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Camille Magneville, Solène Dedieu, Nicolas Loiseau, Thomas Claverie,
Sébastien Villéger

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1 **Detecting benefits of protection level on diversity facets in a sea of temporal scarcity**

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4 **Authors:**

5 Camille Magneville ^{1,2*} (<https://orcid.org/0000-0003-0489-3822>)

6 Solène Dedieu ¹

7 Nicolas Loiseau ¹ (<https://orcid.org/0000-0003-3783-0879>)

8 Thomas Claverie ^{1,3,4} (<https://orcid.org/0000-0002-6258-4991>)

9 Sébastien Villéger ¹ (<https://orcid.org/0000-0002-2362-7178>)

10

11 ¹ MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France.

12 ² Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, Aarhus
13 University, Ny Munkegade 114, DK-8000 Aarhus, Denmark

14 ³ Centre Universitaire de Formation et de Recherche de Mayotte, France.

15 ⁴ UMR ENTROPIE, Univ La Réunion, IRD, IFREMER, Univ Nouvelle-Calédonie, CNRS, Saint-Denis,
16 Réunion, France

17

18 * corresponding author (camille.magneville@gmail.com)

19

20 **Data availability statement:**

21 Data and scripts are available on Github (<https://github.com/CmlMagneville/MPAfacetsdivaccum>).

22 **Conflict of Interest disclosure:**

23 The authors have no conflict of interest to declare.

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29

30

31 **Authors' contributions:**

32 CM and SV conceived the ideas and designed methodology; SD, NL, TC, SV and CM collected the
33 data; SD and CM analyzed the data; CM led the writing of the manuscript. All authors contributed
34 critically to the drafts and gave final approval for publication.

35

36

37

38 **Abstract:**

- 39 1. The establishment of protected areas to face global diversity declines has mainly prioritized
40 taxonomic diversity, leaving aside phylogenetic and functional diversities which determine
41 ecosystem functioning and resilience. Furthermore, the assessment of protected areas
42 effectiveness is mainly done using short duration surveys (<2h) which may undermine the
43 detection of rare species.
- 44 2. Using a long-duration video approach, reef fish taxonomic, phylogenetic and functional facets
45 of diversity were assessed for three days within a fully protected area and a nearby poorly
46 protected area in Mayotte island (Western Indian Ocean).
- 47 3. We found that temporally rare species contributed to more than 60% of the taxonomic and 85%
48 of the functional facets of biodiversity found on each site. Those rare species which harbour
49 the most distinct trait values, also make reef fish diversity particularly vulnerable to their loss.
50 Taxonomic, phylogenetic and functional richness were similar between the fully protected area
51 and the poorly protected area while the species, lineages and traits compositions were
52 markedly different.
- 53 4. These results pinpoint the importance of considering taxonomic, functional and phylogenetic
54 dissimilarities while accessing protected areas effectiveness, instead of only using richness. In
55 addition, benefits of the fully protected area were only detected using more than 15 hours of
56 video survey, which emphasises the importance of long duration remote approaches to capture
57 the within and between day's temporal variations.

58

59 **Keywords:** coral reef fishes, diversity survey, functional diversity, long duration video approach,

60 phylogenetic diversity, protection level, rarity, taxonomic diversity

61 **Author for correspondence:**

62

63 Magneville Camille

64

65 UMR MARBEC, Université de Montpellier

66 93 Place Eugène Bataillon

67 34090 Montpellier

68 FRANCE

69

70 camille.magneville@gmail.com

71 1 - Introduction

72

73 Human activities synergistically threaten biodiversity through climate change, habitat
74 fragmentation, overexploitation, pollution or biological invasions (Bellard et al. 2022). These threats
75 have led to changes in species composition, abundance and richness which ultimately disrupt
76 ecosystem functioning (Ceballos & Ehrlich 2002; Gaston & Fuller 2008). In order to safeguard
77 biodiversity in the face of such declines, the number of protected areas has been growing for the last
78 two decades, leading to 16% of lands and 7.5% of the oceans being currently designated as protected
79 (Sala et al. 2021). The effectiveness of Protected Areas mostly depends on their protection level (Zupan
80 et al. 2018; Friedlander et al. 2019; Turnbull et al. 2021) which ranges from poor protection where
81 activities with high impact on species are poorly or not restricted, to full protection where no extractive
82 activities are allowed (Horta e Costa et al. 2016). In the marine realm, numerous studies have found a
83 positive effect of protected areas, particularly old and large areas with no-take policy, on fish biomass
84 (Mosquera et al. 2000; Russ et al. 2008; Lester et al. 2009; Emslie et al. 2015; Cox et al. 2017; Strain
85 et al. 2019) and fish size (Lester et al. 2009; Emslie et al. 2015), especially for species targeted by
86 fisheries. However, most studies focused on comparing fish diversity in protected areas *versus* fished
87 areas while few compared within levels of protection (but see (Hall et al. 2023)) which prevents from
88 fully understanding whether banning only some fishing technique in poorly protected areas is as
89 effective as no-take policies in fully protected areas.

90

91 In addition, the establishment of protected areas has most often focused on threatened,
92 umbrella, endemic species or species with an economic value (Isaac et al. 2007), thus protecting
93 taxonomic diversity (TD). In doing so, current conservation efforts disregard other key facets of
94 biodiversity such as phylogenetic diversity (PD). This biodiversity facet represents the evolutionary
95 heritage and losing PD could lead to a reduced potential of communities to respond to environmental
96 changes because of a reduced evolutionary potential (Purvis, Gittleman and Brooks, 2005). However,
97 the existing network of protected areas falls short in adequately safeguarding this facet of diversity, as
98 the global marine protected area network only covers 17.6% of fishes' Tree of Life (Mouillot et al. 2016).
99 Functional diversity (FD) which reflects the value and range of those species and organismal traits that
100 influence ecosystem functioning (Tilman, 2001), is also poorly represented in the current protected area

101 network (e.g. Mouillot et al. 2011, Guilhaumon et al. 2015, Devictor et al. 2010). This diversity facet is
102 key for understanding both ecosystem functioning (Cardinale et al. 2012, Naeem et al. 2012) and
103 ecosystem resilience (Yachi and Loreau, 1997, Bellwood et al. 2003). Taxonomic, phylogenetic and
104 functional diversities are not necessarily congruent (Devictor et al. 2010, Strecker et al. 2011, Brum et
105 al. 2017, Cadotte & Tucker 2018) and thus do not necessarily act as good surrogates for each other's
106 (Devictor et al. 2010, D'Agata et al. 2014, Mazel et al. 2018). For instance, an assemblage with a high
107 number of species (high TD) which are functionally redundant (i.e. have similar functional roles), has a
108 lower FD than an assemblage with a lower number of species (low TD) with distinct functional roles.
109 Thus, biodiversity conservation requires studying the three facets altogether (Pollock et al. 2017). But
110 the extent to which Marine Protected Areas enhance the complementary facets of biodiversity remains
111 largely unknown.

112

113 While there is evidence that taxonomic diversity varies over years, months and seasons, few
114 studies, mostly marine ones, have focused on its variation on short temporal scales, displaying
115 ambivalent results (Colton & Alevizon 1981; Thompson & Mapstone 2002; Santos et al. 2002; Willis et
116 al. 2006; Birt et al. 2012; Chabanet et al. 2012; Myers et al. 2016; Luise Bach & Smith 2021). The
117 causes of these within- and between- day variations remains uncertain but may be linked to species
118 behaviour, for instance to their foraging activity which has been shown to vary at these short temporal
119 scales (Choat & Clements, 2002; White et al. 2002; Magneville et al. 2022a). To our knowledge, there
120 have been no studies to explore such variations of functional and phylogenetic diversities. Yet, these
121 short temporal scale variations could affect the assessment of conservation benefit through bias in
122 detection of rare species which could belong to unique lineages and/or support unique combinations of
123 traits. A comprehensive survey of all rare species is needed as those species can enhance resistance
124 to species invasions (Lyons and Schwarz, 2001) or play a key role in trophic control (Bellwood, Hugues
125 and Hoey, 2006) and nutrient cycling (Theodose et al. 1996) and are particularly vulnerable to global
126 changes and other human-induced disturbances (Davies et al. 2004).

127

128 Using long-duration remote underwater cameras, we assessed reef fish diversity within a fully
129 protected Marine Protected Area (MPA) and in a nearby poorly protected MPA from Mayotte island
130 (Western Indian Ocean). We specifically address the following questions: (i) How do the taxonomic,

131 phylogenetic and functional diversities vary within a day and across days? (ii) Is there an effect of the
132 protection level on taxonomic, phylogenetic and functional diversities and species, lineages and traits
133 composition? (iii) How do short temporal variations of biodiversity facets impact our perception of
134 protection effect?

135

136 **2 - Methods**

137

138 **Remote Underwater Video recording**

139 This study was carried out in two sites in Mayotte lagoon (Western Indian Ocean) (see
140 Supplementary Figure 1). The first sampling site, N'Gouja (-12.9639° lat; 45.0870 long), is within a fully
141 protected marine area ("Parc Naturel Marin de Mayotte" <https://parc-marin-mayotte.fr/>) where fishing is
142 prohibited. The second sampling site, Bouéni (-12.9162° lat; 45.0807 long), is within a poorly protected
143 marine area. It is 5.3 km away from the fully protected area and is used by local artisanal fishers using
144 only hooks from pirogues (nets and spearfishing are prohibited). The fringing reefs from the two sites
145 were similar with an average depth of three meters and a benthic habitat comprising a mix of branching
146 and encrusting living corals, turf and detritic substrates. Survey was carried out on six days spanning
147 from 03/11/2020 to 06/11/2020 and from 08/11/2020 to 09/11/2020, surveying each site every other
148 day. Two GoPro Hero 5 (GoPro Inc, United States) with external batteries were placed in two waterproof
149 housings (four inches water tight enclosure, Blue Robotics, United States) mounted on a 35 cm high
150 tripod. Cameras were set to record high-definition videos (1920 by 1080 pixels at 25 frames per second)
151 with a 90° field-of-view.

152 Cameras were set up 40m apart with no substrate obstructing the camera's field-of-view. After
153 the start of the recording, cameras were synchronized with a one second precision (passing the same
154 digital watch in front of each camera at the beginning of their respective recording). Then, a 2m² quadrat
155 was briefly placed in front of each camera to enable the measurement of fish diversity across this
156 standardized area (Longo et al. 2014). The microhabitats present in each quadrat were similar between
157 the two survey sites.

158 Cameras recorded continuously between 06:30 and 18:00, thus recording from 1h after dusk
159 and 30 minutes before dawn. To reduce the diver's effect on fish detection, only videos starting one
160 hour after the divers left the surveyed area and videos finishing one hour before divers came back were

161 kept. Overall, ten hours of videos (from 07:30:00 to 17:30:00) were thus analysed for each day and
162 each camera, representing a total of 120 hours of video.

163

164 **Measuring species, functional and phylogenetic diversities on videos**

165 For each day and each camera, the ten hours of continuous recording were divided into 33
166 video files of 17min42s (due to the 4Go size limit when used by GoPro saved files). Frames were
167 extracted from each video file at a rate of one frame per second. The first occurrence of each species
168 appearing on a given video file on the water column above the 2m² surveyed area was recorded. Thus,
169 we noted the identity of all species appearing in each video sequence of 17min42s. Then, we merged
170 at a second level the data from the two cameras per day and site. Species richness was computed on
171 each sequence as the number of species then standardised by dividing by the overall number of species
172 seen on both sites in this study.

173 Phylogenetic distances between species were calculated using the phylogeny from Rabosky et
174 al. (2018) through the *fishtree* R package (Chang et al. 2019). Of the total 130 species seen on both
175 sites, six species were not present in the phylogeny. Therefore, we selected sister species that included
176 in phylogeny from Rabosky et al. (2018) (see Supplementary Table 1 for species replacement).
177 Phylogenetic richness was calculated on each sequence as the Faith's PD index (Faith 1992) *i.e.* the
178 sum of the length of the branches of the minimum spanning path linking species seen on the studied
179 sequence divided by the sum of the entire phylogeny branches length.

180 Functional diversity was assessed accounting for six traits related to the key functions
181 supported by reef fishes: activity period, mobility, position in the water column, size class, schooling
182 size and diet (Villéger et al. 2017). Traits values were collected in the database collected in Parravicini
183 et al. (2020): all traits were coded as ordinal variables and diet was coded as a categorical variable (see
184 Supplementary Table 2 for traits categories). Species with same trait values were grouped into 76
185 functional entities *i.e.* groups of species sharing the same combinations of functional traits (Mouillot et
186 al 2014). Trait-based distances between all pairs of entities were computed using the Gower distance
187 (Villéger et al 2008). The functional space was computed using a PCoA based on the distances between
188 functional entities (Mouillot et al 2014). The quality of functional spaces from two to ten PC axes was
189 computed using the mean absolute deviation index which computes the absolute deviation between
190 species traits-based distances and species distances in the functional space (Magneville et al. 2022b).

191 The five-dimensional space was chosen as the one with the best quality *i.e.* the one which reflects the
192 best species trait-based distances (Maire et al 2015). The first functional axis was correlated with the
193 six functional traits, with big-sized, very mobile, piscivore species and species with a high position in
194 the water column being associated with positive values of the first axis (Supp Fig 2). The second
195 functional axis was mainly correlated with home range, activity period, schooling and diet, with solitary
196 species being associated with positive values of the second functional axis. Functional richness (FRic)
197 (Villéger et al. 2008) was computed as the volume of the convex hull shaping all species of a given
198 assemblage in the functional space. Two additional functional facets were measured: functional
199 dispersion (FDis) computed as the mean distance of each species to the centre of gravity of the species
200 from the studied assemblage (Laliberté & Legendre, 2010) and functional specialization (FSpe)
201 calculated as the mean distance of each species to the center of gravity of the functional space
202 (Bellwood et al. 2006; Mouillot et al. 2013b). In addition, the functional specialisation of each species
203 was computed as the distance to the gravity centre of the functional space. This measure was then
204 standardized by dividing all values by the maximal value across all species. Computation of all
205 functional diversity indices was performed using the *mFD* R package *version 1.0.3* (Magneville et al.,
206 2022b).

207 To draw the accumulations curves of each biodiversity facet (species richness, phylogenetic richness,
208 functional richness, functional specialisation and functional dispersion) in each site over the three
209 survey days, the indices were computed taking into account all the species seen before the end of the
210 increasing number of video sequences (from 1 to 99).

211

212 **Species rarity**

213 The temporal rarity of each species was measured for each site as the number of videos of
214 17min42s on which the species has been detected over the three days of recording within a given site,
215 divided by the total number of videos of a given site. Super rare species were defined as species
216 occurring in at most 5% of videos of a given site (Mouillot et al. 2013a), rare species were species
217 whose percentage of video occurrence was $> 5\%$ and $< 25\%$ and common species were defined as
218 species occurring in $\geq 25\%$ of videos of a given site. A species can belong to different rarity categories
219 on the two studied sites.

220 To test for a phylogenetic signal of temporal rarity within each site, we computed the
221 phylogenetic D index (Fritz & Purvis 2010). This index tests whether temporal rarity of species is
222 randomly distributed along the phylogenetic tree or if they are clustered according to their temporal
223 rarity. A low value indicates common species and rare/super rare species are clustered in distinct parts
224 of the phylogenetic tree. The index was computed using the *phylo.d()* function of the *caper* R package
225 *version 1.0.1*.

226

227 **Dissimilarity between species assemblages**

228 Taxonomic dissimilarity in species composition was computed with the Jaccard index between
229 all pairs of videos. Its turnover component which represents the rate of species replacement,
230 independently from difference in species richness was computed following Baselga, (2012).
231 Phylogenetic dissimilarity (i.e. dissimilarity in lineage composition) was computed using a Jaccard-like
232 index. Its turnover component (Leprieur et al. 2012) represents the degree of replacement of a lineage
233 part between two assemblages. Functional dissimilarity was computed using a Jaccard-like index
234 applied to convex hulls shaping species in the functional space. Its turnover component (Villéger et al.
235 2013) quantifies the degree of replacement of a functional strategies between two assemblages.
236 Taxonomic and phylogenetic dissimilarities and their turnover components were computed using the
237 *betapart* package version 1.5.6 (Baselga & Orme 2012) and functional dissimilarity and its turnover
238 component were computed using the *mFD* package (Magneville et al. 2022b).

239 To test if dissimilarity in species, lineage and trait compositions were different across days and
240 sites, we computed three PERMANOVA using the dissimilarity in species, lineage and traits between
241 all pairs of videos.

242 Dissimilarity and its turnover component were also computed in each site among the 3 pairs of
243 survey days (i.e. accounting for all species seen during each day), and between the two sites (i.e.
244 accounting for all species seen during the 3 days).

245

246 **Vulnerability of biodiversity to Species Loss**

247 The vulnerability of functional richness and of phylogenetic richness of each site to species
248 loss was studied according to three scenarios (following Leitão et al., 2016). The first scenario
249 simulates the random loss of species by randomly removing species from one to the number of species

250 present in the studied site. One hundred iterations of such random species loss were computed. The
251 second scenario simulates the loss of species going from the most common to the rarest in each site,
252 while the third scenario simulates the loss of species going from the rarest to the most common.

253

254 **3 - Results**

255

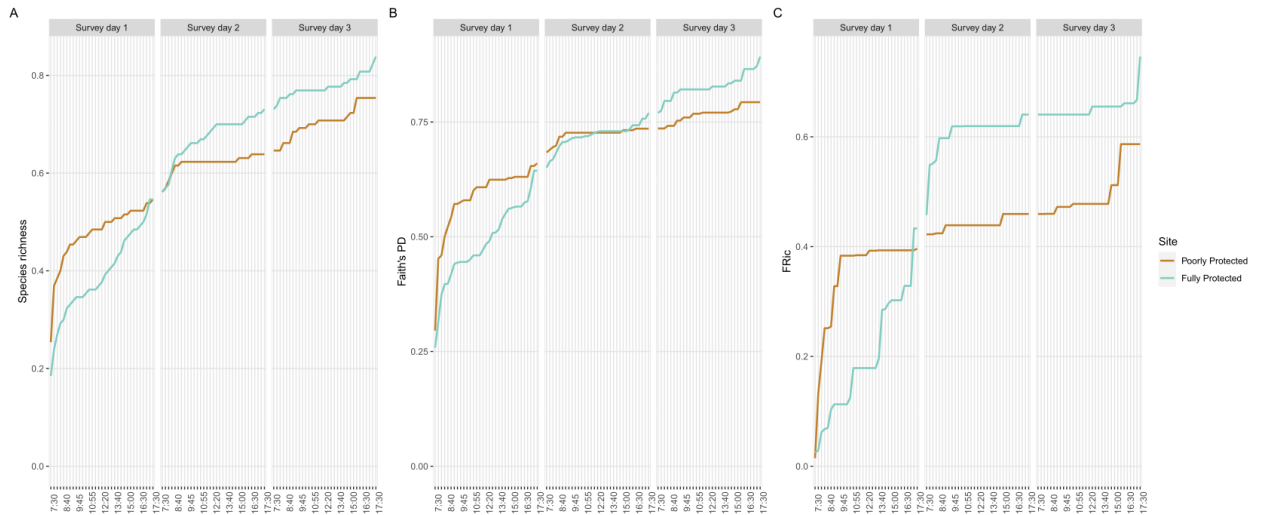
256 **Accumulation of TD, FD and PD across days and within each day**

257 After the three days, 130 species were recorded on both sites with 109 species seen in the fully
258 protected area, 98 species seen in the poorly protected area and 77 species being common between
259 the two sites. Diversity estimate increased during the three days for the three facets of biodiversity, TD,
260 PD and FD (Figure 1). TD showed a steady increase across the survey days especially in the fully
261 protected area with a cumulated richness of 55% of the total richness at the end of the first survey day,
262 73% of the total richness at the end of the second survey day and 84% of the total richness at the end
263 of the third survey day. FD and PD displayed increases interspersed with “plateaux” particularly on the
264 second and third sampling days. Functional dispersion (FDis) and functional specialisation (FSpe)
265 values showed high variations across days with a mean FDis of 0.52 (sd = 0.03) and a mean FSpe of
266 0.37 (sd = 0.02) in the fully protected area, a mean FDis of 0.53 (sd = 0.01) and a mean FSpe of 0.38
267 (sd = 0.007) in the poorly protected area with low values at the beginning of the first day (Supp Fig. 1).

268 Within each site, the inter-day dissimilarity between videos was significantly higher than intra-
269 day dissimilarity for TD and PD (See Supp Table 3 and Supp Table 4 for associated Wilcoxon’s tests).

270

271



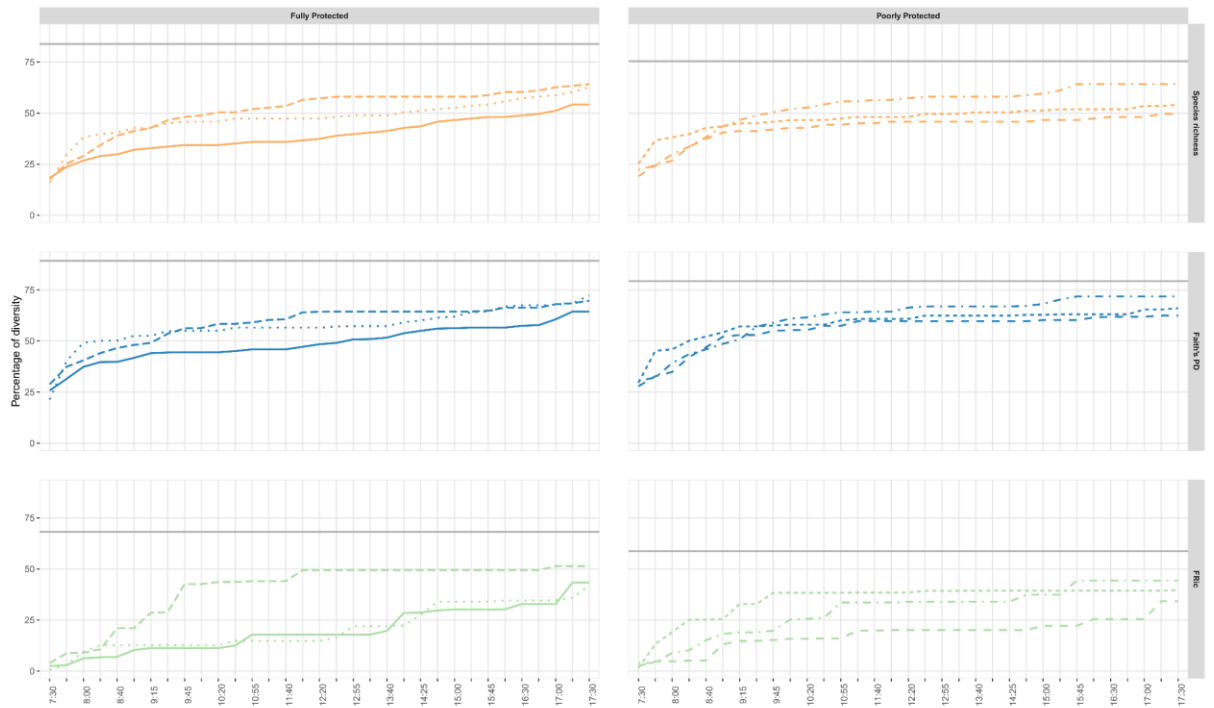
272

273 **Figure 1: Census of taxonomic, phylogenetic and functional richness across days.** Accumulation
 274 of detected species richness (A), phylogenetic richness (B) and functional richness (C) across the three
 275 days for the two sites. Values are expressed as a proportion relative to the total richness present in the
 276 two sites over the three days. The site in the fully protected area (N’Gouja) is represented in green while
 277 the site in the poorly protected area (Bouéni) is represented in brown.

278

279 Taxonomic richness increases throughout the day, with a sharp increase at the beginning of
 280 the recording (Figure 2). Between 25.61% and 46.48% of the total species richness observed within a
 281 single day was captured in the first video (i.e. first 17min42s). Species richness does not reach a
 282 “plateau” at the end of each day. The mean taxonomic dissimilarity between days was 36.57% in the
 283 fully protected area (sd: 0.8%) and 36.42% in the poorly protected area (sd: 0.4%). Overall, the fully
 284 protected area hosted 68% of functional richness detected on both sites and 89% of phylogenetic
 285 richness detected on both sites and the poorly protected area counted 59% of functional richness
 286 detected on both sites and 79% of phylogenetic richness detected on both sites. Functional and
 287 phylogenetic richness accumulation curves were similar to the taxonomic accumulation curve with a
 288 sharp increase at the beginning of the day and no asymptote at the end of the day (Figure 2). The mean
 289 functional dissimilarity between days in the fully protected area was 40.86% (sd: 4.25%) and 37.98%
 290 (sd: 6.67%) in the poorly protected area. The mean phylogenetic dissimilarity between days was of
 291 30.02% (sd: 4.27%) in the fully protected area and of 24.43% (sd: 0.8%) in the poorly protected area.

292



293

294 **Figure 2: Accumulation of species richness (orange), phylogenetic richness (blue) and**
 295 **functional richness (green) within a day.** The percentage of diversity seen on both sites is
 296 represented with the colored lines with different shapes for each survey days. The horizontal grey lines
 297 represent the percentage of total diversity seen on each site: on the left, the fully protected area
 298 (N’Gouja) and on the right, the poorly protected area (Bouéni).

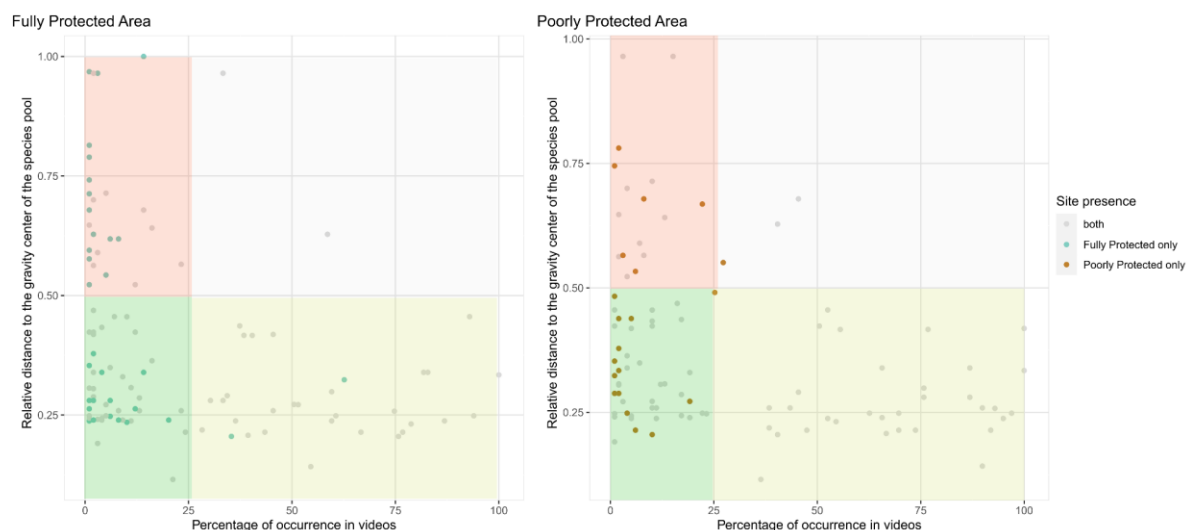
299

300 Altogether super rare (i.e. seen in $\leq 5\%$ of videos from a given site) and rare species (i.e. seen
 301 in $>5\%$ and $< 25\%$ of the videos), represented 69.72% of the fully protected areas species (76 species)
 302 and 63.26% of the poorly protected area’s species (62 species) (Supplementary Figure 5). Super rare
 303 species represented 36.70% of the fully protected area’s species (40 species) and 28.57% of the poorly
 304 protected area species (28 species). Rare species present in the two sites represented 19.27% of the
 305 species present in the fully protected area (36 species) and 16.33% of the species present in the poorly
 306 protected area (34 species). Common species (i.e. seen in $\geq 25\%$ of videos from a given site) present
 307 on both sites represented 20% of the total species number (33 species in the fully protected area and
 308 36 species in the poorly protected area). Four species (3.08% of the total species number) were present
 309 in more than 75% of videos for both sites, *Ctenochaetus striatus*, *Chaetodon trifasciatus*, *Gomphosus*
 310 *caeruleus* and *Thalassoma hardwicke*.

311

312 Super- rare and rare species represented 92% of the FRic seen in the fully protected area and
 313 85% of the FRic seen in the poorly protected area. They showed significantly higher distances to the
 314 gravity centre of the functional space than common species, for both sites (see Supplementary Table
 315 5). Species with the highest functional specialization (i.e. >75% of the maximal distance) were all super
 316 rare or rare species in each site, except *Caranx melampyus* which is common in the fully protected
 317 area but super rare in the poorly protected area (Figure 3). However, some super- rare species had low
 318 functional specialisation. Respectively 93.75% and 90.48% of species being unique to each site (32
 319 species in the fully protected area and 21 species in the poorly protected area are unique) were super
 320 rare or rare in the fully protected area and in the poorly protected area. Respectively 93.93% and
 321 94.44% of temporally common species i.e., seen in >25% of videos (33 species in the fully protected
 322 area and 36 in the poorly protected area are common) were present at both sites. There were only two
 323 functionally distinct and common species in the fully protected area and three functionally distinct and
 324 common species in the poorly protected area.

325



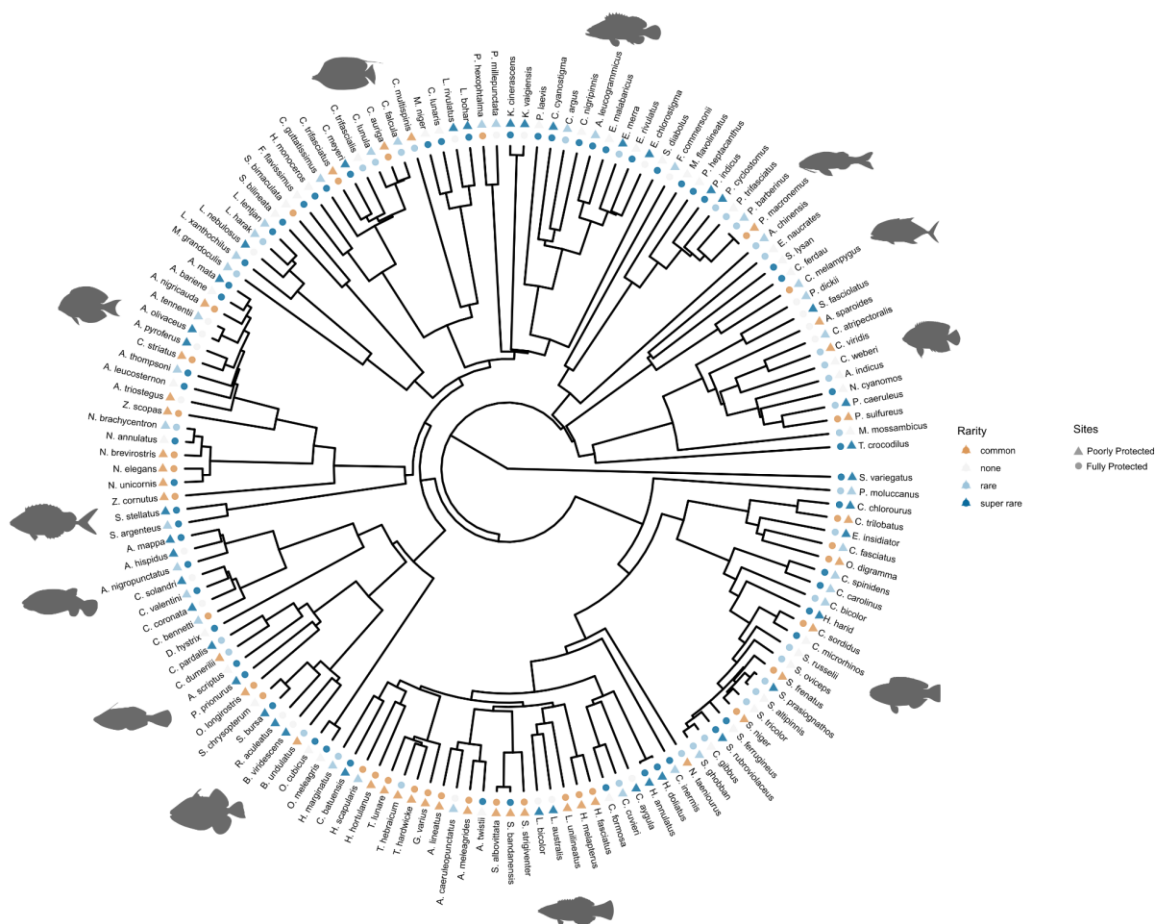
326

327 **Figure 3: Species functional specialisation according to their rarity.** Functional specialisation of
 328 each species seen in the fully protected area (N'Gouja, left) and in the poorly protected area (Bouéni,
 329 right) according to their temporal rarity. Functional specialisation is measured as the distance to the
 330 gravity centre of the global pool (y axis). Green and brown circles show species unique to each site
 331 respectively the fully protected area (N'Gouja) and the poorly protected area (Boueni), while grey circles
 332 show species present in both sites. The red area (top left) reflects rare and distinct species (Temporal
 333 occurrence < 25%, Species functional specialisation > 50%), the green area (bottom left) reflects rare

334 and not distinct species (Temporal occurrence < 25%, Species functional specialisation < 50%), the
 335 yellow area (bottom right) reflects common and not distinct species (Temporal occurrence > 25%,
 336 Species functional specialisation < 50%) and the grey area (top right) reflects common and distinct
 337 species (Temporal occurrence > 25%, Species functional specialisation > 50%).

338

339 The super rare and rare species were randomly distributed along the phylogenetic tree (D = 0.80 in
 340 poorly protected area and D = 0.83 in fully protected area) (Figure 4).



341

342 **Figure 4: Species rarity in the phylogenetic tree.** Phylogenetic tree representing species seen in the
 343 fully protected area (N’Gouja) and in the poorly protected area (Bouéni). The rarity of each species is
 344 represented as circles for species seen in the fully protected area and triangles for species seen in the
 345 poorly protected area. Shape colours reflect their presence and/or temporal rarity. Fishes silhouettes
 346 represent the main families of the phylogenetic tree and are taken from the *Fishape* github repository
 347 <https://github.com/simonjbrandl/fishape/tree/master/shapes>

348

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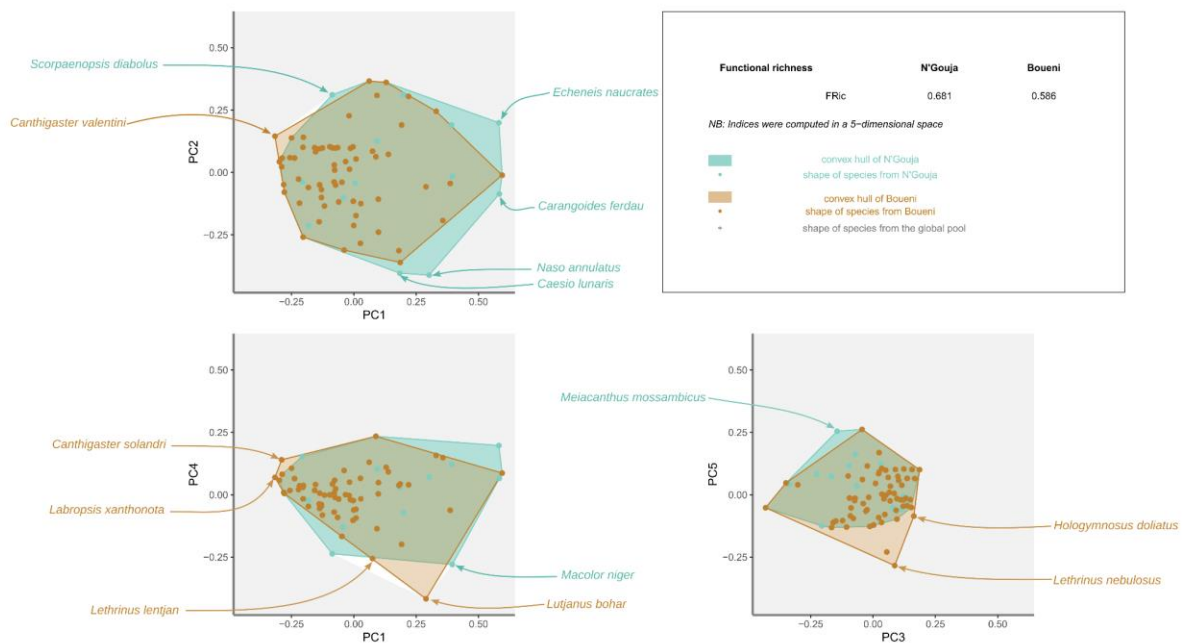
350 **Effect of the protection on TD, FD and PD**

351

352 Overall dissimilarity in species composition between the two sites was 0.41 due mostly to taxonomic
353 turnover (TD turnover = 0.35). Dissimilarity in lineage composition between the two sites was 0.31 due
354 mostly to phylogenetic turnover contributing to 77% of the dissimilarity (PD turnover = 0.24) and
355 dissimilarity in traits composition between the two sites was 0.57 with turnover contributing to 91% of
356 the dissimilarity (FD turnover = 0.51). A PERMANOVA test revealed that site and sampling day affect
357 the dissimilarity in species, lineage and traits composition (Supp Tables 6, 7, 8).

358 Among the 54 species being vertices of the studied pool of species (outermost points shaping the
359 convex hull in the functional space), seven species were only present in the fully protected area and six
360 species were only present in the poorly protected area (Figure 5).

361



362

363 **Figure 5: Difference in fish functional richness between fully protected and poorly protected**
364 **reefs.** Functional richness is illustrated as convex hulls shaping the species present in an assemblage
365 which are plotted along pairs of axes of the 5-dimensional functional space where it was computed.
366 Convex-hulls shaping fish communities found in the fully protected area (N'Gouja) in green and in the
367 poorly protected area (Bouéni) in brown along the first four functional axes of the multidimensional

368 space based on five dimensions. Species being on the edges of the convex-hulls (vertices) and which
369 are unique to each site are labeled in color according to which site they belong.

370

371 **Effect of recording duration on detecting the MPA effect on biodiversity**

372

373 After the first 5h of the first recording day, taxonomic, phylogenetic and functional richness were higher
374 in the poorly protected area than in the fully protected area (Figure 6). At the end of the first recording
375 day, species richness was the same in the fully protected area and in the poorly protected area,
376 phylogenetic richness is 2.95% higher in the poorly protected area and functional richness is 9.28%
377 higher in the fully protected area than in the poorly protected area. After the second recording day,
378 species, functional and phylogenetic richness were higher in the fully protected area than in the poorly
379 protected area by 11.57% for TD, 4.44% for PD and 28.25% for FD. At the end of the third recording
380 day, species, functional and phylogenetic richness were higher in the poorly protected area than in the
381 fully protected area by 10.09% for TD, 11.12% for PD and 21.36% for FD.

382



383

384 **Figure 6: Detection of protection benefit on biodiversity with increasing duration of video**

385 **survey.** (A) Difference in richness between the fully protected area (N'Gouja) and the poorly protected

386 area (Bouéni) according to the duration of video analysed (positive value indicates greater richness in

387 protected area). Taxonomic diversity is computed as the percentage of species richness seen on each

388 video compared to the total species richness of both sites, functional diversity is represented as the

389 functional richness index and phylogenetic diversity is represented as the percentage of the Faith's PD

390 index seen on each video compared to the total Faith's PD of both sites (B) TD dissimilarity computed

391 as the Jaccard index and, PD and FD dissimilarities computed as Jaccard-like indices between the Fully

392 Protected Area and the Poorly Protected Area.

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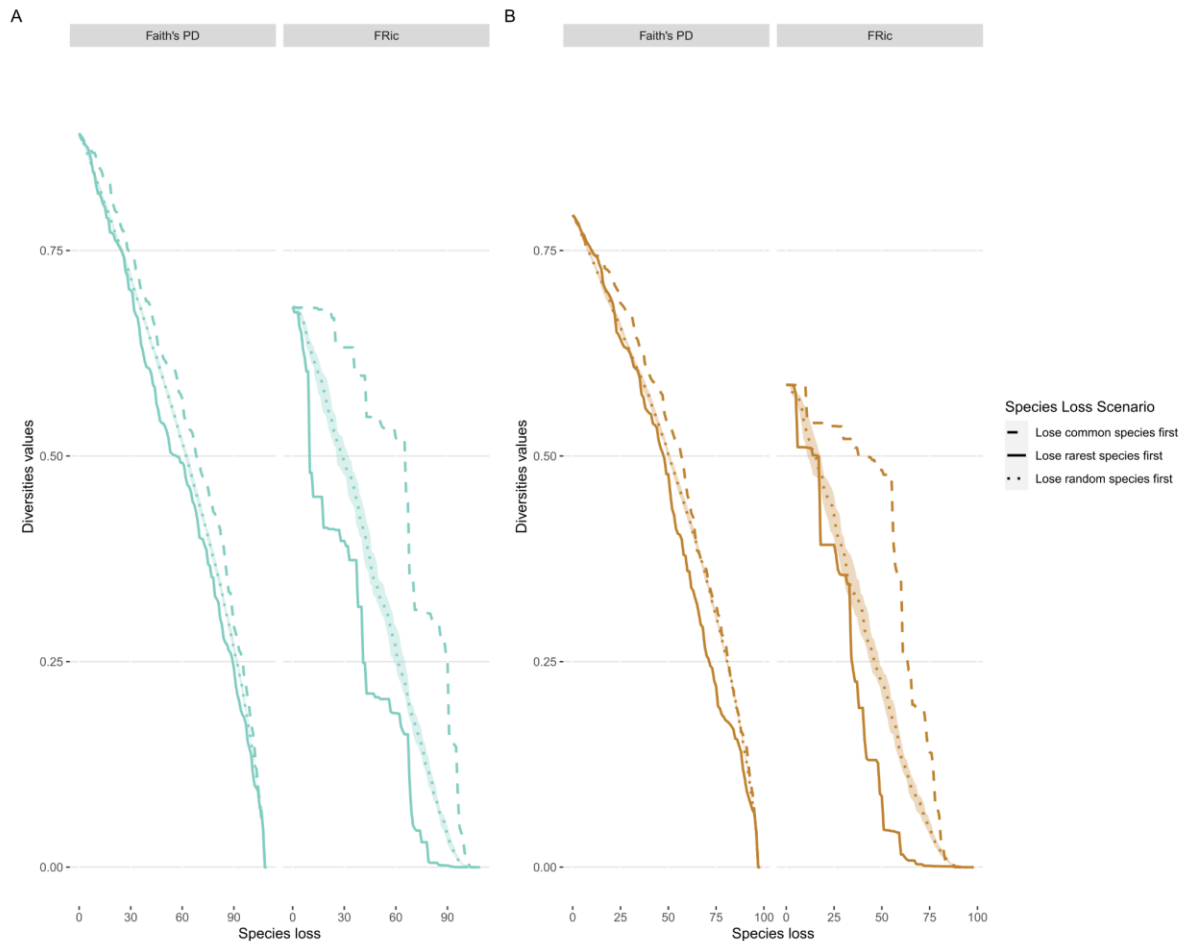
395

396 **Vulnerability of Functional and Phylogenetic Richness to Species Loss**

397

398 Under the scenario of the loss of the 20% rarest species, functional richness would decrease by 39.42
399 % in the fully protected area and 33.14% in the poorly protected area (Figure 7). This scenario
400 represents a supplemental loss of functional richness of 21.50% in the fully protected area and 15.25%
401 in the poorly protected area when compared to the random loss of 20% species and a supplemental
402 loss of 21.50% in the fully protected area and 25.26% in the poorly protected area when compared to
403 the loss of the 20% most common species. Phylogenetic richness would decrease by 12.28 % in the
404 fully protected area and 9.32% in the poorly protected area under the loss of the 20% rarest species.
405 When compared to the random loss of 20% species, this scenario represents a similar phylogenetic
406 richness loss in the fully protected area and the loss of random species realized a supplemental loss of
407 2.73% in the poorly protected area. It represents a supplemental loss of 2.44% in the fully protected
408 area and 0.93% in the poorly protected area when compared to the loss of the 20% most common
409 species.

410



411

412 **Figure 7: Vulnerability of phylogenetic richness and functional richness to species loss.**

413 Vulnerability was measured as the effect of simulated extinction following three scenarios:

414 common species (dashed) or rare species (solid) are lost first or to a random species loss (dotted) for
 415 the fully protected area (N'Gouja) (A) and the poorly protected area (Bouéni) (B). The
 416 rarity/commonness of each species is computed as the percentage of videos on which it occurs. The
 417 effect of the random loss of species was computed on 100 iterations of species loss, the dotted line
 418 represents the median lines surrounded by its confidence interval ($\alpha = 0.5$).

419

420 **4 - Discussion**

421

422 Using a remote long-duration video approach we revealed that species with distinctive
 423 phylogenetic histories and functional strategies were detected throughout three days, especially at the
 424 beginning of each day. After only 20 minutes of recording, up to 50% of the taxonomic diversity (TD)
 425 and up to 30% of phylogenetic diversity (PD) detected during a day have been recorded. Functional

426 diversity (FD) takes more time to be censused as less than 9% of the FD censused during a day was
427 detected after 20 minutes of videos. These results, similar to those from Tropical Eastern Pacific by
428 Marques et al. (2021), call for the use of cameras filming from sunrise to sunset to get a comprehensive
429 view of taxonomic, phylogenetic and functional facets of biodiversity. In addition, we found no significant
430 change in richness before dusk. Yet, variations in species richness between day and night have been
431 reported in other ecosystems (Harvey et al. 2012; Myers et al. 2016). Our cameras were recording from
432 two hours after the sunrise to half an hour before the sunset. They may thus not be recording late
433 enough to study these crepuscular times when predatory species are exploiting the light transitions to
434 hunt (Helfman 1986).

435

436 This high within and between-day variability can be due to the predominance of rare species
437 which contribute most of taxonomic, phylogenetic and functional diversities. Super rare and rare species
438 represented more than 66% of the species detected in the fully protected area and 60% of the species
439 recorded in the poorly protected area. The eight species with the highest species functional
440 specialisation (>75%) were super-rare and rare species at least in one site, which illustrates that distinct
441 combinations of traits are supported by rare species (Mouillot et al., 2013a). Yet, all rare species do not
442 support distinct functions. Temporally common species were the least distinct ones and only four
443 temporally common species had distinct combination of traits (FSpe > 50%) (*Abudefduf sparoides*,
444 *Caranx melampygus*, *Chromis viridis* and *Naso brevirostris*). This highlights the importance of applying
445 long-duration approaches, like the one implemented in this study, to observe species with unique trait
446 combinations that may fulfil unique functional roles. Five of the rare and functionally highly distinct
447 species belonged to functional entities containing only one species (*Carangoides ferdau*, *Echeneis*
448 *naucrates*, *Lutjanus bohar*, *Naso annulatus* and *Macolor niger*) thus being functionally unique. More
449 generally, almost 66% of the functional entities contain only one species, thus having no functional
450 insurance. This functional vulnerability has already been depicted at a larger spatial resolution for
451 tropical reef fish faunas from six biogeographical regions (Mouillot et al., 2014). Across days, both sites
452 display an important dissimilarity in terms of species, lineages and traits composition. It illustrates that
453 each day brings about a variety of different species, functional strategies, and phylogenetic histories.
454 This inter-day variability can be due to the weather differences between the surveyed days as rainfall
455 events occurred during one hour on the second day in the fully protected area and during the morning

456 of the third day in the poorly protected area. The inter-day variability can also be due to the low
457 detectability of rare mobile species which may be present within site but did not swim across the field
458 of view of the two cameras. Using additional cameras would increase the likelihood that all species in
459 the spatial area end up in front of the cameras at least once on the studied days. Thus, further studies
460 are needed to assess the effect of the number of cameras on both within and inter-day variability in
461 diversity estimates.

462

463 As a consequence, the loss of the 20% rarest species would lead to a loss of 40% of its
464 functional richness in the fully protected area and 33% in the poorly protected area. It represents a
465 supplemental loss of up to 25% of functional richness compared to the loss of the 20% most common
466 species and a supplemental loss of up to 20% of functional richness compared to the random loss of
467 20% of species. Reef fish functional diversity from Mayotte is thus vulnerable to the loss of temporally
468 rare species, as already reported for other faunas and floras (Leitão et al., 2016). Super-rare and rare
469 species are scattered in the phylogenetic tree, so that many rare species are from the same genera or
470 family than common species. The loss of rare species thus impacts to a lesser extent phylogenetic
471 richness than functional richness. In fact, the loss of the 20% rarest species represents a similar loss
472 as the loss of the 20% most common species or the loss of 20% of species selected randomly. Yet,
473 rarity is over-represented in some parts of the phylogenetic tree, particularly the one linking groupers.
474 Detecting temporally rare species whose loss can be detrimental to ecosystem functioning is thus
475 crucial when evaluating the effectiveness of conservation measures. While rarity has been computed
476 here as a temporal scarcity, it has several forms based on species geographic range, habitat specificity
477 and local abundance (Rabinowitz 1981; Violle et al. 2017). Integrating the local abundance of each
478 species to its temporal rarity could thus bring a more detailed view on the link between species' roles.
479 However, measuring species temporal rarity can be challenging and costly due to the influence of
480 seasonality, which leads to variations in species assemblages across large temporal scales such as
481 years, seasons, and months (Thompson & Mapstone, 2002; Myers & Worm, 2003; Lamy et al., 2015;
482 Mourier et al., 2016).

483

484 The moderate dissimilarity in species composition between the fully and the poorly protected
485 areas is mainly due to the replacement of species between the two sites. Moreover, the high

486 phylogenetic turnover between the two sites testifies that these replaced species are from distinct
487 lineages. Even if the fully protected area hosts slightly higher functional richness, the high functional
488 turnover between the two areas demonstrates that specific functional strategies are present in each
489 site. In fact, the dissimilar final values of FDis and FSpe indicated that the gravity centres of each site
490 were not close to the gravity center of the functional space, indicating medium functional nestedness
491 between the fully protected area and the poorly protected area. Our results thus confirm that diversity
492 recorded inside *versus* outside protected areas may be a poor indicator of management effectiveness
493 because the identity, composition and function of species they host can be markedly different while
494 diversity remains similar (Boulanger et al. 2021; Loiseau et al. 2021). There were more species
495 categorised as large species (>30cm) in the species only present in the fully protected area (75%) than
496 in the poorly protected area (50%) and more species with a high position in the water column (19% in
497 the fully protected area, 5% in the poorly protected area). In fact, large species are generally the targets
498 of fisheries (Bejarano et al. 2013; Edwards et al. 2014; Edgar et al. 2014) and it has been shown that
499 fully protected areas have a positive impact on such species (Lester et al. 2009; Edgar et al. 2014).
500 Moreover, in the poorly protected area, the use of nets was prohibited and only traditional line fishing
501 was permitted. Therefore, the lower proportion of big species in the poorly protected area can be due
502 to traditional fishing practices using hooks which only attract carnivorous species, mainly large sized
503 species. Using stereo-cameras to quantify individual size would enhance the precision of our results,
504 as the size classes in the trait database may differ from the actual size of individuals. The difference in
505 traits composition was also due to the specific presence of *Echeneis naucrates* in the fully protected
506 area which has been set up to protect marine turtles mainly *Chelonia mydas* and *Eretmochelys*
507 *imbricata* on which shells *Echeneis naucrates* attaches itself. These results show that even if big and
508 old reserves display more benefits for diversity than smaller and younger protected areas (Claudet et
509 al. 2008), small restrictions as a partial prohibition of given fishing practices (as here, nets and
510 spearfishing) can also help to preserve biodiversity (Stanley et al. 2018). However, large, old and
511 connected protected areas are needed to protect ecosystem processes and ecosystem services
512 (Costello & Ballantine 2015).

513

514 The important variations observed at the within and between-day scales highlight the time
515 needed to capture the impact of conservation measures. In fact, the full protection effect is revealed

516 only after a full day of recording videos supporting the use of video based long-duration approaches to
517 assess the effectiveness of conservation measures in high diversity systems. This approach shows that
518 it takes between one to six hours to detect 75% of the TD and PD detected during a day and between
519 four to eight hours to achieve 75% of the total FD seen during a day. Moreover, the low functional
520 distinctiveness (FDis) and specialisation (FSpe) at the beginning of the first survey day illustrate that
521 the species which are seen first are those carrying the most common traits, those with more distinct
522 traits generally appear after. It illustrates the benefits of recording several hours per day to have an
523 adequate picture of the diversity present in a studied site. Species from unique phylogenetic lineages
524 and with unique functional roles are still detected after more than 30 hours of videos which indicates
525 the importance of recording for several days to monitor biodiversity of such speciose ecosystems,
526 mostly made of rare mobile species, instead of conducting short-duration surveys. The effect of short
527 temporal scale variations on our perception of protection effect calls for the development of high
528 frequency tools in terrestrial and marine ecosystems. Yet, while remote cameras are moderately
529 expensive and easy to set up, annotating hundreds of video hours is a time-consuming process. For
530 instance, the annotation time in this study was 12 times higher than the duration of the video collection.
531 Thus, the development of deep-learning algorithms to identify species (Ditria et al. 2020) is essential to
532 ease the use of such remote underwater long duration approaches.

533

534 The findings that reef fish assemblages are dominated by temporally rare species and that these
535 species carry the most distinct functional strategies have important consequences for aquatic
536 conservationists. When monitoring the biodiversity in a specific site, it is crucial to consider the within-
537 day and between-day variabilities, to ensure the detection of the numerous temporally rare species.
538 Neglecting these variabilities can result in biased estimations of biodiversity which may impact our
539 perception of the effect of a conservation measure. Lastly, as distinct species play unique ecological
540 roles, monitoring their temporal occurrences and one step further their abundance is critical for
541 managing ecosystems.

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837

838

Figure legends

839 **Figure 1: Census of taxonomic, phylogenetic and functional richness across days.** Accumulation
840 of detected species richness (A), phylogenetic richness (B) and functional richness (C) across the three
841 days for the two sites. Values are expressed as a proportion relative to the total richness present in the
842 two sites over the three days. The site in the fully protected area (N'Gouja) is represented in green while
843 the site in the poorly protected area (Bouéni) is represented in brown.

844

845 **Figure 2: Accumulation of species richness (orange), phylogenetic richness (blue) and**
846 **functional richness (green) within a day.** The percentage of diversity seen on both sites is
847 represented with the colored lines with different shapes for each survey days. The horizontal grey lines
848 represent the percentage of total diversity seen on each site: on the left, the fully protected area
849 (N'Gouja) and on the right, the poorly protected area (Bouéni).

850

851 **Figure 3: Species functional specialisation according to their rarity.** Functional specialisation of
852 each species seen in the fully protected area (N'Gouja, left) and in the poorly protected area (Bouéni,
853 right) according to their temporal rarity. Functional specialisation is measured as the distance to the
854 gravity centre of the global pool (y axis). Green and brown circles show species unique to each site
855 respectively the fully protected area (N'Gouja) and the poorly protected area (Bouéni), while grey circles
856 show species present in both sites. The red area (top left) reflects rare and distinct species (Temporal
857 occurrence < 25%, Species functional specialisation > 50%), the green area (bottom left) reflects rare
858 and not distinct species (Temporal occurrence < 25%, Species functional specialisation < 50%), the
859 yellow area (bottom right) reflects common and not distinct species (Temporal occurrence > 25%,
860 Species functional specialisation < 50%) and the grey area (top right) reflects common and distinct
861 species (Temporal occurrence > 25%, Species functional specialisation > 50%).

862

863 **Figure 4: Species rarity in the phylogenetic tree.** Phylogenetic tree representing species seen in the
864 fully protected area (N'Gouja) and in the poorly protected area (Bouéni). The rarity of each species is
865 represented as circles for species seen in the fully protected area and triangles for species seen in the
866 poorly protected area. Shape colors reflect their presence and/or temporal rarity. Fishes silhouettes

867 represent the main families of the phylogenetic tree and are taken from the *Fishape* github repository
868 <https://github.com/simonjbrandl/fishape/tree/master/shapes>

869

870 **Figure 5 Difference in fish functional richness between fully protected and poorly protected**

871 **reefs.** Functional richness is illustrated as convex hulls shaping the species present in an assemblage
872 which are plotted along pairs of axes of the 5-dimensional functional space where it was computed.

873 Convex-hulls shaping fish communities found in the fully protected area (N’Gouja) in green and in the
874 poorly protected area (Bouéni) in brown along the first four functional axes of the multidimensional
875 space based on five dimensions. Species being on the edges of the convex-hulls (vertices) and which
876 are unique to each site are labeled in color according to which site they belong.

877

878

879 **Figure 6: Detection of protection benefit on biodiversity with increasing duration of video**

880 **survey.** (A) Difference in richness between the fully protected area (N’Gouja) and the poorly protected
881 area (Bouéni) according to the duration of video analysed (positive value indicates greater richness in
882 protected area). Taxonomic diversity is computed as the percentage of species richness seen on each
883 video compared to the total species richness of both sites, functional diversity is represented as the
884 functional richness index and phylogenetic diversity is represented as the percentage of the Faith’s PD
885 index seen on each video compared to the total Faith’s PD of both sites (B) TD dissimilarity computed
886 as the Jaccard index and, PD and FD dissimilarities computed as Jaccard-like indices between the Fully
887 Protected Area and the Poorly Protected Area.

888

889 **Figure 7: Vulnerability of phylogenetic richness and functional richness to species loss.**

890 Vulnerability was measured as the effect of simulated extinction following three scenarios:
891 common species (dashed) or rare species (solid) are lost first or to a random species loss (dotted) for
892 the fully protected area (N’Gouja) (A) and the poorly protected area (Bouéni) (B). The
893 rarity/commonness of each species is computed as the percentage of videos on which it occurs. The
894 effect of the random loss of species was computed on 100 iterations of species loss, the dotted line
895 represents the median lines surrounded by its confidence interval ($\alpha = 0.5$).

896