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

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### Abstract :

Mesophotic reefs, defined as reefs between 30 m and 150 m, 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

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

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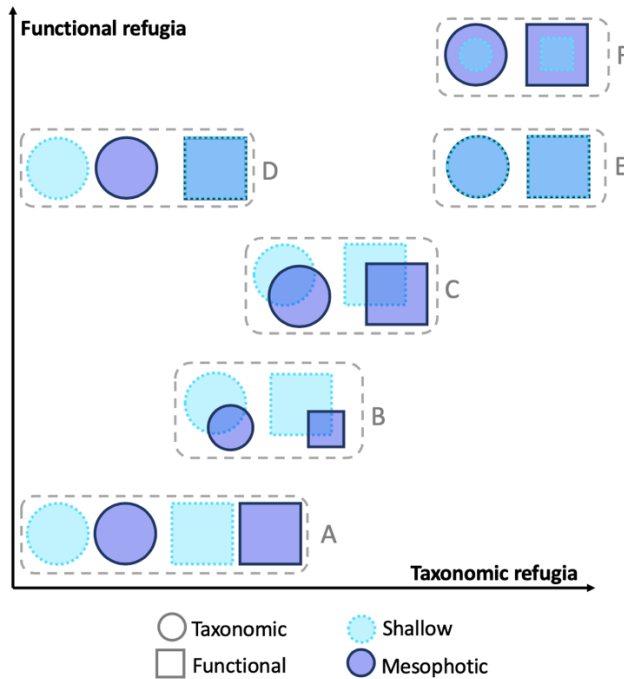
71 Mesophotic coral ecosystems occur in the deeper parts of the ocean's photic zone, with  
72 depth ranging from 30 to 150 m (Eyal et al. 2021), experience reduced temperatures and light, and  
73 may be protected from localized anthropogenic stressors such as pollution and fishing. This  
74 suggests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

75 stressors affecting fishes in shallow water. The deep reef refugia hypothesis emerged from genetic  
76 connectivity research (Lesser et al. 2009; Bongaerts et al. 2010; Assis et al. 2016) and was  
77 reinforced by the fact that many coral reef species occur across a wide depth range (Rocha et al.  
78 2018; Medeiros et al. 2021). However, the increasing frequency and severity of marine heatwaves  
79 (Oliver et al. 2018; Venegas et al. 2019), and accumulating reports of impacts reaching mesophotic  
80 depths (Jackson et al. 2001), cast doubt on the ability of depth refuges to provide protection to fish  
81 communities over the long-term (Rocha et al. 2018).

82  
83 A refugium is defined as an “habitat where some components of biodiversity retreat to, persist in  
84 and can potentially expand from under changing environmental conditions” (sensu, Keppel et al.  
85 2012). The role of refugia to protect species from extinction has been assessed worldwide for  
86 different taxa (Pellissier et al. 2014; Brown et al. 2020). However, biodiversity is multifaceted and  
87 includes other components in addition to the number of species. A largely unexplored dimension  
88 of the role of refugia is their effects on functional diversity, despite the importance of functional  
89 diversity for community and ecosystem functioning. In other words, the ability of refugia to fully  
90 encapsulate diversity has been poorly investigated, especially as it relates to their capacity to  
91 reduce the loss of ecological function (Ordóñez and Svenning 2015). This is particularly true for  
92 mesophotic reefs. Indeed, despite the hypothesis suggesting that mesophotic reefs could be refugia  
93 for reef biodiversity (Jankowski et al. 2015; Lindfield et al. 2016; Coleman et al. 2018; Rocha et  
94 al. 2018; Stefanoudis et al. 2019), there is still a critical lack of evaluation of their role as refugia  
95 for species and trait diversity of fishes (Carrington et al. 2021; Cure et al. 2021).

96  
97 Thus, considering the multifaceted definition of biodiversity, the mesophotic reef refugia  
98 hypothesis could follow several expectations, depending on similarity in species and trait diversity  
99 between shallow and mesophotic reefs (Figure 1): (1) Enriched full refugia: mesophotic reefs host  
100 the same species and trait composition as shallow reefs, plus host unique species and traits not  
101 observed in shallow reefs; (2) Full refugia: mesophotic reefs host the same species and traits  
102 composition than shallow reef while maintaining the same biomass distribution among species;  
103 (3) Functional refugia: mesophotic reefs host different species than shallow reefs but these distinct  
104 species have the same trait values; (4) Not refugia: mesophotic and shallow reefs host distinct  
105 species and traits composition.

106  
107 Here, we tested the potential refugia role of mesophotic ecosystems for multiple facets of  
108 fish diversity using a video-based survey in coral reefs from Mayotte (an island in the Western  
109 Indian Ocean), along a depth gradient from 7.8 to 99.7 m. More specifically, we analyzed how  
110 taxonomic and functional diversity and composition of coral reef fishes changed along the depth  
111 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	$\approx 0$

112  
 113 *Figure 1: A multifaceted approach to test whether deep reefs are refugia for taxonomic (circle)*  
 114 *and functional (square) facets of biodiversity. The size of a circle or square represents the*  
 115 *taxonomic or functional richness of an assemblage while overlapping represents similarity in*  
 116 *species or functional composition between assemblages from mesophotic and shallow reefs. The*  
 117 *associated table shows the expected value of four diversity metrics for each scenario.  $\Delta$ Richness*  
 118 *is the difference in richness between mesophotic and shallow and dissimilarity is the proportion*  
 119 *of richness not shared by shallow and mesophotic reefs. A: No refugia, mesophotic and shallow*  
 120 *reefs host highly distinct species and trait combinations. B & C: Partial refugia, shallow and*  
 121 *mesophotic reefs share a subset of species and traits but also a proportion of unique species and*  
 122 *traits, in B, shallow reefs host more species and trait combinations than mesophotic reef. D:*  
 123 *Functional refugia, mesophotic reef host dissimilar species communities from shallow reefs, but*  
 124 *similar traits composition. E: Full refugia, mesophotic reefs host the same composition of species*  
 125 *and hence of traits as shallow reefs. F: Enriched full refugia, mesophotic reefs host all the species*  
 126 *and trait combinations present in shallow reefs, plus host unique species which have unique traits*  
 127 *(absent in shallow reefs).*

128

129 **MATERIALS AND METHODS**

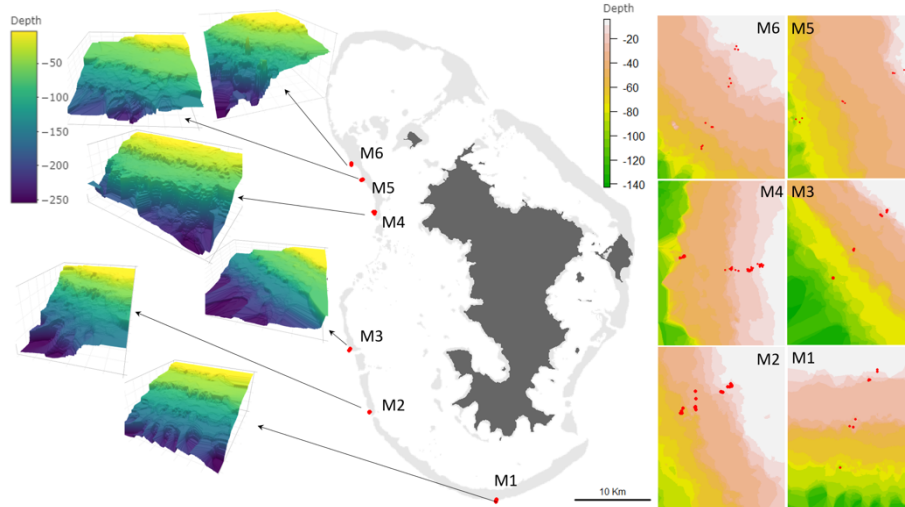
130 **Underwater video surveys of coral reef fishes**

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

136 The choice of study sites was made using two complementary tools: observation of the  
137 habitat using rosette cameras and a 3D reconstruction of the site using data collected by the boat's  
138 sounder. The rosette camera system consisted of four cameras oriented in four different directions.  
139 This system was manually lowered to the bottom over the point of interest using a rope and the  
140 videos were viewed afterwards. For the 3D reconstruction, latitude, longitude and depth  
141 coordinates were recorded every second using a GPS plotter sonar (Lowrance, HDS10). These  
142 traces were then used to reconstruct the 3D profile of the substrate using the *raster* (Hijmans et al.  
143 2015), *gstat* (Pebesma and Heuvelink 2016) and *sp* (Bivand et al. 2008) R packages (Figure 2).  
144 Using to this information, we selected six sites along the west coral reef barrier of the island with  
145 as much similarity as possible in coral cover and complexity within each four different depths,  
146 ranging from 7.8 to 99.7 m deep (Figure 2).

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

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



168  
 169 *Figure 2: Location of surveyed sites around Mayotte Island in the SW Indian Ocean. On the left,*  
 170 *the 3D reconstruction of each site and on the right each red dot represents a drop of a remote*  
 171 *underwater camera.*

172  
 173 **Video analyses**

174 We analyzed data from 121 drops (i.e., assemblages with fewer than five species were not  
 175 included). For each video, the first two minutes were not analyzed to limit disturbance due to the  
 176 video system deployment. As the total duration of video recorded varied among sites and depth  
 177 level, and as analyzing stereovideos is a demanding task we analyzed five, one-minute non-  
 178 overlapping sequences randomly selected within each recording. Hence, we keep a constant  
 179 sampling effort across all replicates for estimating abundance of fish species, even if this sampling  
 180 effort did not allow to reach the asymptote of the species accumulation curve (Supplementary  
 181 materials, Figure S1). For each of these sequences, all fishes up to 5 m from the camera were  
 182 counted and identified to the lowest possible taxonomic level. Abundance of each species was  
 183 estimated as the maximum number of individuals of each species observed in a single frame during  
 184 each one-minute sequence (MaxN; Ellis 1995). A total of 12,891 individuals (50%) belonging to  
 185 182 species were identified. 2206 individuals were identified at the genus level (44 genera) and  
 186 10,382 (40%) at the family level (26 families). We also did not consider cryptobenthic species  
 187 (*Apogonidae* [7 individuals], *Gobiidae* [33 individuals] and *Chondrichthyans* [30 individuals]).  
 188 Because a high proportion of individuals were not identified at the species levels, we also tested  
 189 the sensitivity of our analyses to the taxonomic resolution by rerunning our analyses at the genus  
 190 level. Size calibration calculation and 3D fish measurements were all performed using the open-  
 191 source software VidSync ([www.vidsync.org](http://www.vidsync.org)).

192  
 193 **Biomass estimation**

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

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

206

### 207 **Functional traits**

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

224

### 225 **Taxonomic and functional diversity**

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

232

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

$$236 \quad TD = e^{-\sum_{i=1}^S p_i \log \log p_i} \quad \text{Eq (1)}$$

237

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

240

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

243

$$244 \quad FD = (\sum_{i=1}^S p_i (\sum_{j=1}^S [1 - f(d_{ij}(\tau))] p_j)^{q-1})^{1/(1-q)} \quad \text{Eq (2)}$$

245

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

$$248 \quad FD = \sum_{i=1}^S (\sum_{j=1}^S [1 - f(d_{ij}(\tau))])^{-1} \quad \text{Eq (3)}$$

249  
250 Functional entropy ( $q = 1$ ) was computed on species biomass:

$$251 \quad FD = e^{-\sum_{i=1}^S p_i \log(\sum_{j=1}^S [1 - f(d_{ij}(\tau))] p_j)} \quad \text{Eq (4)}$$

252  
253 This metric is a generalization of the Shannon entropy with functional distance having equal  
254 importance as species dominance.

### 255 256 257 **Taxonomic and functional dissimilarities**

258 The dissimilarity in species and functional entities among assemblages was also computed  
259 using the framework of Chao et al. (2019) with, as for alpha-diversity,  $q=0$  (i.e., dissimilarity in  
260 composition of species or functional entities) and  $q=1$  (i.e., dissimilarity in dominance of species  
261 or functional entities). The dissimilarity indices are bounded between 0 and 1, with 0 indicating  
262 identical assemblages (in terms of species or trait values) and values close to 1 indicating a strong  
263 dissimilarity in species or functional entities. We applied a depth decay analysis (similar to the  
264 distance decay in biogeography, Nekola and White 1999) by comparing the dissimilarity between  
265 0-20m assemblages and each of all other deeper assemblages.

266  
267 Changes in functional richness and structure through depth were illustrated in a functional  
268 space built using Principal Coordinates Analysis (PCoA) computed on functional distances  
269 between species. Indices and functional space were computed and drawn using the *mFD* package  
270 (Magneville et al. 2022).

### 271 272 **Habitat predictors**

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

### 287 288 **Determinants of fish diversity**

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



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

298

### 299 **Determinants of fish dissimilarity**

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

312

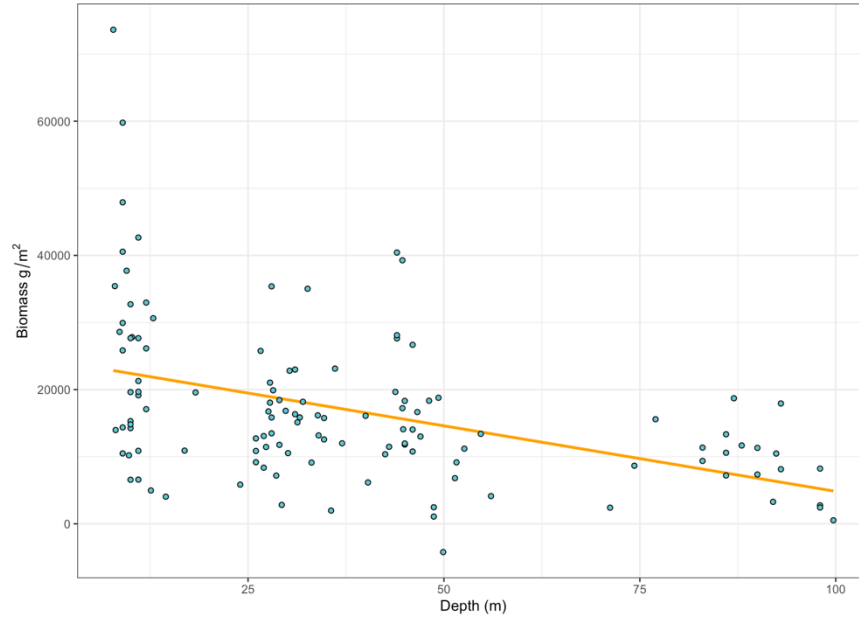
## 313 **RESULTS**

314

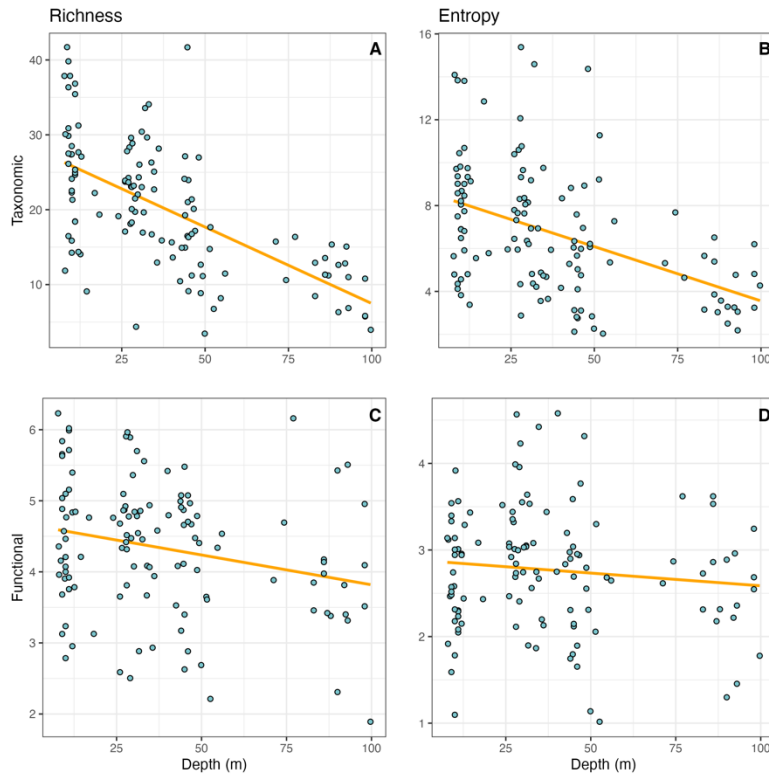
### 315 **Diversity of fishes along depth gradient**

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

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



325  
 326 *Figure 3 Partial regression plot showing changes in biomass of fish along the depth gradient*  
 327 *while accounting for environmental variables. Statistical analyses were carried out using*  
 328 *generalized linear mixed models and related statistics are reported in the Results.*  
 329



330  
 331  
 332 *Figure 4: Partial regression plot showing changes in taxonomic richness ( $q=0$ , A) and entropy*  
 333 *( $q=1$ , B) and functional richness ( $q=0$ ,  $\tau$  = mean functional distance, C) and entropy ( $q=1$ ,  $\tau$  =*  
 334 *mean functional distance, D) of fish communities along the depth gradient, while accounting for*

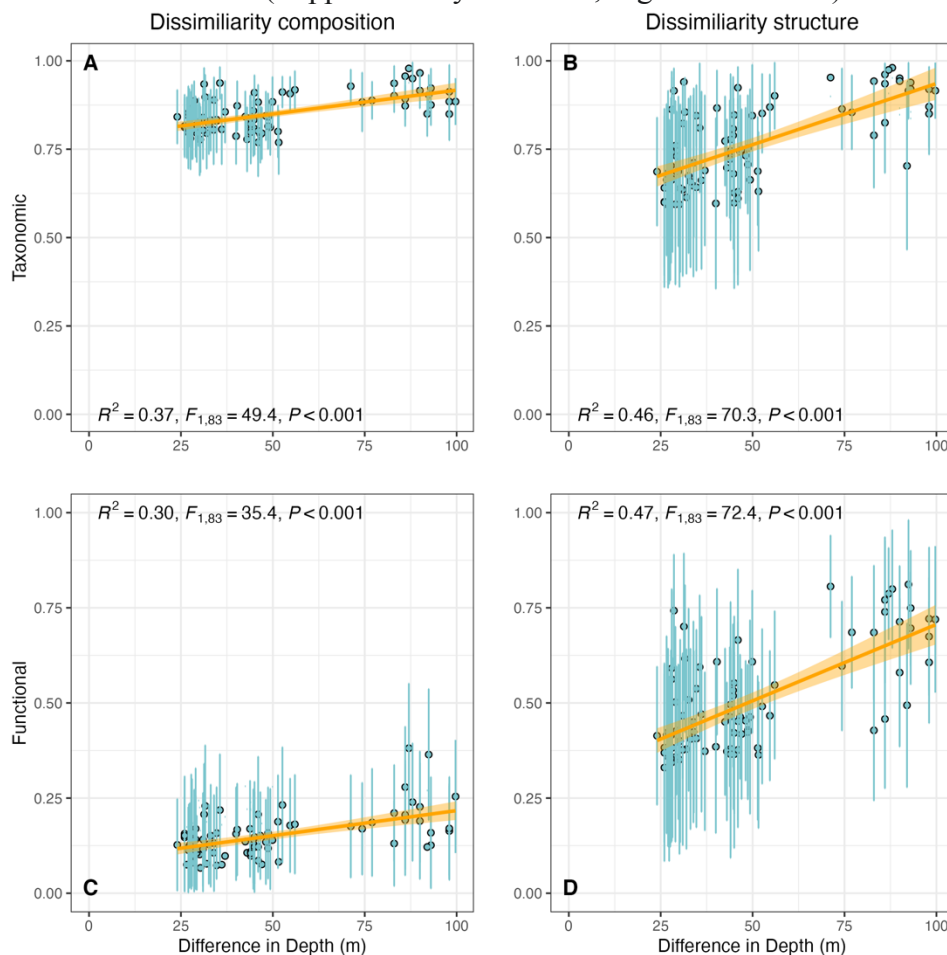
335 *environmental variables. Statistical analyses were carried out using generalized linear mixed*  
 336 *models and related statistics are reported in the Results.*

337

### 338 **Dissimilarity of fish assemblages along depth gradient**

339 The dissimilarity in taxonomic composition and structure between assemblages was high overall,  
 340 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  
 341 values were observed between shallow (0-20 m) and deep assemblages (>60 m) (i.e., high value  
 342 in the difference in depth axis, Figure 5). Limited dissimilarity in functional composition was  
 343 observed between assemblages ( $0.13 \pm 0.13$ ). The dissimilarity in functional structure was higher  
 344 than functional composition ( $0.46 \pm 0.25$ ), highlighting an important change in the distribution of  
 345 biomass between functional entities. Both taxonomic and functional dissimilarities increased with  
 346 an increase in depth difference (all p-values < 0.001 and  $R^2$  ranged between 0.30 and 0.47; Figure  
 347 5).

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

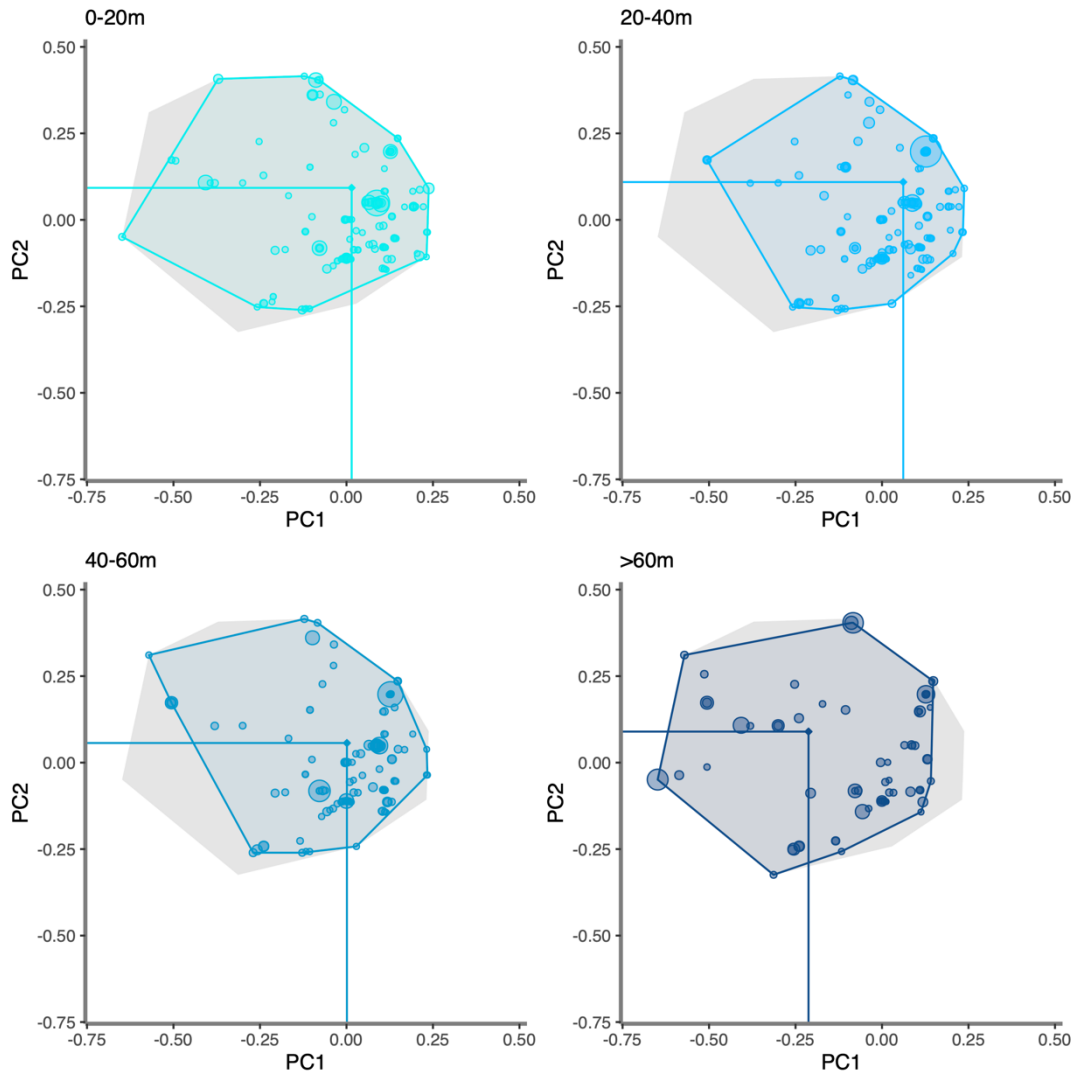


350

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

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

358  
359 Finally, the projection of all species along the first two axes of the PCoA confirmed that  
360 mesophotic and shallow reefs mostly overlap in functional space but distribution of biomass within  
361 this shared functional volume markedly changed (Figure 6).  
362



363  
364 *Figure 6: Changes in functional composition and structure along the depth gradient. The traits*  
365 *space represented is made of the first two axes (Principal Components of a PCoA, relative*  
366 *importance: 32 and 30%, respectively). Species are represented by circles whose size is*  
367 *proportional to the biomass of the species. The gray area represents the portion of the trait space*  
368 *filled by all species present across all depths and colored areas represented the functional*  
369 *richness, i.e., trait space filled by species present in each depth range. Vertical and horizontal*  
370 *lines illustrate the biomass-weighted average position of species from each depth range.*

371  
372 *Environmental drivers of taxonomic and functional diversity*

373 Despite differences in habitat among sites, depth was the most important variable in  
374 explaining biomass, number of species and taxonomic entropy, followed by PC1 of the habitat  
375 data (Table S1). This axis is driven by the shift from scleractinian corals to non-scleractinian corals  
376 with depth (Supplementary materials, Figure S3). For taxonomic richness and taxonomic entropy,  
377 the models explain 66% (conditional  $R^2 = 0.66$  and marginal  $R^2 = 0.45$ ) and 22% (conditional  $R^2$   
378  $= 0.22$  and marginal  $R^2 = 0.19$ ) of the variance, respectively. Visreg confirmed that depth, after  
379 controlling for environmental conditions, significantly explained the biomass, species richness and  
380 entropy pattern between assemblages (Figure 3 and 4). Conversely, environmental conditions and  
381 depth poorly explain variation of functional richness and entropy (25 and 12%, respectively;  
382 conditional  $R^2 = 0.25$ , 0.12 and marginal  $R^2 = 0.21$  and 0.09, respectively).  
383 The GDM explained 41 and 44% of the variation in species composition and structure,  
384 respectively. Depth was the most important explanatory variable for changes in species  
385 composition (Supplementary materials, Figure S6), contributing to 16% and 21% of the explained  
386 deviance, respectively, with a lower effect of environmental PC1 (11% of the deviance explained  
387 for both models). Variation in functional composition was poorly explained by differences in  
388 environmental variables and depth (9% of deviance explained). The GDM explained 41% of the  
389 variation in functional structure, and depth was the greatest driver, contributing to 23% of the  
390 deviance explained.

## 391 392 **DISCUSSION**

393 Here, thanks to a video survey, we documented how taxonomic and trait diversity of reef  
394 fishes changed along a depth gradient from 7.8 to 99.7m around Mayotte Island. Deeper  
395 ecosystems exhibit reduced species richness as already reported (Piacenza et al. 2015). However,  
396 our results demonstrate that shallow reefs and mesophotic reefs contain similar levels of functional  
397 richness with a partial overlap in trait space despite the difference in species composition. While  
398 such convergence has been observed at biogeographic scale (Loiseau et al. 2017; Olivier et al.  
399 2018; McLean et al. 2021), ours is a novel example showing trait convergence in marine fish  
400 communities driven by taxonomically different species.

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

409 Thus, functional space remains relatively constant over the entire water column. This  
410 finding is similar to Carrington et al.'s (2021) findings that temperate shallow-water and deep-sea  
411 ecosystems have similar functional composition. The limited shift in trait composition could be  
412 explained by the relative homogeneity in the temperature of the water column from our sampling  
413 area, ranging only from 24.6 to 31°C. Even if biologically significant, this 6°C degree difference  
414 may not be strong enough to limit the establishment of adapted shallow reef functional entities at  
415 greater depths. For instance, in the Bay of La Paz, across the same range of depth temperature  
416 decreased by 11°C (Hollarsmith et al. 2020). However, conversely to our study Medeiros et al.  
417 (2021) found a divergence in both species and functional composition with depth along the  
418 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 ( $538g \pm 859$ , mean  $\pm$  sd) than between 0 and 20 m ( $191g \pm 222$ ).

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.

465 2021b). However, since biomass distribution across traits determines the influence of fish on  
466 ecosystems functioning, we can easily assume that shallow and mesophotic reef fish communities  
467 do not have the same influence of reef ecosystems. As with all traits-based studies, trait choices  
468 ultimately influence research conclusions. Our results are limited to the set of traits used and to  
469 the depth range scales examined. Future studies should therefore attempt to identify the influence  
470 of depth on physiologic traits such as reproduction and direct functions such as nutrient cycling  
471 (Allgeier et al. 2016) and productivity (Morais and Bellwood 2020) to better understand the  
472 functional complementarity of mesophotic and shallow reefs. Understanding how these functions  
473 vary along depth gradients is critically important to predict how mesophotic reefs may respond to  
474 future environmental change and for their management and conservation. Finally, fishes associated  
475 with mesophotic reefs may perform vertical movements over seasonal and diel time frames  
476 (Bacheler et al. 2021; Brazo et al. 2021). This behavior could increase the similarity between  
477 shallow and mesophotic reefs.

478  
479 Preserving marine ecosystems is a crucial priority, as they support the livelihood and well-being  
480 of millions of citizens (human food provisioning, water purification, disease regulation, cultural  
481 values, etc.) (Cabral et al. 2020). Despite their importance, and although the percentage of the coral  
482 reef surface devoted to protected areas has markedly increased globally (Maxwell et al. 2020),  
483 deep reefs are rarely the focus of conservation strategies. Fishing has historically impacted shallow  
484 coral reefs more than the mesophotic part, but as technology continues to improve, the exploitation  
485 of the deeper areas has been increasing (Audzijonyte and Pecl 2018). Thus, in the context of the  
486 ongoing rise in the severity of threats, mesophotic reefs are an important habitat for conserving  
487 coral reef fish diversity. The unique species composition hosted by mesophotic reefs supports the  
488 recommendation that protected areas should be representative of a broad range of habitats across  
489 depths. Expanding marine protected areas to adjacent mesophotic reefs is required to protect a  
490 mosaic of habitat, maximising the number of species and functional entities protected, critical to  
491 prevent future local population extirpations and maintain coral reef ecosystem functioning and  
492 associated services at all depths. Sustainable management of deep reef ecosystems will also have  
493 strong impacts on the management of fishery resources by providing shelters for targeted species.

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