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

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Authors' contributions:

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

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Abstract:

1. The establishment of protected areas to face global diversity declines has mainly prioritized taxonomic diversity, leaving aside phylogenetic and functional diversities which determine ecosystem functioning and resilience. Furthermore, the assessment of protected areas effectiveness is mainly done using short duration surveys (<2h) which may undermine the detection of rare species.

2. Using a long-duration video approach, reef fish taxonomic, phylogenetic and functional facets of diversity were assessed for three days within a fully protected area and a nearby poorly protected area in Mayotte island (Western Indian Ocean).

3. We found that temporally rare species contributed to more than 60% of the taxonomic and 85% of the functional facets of biodiversity found on each site. Those rare species which harbour the most distinct trait values, also make reef fish diversity particularly vulnerable to their loss. Taxonomic, phylogenetic and functional richness were similar between the fully protected area and the poorly protected area while the species, lineages and traits compositions were markedly different.

4. These results pinpoint the importance of considering taxonomic, functional and phylogenetic dissimilarities while accessing protected areas effectiveness, instead of only using richness. In addition, benefits of the fully protected area were only detected using more than 15 hours of video survey, which emphasises the importance of long duration remote approaches to capture the within and between day's temporal variations.

Keywords: coral reef fishes, diversity survey, functional diversity, long duration video approach, phylogenetic diversity, protection level, rarity, taxonomic diversity

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1 - Introduction

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

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

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

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

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

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

2 - Methods

Remote Underwater Video recording

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

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

Cameras recorded continuously between 06:30 and 18:00, thus recording from 1h after dusk and 30 minutes before dawn. To reduce the diver's effect on fish detection, only videos starting one 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.

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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 ≥ 25% of videos of a given site. A species can belong to different rarity categories

219   on the two studied sites.

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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

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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.

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254   **3 - Results**

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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).

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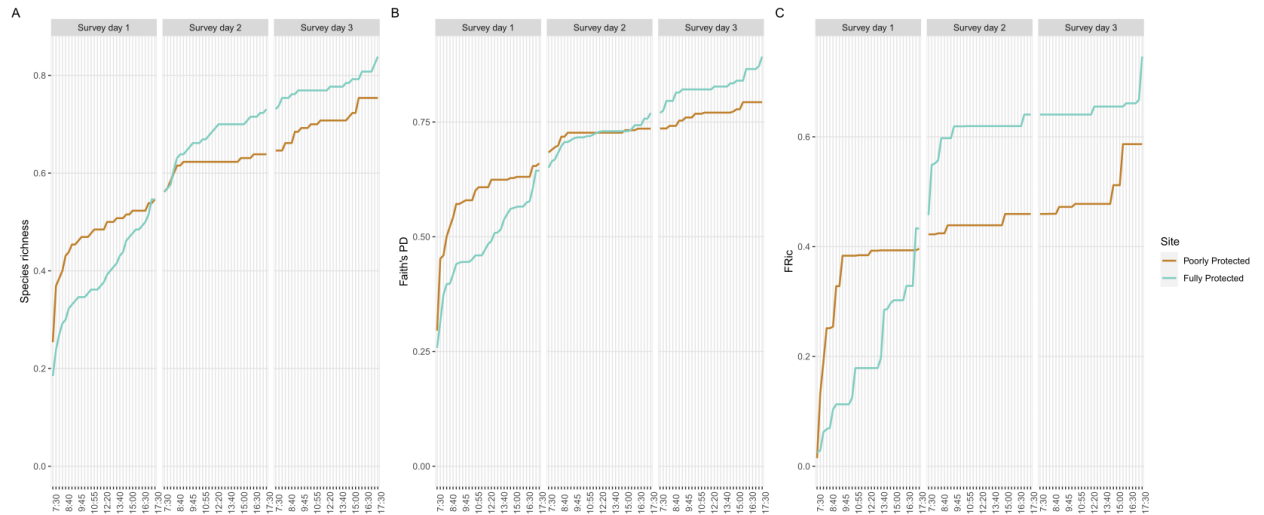
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Figure 1: Census of taxonomic, phylogenetic and functional richness across days. Accumulation of detected species richness (A), phylogenetic richness (B) and functional richness (C) across the three days for the two sites. Values are expressed as a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

Taxonomic richness increases throughout the day, with a sharp increase at the beginning of the recording (Figure 2). Between 25.61% and 46.48% of the total species richness observed within a single day was captured in the first video (i.e. first 17min42s). Species richness does not reach a "plateau" at the end of each day. The mean taxonomic dissimilarity between days was 36.57% in the fully protected area (sd: 0.8%) and 36.42% in the poorly protected area (sd: 0.4%). Overall, the fully protected area hosted 68% of functional richness detected on both sites and 89% of phylogenetic richness detected on both sites and the poorly protected area counted 59% of functional richness detected on both sites and 79% of phylogenetic richness detected on both sites. Functional and phylogenetic richness accumulation curves were similar to the taxonomic accumulation curve with a sharp increase at the beginning of the day and no asymptote at the end of the day (Figure 2). The mean functional dissimilarity between days in the fully protected area was 40.86% (sd: 4.25%) and 37.98% (sd: 6.67%) in the poorly protected area. The mean phylogenetic dissimilarity between days was of 30.02% (sd: 4.27%) in the fully protected area and of 24.43% (sd: 0.8%) in the poorly protected area.
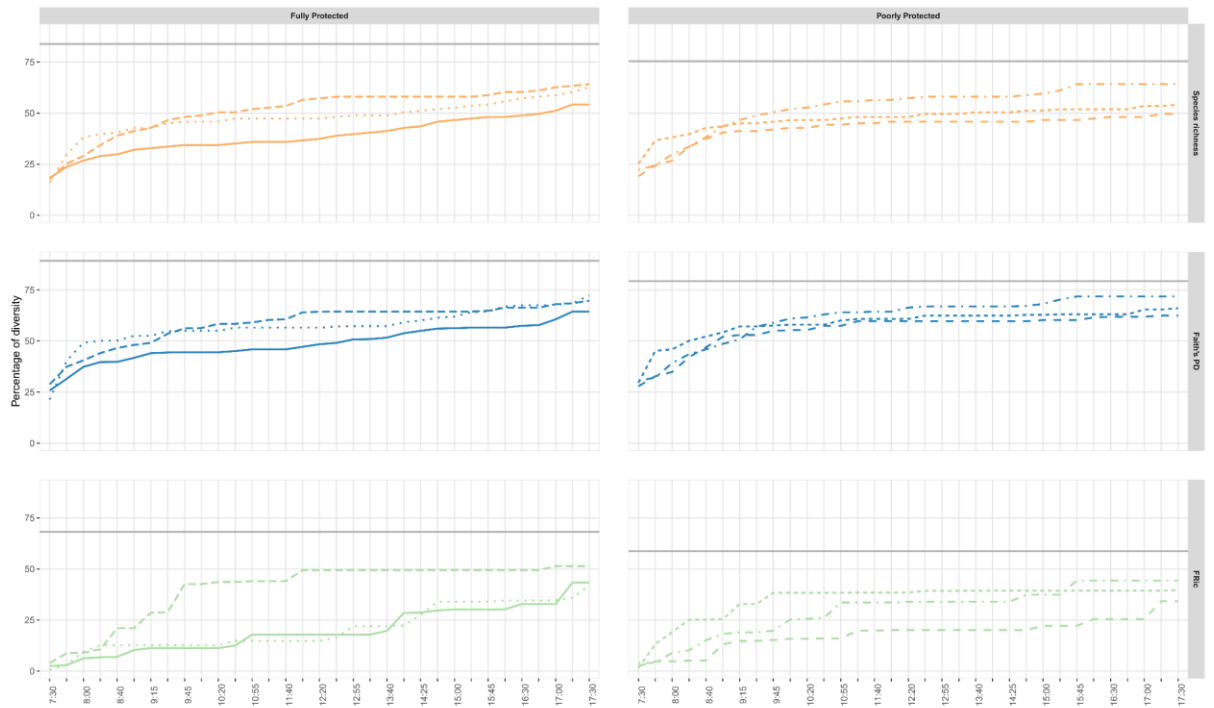
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Figure 2: Accumulation of species richness (orange), phylogenetic richness (blue) and functional richness (green) within a day. The percentage of diversity seen on both sites is represented with the colored lines with different shapes for each survey days. The horizontal grey lines represent the percentage of total diversity seen on each site: on the left, the fully protected area (N'Gouja) and on the right, the poorly protected area (Bouéni).

Altogether super rare (i.e. seen in ≤ 5% of videos from a given site) and rare species (i.e. seen in >5% and < 25% of the videos), represented 69.72% of the fully protected areas species (76 species) and 63.26% of the poorly protected area's species (62 species) (Supplementary Figure 5). Super rare species represented 36.70% of the fully protected area's species (40 species)and 28.57% of the poorly protected area species (28 species). Rare species present in the two sites represented 19.27% of the species present in the fully protected area (36 species) and 16.33% of the species present in the poorly protected area (34 species). Common species (i.e. seen in ≥ 25% of videos from a given site) present on both sites represented 20% of the total species number (33 species in the fully protected area and 36 species in the poorly protected area). Four species (3.08% of the total species number) were present in more than 75% of videos for both sites, *Ctenochaetus striatus, Chaetodon trifasciatus, Gomphosus caeruleus* and *Thalassoma hardwicke.*

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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 melampygus* 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.

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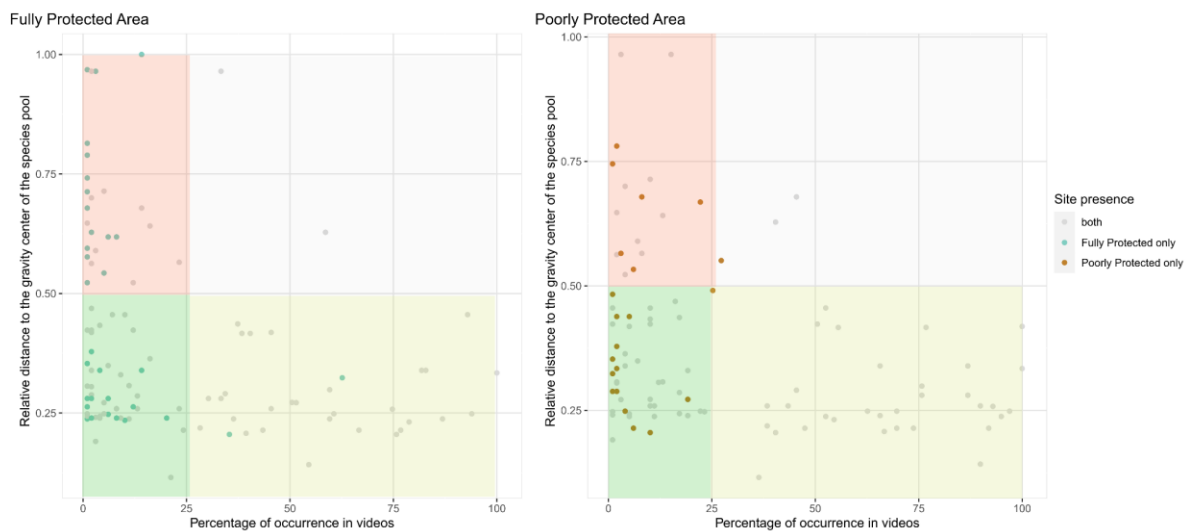
327   **Figure 3: Species functional specialisation according to their rarity.** Functional specialisation of

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

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

The super rare and rare species were randomly distributed along the phylogenetic tree (D = 0.80 in poorly protected area and D = 0.83 in fully protected area) (Figure 4).
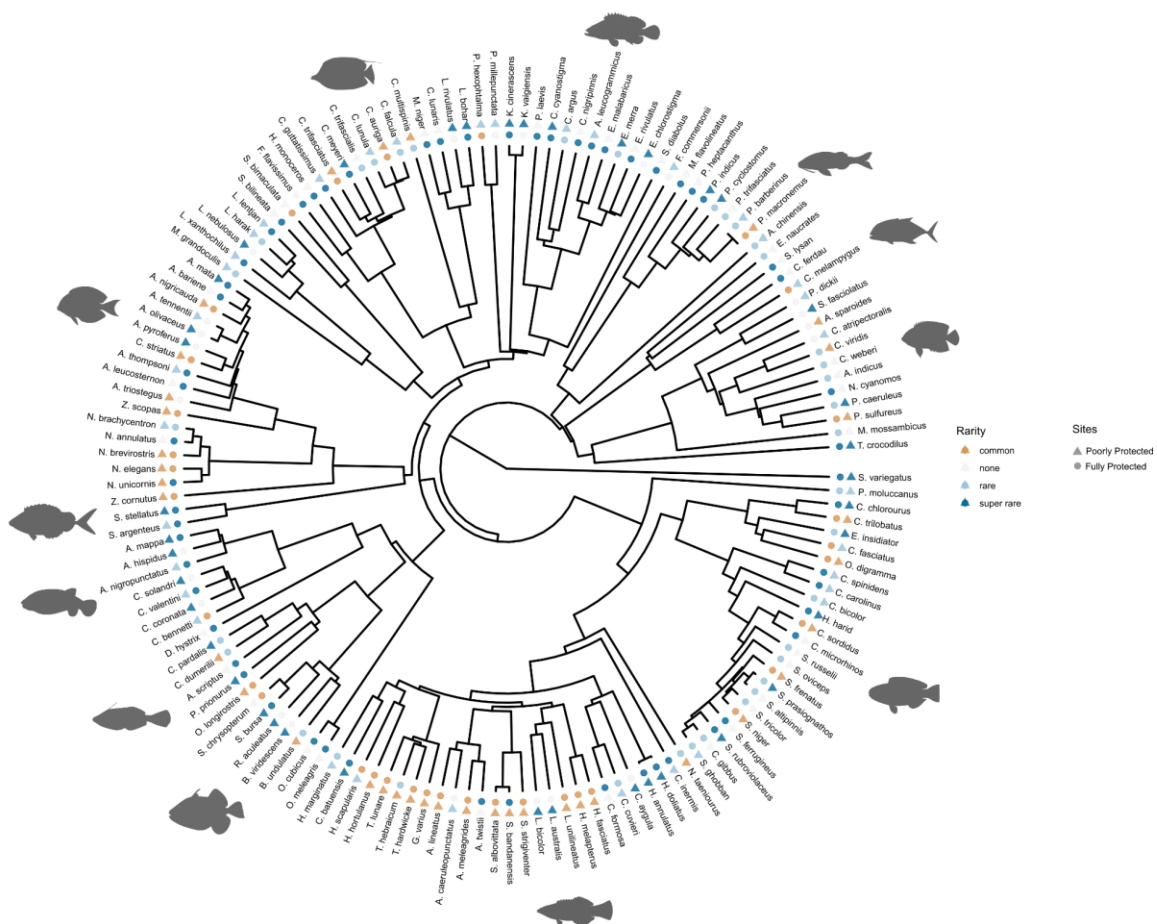
Figure 4: Species rarity in the phylogenetic tree. Phylogenetic tree representing species seen in the fully protected area (N'Gouja) and in the poorly protected area (Bouéni). The rarity of each species is represented as circles for species seen in the fully protected area and triangles for species seen in the poorly protected area. Shape colours reflect their presence and/or temporal rarity. Fishes silhouettes represent the main families of the phylogenetic tree and are taken from the *Fishape* github repository https://github.com/simonjbrandl/fishape/tree/master/shapes

349

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).

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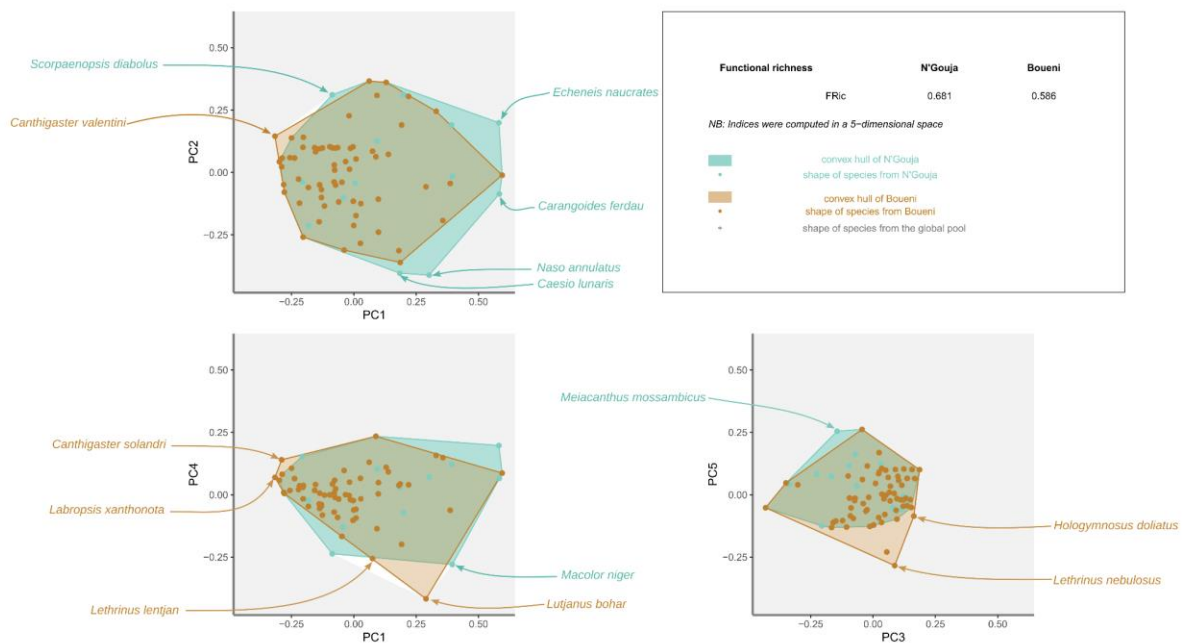
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363 **Figure 5: Difference in fish functional richness between fully protected and poorly protected**

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

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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.

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

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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.

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Figure 6: Detection of protection benefit on biodiversity with increasing duration of video survey. (A) Difference in richness between the fully protected area (N'Gouja) and the poorly protected area (Bouéni) according to the duration of video analysed (positive value indicates greater richness in protected area). Taxonomic diversity is computed as the percentage of species richness seen on each video compared to the total species richness of both sites, functional diversity is represented as the functional richness index and phylogenetic diversity is represented as the percentage of the Faith's PD index seen on each video compared to the total Faith's PD of both sites (B) TD dissimilarity computed as the Jaccard index and, PD and FD dissimilarities computed as Jaccard-like indices between the Fully Protected Area and the Poorly Protected Area.

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Vulnerability of Functional and Phylogenetic Richness to Species Loss

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

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

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

common species (dashed) or rare species (solid) are lost first or to a random species loss (dotted) for

the fully protected area (N'Gouja) (A) and the poorly protected area (Bouéni) (B). The

rarity/commonness of each species is computed as the percentage of videos on which it occurs. The

effect of the random loss of species was computed on 100 iterations of species loss, the dotted line

represents the median lines surrounded by its confidence interval (α = 0.5).

4 - Discussion

      Using a remote long-duration video approach we revealed that species with distinctive

phylogenetic histories and functional strategies were detected throughout three days, especially at the

beginning of each day. After only 20 minutes of recording, up to 50% of the taxonomic diversity (TD)

and up to 30% of phylogenetic diversity (PD) detected during a day have been recorded. Functional

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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 ni 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

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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

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

The important variations observed at the within and between-day scales highlight the time 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 biassed 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

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 (Boueni), 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