

1 **Unexpected high vulnerability of functions in wilderness areas: evidence from coral reef**
2 **fishes**

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31

32 **Abstract**

33

34 High species richness is thought to support the delivery of multiple ecosystems functions and
35 services under changing environments. Yet some species might perform unique functional
36 roles while others are redundant. Thus, the benefits of high species richness in maintaining
37 ecosystem functioning is uncertain if functions have little redundancy, potentially leaving to
38 high vulnerability of functions. We studied the natural propensity of assemblages to be
39 functionally buffered against loss prior to fishing activities, using functional trait
40 combinations, in coral reefs fish assemblages across unfished wilderness areas of the Indo-
41 Pacific: Chagos Archipelago, New Caledonia and French Polynesia. Fish functional diversity
42 in these wilderness areas is highly vulnerable to fishing, explained by species- and
43 abundance-based redundancy packed into a small combination of traits, leaving most other
44 trait combinations (60%) sensitive to fishing, with no redundancy. Functional vulnerability
45 peaks for mobile and sedentary top predators, and large species in general. Functional
46 vulnerability decreases for certain functional entities in New Caledonia, where overall
47 functional redundancy was higher. Uncovering these baseline patterns of functional
48 vulnerability can offer early warning signals of the damaging effects from fishing, and may
49 serve as baselines to guide precautionary and even proactive conservation actions.

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1. Introduction

Human activities have already induced the collapse of many ecosystems around the world [1–3] and, in combination with climate change, have triggered major reductions in biodiversity globally [3–7]. Beyond the loss of species, there is a growing awareness that the loss of ecological functions may be the most critical consequence of human disturbances on ecosystems [8–11]. This diversity of ecological functions sustains ecosystem services on which humanity depends; such as biomass production [10]. Sustaining ecosystem functions requires both high functional diversity, i.e. a large breadth of ecological functions supported by species [12–16], and high functional redundancy, i.e. a large number of species supporting identical functions in the system [17].

In theory, species richness is thought to maintain a high level of both functional diversity and redundancy, thus ensuring the long term functioning of ecosystems in a fluctuating environment [18]. Indeed, high species richness should increase the probability of having both species supporting different functions (functional diversity) and many species supporting the same ecological functions (functional redundancy) [16]. Many experiments confirm this theory, for example demonstrating the vulnerability of ecosystem functioning to species loss [11, 19]. In natural systems, however, the benefits of high species richness to maintaining ecosystem functioning have recently been challenged by three patterns. First, at the scale of ocean basins (and using species checklists), some functions exhibit over-redundancy, i.e. are supported by a disproportionately high number of species, while others are realized by few or one species only, even in the richest regions [20]. Second, species that support specific or unique traits in ecosystems (no redundancy) tend to be rare due to their low abundance in ecosystems [21]. Third, the distribution of species richness and abundance among trophic groups is more critical than simply the number of species to maintain ecosystem functioning and services [22]. These patterns demonstrate the importance of preserving both species and abundance within a wide range of functional groups.

Taken together, these results suggest that high levels of species richness and abundance may not insure ecosystems against functional diversity loss as we once hoped, due to the high vulnerability of some functions that lack redundancy. Yet, this hypothesis has never been tested with empirical data in tropical ecosystems with marginal or no exposure to threats, i.e.

98 where species density and abundances should be close to natural baselines. Assessing the
99 vulnerability of ecological functions to threats in such scenarios would reveal the baseline of
100 functional vulnerability, and the extent to which these ecosystems are buffered against even
101 limited local species declines or extinctions.

102
103 Protected areas (PAs) are often used to assess ecological baselines against which biodiversity
104 levels in exploited areas are compared [23]. However, recent studies have shown that even
105 PAs cannot be considered as true ecological baselines since anthropogenic disturbances
106 typically started long before these areas were established [2, 24–26]. In addition, most of
107 these areas are either too small or embedded in areas influenced by human activities and
108 therefore cannot support the full range of ecological functions [23, 27]. As an alternative,
109 wilderness areas, i.e. large areas geographically isolated from humans by natural geographic
110 barriers or with very limited human presence, may provide ecological baselines close to a
111 ‘natural’ status [2, 25, 27]. Indeed, wilderness areas are traditionally viewed as areas featuring
112 exceptional concentrations of biodiversity and abundance [28], albeit potentially suffering
113 from global changes in a near future [29].

114
115 Here, using coral reef ecosystems along a geographic gradient, we propose to test two
116 hypotheses. First disparate wilderness areas tend to host a similar level of functional diversity,
117 uncovering a consistent baseline for the breadth of functions in ecosystems, despite a high
118 turnover in species composition. Second, this common level of functional diversity remains
119 highly vulnerable to species declines or losses due to a disproportional over-redundancy in
120 some functions and a ‘natural’ lack of redundancy for some critical functions.

121
122 Coral reefs are the most diverse marine ecosystems on Earth [30] and support key services for
123 half a billion people, such as food and income [31]. We quantified the baseline vulnerability
124 to fishing of fish functional diversity in coral reef ecosystems across the Indo-Pacific
125 geographic gradient, taking advantage of extensive surveys in French Polynesia, New
126 Caledonia and Chagos. These three wilderness areas all benefit from a high level of isolation
127 from humans [32] and a high level of enforcement due to the presence of military forces,
128 thereby limiting illegal fishing activities. Since the ecological knowledge to assess the
129 functions carried by individual species is limited, using species functional traits to infer

130 functions offers a viable alternative [33]. Here, we assume that species with more diverse
131 combinations of functional traits are more likely to support different functions (e.g. [34, 35]).

132

133 **2. Material and methods**

134

135 **(a) Study regions**

136

137 Remote atolls and islands in three regions (Chagos Archipelago, New Caledonia, and French
138 Polynesia) were sampled along the Indo-Pacific biogeographic gradient, encompassing 130°
139 of longitude (16,000 km) (ESM, Figure S1). None of these atolls and islands are inhabited:
140 the northern Chagos Archipelago (the Great Chagos Bank, Peros Banhos and Salomon Island)
141 is more than 650 km south of the Maldives and personnel at the Diego Garcia atoll navy base
142 are not permitted to the northern Archipelago; isolated atolls and islands in New Caledonia
143 (Entrecasteaux Archipelago, Astrolabe Reef, and Beautemps-Beaupré) are located between 300
144 to 600 km and > 20 hours by boat from the capital Nouméa [25]; two atolls at the southeast
145 end of the Tuamotu Archipelago (Paraoa and Ahunui) are located approximately 950 km from
146 Papeete, the capital of French Polynesia; and the Acteon Group - a cluster of atolls - is located
147 between 200 and 500 km north of Gambier Island, French Polynesia (Figure 1).

148

149 **(b) Fish surveys**

150

151 Fish data for the Pacific Islands were collected on outer reef slopes using Underwater Visual
152 Census (UVC) along 50 m transects. Briefly, this method involved two divers each recording
153 species identity, abundance and body length [36]. Transects in New Caledonia (18 transects)
154 and French Polynesia (37 transects) were truncated at 10 m wide (10×50m strip transects). In
155 the Chagos Archipelago, fishes were surveyed along outer reef slopes using 50 x 5 m strip
156 transects (79 transects). To make surveys comparable among regions, a common area of 500
157 m² was obtained by randomly aggregating two Chagos transects (250 m²). Accumulation
158 curves of species richness were performed for each region to test for potential biases due to
159 survey techniques (ESM, Figure S1). Species densities and abundances were estimated for
160 500 m² transects and averaged for each region. Sharks and rays were removed from the main
161 species list due to their specific traits, some poaching in Chagos, and difficulties in assessing

162 their abundance using UVC [37]. As such, this study focused on 412 fish species belonging to
163 35 teleost families.

164

165 **(c) Functional traits and entities**

166

167 To estimate functional diversity, we used six functional traits related to major fish attributes:
168 1) maximum body size, 2) diet, 3) home range, 4) position over the reef, 5) activity, and 6)
169 gregariousness [20, 38].

170

171 Fish sizes were coded using six ordered categories: 0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50
172 cm, 50.1–80 cm, and >80 cm. Diet was characterized based on the main items consumed by
173 each species, which led to seven trophic categories: herbivorous-detritivorous (i.e., fishes
174 feeding on turf or filamentous algae and/or undefined organic material), macroalgal
175 herbivorous (i.e., fishes eating large fleshy algae and/or seagrass), invertivorous targeting
176 sessile invertebrates (i.e., corals, sponges, ascidians), invertivorous targeting mobile
177 invertebrates (i.e., benthic species such as crustaceans, echinoderms), planktivores (i.e., fishes
178 eating small organisms in the water column), piscivorous (including fishes and cephalopods),
179 and omnivorous (i.e., fishes for which both vegetal and animal material are important in their
180 diet) [20, 39]. Home range was coded using three ordered categories: sedentary (including
181 territorial species), mobile within a reef, and mobile between reefs. Position in the water
182 column was coded using three ordered categories: benthic, benthopelagic, and pelagic.
183 Activity period was coded using three ordered categories: diurnal, both diurnal and nocturnal,
184 and nocturnal. Schooling was coded using five ordered categories: solitary, pairing, or living
185 in small (3–20 individuals), medium (20–50 individuals), or large (>50 individuals) groups.
186 This functional traits database was built using information about the ecology of adult life-
187 stages available in the literature and according to observations made in the Indo – Pacific by
188 the survey team [38, 40, 41].

189

190 More detailed descriptions linking these traits to ecological processes can be found in the
191 Supplemental Material of published articles [20, 27]. Since all traits were coded using
192 categories, we defined functional entities (FEs) as groups of species sharing the same trait
193 categories. In total, 412 fish species were clustered into 157 different FEs [20, 27].

194

195 **(d) Fish functional diversity**

196

197 In order to compare the level of functional richness among the wilderness areas, we measured
198 the functional richness (FRic) of fishes for each region defined as the volume inside the
199 convex hull occupied by species within a functional space [42, 43]. To build a functional
200 space, we calculated pairwise functional distances between species pairs based on the six
201 functional traits using the Gower metric, which allows mixing different types of variables
202 while giving them equal weight [44]. A Principal Coordinates Analysis (PCoA) was
203 performed on this distance matrix to build a multidimensional functional space. We retained
204 the first four principal axes (PCs), which faithfully represent the Gower distance between
205 species [42, 43, 45].

206

207 **(e) Taxonomic and Functional β -diversity**

208

209 In order to determine if wilderness areas host different species and functional compositions
210 across the Indo-Pacific we assessed taxonomic and functional β -diversity among regions. We
211 used the β -diversity partitioning framework based on the Jaccard dissimilarity index [46, 47].
212 Taxonomic β -diversity (β_{jac}) equals (Eq.1):

213

214
$$\beta_{jac} = \frac{b+c}{a+b+c} \quad \text{Eq. 1}$$

215

216 where, a is the number of species in both regions A and B, b is the number of species present
217 in region A but not in region B, and c is the number of species present in region B but not in
218 region A.

219

220 To distinguish between the species replacement vs. nestedness components of β -diversity, we
221 decomposed the pairwise Jaccard dissimilarity index (Eq. 1) into two additive components
222 [46, 47]. The replacement component of the Jaccard dissimilarity index (β_{jtu} , Eq. 2) describes
223 species replacement without the influence of richness difference between regions. This index
224 is formulated as follows:

225

226
$$\beta_{jtu} = \frac{2 \min(b,c)}{a+2 \min(b,c)} \quad \text{Eq. 2}$$

227

228 where a , b , and c are the same as in Eq. 1.

229

230 The nestedness component of the Jaccard dissimilarity index (β_{jne} , Eq. 3) is the difference
231 between β_{jac} and β_{ju} . This index accounts for the fraction of dissimilarity due to richness
232 difference and is formulated as follows:

233

$$\beta_{jne} = \frac{\max(b,c) - \min(b,c)}{a+b+c} \times \frac{a}{a+2\min(b,c)} \quad \text{Eq. 3}$$

235

236 where a , b , and c are the same as in Eq. 1 and 2. The first term in Eq. 3 expresses a measure
237 of richness difference, whereas the second term corresponds to the dissimilarity version of β_{ju}
238 that is independent of richness difference ($1 - \beta_{ju}$, [47]).

239

240 The functional β -diversity among regions was decomposed into functional turnover and
241 functional nestedness-resultant components following the same framework [48, 49].

242 Taxonomic and functional β -diversity and their respective components were computed using
243 the R functions from the “betapart” R package (R 2.15.2, R development Core Team, 2012).

244

245 **(f) Functional vulnerability to fishing**

246

247 Despite the variety of conceptual approaches, there is growing agreement in defining
248 vulnerability as the combination of three components: i) *sensitivity*, or the susceptibility of a
249 system to threats, ii) *exposure*, or the level of those threats on a system, and iii) *adaptive*
250 *capacity*, or the capacity of the system to prepare for and respond to those threats [39, 50, 51].
251 By analogy, the level of "functional vulnerability" in a given ecosystem relies on i) *functional*
252 *sensitivity*, i.e. the extent to which particular traits are more prone to decline in the face of
253 certain threats [52], ii) *exposure* or the level of threats, and iii) *functional redundancy*, i.e. the
254 degree to which the same functional traits are supported by many and/or abundant species.

255

256 In wilderness areas, exposure to fishing is absent or extremely low [28]. Therefore, the
257 vulnerability to fishing in wilderness areas, termed here as “baseline vulnerability”, is solely
258 defined as the combination of species sensitivity to fishing, driven by their biological traits
259 (e.g. size, growth, reproductive capacity), and the level of functional redundancy which is

260 determined by the natural distribution of species density and abundances among functional
261 entities (ESM, Figure S2).

262

263 The sensitivity of each fish species to fishing was estimated using a fuzzy logic expert system
264 to take into account eight life history characteristics that are linked to species productivity and
265 other factors that make fish species more or less sensitive to fishing [53]. This indicator has
266 accurate predictive capacity [53] and has been widely recognized as a comprehensive and
267 suitable indicator of fish sensitivity to fishing [54]. The sensitivity to fishing was aggregated
268 at the level of FEs by averaging the sensitivity of all species belonging to the given FE. The
269 scale ranged from 0 to 24.

270

271 Functional redundancy is defined as the level of functional equivalence among species in an
272 ecosystem, such that one function may be performed by one or many species, and one species
273 may substitute for another in the latter case [55]. Here redundancy was assessed using three
274 complementary indices. First we used the number of species composing each FE in each
275 region (FR_S). However, the number of species per FE is only one aspect of functional
276 redundancy. The distribution of species abundances within FEs represents a complementary
277 aspect of redundancy [56–58]. Therefore, secondly we took into account the number of
278 individuals in each FE (FR_{ab}).

279 The mean abundance per 500m² of a species i in each region was calculated according to the
280 formula:

281

$$282 \quad \overline{ab}_i = \frac{\sum_{i=1}^N n_i}{N} \quad \text{Eq. 4}$$

283

284 where N is the number of transects per region and n_i is the number of individuals of species i .
285 Then functional redundancy of a given FE for a given region FR_{ab} was obtained as follows:

286

$$287 \quad FR_{ab} = \sum_{i=1}^S \overline{ab}_i \quad \text{Eq. 5}$$

288

289 with \overline{ab}_i representing the mean number of individuals of species i per 500m² and S is the
290 number of species in the given FE for that given region.

291

292 Thirdly, we computed a redundancy index accounting for both the number of species and
293 their abundances in each FE. We used the Shannon entropy index $FR_{Shannon}$ with the rationale
294 that a given FE will have more redundancy if represented by many abundant species.
295 Conversely, FEs will have low redundancy if represented by few and rare species.
296 Accordingly, in each region, $FR_{Shannon}$ for each FE was computed as:

297

$$298 \quad FR_{Shannon} = - \sum_{i=1}^S p_i \ln p_i \quad (\text{Eq. 6})$$

299

$$300 \quad \text{with } p_i = \frac{\overline{ab}_i}{\sum_{i=1}^S \overline{ab}_i} \quad (\text{Eq. 7})$$

301

302 where, p_i is the individuals' proportion of species i in the FE, and S is the number of species
303 per FE.

304

305 We applied the correction derived from the equivalent number of species [59]:

306

$$307 \quad FR_{Shannon_{EQ}} = \exp (FR_{Shannon}) \quad (\text{Eq. 8})$$

308

309 The equivalent number of species is an unbiased measure of Shannon entropy, following
310 Hill's "doubling" property that ensures that the diversity index doubles with the level of
311 diversity, as opposed to non-linear diversity indices that behave counter intuitively [60].

312

313 Quantitatively, the vulnerability of fish FEs to fishing for each region was assessed using a
314 framework based on multi-criteria decision-making (MCDM) and the TOPSIS method
315 (Technique for Order Preference by Similarity to an Ideal Solution). Applied to our specific
316 case, this technique ranks FEs according to their relative distance to the positive and negative
317 ideal solutions, which represent the conditions obtained when the criteria have extreme values
318 [39, 61]. The positive ideal solution (A^+) corresponds to the conditions where sensitivity to
319 threats is minimum while redundancy is maximum (ESM, Figure S3). Conversely, the
320 negative ideal solution (A^-) corresponds to the conditions where sensitivity to threats is
321 maximum while redundancy is minimum.

322 Functional vulnerability was then expressed as the relative distance to these positive and
323 negative ideal solutions according to Eq. 9:

324

$$325 \quad V_i = \frac{d^+}{d^- + d^+} \quad \text{Eq. 9}$$

326

327 where V_i is the vulnerability of functional entity i , d^+ is the distance to A^+ and d^- the distance
328 to A^- in Euclidean space. The vulnerability index ranges from 0 if the criteria scores
329 correspond to A^+ and to 1 when the criteria scores correspond to A^- [39, 61].

330 The vulnerability of a FE is high when both the fishing sensitivity of that FE is high and when
331 redundancy is low [39, 62].

332

333 **(g) Mapping functional sensitivity, redundancy and vulnerability in** 334 **functional space**

335

336 The density distribution of functional redundancy, sensitivity and vulnerability within the
337 functional space was estimated using the kernel method with a Gaussian estimation [63]. The
338 smoothing parameter h was estimated using the *ad hoc* method, which is the optimum h value
339 obtained for the normal distribution [63]:

$$340 \quad h = \sigma n^{-\frac{1}{6}} \quad \text{Eq. 10}$$

341

342 where, n is the number of FEs, and σ^2 being the estimated variance for x and y coordinates.

343

$$344 \quad \sigma = 0.5(\sigma_x^2 + \sigma_y^2) \quad \text{Eq. 11}$$

345

346 The kernel density estimation was computed using the “adehabitatHR” R package (R 2.15.2,
347 R development Core Team, 2014).

348

349 Functional redundancy, sensitivity and vulnerability were mapped onto the functional space
350 for each region and their match was estimated with the Pearson product-moment correlation.

351

352 **3. Results**

353

354 **(a) Similar level of functional diversity across wilderness areas**

355

356 The greatest number of species and FEs were found in New Caledonia, encompassing 83% of
357 FEs recorded in the three regions (Figure 2). In contrast, French Polynesia showed the lowest
358 number of species (42%) and FE (69%) (Figure 2 and Additional Information in ESM).
359 Overall, 45% of the total FEs (71) were common to the three regions, whereas only 13% (56)
360 of the species were shared (Figure 2 and Additional Information in ESM).

361
362 The functional richness in each region (FRic) ranged from 82% of the global functional
363 volume (French Polynesia) to 94.4% (New Caledonia) (ESM, Figure S4). The low variability
364 of functional diversity between biogeographic regions is consistent with the weak level of β -
365 functional diversity (functions turnover) between regions ranging from 0.14 to 0.18
366 (maximum is 1). Conversely, the β – taxonomic diversity was higher, ranging between 0.66
367 and 0.79 (maximum at 1) (ESM, Figure S5, Table S1 and Additional Information), implying
368 that most functional entities are present independent of species identities.

369
370 **(b) Heterogeneous distribution of functional redundancy across wilderness areas and**
371 **functional entities**

372
373 Despite the overall stability of functional diversity across the biogeographic gradient, the
374 highest functional redundancy of both species per FE (15) and Shannon entropy (17) was
375 found in New Caledonia, whereas Chagos and French Polynesia only reached 8-9 species
376 (Figure 3b & Additional Information in ESM). In each region, more than 60% of FEs were
377 represented by only one species, and 12% to 20% of the FEs were represented by only 2
378 species (Figure 3a & Additional Information in ESM), showing that the majority of FEs had
379 low species redundancy.

380
381 Mapping variation of Shannon entropy across the functional space showed a highly
382 heterogeneous distribution of functional redundancy for each region, with the highest values
383 disproportionally packed into some parts of the functional space (Figure 4a & ESM Figure
384 S7), leaving most of the functional space with low or no redundancy. The extreme
385 concentration of functional redundancy in the top left of the figure (Figure 4a) was
386 represented by sedentary small to medium size detritivorous, invertivorous, planktivores and
387 omnivorous feeders (e.g. surgeonfishes, damselfishes, butterflyfishes) (Figure 4a & ESM

388 Figure S6). The top right concentration of redundancy (Figure 4a) was characterized by small
389 to medium size invertivorous feeders (mobile prey) (see also Additional Information in ESM).

390

391 **(c) High vulnerability of functional entities in wilderness areas**

392

393 Since most of the functional space had low functional redundancy, the variation in
394 vulnerability to fishing was partly driven by sensitivity to fishing (mean Pearson coefficient
395 across regions = 0.93, $p < 0.001$). Variations in functional sensitivity and redundancy across
396 the functional space were independently distributed (mean Pearson coefficient across
397 locations = -0.09, $p > 0.1$) albeit the most sensitive species systematically showed very low
398 redundancy (ESM Figure S8).

399

400 Medium to large top predators, both solitary and sedentary, such as groupers (top right) and
401 moray eels (top right), as well as mobile and medium sized schooling species such as the
402 Bluefin trevally (*Caranx melampygus*) and the Great barracuda (*Sphyraena barracuda*)
403 (bottom right) were highly vulnerable to fishing in the three regions (Figure 4c, 4d & ESM
404 Figure S6) due to their high sensitivity to fishing (Figure 4b) and low redundancy (1 species
405 per FE (Figure 4a). For the same reasons, large invertivores species feeding on mobile prey
406 such as the Humphead wrasse (*Cheilinus undulatus*), large invertivores (sedentary and
407 mobile), detritivores and planktivores, located in the upper right side of the functional space
408 (Figure 4b & ESM Figure S6) showed a high vulnerability to fishing (Figure 4b & Addition
409 Information in ESM).

410

411 At the center of the functional space we observed a high fishing vulnerability peak due to the
412 presence of two large, mobile, and medium sized schooling species; the bumphead parrotfish
413 (*Bolbometopon muricatum*), an invertebrate sessile feeder, and the humpback unicornfish
414 (*Naso brachycentron*), a macroalgae feeder (Figure 4b & ESM Figure S6). At the right side of
415 the functional space we observed a second peak of vulnerability to fishing (hence high
416 sensitivity coupled with low redundancy) characterized by the bicolor parrotfish (*Cetoscarus*
417 *ocellatus*), a large bioeroder [64] and the bluespine unicornfish (*Naso unicornis*), a
418 macroalgae feeder, both being the only species in their respective FEs and highly sensitive to
419 fishing, explaining their high vulnerability.

420

421 Conversely, the high diversity of small to medium size herbivorous-detrivorous,
422 omnivorous, invertivorous and planktivores species in some FEs (top left of the functional
423 space), contributed to their high functional redundancy, counterbalancing (mean Pearson
424 coefficient across locations of -0.21, $p < 0.001$) their high sensitivity to fishing and making
425 them less vulnerable (Figure 4). The higher functional redundancy in New Caledonia
426 decreased the vulnerability of certain FE. For example the functional entity composed of
427 medium size invertebrates feeders (mainly from the triggerfishes family) was composed of 9
428 species in NC and 5 in French Polynesia, thereby, in concert with Shannon entropy, reducing
429 its vulnerability 12% compared to French Polynesia. Variation in redundancy and
430 vulnerability across the functional space depicted by the 3rd and 4th axes of PCoA are showed
431 in Figure S9 (ESM).

432

433 **4. Discussion**

434

435 **(a) Homogeneous level of functional diversity and functional vulnerability across the** 436 **Indo-Pacific biogeographic gradient**

437

438 Surprisingly, despite the large differences in species richness and identity among the three
439 regions, we found very consistent patterns of functional diversity along the species richness
440 biogeographic gradient [65], suggesting that the set of ecological functions for the growth and
441 persistence of coral reefs are supported independently of species identity and richness, thus
442 serving as a “natural” baseline indicator. As such, the presence/absence of functional entities
443 compared to wilderness areas may be a useful indicator to assess ecosystem conditions under
444 human pressure. This result is in line with a previous study on the scale of biogeographic
445 regions demonstrating that functions are maintained along a gradient of species richness [20].
446 Similar consistency was found for functional vulnerability, suggesting that combinations of
447 fish traits have quasi-similar levels of redundancy across coral reefs and the biogeographic
448 gradient, albeit New Caledonia had lower levels of vulnerability for several functional entities
449 due to higher functional redundancy.

450

451 **(b) High vulnerability of ecosystem functioning**

452

453 Studies of vulnerability have typically focussed on species rather than ecological functions
454 [39], and often overlook abundance distributions among species [20, 39]. In addition, the
455 assumption that functional diversity in wilderness areas, seen as a reference, is not buffered
456 against extinction due to relatively high functional vulnerability has never been tested. Here
457 we filled this gap by assessing the baseline functional vulnerability of fish assemblages to
458 fishing in some of the most isolated coral reef ecosystems across the Indo-Pacific. We found
459 that even in the near-absence of fishing and considering species abundance, most functional
460 entities remain highly vulnerable in each wilderness ecosystem since species diversity is
461 overwhelmingly packed into a small set of FEs, leaving most FEs with no redundancy or
462 functional insurance. Importantly, functional sensitivity and functional redundancy are
463 independently distributed among the combinations of traits. As such, redundancy is seldom
464 compensating for the high sensitivity of some traits, the most sensitive ones often having no
465 redundancy.

466
467 Our study is complementary to previous macro-ecological investigations showing the
468 heterogeneous distribution of redundancy across FEs [20, 39], and attests that the same
469 pattern translates to the local scale when considering species abundances. This result is not
470 trivial since even FEs with low species redundancy may be preserved if those species are
471 widespread, abundant, and weakly sensitive to threats. This is not the case for fishes on coral
472 reefs. Consequently, high biodiversity and abundance of fishes is unlikely to buffer coral reef
473 ecosystems against functional diversity loss. This result is consistent with the observations
474 that marine ecosystem functions and services scale positively and do not saturate with the
475 level of species and FE richness within local faunas [66, 67].

476
477 Vulnerability can provide early warning signals of fishing pressure, since the processes
478 performed by vulnerable traits are most likely to be the first to decline, even under low
479 pressure [68]. Indeed, from a sustainable management perspective this study highlights key
480 vulnerable functional entities that should be under particular conservation measures. For
481 example, the bluespine unicornfish (*N. unicornis*) has been identified as one of the most
482 important macroalgal consumers on coral reefs [69] yet is targeted by commercial,
483 recreational and artisanal fisheries [70]. Macroalgal feeders play a critical role in preventing
484 and reversing coral-algal shifts and the finding of their high baseline vulnerability to fishing is
485 worrying [8, 9]. Despite recent studies demonstrating signs of overexploitation in the Pacific

486 [70], this species is listed as “Least concern” in the Red list of Threatened Species by the
487 International Union for Conservation of Nature (IUCN). This is also the case for top predators
488 such as the Bluefin trevally (*C.melampygus*) and the great barracuda (*S. barracuda*) which are
489 highly sensitive to fishing [71, 72], while the Bluefin trevally has also been found in very low
490 abundance in marine protected areas compared to wilderness [27]. The IUCN Red list criteria
491 could benefit from taking a trait based approach to uncover the species vulnerability from a
492 functional perspective.

493

494 **5. Conclusion**

495

496 With biodiversity being lost in the Anthropocene, the need to carefully manage functional
497 diversity has never been greater. The slow decrease in abundance of functionally important
498 species is insidious, despite strong implications for coral ecosystem functioning and resilience
499 [9]. High redundancy can highlight the core processes that may persist even under high levels
500 of fishing pressure since they are highly buffered against local species extinction. While
501 fishing pressure should decrease on the most vulnerable functional entities, it could
502 potentially be directed toward the least vulnerable functional entities highlighted in the
503 functional space. Local adaptive management measures toward those species could focus on
504 gear restrictions, minimum size limits [73], quotas or fishing bans during spawning times [74,
505 75], or modified angling techniques (e.g. [76–78]). However, those species often do not
506 represent the same fishing interest due to their low commercial values [79]. Therefore the
507 burden of reducing fishing pressure on the most vulnerable functional entities should be
508 shared along market value chains [80], as fisherman targeting certain species operate under
509 incentives determined by trade and the agents involved at both local and international scales
510 [81, 82]. Ultimately, a multilayer management approach considering the complexity of the
511 socio-ecological system is necessary to maintain ecosystem functioning [80].

512

513 **Data accessibility**

514 Functional entity fishing sensitivity and vulnerability on Dryad doi:10.5061/dryad.24gs0

515

516 **Author’s contributions**

517 D.M. and L.V conceived the project; S.D., M.K., L.V., L.W., G.M., P.F., N.A.J.G and many
518 others collected the data; S.D., D.M. and L.V. prepared the figures; S.D., D.M. and L.V.
519 drafted the initial manuscript; all authors contributed to analyses, writing and interpretation.

520

521 **Competing interests**

522 The authors declare no competing interests

523

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781 **Figure captions**

782

783 **Figure 1.**

784 Sampled coral reef ecosystems across three regions of the Indo-Pacific. Fish were identified
785 and counted at the outer reefs of remote atolls (blue stars) in Chagos (79 transects), New
786 Caledonia (18 transects) and French Polynesia (37 transects).

787

788 **Figure 2.**

789 Sharing of species and functional entities between regions. Venn diagram (top) for the
790 number of species (A) and the number of functional entities (B) for Chagos (orange), New
791 Caledonia (green), and French Polynesia (blue).
792 Percentages indicate the proportion of species and functional entities in each region compared
793 to the total pool. Histograms (bottom) show the proportion (left-axis) and the number of
794 species (A) or functional entities (B) (right-axis) in each region (color bars), the proportion of
795 unique species (A) or functional entities (B) in each region (black segments on colored bars),
796 the number of species (A) or functional entities (B) for each pair of regions, and the number
797 of species (A) or functional entities (B) common to the three regions.

798

799 **Figure 3.**

800 The levels of functional redundancy in terms of species richness and Shannon entropy across
801 functional entities for the three regions. Distribution of functional entities (in percentage)
802 along a gradient of functional redundancy in terms of the number of species by functional
803 entity in each region (a). Relationships between the number of species per functional entity
804 and the Shannon entropy (expressed as equivalent number of species, Material and Methods)
805 for each functional entity are shown for each region (b). The bottom panel demonstrates the
806 variation of Shannon entropy for a fixed number of species per functional entity.
807 #S/FE is the number of species per functional entity.

808

809 **Figure 4.**

810 Mapping redundancy, sensitivity and vulnerability in the functional space for fish faunas of
811 the three regions. The top row (a) shows for each region the distribution of functional
812 redundancy within functional entities, measured using the Shannon entropy, across the
813 functional space. The middle row (b) shows the distribution of sensitivity to fishing across the
814 functional space while the bottom row (c) shows the distribution of vulnerability to fishing in
815 this space, d) position of vulnerable functional entities in the functional space. Colors indicate
816 the level of vulnerability of functional entities and fish shapes were chosen to illustrate the
817 main genus of each functional entity (see also ESM, Figure S6).

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