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

Stéphanie D'agata[1,2,3], Laurent Vigliola[2], Nicholas A.J. Graham[4,5], Laurent Wantiez[6], Valeriano Parravicini[7], Sébastien Villéger[1], Gerard Mou-Tham[2], Philippe Frolla[8], Alan M. Friedlander[9,10], Michel Kulbicki[11] & David Mouillot[1,4]

1. MARBEC, UMR IRD-CNRS-UM-IFREMER 9190, Université Montpellier, 34095 Montpellier Cedex, France
2. ENTROPIE, UMR IRD-UR-CNRS 9220, Laboratoire d'Excellence LABEX CORAIL, Institut de Recherche pour le Développement, BP A5, 98848 Nouméa Cedex, New Caledonia
3. Wildlife Conservation Society, Marine Programs, 2300 Southern Boulevard, Bronx, NY, 10460, USA
4. Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, 4811 Qld, Australia
5. Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK
6. Université de Nouvelle Calédonie- Laboratoire « LIVE » EA4243 – BP R4 – 98851 – Nouméa- Nouvelle Calédonie
7. Ecole Pratique des Hautes Etudes, USR 3278 EPHE-CNRS-UPVD CRIOBE, University of Perpignan, 66860 Perpignan cedex, France
8. Entreprise Générale de Logistique Environnementale (EGLE SARL), Tribu de Fatanaoué 98833 Voh-Temala, New caledonia
9. Fisheries Ecology Research Lab, University of Hawaii, 2538 McCarthy Mall, Honolulu, Hawaii 96822
10. Pristine Seas, National Geographic Society, 1145 17th St NW, Washington, DC 20036
11. ENTROPIE, UMR IRD-UR-CNRS 9220, Laboratoire d'Excellence LABEX CORAIL, Institut de Recherche pour le Développement, University of Perpignan, 66860 Perpignan Cedex 9, France

Abstract

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

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.

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

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

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

Coral reefs are the most diverse marine ecosystems on Earth [30] and support key services for half a billion people, such as food and income [31]. We quantified the baseline vulnerability to fishing of fish functional diversity in coral reef ecosystems across the Indo-Pacific geographic gradient, taking advantage of extensive surveys in French Polynesia, New Caledonia and Chagos. These three wilderness areas all benefit from a high level of isolation from humans [32] and a high level of enforcement due to the presence of military forces, thereby limiting illegal fishing activities Since the ecological knowledge to assess the functions carried by individual species is limited, using species functional traits to infer functions offers a viable alternative [33]. Here, we assume that species with more diverse combinations of functional traits are more likely to support different functions (e.g. [34, 35]).

2. Material and methods

(a) Study regions

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

(b) Fish surveys

Fish data for the Pacific Islands were collected on outer reef slopes using Underwater Visual Census (UVC) along 50 m transects. Briefly, this method involved two divers each recording species identity, abundance and body length [36]. Transects in New Caledonia (18 transects) and French Polynesia (37 transects) were truncated at 10 m wide (10×50m strip transects). In the Chagos Archipelago, fishes were surveyed along outer reef slopes using 50 x 5 m strip transects (79 transects). To make surveys comparable among regions, a common area of 500 m^2 was obtained by randomly aggregating two Chagos transects (250 m^2). Accumulation curves of species richness were performed for each region to test for potential biases due to survey techniques (ESM, Figure S1). Species densities and abundances were estimated for 500 m^2 transects and averaged for each region. Sharks and rays were removed from the main species list due to their specific traits, some poaching in Chagos, and difficulties in assessing their abundance using UVC [37]. As such, this study focused on 412 fish species belonging to 35 teleost families.

(c) Functional traits and entities

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

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

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

(d) Fish functional diversity

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

(e) Taxonomic and Functional β-diversity

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

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

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

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

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

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

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

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

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

The functional β-diversity among regions was decomposed into functional turnover and functional nestedness-resultant components following the same framework [48, 49].
Taxonomic and functional β-diversity and their respective components were computed using the R functions from the "betapart" R package (R 2.15.2, R development Core Team, 2012).

(f) Functional vulnerability to fishing

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

In wilderness areas, exposure to fishing is absent or extremely low [28]. Therefore, the vulnerability to fishing in wilderness areas, termed here as "baseline vulnerability", is solely defined as the combination of species sensitivity to fishing, driven by their biological traits (e.g. size, growth, reproductive capacity), and the level of functional redundancy which is determined by the natural distribution of species density and abundances among functional entities (ESM, Figure S2).

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

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

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

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

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

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

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

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

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

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

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

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

$$FR_{shannon\_EQ} = \exp\left(FR_{shannon}\right) \qquad \text{(Eq. 8)}$$

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

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

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

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

where V_i is the vulnerability of functional entity i, d^+ is the distance to A^+ and d^- the distance to A^- in Euclidean space. The vulnerability index ranges from 0 if the criteria scores correspond to A^+ and to 1 when the criteria scores correspond to A^- [39, 61].
The vulnerability of a FE is high when both the fishing sensitivity of that FE is high and when redundancy is low [39, 62].

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

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

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

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

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

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

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

3. Results

(a) Similar level of functional diversity across wilderness areas

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

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

(b) Heterogeneous distribution of functional redundancy across wilderness areas and functional entities

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

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

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

(c) High vulnerability of functional entities in wilderness areas

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

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

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

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

4. Discussion

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

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

(b) High vulnerability of ecosystem functioning

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

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

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

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

5. Conclusion

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

Data accessibility

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

Author's contributions

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 others collected the data; S.D., D.M. and L.V. prepared the figures; S.D., D.M. and L.V. drafted the initial manuscript; all authors contributed to analyses, writing and interpretation.

Competing interests

The authors declare no competing interests

Funding

This work is an outcome of the Pristine Reefs project funded by the Total Foundation.

It also benefited from several databases from the GASPAR program financed by the French Foundation for Research on Biodiversity (FRB) within the CESAB initiative.

D.M. was supported by a Marie Curie International Outgoing Fellowship (FISHECO) with agreement number IOF-GA-2009-236316. The Australian Research Council and Royal Society funded N.A.J.G.

Ackowledgements

We thank the crew of research vessels Amborella (Government of New Caledonia), Alis (IRD), Plan B (Waitt Institute), and the Pacific Marlin (FCO), for help in data collection during oceanographic campaigns Pristine Reefs, APEX, and National Geographic Pristine Seas. We thank Dr. Nathalie Sedon and Dr. Alexandre Pigot as well as three anonymous reviewers for their comments, which prompted significant improvements.

References

1. Vitousek PM (1997) Human Domination of Earth's Ecosystems. Science 277:494–499. doi: 10.1126/science.277.5325.494

2. Jackson JB, Kirby MX, Berger WH, et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637. doi: 10.1126/science.1059199

3. Waters CN, Zalasiewicz J, Summerhayes C, et al (2016) The Anthropocene is

functionally and stratigraphically distinct from the Holocene. Science 351:137–147. doi: 10.1126/science.aad2622

4. Costello MJ, May RM, Stork NE (2013) Can we name Earth's species before they go extinct? Science 339:413–6. doi: 10.1126/science.1230318

5. Worm B, Barbier EB, Beaumont N, et al (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790. doi: 10.1126/science.1132294

6. Barnosky AD, Hadly EA, Bascompte J, et al (2012) Approaching a state shift in Earth's biosphere. Nature 486:52–8. doi: 10.1038/nature11018

7. Pimm SL, Jenkins CN, Abell R, et al (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752. doi: 10.1126/science.1246752

8. Hughes TP, Rodrigues MJ, Bellwood DR, et al (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365. doi: 10.1016/j.cub.2006.12.049

9. Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833. doi: 10.1038/nature02691

10. Naeem S (2012) Ecological consequences of declining biodiversity: A biodiversity-ecosystem function (BEF) framework for marine systems. Mar Biodivers Ecosyst Funct Fram Methodol Integr. doi: 10.1093/acprof:oso/9780199642250.001.0001

11. Hooper DU, Adair EC, Cardinale BJ, et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108. doi: 10.1038/nature11118

12. Lefcheck JS, Byrnes JEK, Isbell F, et al (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936. doi: 10.1038/ncomms7936

13. Gascon C, Brooks TM, Contreras-MacBeath T, et al (2015) The Importance and Benefits of Species. Curr Biol 25:R431–R438. doi: 10.1016/j.cub.2015.03.041

14. Duffy JE, Lefcheck JS, Stuart-Smith RD, et al (2016) Biodiversity enhances reef fish biomass and resistance to climate change. Proc Natl Acad Sci 201524465. doi: 10.1073/pnas.1524465113

15. Norkko A, Villnäs A, Norkko J, et al (2013) Size matters: implications of the loss of large individuals for ecosystem function. Sci Rep 3:2646. doi: 10.1038/srep02646

16. Tilman D, Knops J, Wedin D, et al (1997) The Influence of Functional Diversity and Composition on Ecosystem Processes. Science (80-) 277:1300–1302. doi: 10.1126/science.277.5330.1300

17. Naeem S, Li S (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509. doi: 10.1038/37348

18. Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating

environment : The insurance hypothesis. Proc Natl Acad Sci 96:1463–1468.

19. Isbell F, Craven D, Connolly J, et al (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577. doi: 10.1038/nature15374

20. Mouillot D, Villéger S, Parravicini V, et al (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci 111:13757–13762. doi: 10.1073/pnas.1317625111

21. Mouillot D, Bellwood DR, Baraloto C, et al (2013) Rare Species Support Vulnerable Functions in High- Diversity Ecosystems. doi: 10.1371/journal.pbio.1001569

22. Soliveres S, van der Plas F, Manning P, et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459. doi: 10.1038/nature19092

23. Edgar GJ, Stuart-Smith RD, Willis TJ, et al (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–20. doi: 10.1038/nature13022

24. Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol 6:e54. doi: 10.1371/journal.pbio.0060054

25. McClanahan TR, Omukoto JO (2011) Comparison of modern and historical fish catches (AD 750-1400) to inform goals for marine protected areas and sustainable fisheries. Conserv Biol 25:945–55. doi: 10.1111/j.1523-1739.2011.01694.x

26. Kathleen Lyons S, Amatangelo KL, Behrensmeyer AK, et al (2015) Holocene shifts in the assembly of plant and animal communities implicate human impacts. Nature 529:80–83. doi: 10.1038/nature16447

27. D'agata S, Mouillot D, Wantiez L, et al (2016) Marine reserves lag behind wilderness in the conservation of key functional roles. Nat Commun 7:12000. doi: 10.1038/ncomms12000

28. Mittermeier R a, Mittermeier CG, Brooks TM, et al (2003) Wilderness and biodiversity conservation. Proc Natl Acad Sci U S A 100:10309–13.

29. Watson JEM, Shanahan DF, Di Marco M, et al (2016) Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. Curr Biol 0:81–98. doi: 10.1016/j.cub.2016.08.049

30. Spalding MD, Ravilious C, Green EP (2001) Word Atlas of Coral Reefs. University of California Press, Berkeley. USA, Prepared at the UNEP World Conservation Monitoring Centre

31. Cinner JE (2014) Coral reef livelihoods. Curr Opin Environ Sustain 7:65–71. doi: 10.1016/j.cosust.2013.11.025

32. Maire E, Cinner J, Velez L, et al (2016) How accessible are coral reefs to people? A global assessment based on travel time. Ecol Lett 19:351–364. doi: 10.1111/ele.12577

33. Violle C, Navas M, Vile D, et al (2007) Let the concept of trait be functional ! Oikos 882–892. doi: 10.1111/j.2007.0030-1299.15559.x

34. Coux C, Rader R, Bartomeus I, Tylianakis JM (2016) Linking species functional roles to their network roles. Ecol Lett 19:762–70. doi: 10.1111/ele.12612

35. Murray F, Douglas A, Solan M (2014) Species that share traits do not necessarily form distinct and universally applicable functional effect groups. Mar Ecol Prog Ser 516:23–34. doi: 10.3354/meps11020

36. Labrosse, P., Kulbicki, M. and Ferraris J (2002) Underwater visual fish census surveys. Proper use and implementation. Reef Resour Assess tools Noumea, New Caledonia Secr Pacific Community 54 pp.

37. Ward-Paige C, Mills Flemming J, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. PLoS One 5:e11722. doi: 10.1371/journal.pone.0011722

38. Kulbicki M, Mou-tham G, Vigliola L, et al (2011) Major coral reef fish species of the South pacific with basic information on their biology and ecology. Cris. report. Noumea SPC. 107 pp. + Annex.

39. Parravicini V, Villéger S, McClanahan TR, et al (2014) Global mismatch between species richness and vulnerability of reef fish assemblages. Ecol Lett 17:1101–10. doi: 10.1111/ele.12316

40. Kulbicki M, Bozec Y, Labrosse P, et al (2005) Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. Aquat Living Resour 18:231–250. doi: 10.1051/alr

41. Chabanet P, Guillemot N, Kulbicki M, et al (2010) Baseline study of the spatio-temporal patterns of reef fish assemblages prior to a major mining project in New Caledonia (South Pacific). Mar Pollut Bull 61:598–611. doi: 10.1016/j.marpolbul.2010.06.032

42. Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. doi: 10.1890/07-1206.1

43. Mouillot D, Graham NAJ, Villéger S, et al (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–77. doi: 10.1016/j.tree.2012.10.004

44. Legendre P, Legendre L (1998) Numerical Ecology. Dev Environ Model. doi: 10.1016/S0167-8892(98)80061-4

45. Maire E, Grenouillet G, Brosse S, Villéger S (2015) How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Glob Ecol Biogeogr 24:728–740. doi: 10.1111/geb.12299

46. Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Glob Ecol Biogeogr 21:1223–1232. doi: 10.1111/j.1466-8238.2011.00756.x

47. Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19:134–143. doi: 10.1111/j.1466-8238.2009.00490.x

48. Villéger S, Grenouillet G, Brosse S (2013) Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Glob Ecol Biogeogr 22:671–681. doi: 10.1111/geb.12021

49. Villéger S, Novack-Gottshall PM, Mouillot D (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol Lett 14:561–8. doi: 10.1111/j.1461-0248.2011.01618.x

50. Foden WB, Butchart SHM, Stuart SN, et al (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS One 8:e65427. doi: 10.1371/journal.pone.0065427

51. Cinner JE, McClanahan TR, Graham NAJ, et al (2012) Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. Glob Environ Chang 22:12–20. doi: 10.1016/j.gloenvcha.2011.09.018

52. Graham NAJ, Chabanet P, Evans RD, et al (2011) Extinction vulnerability of coral reef fishes. Ecol Lett 14:341–348. doi: 10.1111/j.1461-0248.2011.01592.x

53. Cheung WWL, Pitcher TJ, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. Biol Conserv 124:97–111. doi: 10.1016/j.biocon.2005.01.017

54. Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA (2005) Biology of extinction risk in marine fishes. Proc Biol Sci 272:2337–44. doi: 10.1098/rspb.2005.3281

55. Naeem S (1998) Species Redundancy and Ecosystem Reliability. Conserv Biol 12:39–45. doi: 10.1111/j.1523-1739.1998.96379.x

56. Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral-reef recovery. Curr Biol 16:2434–9. doi: 10.1016/j.cub.2006.10.030

57. Stevens RD, Cox SB, Strauss RE, Willig MR (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. Ecol Lett 6:1099–1108. doi: 10.1046/j.1461-0248.2003.00541.x

58. Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. Ecol Lett 8:391–400. doi: 10.1111/j.1461-0248.2005.00731.x

59. Jost L (2006) Entropy and diversity. Oikos 113:363–375. doi: 10.1111/j.2006.0030-1299.14714.x

60. Hill MO (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432. doi: 10.2307/1934352

61. Turner BL, Kasperson RE, Matson PA, et al (2003) A framework for vulnerability analysis in sustainability science. Proc Natl Acad Sci U S A 100:8074–9. doi: 10.1073/pnas.1231335100

62. Cinner JE, Huchery C, Darling ES, et al (2013) Evaluating Social and Ecological

Vulnerability of Coral Reef Fisheries to Climate Change. PLoS One 8:e74321. doi: 10.1371/journal.pone.0074321

63. Worton BJ (1995) Using Monte Carlo Simulation to Evaluate Kernel-Based Home Range Estimators. J Wildl Manage 59:794–800. doi: 10.2307/3801959

64. Green AL, Bellwood DR (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region. IUCN, Gland, Switzerland

65. Allen GR (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. Aquat Conserv Mar Freshw Ecosyst 556:541–556. doi: 10.1002/aqc

66. Danovaro R, Gambi C, Dell'Anno A, et al (2008) Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr Biol 18:1–8. doi: 10.1016/j.cub.2007.11.056

67. Mora C, Aburto-Oropeza O, Ayala Bocos A, et al (2011) Global Human Footprint on the Linkage between Biodiversity and Ecosystem Functioning in Reef Fishes. PLoS Biol 9:e1000606. doi: 10.1371/journal.pbio.1000606

68. Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc Biol Sci 279:1621–9. doi: 10.1098/rspb.2011.1906

69. Hoey AS, Bellwood DR (2009) Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. Ecosystems 12:1316–1328. doi: 10.1007/s10021-009-9291-z

70. Ford AK, Bejarano S, Marshell A, Mumby PJ (2016) Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. Aquat Conserv Mar Freshw Ecosyst 26:790–805. doi: 10.1002/aqc.2623

71. Friedlander A, DeMartini E (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264. doi: 10.3354/meps230253

72. Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2001) Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. Fish Res 53:105–113. doi: 10.1016/S0165-7836(00)00285-X

73. Bozec Y-M, O'Farrell S, Bruggemann JH, et al (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc Natl Acad Sci U S A 1601529113-. doi: 10.1073/pnas.1601529113

74. Bejarano Chavarro S, Mumby PJ, Golbuu Y (2014) Changes in the spear fishery of herbivores associated with closed grouper season in Palau, Micronesia. Anim Conserv 17:133–143. doi: 10.1111/acv.12066

75. Cohen PJ, Alexander TJ (2013) Catch rates, composition and fish size from reefs managed with periodically-harvested closures. PLoS One 8:e73383. doi: 10.1371/journal.pone.0073383

76. Hicks CC, McClanahan TR (2012) Assessing Gear Modifications Needed to Optimize Yields in a Heavily Exploited, Multi-Species, Seagrass and Coral Reef Fishery. PLoS One 7:e36022. doi: 10.1371/journal.pone.0036022

77. Mbaru EK, McClanahan TR (2013) Escape gaps in African basket traps reduce bycatch while increasing body sizes and incomes in a heavily fished reef lagoon. Fish Res 148:90–99. doi: 10.1016/j.fishres.2013.08.011

78. McClanahan TR, Sebastian CR, Cinner J, et al (2010) Managing fishing gear to encourage ecosystem-based management of coral reefs fisheries. Proc 11th Int Coral Reef Symp Ft Lauderdale, Florida 2:10190–1023 (Session number 22).

79. Thyresson M, Crona B, Nyström M, et al (2013) Tracing value chains to understand effects of trade on coral reef fish in Zanzibar, Tanzania. Mar Policy 38:246–256. doi: 10.1016/j.marpol.2012.05.041

80. McClanahan TR, Cinner JE (2012) Adapting to a changing environment : confronting the consequences of climate change. Oxford University Press

81. Thyresson M, Nyström M, Crona B (2011) Trading with Resilience: Parrotfish Trade and the Exploitation of Key-Ecosystem Processes in Coral Reefs. Coast Manag 39:396–411. doi: 10.1080/08920753.2011.589226

82. Williams ID, White DJ, Sparks RT, et al (2016) Responses of Herbivorous Fishes and Benthos to 6 Years of Protection at the Kahekili Herbivore Fisheries Management Area, Maui. PLoS One 11:e0159100. doi: 10.1371/journal.pone.0159100

Figure captions

Figure 1.

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

Figure 2.

Sharing of species and functional entities between regions. Venn diagram (top) for the number of species (A) and the number of functional entities (B) for Chagos (orange), New Caledonia (green), and French Polynesia (blue).

Percentages indicate the proportion of species and functional entities in each region compared to the total pool. Histograms (bottom) show the proportion (left-axis) and the number of species (A) or functional entities (B) (right-axis) in each region (color bars), the proportion of unique species (A) or functional entities (B) in each region (black segments on colored bars), the number of species (A) or functional entities (B) for each pair of regions, and the number of species (A) or functional entities (B) common to the three regions.

Figure 3.

The levels of functional redundancy in terms of species richness and Shannon entropy across functional entities for the three regions. Distribution of functional entities (in percentage) along a gradient of functional redundancy in terms of the number of species by functional entity in each region (a). Relationships between the number of species per functional entity and the Shannon entropy (expressed as equivalent number of species, Material and Methods) for each functional entity are shown for each region (b). The bottom panel demonstrates the variation of Shannon entropy for a fixed number of species per functional entity.

#S/FE is the number of species per functional entity.

Figure 4.

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