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

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

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The authors have no conflict of interest to declare.

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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.

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

Measuring species, functional and phylogenetic diversities on videos

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

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

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

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

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

Species rarity

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

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

Dissimilarity between species assemblages

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

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

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

Vulnerability of biodiversity to Species Loss

The vulnerability of functional richness and of phylogenetic richness of each site to species loss was studied according to three scenarios (following Leitão et al., 2016). The first scenario simulates the random loss of species by randomly removing species from one to the number of species present in the studied site. One hundred iterations of such random species loss were computed. The second scenario simulates the loss of species going from the most common to the rarest in each site, while the third scenario simulates the loss of species going from the rarest to the most common.

3 - Results

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

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

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

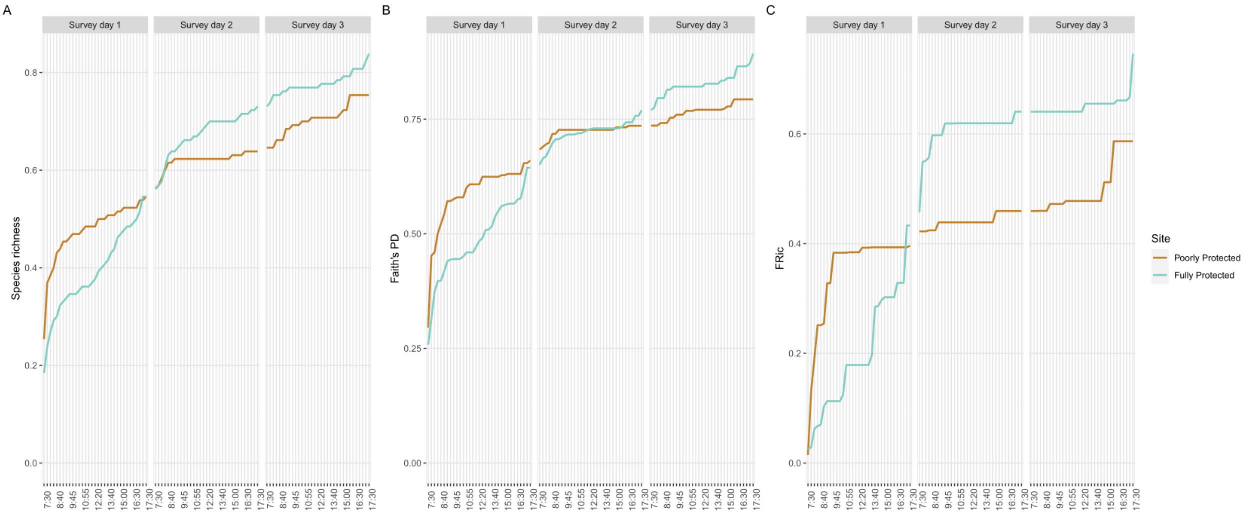

Figure 1: Census of taxonomic, phylogenetic and functional richness across days. Accumulation of detected species richness (A), phylogenetic richness (B) and functional richness (C) across the three days for the two sites. Values are expressed as a proportion relative to the total richness present in 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.

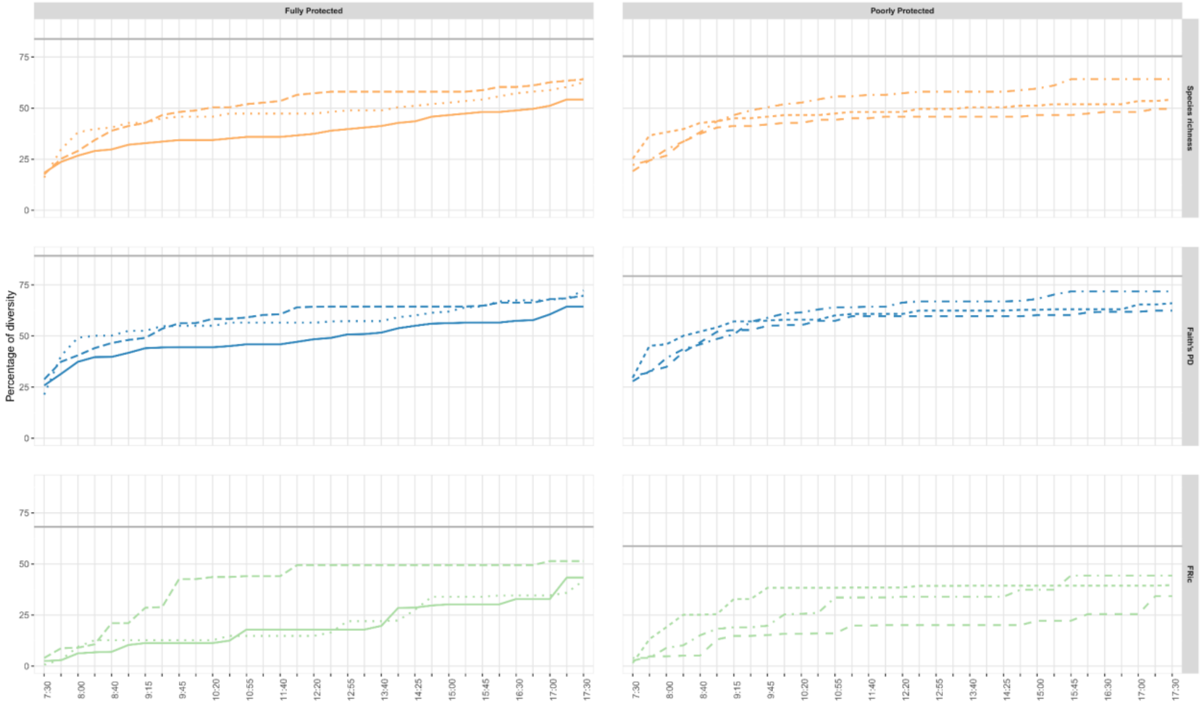

Figure 2: Accumulation of species richness (orange), phylogenetic richness (blue) and functional richness (green) within a day. The percentage of diversity seen on both sites is represented with the colored lines with different shapes for each survey days. The horizontal grey lines represent the percentage 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*.

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

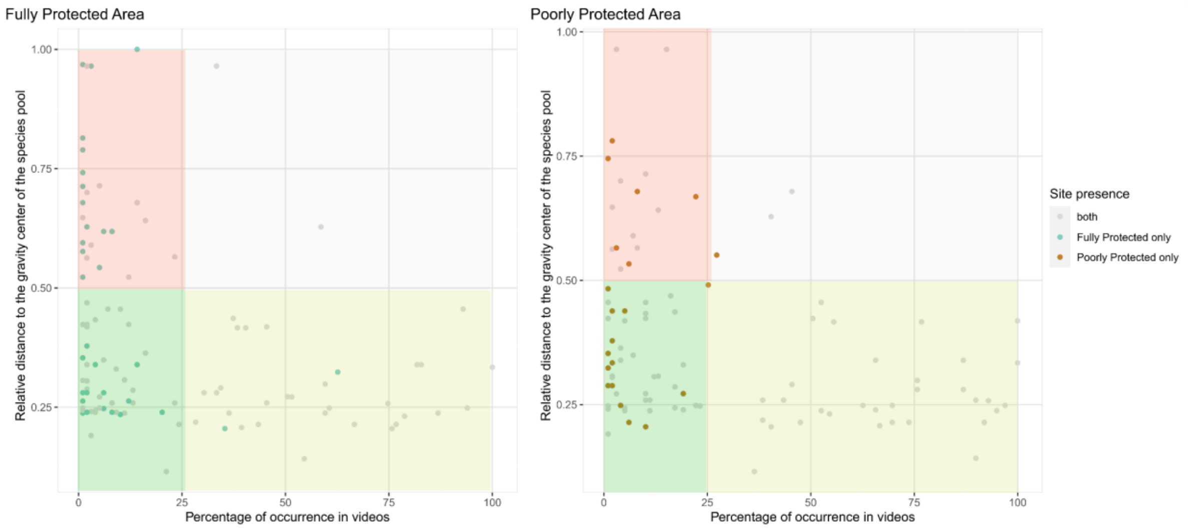

Figure 3: Species functional specialisation according to their rarity. Functional specialisation of each species seen in the fully protected area (N'Gouja, left) and in the poorly protected area (Bouéni, right) according to their temporal rarity. Functional specialisation is measured as the distance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

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).

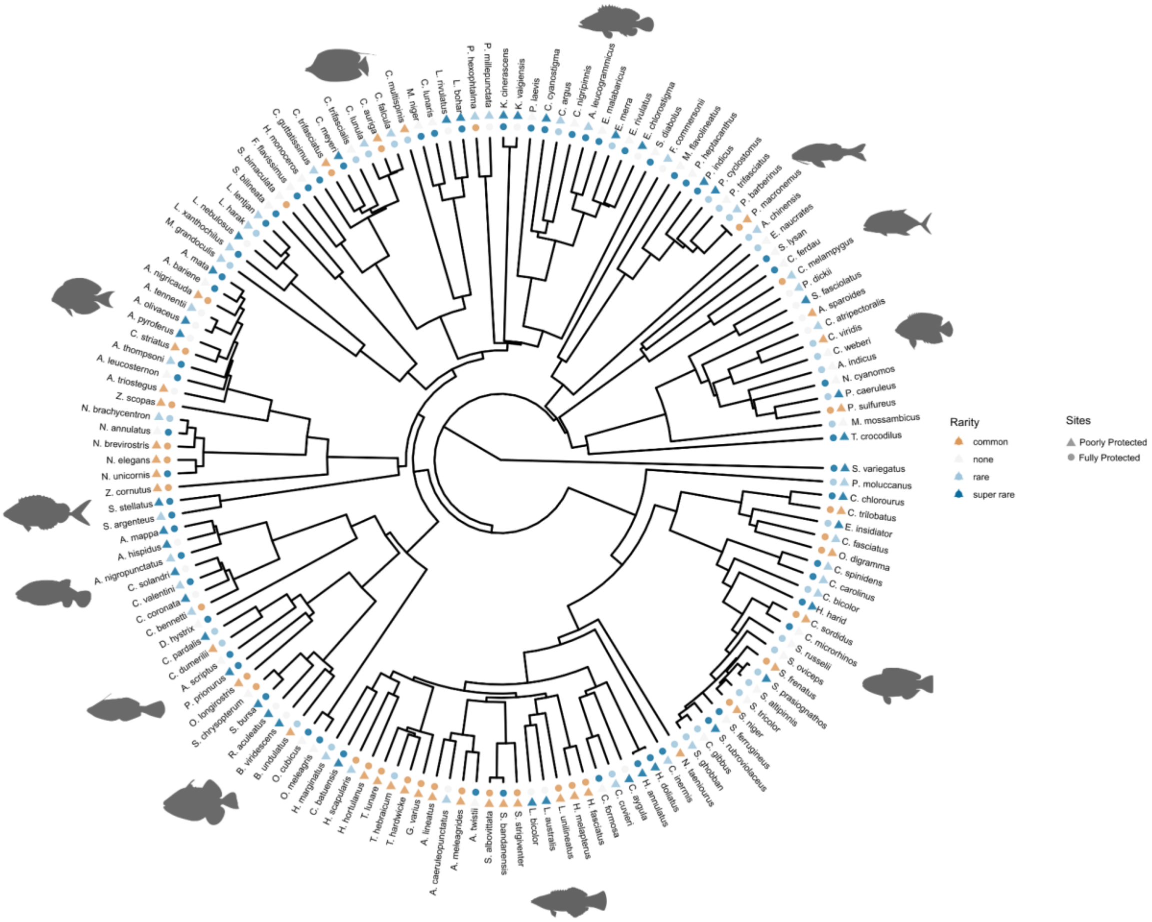

Figure 4: Species rarity in the phylogenetic tree. Phylogenetic tree representing species seen in the fully protected area (N'Gouja) and in the poorly protected area (Bouéni). The rarity of each species is represented as circles for species seen in the fully protected area and triangles for species seen 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

Effect of the protection on TD, FD and PD

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

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

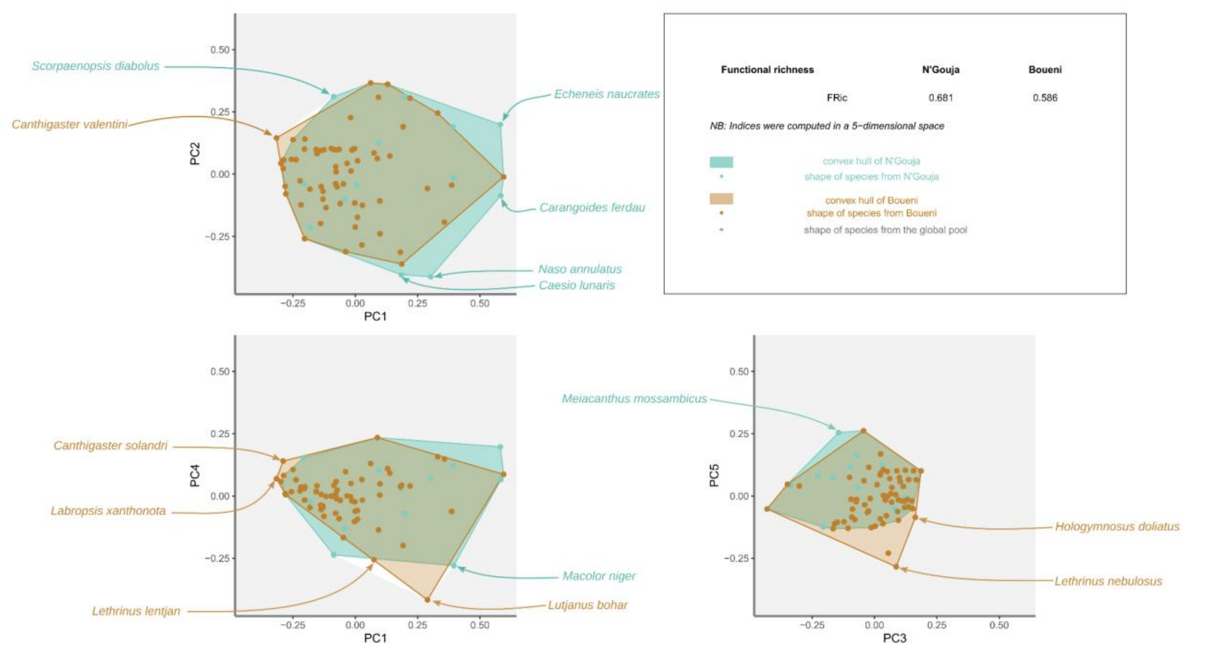

Figure 5: Difference in fish functional richness between fully protected and poorly protected reefs. Functional richness is illustrated as convex hulls shaping the species present in an assemblage which are plotted along pairs of axes of the 5-dimensional functional space where it was computed. Convex-hulls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

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

Effect of recording duration on detecting the MPA effect on biodiversity

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

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.

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.

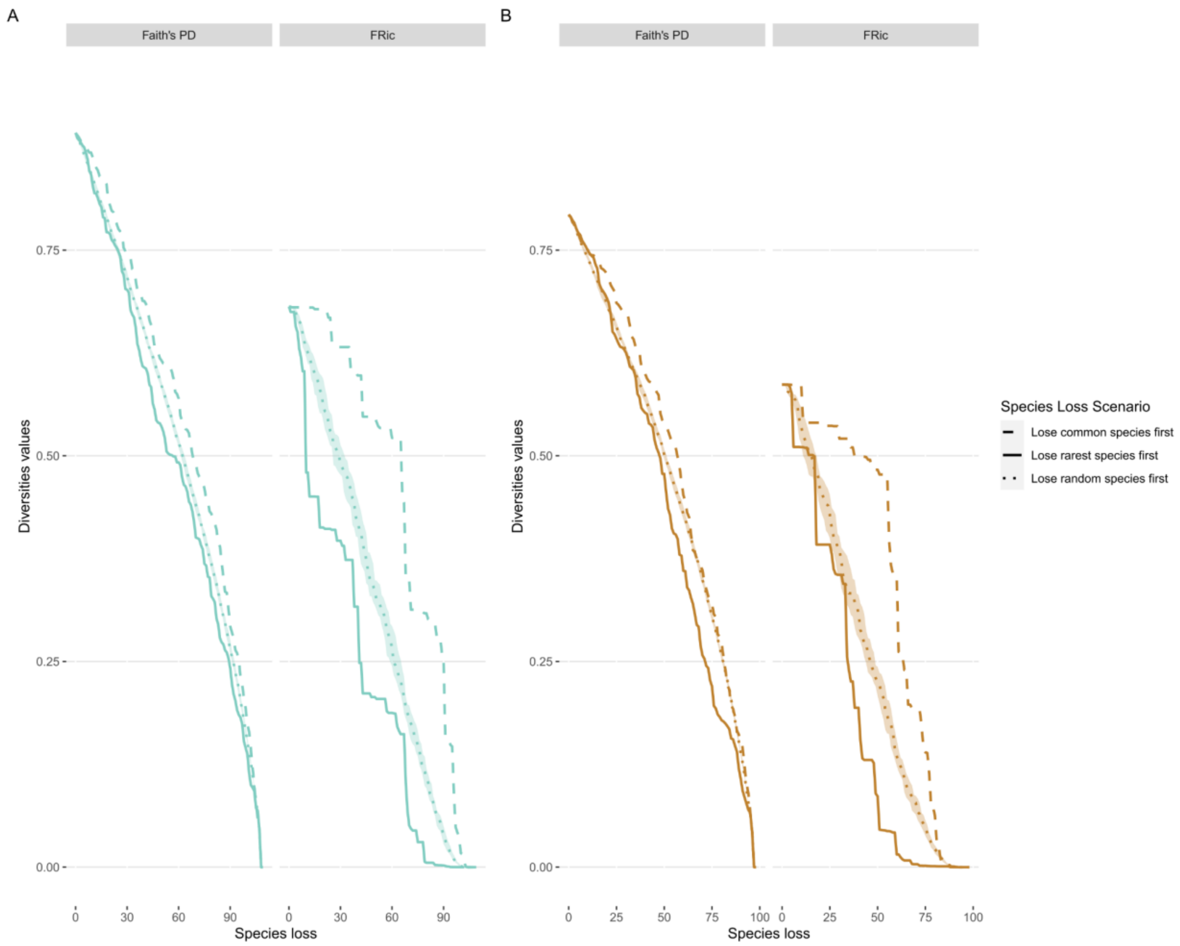

Figure 7: Vulnerability of phylogenetic richness and functional richness to species loss. Vulnerability was measured as the effect of simulated extinction following three scenarios: common species (dashed) or rare species (solid) are lost first or to a random species loss (dotted) for the fully protected 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 diversity (FD) takes more time to be censused as less than 9% of the FD censused during a day was detected after 20 minutes of videos. These results, similar to those from Tropical Eastern Pacific by Marques et al. (2021), call for the use of cameras filming from sunrise to sunset to get a comprehensive view of taxonomic, phylogenetic and functional facets of biodiversity. In addition, we found ni significant change in richness before dusk. Yet, variations in species richness between day and night have been reported in other ecosystems (Harvey et al. 2012; Myers et al. 2016). Our cameras were recording from two hours after the sunrise to half an hour before the sunset. They may thus not be recording late enough to study these crepuscular times when predatory species are exploiting the light transitions to hunt (Helfman 1986).

This high within and between-day variability can be due to the predominance of rare species which contribute most of taxonomic, phylogenetic and functional diversities. Super rare and rare species represented more than 66% of the species detected in the fully protected area and 60% of the species recorded in the poorly protected area. The eight species with the highest species functional specialisation (>75%) were super- rare and rare species at least in one site, which illustrates that distinct combinations of traits are supported by rare species (Mouillot et al., 2013a). Yet, all rare species do not support distinct functions. Temporally common species were the least distinct ones and only four temporally common species had distinct combination of traits (FSpe > 50%) (*Abudefduf sparoides, Caranx melampygus, Chromis viridis* and *Naso brevirostris*). This highlights the importance of applying long-duration approaches, like the one implemented in this study, to observe species with unique trait combinations that may fulfil unique functional roles. Five of the rare and functionally highly distinct species belonged to functional entities containing only one species (*Carangoides ferdau*, *Echeneis naucrates*, *Lutjanus bohar*, *Naso annulatus* and *Macolor niger*) thus being functionally unique. More generally, almost 66% of the functional entities contain only one species, thus having no functional insurance. This functional vulnerability has already been depicted at a larger spatial resolution for tropical reef fish faunas from six biogeographical regions (Mouillot et al., 2014). Across days, both sites display an important dissimilarity in terms of species, lineages and traits composition. It illustrates that each day brings about a variety of different species, functional strategies, and phylogenetic histories. This inter-day variability can be due to the weather differences between the surveyed days as rainfall events occurred during one hour on the second day in the fully protected area and during the morning of the third day in the poorly protected area. The inter-day variability can also be due to the low detectability of rare mobile species which may be present within site but did not swim across the field of view of the two cameras. Using additional cameras would increase the likelihood that all species in the spatial area end up in front of the cameras at least once on the studied days. Thus, further studies are needed to assess the effect of the number of cameras on both within and inter-day variability in diversity estimates.

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

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

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

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Figure legends

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.

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).

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

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 colors 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

Figure 5 Difference in fish functional richness between fully protected and poorly protected reefs. Functional richness is illustrated as convex hulls shaping the species present in an assemblage which are plotted along pairs of axes of the 5-dimensional functional space where it was computed. Convex-hulls shaping fish communities found in the fully protected area (N'Gouja) in green and in the poorly protected area (Bouéni) in brown along the first four functional axes of the multidimensional space based on five dimensions. Species being on the edges of the convex-hulls (vertices) and which are unique to each site are labeled in color according to which site they belong.

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.

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 ($\alpha = 0.5$).