots of known coordinates situated 4 m from the system underwater. Distortion of the cameras was calibrated with an 80x50 cm chessboard situated 1 m from the cameras underwater (Neuswanger et al. 2016). Measurement accuracy was verified by filming a graduated ruler underwater with each system.

Each of the 6 sites was surveyed several times (between 9 and 64 times,  $20.2 \pm 21.6$ , mean  $\pm$  sd) from 26-Feb to 23-Mar 2019. All surveys were performed between 9:00 and 17:00. Weather ranged from warm and calm sunny days to rainy and windy days with as much as 1.5 m waves in that period. Current did not exceed 0.8 knots. To minimize fishes moving between drops, and potential spatial pseudo-replication, the four depths within a site were simultaneously surveyed, and video systems within a depth level were dropped at least 100m apart from each other (Langlois et al. 2020). Videos recording lasted from 55 minutes to 171 minutes ( $98.9 \pm 36.3$ ).

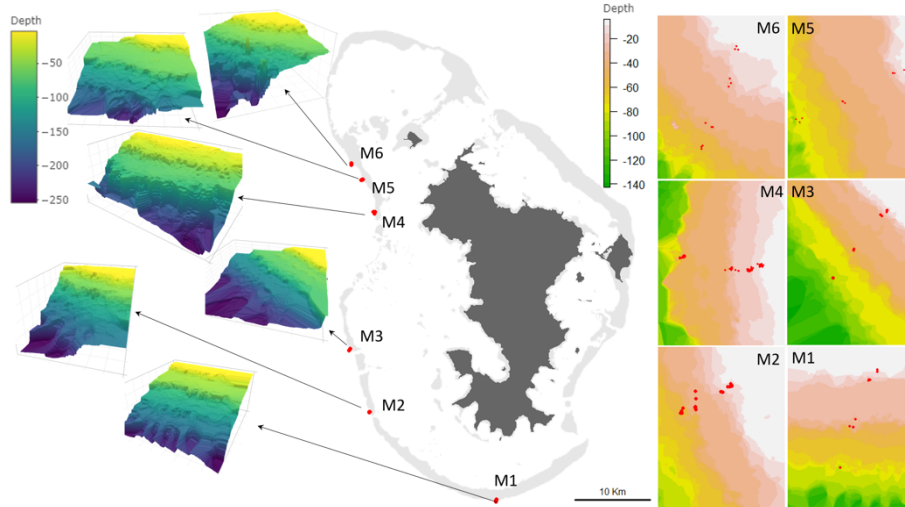


Figure 2: Location of surveyed sites around Mayotte Island in the SW Indian Ocean. On the left, the 3D reconstruction of each site and on the right each red dot represents a drop of a remote underwater camera.

### Video analyses

We analyzed data from 121 drops (i.e., assemblages with fewer than five species were not included). For each video, the first two minutes were not analyzed to limit disturbance due to the video system deployment. As the total duration of video recorded varied among sites and depth level, and as analyzing stereovideos is a demanding task we analyzed five, one-minute non-overlapping sequences randomly selected within each recording. Hence, we keep a constant sampling effort across all replicates for estimating abundance of fish species, even if this sampling effort did not allow to reach the asymptote of the species accumulation curve (Supplementary materials, Figure S1). For each of these sequences, all fishes up to 5 m from the camera were counted and identified to the lowest possible taxonomic level. Abundance of each species was estimated as the maximum number of individuals of each species observed in a single frame during each one-minute sequence (MaxN; Ellis 1995). A total of 12,891 individuals (50%) belonging to 182 species were identified. 2206 individuals were identified at the genus level (44 genera) and 10,382 (40%) at the family level (26 families). We also did not consider cryptobenthic species (Apogonidae [7 individuals], Gobiidae [33 individuals] and Chondrichthyans [30 individuals]). Because a high proportion of individuals were not identified at the species levels, we also tested the sensitivity of our analyses to the taxonomic resolution by rerunning our analyses at the genus level. Size calibration calculation and 3D fish measurements were all performed using the open-source software VidSync ([www.vidsync.org](http://www.vidsync.org)).

### Biomass estimation

Measuring manually each individual for the 121 videos was impractical given their number. Thus, we measured all individuals for 45 videos (for a total of 7h18min) at one of the six sites. Then, for each individual in the present study, we assigned the measured average size at the lowest taxonomic level (species, genus, family) possible according to available data. This process may reduce the dissimilarity in species size between shallow and mesophotic reefs. However, comparison of the distribution in size between shallow reef (from 0 to 30m) and mesophotic reef (from 30 to 99m) for the most measured common species (37) show that body size did not

significantly vary across the depth gradient (Supplementary materials, Figure S2). Some species or genera were not observed at the selected site for fish measurement (59%). Thus, we associated the average size for the given taxonomic level from the Reef Life Survey database (highly correlated with the average size from our dataset,  $\text{cor} = 0.78$ ,  $\text{p-value} < 0.001$ , <https://reeflifesurvey.com/>, Edgar et al. 2020).

### Functional traits

Five traits linked to the key functions performed by fishes were selected: Diet, Position in the water column, Gregariousness, Activity, Mobility, Size. These traits linked to food acquisition, locomotion and behaviour are a proxy of the ability of each species to impact ecosystem processes. Values were taken from the dataset used by (Mouillot et al. 2014). Diet characterized each species' main food source and was coded using seven categories: herbivore and detritivore, macro-algae herbivore, sessile invertebrate feeder, mobile invertebrate feeder, planktivore, piscivore and omnivore. Position in the water column was coded using four ordered categories: benthic (sedentary on the bottom), demersal (swimming near the bottom), pelagic site-attached (swimming off the bottom within a reef), and pelagic mobile (swimming off the bottom between reefs). Mobility was coded using three ordered categories: sedentary, mobile within a reef, and mobile between reefs. Active period was coded as either diurnal (active during the day), nocturnal (active during the night) or both. Gregariousness was coded using five ordered categories from solitary to large schooling. Body size was coded using six ordered categories: 0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm, and >80 cm. For individuals identified at the genus or family level, we used the average modality of each trait for the given genus or family. Functional distance between all pairs of species was computed using Gower's metric (Gower and Legendre 1986).

### Taxonomic and functional diversity

To evaluate the influence of depth on reef fish diversity of each assemblage we applied a framework based on a generalization of Hill numbers to measure taxonomic and functional diversity in all assemblages (Chao et al. 2019). Hill numbers provide a parametric family of diversity indices, differing by a parameter “ $q$ ” that determines their sensitivity to species relative abundances, all expressed in the same unit as “equivalent number of species” (*sensu* species with even dominance and even functional distance).

Taxonomic diversity was described using two indices: species richness (i.e.,  $q = 0$  indicates that all species have equal weight) and taxonomic entropy (i.e.,  $q=1$ , as exponential of the Shannon index):

$$\text{TD} = e^{-\sum_{i=1}^S p_i \log p_i} \quad \text{Eq (1)}$$

where  $i$  is the number of species in an assemblage and  $p_i$  is the relative dominance (abundance or biomass) of the  $i$ th species.

To estimate functional diversity, we also used the framework from Chao et al. (2019) setting the parameter  $\tau$  to the mean functional distance over all pairs of species:

$$\text{FD} = (\sum_{i=1}^S p_i (\sum_{j=1}^S [1 - f(d_{ij}(\tau))] p_j)^{q-1})^{1/(1-q)} \quad \text{Eq (2)}$$

Functional richness ( $q = 0$ ) was computed with species presence/absence (i.e., all  $p_i$  equals to 1/S):

$$FD = \sum_{i=1}^S (\sum_{j=1}^S [1 - f(d_{ij}(\tau))])^{-1} \quad \text{Eq (3)}$$

Functional entropy ( $q = 1$ ) was computed on species biomass:

$$FD = e^{-\sum_{i=1}^S p_i \log(\sum_{j=1}^S [1 - f(d_{ij}(\tau))] p_j)} \quad \text{Eq (4)}$$

This metric is a generalization of the Shannon entropy with functional distance having equal importance as species dominance.

### **Taxonomic and functional dissimilarities**

The dissimilarity in species and functional entities among assemblages was also computed using the framework of Chao et al. (2019) with, as for alpha-diversity,  $q=0$  (i.e., dissimilarity in composition of species or functional entities) and  $q=1$  (i.e., dissimilarity in dominance of species or functional entities). The dissimilarity indices are bounded between 0 and 1, with 0 indicating identical assemblages (in terms of species or trait values) and values close to 1 indicating a strong dissimilarity in species or functional entities. We applied a depth decay analysis (similar to the distance decay in biogeography, Nekola and White 1999) by comparing the dissimilarity between 0-20m assemblages and each of all other deeper assemblages.

Changes in functional richness and structure through depth were illustrated in a functional space built using Principal Coordinates Analysis (PCoA) computed on functional distances between species. Indices and functional space were computed and drawn using the *mFD* package (Magneville et al. 2022).

### **Habitat predictors**

To include the environment of each assemblage as covariate, we measured variables related to abiotic and biotic habitat recorded by the video systems. It is however important to note that hard substrate was mainly targeted and any results on variation among habitat should be interpreted with caution. For the abiotic variables, we recorded the substrate type (soft, mix, hard), topography, habitat complexity (from 0 to 3), temperature and depth. For temperature and depth measurements, we used a custom-made data logger built by the company Syera (<https://syera.fr/wp/glog/>) and using the Bar30 temperature-depth sensor from the company blue robotics (<https://bluerobotics.com/>). Moreover, categorical abundance of dominant coral biota, sponge, non-scleractinian coral and scleractinian coral were recorded. We performed a principal component analysis of a mixture of numerical and categorical variables (Factor analysis of mixed data, FAMD, using *FactoMineR*). Depth was not included in this analysis. The first four orthogonal PCA axes explained 62% of the total variance in habitat predictors among assemblages and were retained as explanatory variables in the analyses to test environmental influence on fish assemblages (Supplementary materials, Figure S3).

### **Determinants of fish diversity**

We used generalized linear mixed models (GLMMs) to investigate the effect of depth while controlling for environmental differences in the four diversity indices and biomass hypothesized

to influence composition, entropy and traits of reef fish communities. Variables included the first four axes of the environmental FAMD and depth while accounting for the site and date of the sampling as random effects. For each model, we computed marginal  $R^2$  providing the variance explained only by fixed effects and conditional  $R^2$  providing the variance explained by the entire model, i.e., both fixed effects and random effects. Finally, we performed visreg analyses (Breheny and Burchett 2017) to isolate the exclusive effect of depth on diversity after accounting for environmental confounding factors.

### **Determinants of fish dissimilarity**

To test if depth was the best predictor of taxonomic and functional dissimilarities, we applied generalized dissimilarity modelling (GDM, Ferrier et al. 2007). GDM examines the dissimilarities among pairs of assemblages as a non-linear multivariate function of the depth and environment of those assemblages. GDM thus overcomes two potential problems: non-linearity in dissimilarity between assemblages and environmental dissimilarities, and uneven rates of dissimilarities along environmental gradients (Ferrier et al. 2007; Manion et al. 2016). We selected the three I-spline basis function options and accounted for spatial autocorrelation by including the geographic distance between pairs of assemblages as a predictor variable. To assess the impact of each environmental variable, multiple GDMs were run by removing one variable at a time. Percentage contribution of each variable was determined by comparing deviance of the full model to deviance of models without the variable of interest. Variables included the first four axes of the environmental PCA and depth.

## **RESULTS**

### **Diversity of fishes along depth gradient**

Total fish biomass and taxonomic richness ( $q = 0$ ) significantly decreased with depth (Figure 3 & 4,  $p$ -value  $< 0.001$ , Table S1). On average,  $29.3 (\pm 10.7 \text{ sd})$  species were observed between 0-20 m, and  $8.4 (\pm 3.6 \text{ sd})$  beyond 80 m. Taxonomic entropy ( $q = 0$ ) also decreased with depth, but less steeply than taxonomic richness, indicating that decreasing species richness was associated with an increase in species dominance ( $p$ -value = 0.002).

Functional richness values varied from 1.7 to 6.2 among assemblages ( $4.3 \pm 1.0$ , Figure 4). Functional entropy varied from 1.1 to 4.8 among assemblages ( $2.8 \pm 0.7$ , Figure 4). Unlike taxonomic diversity, functional richness and functional entropy were not significantly influenced by depth ( $p$ -value = 0.134, 0.498, respectively, Table S1).

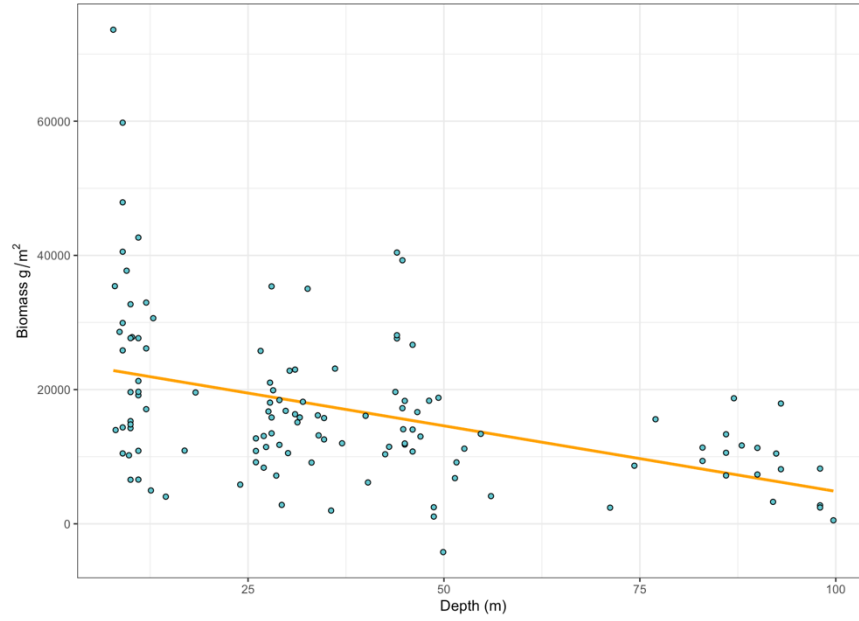


Figure 3 Partial regression plot showing changes in biomass of fish along the depth gradient while accounting for environmental variables. Statistical analyses were carried out using generalized linear mixed models and related statistics are reported in the Results.

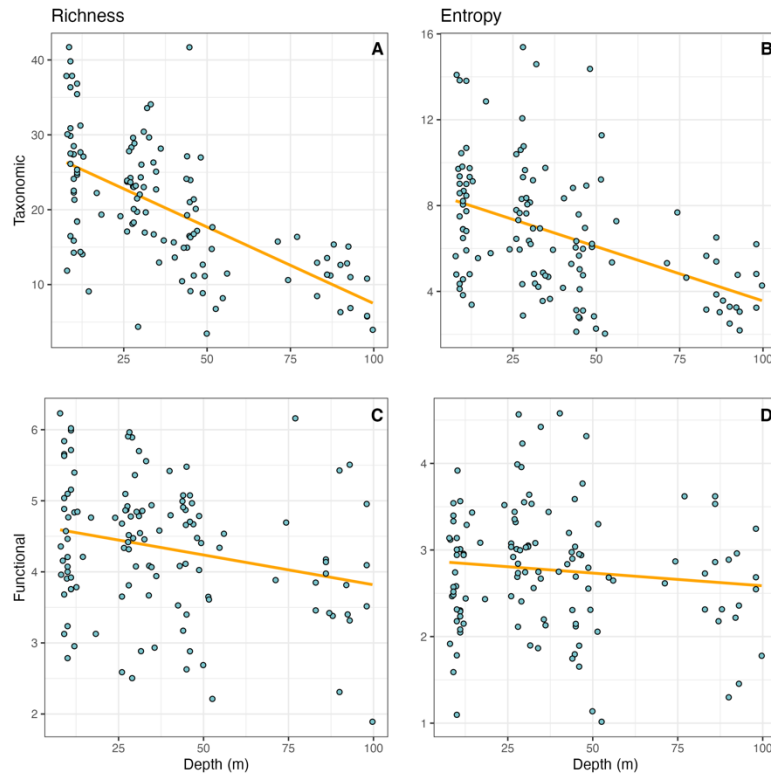


Figure 4: Partial regression plot showing changes in taxonomic richness ( $q=0$ , A) and entropy ( $q=1$ , B) and functional richness ( $q=0$ ,  $\tau$  = mean functional distance, C) and entropy ( $q=1$ ,  $\tau$  = mean functional distance, D) of fish communities along the depth gradient, while accounting for

environmental variables. Statistical analyses were carried out using generalized linear mixed models and related statistics are reported in the Results.

### Dissimilarity of fish assemblages along depth gradient

The dissimilarity in taxonomic composition and structure between assemblages was high overall, ranging from 0.4 to 1 ( $0.86 \pm 0.09$ ) and 0.1 to 1 ( $0.77 \pm 0.2$ ), respectively. The highest dissimilarity values were observed between shallow (0-20 m) and deep assemblages (>60 m) (i.e., high value in the difference in depth axis, Figure 5). Limited dissimilarity in functional composition was observed between assemblages ( $0.13 \pm 0.13$ ). The dissimilarity in functional structure was higher than functional composition ( $0.46 \pm 0.25$ ), highlighting an important change in the distribution of biomass between functional entities. Both taxonomic and functional dissimilarities increased with an increase in depth difference (all p-values < 0.001 and  $R^2$  ranged between 0.30 and 0.47; Figure 5).

The diversity patterns described above were very similar to those computed only with the genus presence and dominance (Supplementary materials, Figure S4 and S5).

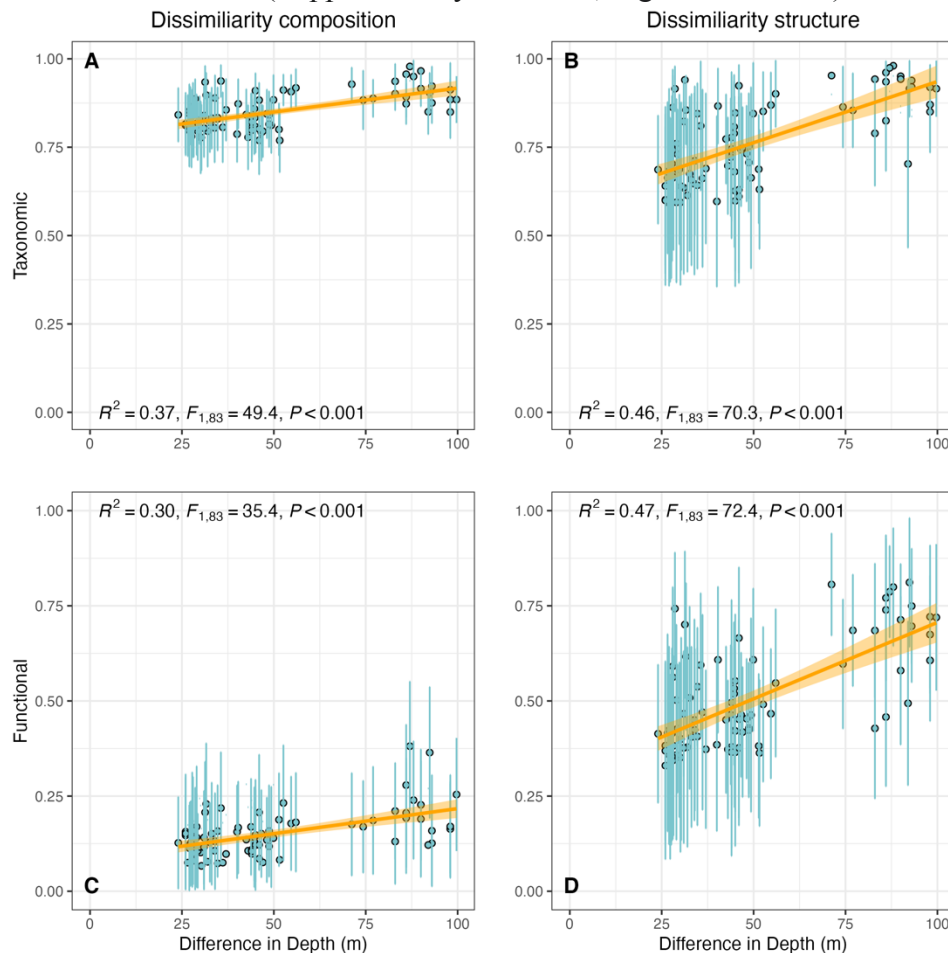


Figure 5: Depth decay of fish diversity, mean dissimilarity (whiskers representing sd) in taxonomic and functional composition and structure between 0-20m assemblages (coded as being at 0m) and each all other deeper assemblages. The first row shows dissimilarity in species composition ( $q=0$ ) and structure ( $q=1$ ). The second row dissimilarity in functional composition ( $q=0$ ,  $\tau$  = mean functional distance) and structure ( $q=0$ ,  $\tau$  = mean functional distance). Yellow lines are linear

regressions (with associated statistics) between the difference in depth and beta diversity indices. Shaded areas represent the 95% confidence interval of the regression.

Finally, the projection of all species along the first two axes of the PCoA confirmed that mesophotic and shallow reefs mostly overlap in functional space but distribution of biomass within this shared functional volume markedly changed (Figure 6).

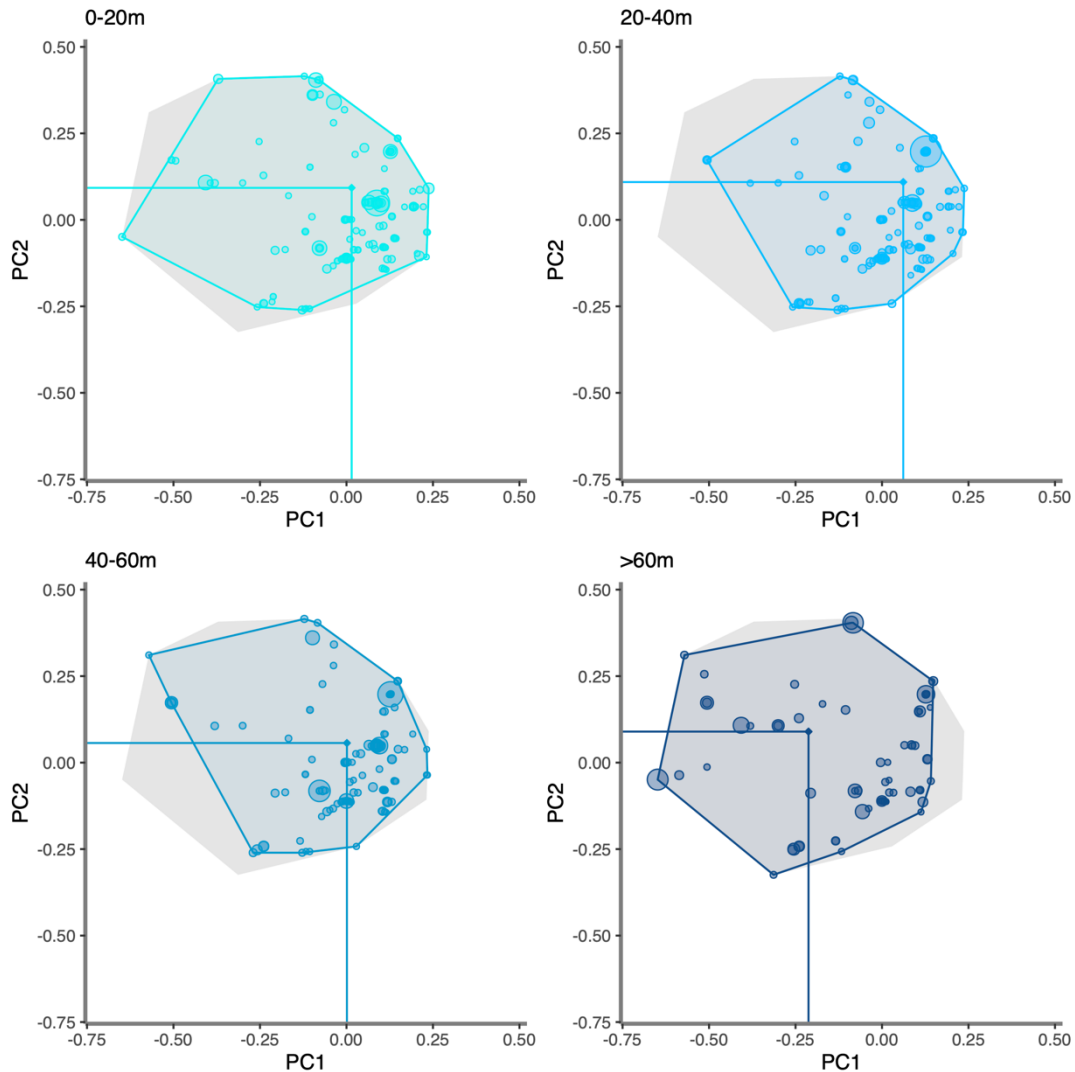


Figure 6: Changes in functional composition and structure along the depth gradient. The traits space represented is made of the first two axes (Principal Components of a PCoA, relative importance: 32 and 30%, respectively). Species are represented by circles whose size is proportional to the biomass of the species. The gray area represents the portion of the trait space filled by all species present across all depths and colored areas represented the functional richness, i.e., trait space filled by species present in each depth range. Vertical and horizontal lines illustrate the biomass-weighted average position of species from each depth range.

Environmental drivers of taxonomic and functional diversity

Despite differences in habitat among sites, depth was the most important variable in explaining biomass, number of species and taxonomic entropy, followed by PC1 of the habitat data (Table S1). This axis is driven by the shift from scleractinian corals to non-scleractinian corals with depth (Supplementary materials, Figure S3). For taxonomic richness and taxonomic entropy, the models explain 66% (conditional  $R^2 = 0.66$  and marginal  $R^2 = 0.45$ ) and 22% (conditional  $R^2 = 0.22$  and marginal  $R^2 = 0.19$ ) of the variance, respectively. Visreg confirmed that depth, after controlling for environmental conditions, significantly explained the biomass, species richness and entropy pattern between assemblages (Figure 3 and 4). Conversely, environmental conditions and depth poorly explain variation of functional richness and entropy (25 and 12%, respectively; conditional  $R^2 = 0.25$ , 0.12 and marginal  $R^2 = 0.21$  and 0.09, respectively). The GDM explained 41 and 44% of the variation in species composition and structure, respectively. Depth was the most important explanatory variable for changes in species composition (Supplementary materials, Figure S6), contributing to 16% and 21% of the explained deviance, respectively, with a lower effect of environmental PC1 (11% of the deviance explained for both models). Variation in functional composition was poorly explained by differences in environmental variables and depth (9% of deviance explained). The GDM explained 41% of the variation in functional structure, and depth was the greatest driver, contributing to 23% of the deviance explained.

## DISCUSSION

Here, thanks to a video survey, we documented how taxonomic and trait diversity of reef fishes changed along a depth gradient from 7.8 to 99.7m around Mayotte Island. Deeper ecosystems exhibit reduced species richness as already reported (Piacenza et al. 2015). However, our results demonstrate that shallow reefs and mesophotic reefs contain similar levels of functional richness with a partial overlap in trait space despite the difference in species composition. While such convergence has been observed at biogeographic scale (Loiseau et al. 2017; Olivier et al. 2018; McLean et al. 2021), ours is a novel example showing trait convergence in marine fish communities driven by taxonomically different species.

Thus, while the taxonomic composition of the fish fauna varied over depth, species were often replaced by another with similar functional roles such that only minor differences in functional entities occurred across depth ranges. For instance, small planktivorous *Chromis* spp. were progressively replaced by *Pseudanthias* spp. another small planktivorous species, with a ratio of two *Pseudanthias* spp. per 100 *Chromis* spp. between 0 and 20 m versus a ratio of 49 per 100 beyond 60 m. This trait similarity across the depth gradient could limit the competition between species that have different distributions along the depth gradient and thus promote coexistence of fishes on the seascape (Goetze et al. 2021; Bosch et al. 2021).

Thus, functional space remains relatively constant over the entire water column. This finding is similar to Carrington et al.'s (2021) findings that temperate shallow-water and deep-sea ecosystems have similar functional composition. The limited shift in trait composition could be explained by the relative homogeneity in the temperature of the water column from our sampling area, ranging only from 24.6 to 31°C. Even if biologically significant, this 6°C degree difference may not be strong enough to limit the establishment of adapted shallow reef functional entities at greater depths. For instance, in the Bay of La Paz, across the same range of depth temperature decreased by 11°C (Hollarsmith et al. 2020). However, conversely to our study Medeiros et al. (2021) found a divergence in both species and functional composition with depth along the Northeastern Brazilian subprovince characterized by a temperature range similar to ours (7°C).

419 However, despite the functional richness of shallow and mesophotic reefs remaining  
420 relatively similar, traits dependent on light energy, like herbivory, do not occur beyond 60m depth  
421 (Supplementary materials, Figure S7). Such a decrease is expected to be due to harsher  
422 environmental conditions in deep habitat that filter out some species present on shallow reefs  
423 (Price et al. 1999; Costello and Chaudhary 2017). Moreover, the overlap in trait space (i.e.,  
424 functional similarity) is accompanied by changes in the structure of the traits with a significant  
425 shift in biomass between functional entities. Indeed, the increase in the dissimilarity of functional  
426 structure with depth highlights the fact that dominant and rare functional entities are different  
427 between shallow reefs and deep reefs (Figure 5). For instance, 75% of *Chaetodontidae*,  
428 corallivores, were observed between 0 and 34 m and only 5% were observed beyond 48 m.  
429 Conversely, 50% of *Carangidae*, which are highly mobile and piscivorous, were recorded beyond  
430 48 m. Overall, variation in trait structure was characterized by a greater relative biomass and  
431 abundance of piscivores on deep reefs, while herbivorous fishes were relatively more abundant on  
432 shallow reefs (Supplementary materials, Figure S7). In fact, piscivorous species represent 8% of  
433 the total biomass in shallow reefs (0-20m), but represent 48% of the biomass beyond 60 m. The  
434 biomass of piscivorous and mobile fishes within reefs, such as grouper, is even higher beyond  
435 60 m ( $538\text{g} \pm 859$ , mean  $\pm$  sd) than between 0 and 20 m ( $191\text{g} \pm 222$ ).

436 Coral reef ecosystems have been heavily impacted by temperature rise over the last few  
437 decades, with documented increases in intense heatwaves leading to massive bleaching events  
438 (Genevier et al. 2019). Synergistically, fisheries strongly impact coral reef fish communities  
439 (MacNeil et al. 2015). Deep-sea ecosystems have been described as stable, with the incidence and  
440 intensity of heatwaves, occurrence of storms and fishing activities lower in mesophotic depths than  
441 in shallow water (Kahng et al. 2017). This “stability” suggests that mesophotic reefs could provide  
442 protection to fish communities (Bongaerts et al. 2010). In the same vein, we found that the upper  
443 mesophotic (30-60 m) zone holds the greatest potential to aid in reef recovery following  
444 disturbance due to the functional overlap with the shallow reef, suggesting that the upper  
445 mesophotic could be a “functional refugia”. However, the limited similarity in species composition  
446 between mesophotic assemblages and shallow reef assemblages suggests that only a relatively  
447 small number of deeper species may be able to live on shallow reefs. Moreover, the strong decrease  
448 in biomass with depth supports the hypothesis that mesophotic reefs are a limited functional  
449 refugia in the face of climate change (i.e. they host dissimilar species, but similar traits while  
450 exhibiting a decrease and a shift in biomass distribution across traits). Lastly, despite the minimal  
451 shift in functional trait composition, there is a marked shift from dominance of herbivorous fishes  
452 to piscivorous fishes with increasing depth. Herbivorous species can have positive effects on coral  
453 cover by controlling macroalgae populations, which can prevent coral mortality and promoting  
454 resilience of coral reefs in the face of anthropogenic disturbance and heatwaves (Burkepile and  
455 Hay 2008). Maintaining high herbivore biomass and diversity is an important goal for sustaining  
456 coral reef functioning (Lefcheck et al. 2019) that cannot be supported by mesophotic reefs deeper  
457 than 60m. However, our results demonstrate the importance of mesophotic reefs to fishery-targeted  
458 species, since the biomass of some piscivorous fishes that are targets of fisheries increase with  
459 depth (Lindfield et al. 2016; Weijerman et al. 2019; Bosch et al. 2021). Even low fishing pressure  
460 on shallow reefs of Mayotte could also create a decreasing gradient of biomass of targeted  
461 piscivorous (Doherty et al. 2015).

462 While we documented the convergence of trait diversity over depth, we are unable to  
463 explain the potential consequences for the ecosystem functioning, since studies linking fish traits  
464 to ecosystem functioning are still lacking (Villéger et al. 2017; Bellwood et al. 2018; Bosch et al.

2021b). However, since biomass distribution across traits determines the influence of fish on ecosystems functioning, we can easily assume that shallow and mesophotic reef fish communities do not have the same influence of reef ecosystems. As with all traits-based studies, trait choices ultimately influence research conclusions. Our results are limited to the set of traits used and to the depth range scales examined. Future studies should therefore attempt to identify the influence of depth on physiologic traits such as reproduction and direct functions such as nutrient cycling (Allgeier et al. 2016) and productivity (Morais and Bellwood 2020) to better understand the functional complementarity of mesophotic and shallow reefs. Understanding how these functions vary along depth gradients is critically important to predict how mesophotic reefs may respond to future environmental change and for their management and conservation. Finally, fishes associated with mesophotic reefs may perform vertical movements over seasonal and diel time frames (Bacheler et al. 2021; Brazo et al. 2021). This behavior could increase the similarity between shallow and mesophotic reefs.

Preserving marine ecosystems is a crucial priority, as they support the livelihood and well-being of millions of citizens (human food provisioning, water purification, disease regulation, cultural values, etc.) (Cabral et al. 2020). Despite their importance, and although the percentage of the coral reef surface devoted to protected areas has markedly increased globally (Maxwell et al. 2020), deep reefs are rarely the focus of conservation strategies. Fishing has historically impacted shallow coral reefs more than the mesophotic part, but as technology continues to improve, the exploitation of the deeper areas has been increasing (Audzijonyte and Pecl 2018). Thus, in the context of the ongoing rise in the severity of threats, mesophotic reefs are an important habitat for conserving coral reef fish diversity. The unique species composition hosted by mesophotic reefs supports the recommendation that protected areas should be representative of a broad range of habitats across depths. Expanding marine protected areas to adjacent mesophotic reefs is required to protect a mosaic of habitat, maximising the number of species and functional entities protected, critical to prevent future local population extirpations and maintain coral reef ecosystem functioning and associated services at all depths. Sustainable management of deep reef ecosystems will also have strong impacts on the management of fishery resources by providing shelters for targeted species.

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## REFERENCES

- Allgeier JE, Valdivia A, Cox C, Layman CA (2016) Fishing down nutrients on coral reefs. *Nat Commun* 7:12461
- Assis J, Coelho NC, Lamy T, Valero M, Alberto F, Serrão EÁ (2016) Deep reefs are climatic refugia for genetic diversity of marine forests. *Journal of biogeography* 43:833-844
- Audzijonyte A, Pecl GT (2018) Deep impact of fisheries. *Nature ecology & evolution* 2:1348-1349
- Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021) Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. *Scientific Reports* 11:1-16
- Bellwood DR, Streit RP, Brandl SJ, Tebbett SB (2019) The meaning of the term ‘function’ in ecology: A coral reef perspective. *Functional Ecology*, 33:948-961.
- Bivand RS, Pebesma EJ, Gómez-Rubio V, Pebesma EJ (2008) *Applied spatial data analysis with R*. Springer
- Bongaerts P, Ridgway T, Sampayo E, Hoegh-Guldberg O (2010) Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral reefs* 29:309-327
- Bosch NE, Monk J, Goetze J, Wilson S, Babcock RC, Barrett N, ... & Langlois, TJ (2022) Effects of human footprint and biophysical factors on the body-size structure of fished marine species. *Conservation Biology*, 36(2), e13807.
- Bosch NE, McLean M, Zarco-Perello S, Bennett S, Stuart-Smith RD, Vergés A, ... & Wernberg, T (2022) Persistent thermally driven shift in the functional trait structure of herbivorous fishes: Evidence of top-down control on the rebound potential of temperate seaweed forests?. *Global Change Biology*, 28:2296-2311.
- Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, Duffy JE (2019) Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment* 17:445-454
- Brazo A, Marques R, Zimmermann M, Aspillaga E, Hereu B, Saragoni G, Mercière A, Crec’Hriou R, Mercader M, Verdoit-Jarraya M (2021) Seasonal influence on the bathymetric distribution of an endangered fish within a marine protected area. *Scientific Reports* 11:1-16
- Breheny P, Burchett W (2017) Visualization of regression models using visreg. *R J* 9:56
- Brown SC, Wigley TM, Otto-Bliesner BL, Rahbek C, Fordham DA (2020) Persistent Quaternary climate refugia are hospices for biodiversity in the Anthropocene. *Nature Climate Change* 10:244-248
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* 105:16201-16206
- Cabral RB, Bradley D, Mayorga J, Goodell W, Friedlander AM, Sala E, Costello C, Gaines SD (2020) A global network of marine protected areas for food. *Proceedings of the National Academy of Sciences* 117:28134-28139
- Carrington VG, Papa Y, Beese CM, Hall J, Covain R, Horn P, Ladds MA, Rogers A, Yeo D (2021) How functionally diverse are fish in the deep? A comparison of fish communities in deep and shallow-water systems. *Diversity and Distributions*

- Chao A, Chiu CH, Villéger S, Sun IF, Thorn S, Lin YC, Chiang JM, Sherwin WB (2019) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis) similarity measures. *Ecological Monographs* 89:e01343
- Cinner JE, Huchery C, MacNeil MA, Graham NA, McClanahan TR, Maina J, Maire E, Kittinger JN, Hicks CC, Mora C (2016) Bright spots among the world's coral reefs. *Nature* 535:416-419
- Cinner JE, Zamborain-Mason J, Gurney GG, Graham NA, MacNeil MA, Hoey AS, ... & Mouillot D. (2020). Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science*, 368(6488), 307-311.
- Coleman RR, Copus JM, Coffey DM, Whitton RK, Bowen BW (2018) Shifting reef fish assemblages along a depth gradient in Pohnpei, Micronesia. *PeerJ* 6:e4650
- Costello MJ, Chaudhary C (2017) Marine biodiversity, biogeography, deep-sea gradients, and conservation. *Current Biology* 27:R511-R527
- Cure K, Currey-Randall L, Galaiduk R, Radford B, Wakeford M, Heyward A (2021) Depth gradients in abundance and functional roles suggest limited depth refuges for herbivorous fishes. *Coral Reefs* 40:365-379
- Doherty B, Herfaut J, Le Manach F, Harper S, Zeller D (2015) Reconstructing domestic marine fisheries in Mayotte from 1950–2010. *Fisheries Catch Reconstructions in the Western Indian Ocean*, eds F Le Manach and D Pauly (Vancouver: University of British Columbia):53-65
- Eddy TD, Lam VW, Reygondeau G, Cisneros-Montemayor AM, Greer K, Palomares MLD, Bruno JF, Ota Y, Cheung WW (2021) Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* 4:1278-1285
- Edgar GJ, Cooper A, Baker SC, Barker W, Barrett NS, Becerro MA, Bates AE, Brock D, Ceccarelli DM, Clausius E (2020) Reef Life Survey: Establishing the ecological basis for conservation of shallow marine life. *Biological Conservation* 252:1-14
- Ellis D (1995) Evaluation of video camera technique for indexing abundances of juvenile pink snapper *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. *Fishery Bulletin* 93:67-77
- Eyal G, Laverick JH, Bongaerts P, Levy O, Pandolfi JM (2021) Mesophotic coral ecosystems of the Great Barrier Reef are understudied and underexplored. *Frontiers in Marine Science* 8:83
- Ferrier S, Manion G, Elith J, Richardson K (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and distributions* 13:252-264
- Genevier LG, Jamil T, Raitsos DE, Krokos G, Hoteit I (2019) Marine heatwaves reveal coral reef zones susceptible to bleaching in the Red Sea. *Global change biology* 25:2338-2351
- Goetze JS, Wilson S, Radford B, Fisher R, Langlois TJ, Monk J, Knott NA, Malcolm H, Currey-Randall LM, Ierodiaconou D (2021) Increased connectivity and depth improve the effectiveness of marine reserves. *Global Change Biology*
- Gower JC, Legendre P (1986) Metric and Euclidean properties of dissimilarity coefficients. *Journal of classification* 3:5-48
- Hijmans RJ, Van Etten J, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, Lamigueiro OP, Bevan A, Racine EB, Shortridge A (2015) Package 'raster'. *R package* 734

- Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA (2001) Historical overfishing and the recent collapse of coastal ecosystems. *science* 293:629-637
- Hollarsmith JA, Ramirez-Ortiz G, Winquist T, Velasco-Lozano M, DuBois K, Reyes-Bonilla H, Neumann KC, Grosholz ED (2020) Habitats and fish communities at mesophotic depths in the Mexican Pacific. *Journal of Biogeography*, 47:1552-1563.
- Jankowski M, Graham N, Jones G (2015) Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth-refuge hypothesis. *Marine Ecology Progress Series* 540:203-215
- Kahng S, Copus JM, Wagner D (2017) Mesophotic coral ecosystems. *Marine animal forests: the ecology of benthic biodiversity hotspots*:185-206
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AG, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* 21:393-404
- Langlois T, Goetze J, Bond T, Monk J, Abesamis RA, Asher J, ... & Harvey ES (2020) A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution* 11: 1401-1409.
- Lefcheck JS, Innes-Gold AA, Brandl SJ, Steneck RS, Torres RE, Rasher DB (2019) Tropical fish diversity enhances coral reef functioning across multiple scales. *Science advances* 5:eaav6420
- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology* 375:1-8
- Letessier TB, Juhel J-B, Vigliola L, Meeuwij JJ (2015) Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *Journal of Experimental Marine Biology and Ecology* 466:120-126
- Lindfield SJ, Harvey ES, Halford AR, McIlwain JL (2016) Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs* 35:125-137
- Loiseau N, Legras G, Kulbicki M, Mérigot B, Harmelin-Vivien M, Mazouni N, Galzin R, Gaertner J-C (2017) Multi-component  $\beta$ -diversity approach reveals conservation dilemma between species and functions of coral reef fishes. *Journal of Biogeography* 44:537-547
- MacNeil MA, Graham NA, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NV (2015) Recovery potential of the world's coral reef fishes. *Nature* 520:341-344
- Magneville C, Loiseau N, Albouy C, Casajus N, Claverie T, Escalas A, Leprieur F, Maire E, Mouillot D, Villéger S (2022) mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* 2022
- Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research* 154:44-62
- Manion G, Lisk M, Ferrier S, Nieto-Lugilde D, Fitzpatrick M (2016) gdm: Functions for generalized dissimilarity modeling. Rpackage version 1
- Marie C-V, Breton D, Crouzet M (2018) More than half of all adults living in Mayotte were born elsewhere. *Population Societies*:1-4
- Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues AS, Stolton S, Visconti P, Woodley S, Kingston N, Lewis E (2020) Area-based conservation in the twenty-first century. *Nature* 586:217-227

- Medeiros APM, Ferreira BP, Alvarado F, Betancur RR, Soares MO, Santos BA (2021) Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic. *Ecol Evol* 11:4413-4427
- Morais RA, Bellwood DR (2020) Principles for estimating fish productivity on coral reefs. *Coral Reefs* 39:1221-1231
- Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-González JE, Bender M, Chabanet P, Floeter SR, Friedlander A, Vigliola L (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences* 111:13757-13762
- Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. *Journal of biogeography* 26:867-878
- Neuswanger JR, Wipfli MS, Rosenberger AE, Hughes NF (2016) Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1861-1873
- Olivier D, Loiseau N, Petatán-Ramírez D, Millán OT, Suárez-Castillo AN, Torre J, Munguia-Vega A, Reyes-Bonilla H (2018) Functional-biogeography of the reef fishes of the islands of the Gulf of California: integrating functional divergence into marine conservation. *Global Ecology and Conservation* 16:e00506
- Ordóñez A, Svenning JC (2015) Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. *Global Ecology and Biogeography* 24:826-837
- Oliver EC, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuisen JA, Feng M, Gupta AS, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC, Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature communications*, 9(1), 1-12.
- Pebesma E, Heuvelink G (2016) Spatio-temporal interpolation using gstat. *RFID Journal* 8:204-218
- Pellissier L, Leprieur F, Parravicini V, Cowman PF, Kulbicki M, Litsios G, Olsen SM, Wisz MS, Bellwood DR, Mouillot D (2014) Quaternary coral reef refugia preserved fish diversity. *Science* 344:1016-1019
- Piacenza SE, Barner AK, Benkwitt CE, Boersma KS, Cerny-Chipman EB, Ingeman KE, Kindinger TL, Lee JD, Lindsley AJ, Reimer JN (2015) Patterns and variation in benthic biodiversity in a large marine ecosystem. *PLoS One* 10:e0135135
- Price A, Keeling M, O'callaghan C (1999) Ocean-scale patterns of 'biodiversity' of Atlantic asteroids determined from taxonomic distinctness and other measures. *Biological Journal of the Linnean Society* 66:187-203
- Roberts TE, Bridge TC, Caley MJ, Madin JS, Baird AH (2019) Resolving the depth zonation paradox in reef-building corals. *Ecology* 100:e02761
- Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science* 361:281-284
- Sala E, Mayorga J, Bradley D, Cabral RB, Atwood TB, Auber A, Cheung W, Costello C, Ferretti F, Friedlander AM (2021) Protecting the global ocean for biodiversity, food and climate. *Nature* 592:397-402
- Sale PF (2013) *The ecology of fishes on coral reefs*. Elsevier

681 Spalding M, Spalding MD, Ravilious C, Green EP (2001) World atlas of coral reefs. Univ of  
682 California Press

683 Stefanoudis PV, Gress E, Pitt JM, Smith SR, Kincaid T, Rivers M, Andradi-Brown DA, Rowlands  
684 G, Woodall LC, Rogers AD (2019) Depth-dependent structuring of reef fish assemblages  
685 from the shallows to the rariphotic zone. *Frontiers in Marine Science* 6:307

686 Venegas RM, Oliver T, Liu G, Heron SF, Clark SJ, Pomeroy N, Young C, Eakin CM, Brainard  
687 RE (2019) The rarity of depth refugia from coral bleaching heat stress in the western and  
688 central Pacific Islands. *Scientific reports* 9:1-12

689 Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ (2017) Functional ecology of fish: current  
690 approaches and future challenges. *Aquatic Sciences* 79:783-801

691 Weijerman M, Grüss A, Dove D, Asher J, Williams ID, Kelley C, Drazen JC (2019) Shining a  
692 light on the composition and distribution patterns of mesophotic and subphotic fish  
693 communities in Hawai ‘i. *Marine Ecology Progress Series* 630:161-182

694 Wickel J, Jamon A, Pinault M, Durville P, Chabanet P (2014) Composition et structure des  
695 peuplements ichtyologiques marins de l’île de Mayotte (sud-ouest de l’océan Indien).  
696 *Cybium: Revue Internationale d’Ichtyologie* 38:179-203