

LETTER

Global mismatch between species richness and vulnerability of reef fish assemblages

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Abstract

The impact of anthropogenic activity on ecosystems has highlighted the need to move beyond the biogeographical delineation of species richness patterns to understanding the vulnerability of species assemblages, including the functional components that are linked to the processes they support. We developed a decision theory framework to quantitatively assess the global taxonomic and functional vulnerability of fish assemblages on tropical reefs using a combination of sensitivity to species loss, exposure to threats and extent of protection. Fish assemblages with high taxonomic and functional sensitivity are often exposed to threats but are largely missed by the global network of marine protected areas. We found that areas of high species richness spatially mismatch areas of high taxonomic and functional vulnerability. Nevertheless, there is strong spatial match between taxonomic and functional vulnerabilities suggesting a potential win–win conservation–ecosystem service strategy if more protection is set in these locations.

Keywords

Conservation, macroecology, risk assessment, sensitivity, vulnerability.

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INTRODUCTION

Global climate changes and more localised human impacts are undermining populations of vulnerable taxa and may ultimately induce profound losses of biodiversity and associated functions (Worm *et al.* 2006; Barnosky *et al.* 2011). Accumulating evidence suggests, however, that ecosystem functions, such as productivity, nutrient cycling and responses to climate disturbances, are not tightly related to species richness but rather to the breadth of functions performed by species, that is encapsulated by the term functional diversity (Cardinale *et al.* 2012; Naeem *et al.* 2012). The assurance of long-term functioning of ecosystems also depends on the number of species supporting each function. This functional redundancy, i.e. the number of species playing the same set of functions in ecosystems, is a key to the resilience of ecological processes when disturbances are strong enough to deplete or remove species from assemblages (Yachi & Loreau 1999; Bellwood *et al.* 2003). Functions performed by many species thus bene-

fit from an insurance against local extinctions while functions supported by one or few species are more prone to local threats and associated extinctions (Boyer & Jetz 2014). Even if well-established conservation tools, such as the IUCN Red List, recognise that the loss of endangered species may dramatically change the functioning of ecosystems through the alteration of functional diversity (Gaston *et al.* 2009), the quantitative delineation of functional vulnerability within assemblages is still largely overlooked and its large-scale distribution is virtually unknown (Naeem *et al.* 2012). A critical issue is thus to understand how the increasing vulnerability at the species level is transferred at the functional level, the cornerstone of this relationship being the extent of functional redundancy. However, a quantitative framework to assess taxonomic and functional vulnerability of species assemblages that takes into account the exposure to human threats and protection effort, especially at large spatial scale, is lacking.

Vulnerability is recognised as an important criterion for evaluating responses to disturbances in many different

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research areas and for estimating the likelihood that structural and functional changes will occur in ecosystems (Carpenter *et al.* 2001; Turner *et al.* 2003; Eakin & Luers 2006). The emerging consensus is to define vulnerability as a combination of sensitivity and exposure minus the adaptive capacity of the system (Allison *et al.* 2009; Hughes *et al.* 2012; Cinner *et al.* 2013b). Sensitivity is the propensity of the system to be influenced by threats while exposure is the level of these threats. Furthermore, adaptive capacity is the latent ability of the system to prepare for and respond to increasing threats, which is often pragmatically considered as a result of management measures (Micheli *et al.* 2012; Cinner *et al.* 2013b). In this study, we defined vulnerability of species assemblages as a combination of (1) sensitivity seen as the intrinsic propensity to lose biodiversity, (2) exposure to the threats, which may increase the likelihood to experience biodiversity loss and (3) the level of protection that mitigates the likelihood of biodiversity loss for a given level of sensitivity and exposure.

We applied this framework globally to assemblages of tropical reef fishes that experience severe threats while being subject to increasing conservation efforts, specifically the implementation of marine protected areas (MPAs). Fish biodiversity supports key functions of tropical reef ecosystems and a major source of protein for millions of people in the tropical coastal zones (Bellwood *et al.* 2004). Consequently, by identifying the most vulnerable regions, taxonomically and functionally, we provide spatially explicit warns of potential threats to ecosystem functioning and food production on tropical reefs.

METHODS

Global geographic distributions of tropical reef fishes

We compiled a global database on tropical coastal fish occurrences from 169 locations (Kulbicki *et al.* 2013; Parravicini *et al.* 2013). We focused our analysis on shallow water species, which were defined as those recordable within the depth range between 0 and 50 m. Overall, we obtained information on the distribution of 6316 tropical reef fish species. From these distributional data we obtained a range map for each species, defined as the convex polygon shaping the area where each species is present (Buckley & Jetz 2007). Range maps were visually checked and reviewed by the authors according to their expertise. When discontinuities were detected, the initial convex hull was divided into multiple polygons to avoid merging disjointed distributions. Species composition was then extracted for each $5^\circ \times 5^\circ$ grid cell, corresponding to approximately 550×550 km at the equator. The grid grain size of $5^\circ \times 5^\circ$ was chosen because it represents an appropriate compromise between resolution and the density of the available geographical information.

Fish traits and functional entities

The functional niche of reef fishes was described using a set of six complementary functional traits that define, in combinations, the main facets of fish ecology (Guillemot *et al.* 2011; see Supporting Information). Fish size was coded using six

ordered categories: 0–7, 7.1–15, 15.1–30, 30.1–50, 50.1–80 and > 80 cm. Mobility was coded using three ordered categories: sedentary (including territorial species), mobile within a reef and mobile between reefs. Period of activity 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 groups (> 50 groups). Position in the water column was coded using three ordered categories: benthic, benthopelagic and pelagic. Diet was characterised based on the main items consumed by each species and this led to seven trophic categories: herbivorous-detritivorous (i.e. fish feeding on turf or filamentous algae and undefined organic material), macroalgal herbivorous (i.e. fish eating large fleshy algae and seagrass), invertivorous targeting sessile invertebrates (i.e. corals, sponges, ascidians), invertivorous targeting mobile invertebrate (i.e. benthic species such as crustaceans), planktivorous (i.e. fish eating small organisms in the water column), piscivorous (including fish and cephalopods) and omnivorous, or fish for which both plant and animal material are important. Trait values for adult life stage were extracted from specific works for the Indo-Pacific (Mouillot *et al.* 2013), the Atlantic (Halpern & Floeter 2008) and from FishBase. The six categorical traits define 5670 unique combinations that we coin potential functional entities (FEs). The 6316 species were then gathered into 646 realised FEs.

Taxonomic and functional sensitivity

Following Wilson *et al.* (2006), we defined the taxonomic sensitivity to species loss (St) as the proportion of species in an assemblage (1) that are threatened (i.e. having a high propensity to become locally rare or extinct when facing threats):

$$St_i = \frac{Ext_i}{Ric_i} \quad (1)$$

where St_i is the taxonomic sensitivity of the assemblage at the cell i , Ext_i is the number of threatened species at the cell i , and Ric_i is the overall species richness at the cell i . In our case, we considered species with a high propensity to become locally extinct as those belonging to the threatened categories of the IUCN Red List, specifically those listed as vulnerable, endangered and critically endangered. As the IUCN assessment of reef fishes has been completed only for seven of the 170 families of reef fishes, species with a small geographical range were also considered as threatened (Roberts *et al.* 2002; Wilson *et al.* 2006). Recent works demonstrating that geographical range is the main correlate of IUCN extinction risk justify these choices (Harnik *et al.* 2012; Strona 2014). Following Hughes *et al.* (2002) we employed two different definitions of small-ranged species as those showing the smallest 5% and 10% geographical ranges (corresponding to ~8% and ~13% of the global pool respectively). Since both definitions return almost identical results, only the results obtained from employing the latter more cautionary threshold are reported.

Consistent with the definition of sensitivity to species loss, the sensitivity of functional diversity to species loss (Sf) was defined as the proportion of functions in a species assemblage

with the highest propensity to be lost under external threats. Functional sensitivity was then operationally defined as the proportion of FEs in an assemblage that showed no redundancy (i.e. represented by just one species). These FEs were assumed to be highly sensitive to taxonomic erosion since the loss of only one species may induce the loss of one unique combination of traits.

The functional sensitivity (Sf) of fish assemblages was thus calculated in each cell according to the following formula:

$$Sf_i = \frac{FEric_i - \sum_{j=1}^{FEric_i} \min(nj_i - 1, 1)}{FEric_i} \quad (2)$$

where Sf_i is the functional sensitivity of fish assemblage at the cell i , $FEric_i$ (FE richness) represents the total number of FEs in the cell i and nj_i represents the number of species within the FE j in the cell i . This index ranges between 0 when all FEs have more than one species to 1 when all FEs have only one species.

Exposure to human threats and protection effort

Global distribution of human threats was derived from the global map of human impact developed by Halpern *et al.* (2008) and available at: <http://www.nceas.ucsb.edu/globalmarine>. This map provides a cumulative impact score accounting for 17 human activities that more generally quantify the intensity of fishing, pollution and climate change. As an integrated estimator of the intensity of human threats on fish assemblages, we extracted for each grid cell the mean cumulative impact score for ocean regions between 0 m and 50 m depth. To estimate the protection status, we collected spatial information on MPAs from the WDPA (World Database on Protected Areas, available at <http://protectedplanet.net/>). To reduce the risk of overestimating protection effort, the original database was partitioned into two distinct MPA databases corresponding to different levels of protection (see Fig. S1).

Taxonomic and functional vulnerability

Vulnerability of a system or assemblage is high when it has a high sensitivity to threats, a high exposure to those threats and a low adaptive capacity or protection against these threats (Cinner *et al.* 2013b). A decision theory framework can be used to quantify vulnerability (Huang *et al.* 2011), where a multicriteria decision-making (MCDM) problem can be concisely expressed in matrix form as:

$$D = \begin{matrix} & C_1 & C_2 & \dots & C_n \\ A_1 & x_{11} & x_{12} & \dots & x_{1n} \\ A_2 & x_{21} & x_{22} & \dots & x_{2n} \\ \dots & \dots & \dots & \dots & \dots \\ A_m & x_{m1} & x_{m2} & \dots & x_{mn} \end{matrix} \quad (3)$$

where D is the decision matrix, A_1, A_2, \dots, A_m are the possible alternatives (i.e. grid cells in our case) and C_1, C_2, \dots, C_n are the criteria used to evaluate vulnerability. To solve the decision matrix we used the TOPSIS method (Technique for Order Preference by Similarity to an Ideal Solution). This technique ranks the alternatives according to their relative distance to positive

and negative ideal solutions, which represent the conditions obtained when the criteria have extreme values. In our case, vulnerability was considered as a function of three criteria: sensitivity (either taxonomic or functional), exposure to anthropogenic threats and protection. We defined the positive ideal (A^+) and the negative ideal (A^-) solutions as follows:

$$A^+ = \{v_1^+, \dots, v_n^+\} = \{(\min v_{ij}|j \in F), (\max v_{ij}|j \in P)\} \quad (4)$$

$$A^- = \{v_1^-, \dots, v_n^-\} = \{(\max v_{ij}|j \in F), (\min v_{ij}|j \in P)\} \quad (5)$$

where v_{ij} is the standardised elements of the decision matrix (3), F is the criteria favouring vulnerability (i.e. exposure and sensitivity) and P is the criteria expected to reduce vulnerability (i.e. protection in our case). Hence, the positive ideal solution (A^+ ; eqn 4) corresponds to the condition where sensitivity and exposure to threats are minimised and protection is maximised. More practically this case corresponds to a hypothetical MPA protecting an area under low human pressure and having a fish fauna with no threatened species and no FE represented by one species. On the other hand, the negative ideal solution (A^- ; eqn 5) corresponds to a condition of minimum protection, maximum exposure to threats and maximum sensitivity, or an area with only endemic species, each one filling a different FE. Vulnerability, either taxonomic or functional, was then expressed as the relative distance to the positive ideal solution according to the following formula:

$$V_i = \frac{d_i^+}{d_i^+ + d_i^-} \quad (6)$$

where V_i is the vulnerability (either taxonomic or functional) of fish assemblage at the cell i , d_i^+ is the distance to A^+ of the cell i in the Euclidean space and d_i^- is the distance to A^- of the cell i (Fig. 1). The vulnerability index obtained ranges

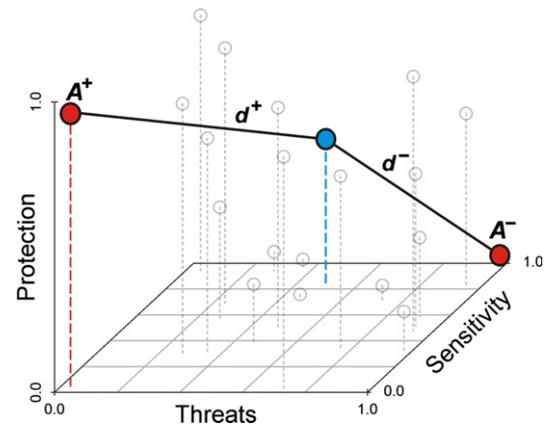


Figure 1 Conceptual plot exemplifying the multicriteria method employed for the quantification of reef fish assemblage vulnerability. Vulnerability is the result of threats exposure, sensitivity (either taxonomic or functional) and protection. Each point represents an assemblage to be evaluated (i.e. a grid cell). The vulnerability of the focal assemblage (in blue) is quantified as its relative distances to the positive ideal solution A^+ and the negative ideal solution A^- , where A^+ represents an ideal assemblage with minimum vulnerability (i.e. minimum threats, minimum sensitivity and maximum protection), while A^- represents an ideal assemblage with maximum vulnerability (maximum threats, maximum sensitivity and minimum protection). Vulnerability (V) is then numerically quantified as $V = d^+ / (d^+ + d^-)$.

from 0 if the criteria scores correspond to A^+ (eqn 4), to 1 when the criteria scores correspond to A^- (eqn 5).

Robustness of vulnerability indices

We assessed the robustness of our vulnerability indices to (1) the criteria employed to estimate the protection effort, (2) the criteria employed to estimate exposure, (3) the identity of traits and (4) the categorisation of functional traits. To evaluate the protection effort, we built two distinct databases on MPAs derived from distinct filters applied to the original WDPA information. The first database was a result of filtering the original database to eliminate MPAs found on land and a careful exclusion of MPAs not designed to protect ecosystem components of our interest, such as MPAs focusing on protecting birds and dugongs. A second more conservative database included only MPAs belonging to IUCN categories I–IV. We then used a Kruskal–Wallis test to evaluate the robustness of our vulnerability assessment to the criteria employed in estimating protection effort.

To verify that biogeographical gradients of vulnerability were not disproportionately influenced by the estimate of human threats, we performed the analyses using human population density (<http://www.nceas.ucsb.edu/globalmarine/impacts>), instead of the cumulative impact score, as a proxy for exposure to human threats. Among the various layers available, human population density was chosen because it is known to be a valuable proxy of the anthropogenic effects on reef fish assemblages (Bellwood *et al.* 2012; Cinner *et al.* 2013a; D'agata *et al.* 2014).

Functional sensitivity estimates may be affected by the identity of traits. Therefore, we performed an analysis testing the robustness of our findings to the potential disproportional influence of one particular trait by calculating functional vulnerability using all combinations of five out of six traits. We did not reduce the number of traits lower than 5 since this may eliminate important information on the fish niches, thus providing an oversimplistic definition of FEs. Furthermore, we tested whether our functional vulnerability estimates were robust to the resolution of the categorisation of functional traits. A coarse categorisation could potentially produce low functional sensitivity since FEs would be likely represented by many species while a fine categorisation would lead to the opposite, a high sensitivity with many FEs having only one species. Consequently, we reduced the number of functional categories to 86 coarse FEs as compared to the original 646 fine categorisations. For this we defined coarser categories for each trait: size classes (0–15, 15.1–50 and > 50 cm), schooling behaviour (solitary, small groups: 2–20 individuals, gregarious: > 20 individuals), mobility (sedentary vs. mobile), position in the water column (strictly pelagic vs. benthic/benthopelagic), period of activity (strictly nocturnal vs. diurnal/diurnal-nocturnal) and main diet (primary consumers: detritivores, herbivores and omnivores; invertivores: sessile, mobile benthos and plankton; and piscivores). The robustness of functional vulnerability to trait choices was tested using Kruskal–Wallis tests.

To determine, for each assemblage, which was the main component (i.e. exposure, sensitivity or protection) contribut-

ing more to taxonomic and functional vulnerability, we computed vulnerability values for each pair of components and measured the absolute difference to the original vulnerability estimate. Finally, we also tested whether the observed patterns may be obtained by chance alone. For this we constructed a null model where, for each assemblage, the observed richness of sensitive functions was compared with values obtained after randomly assigning species to FEs.

Spatial congruence estimations

We tested for spatial congruence among species richness, taxonomic and functional sensitivity and vulnerability, exposure and management protection effort to assess whether classical richness-based conservation criteria may match with those based on our vulnerability estimates. First, we calculated the coefficients of correlation between all pairs of variables across cells. Due to potential spatial autocorrelation we assessed correlation significance according to the Dutilleul-corrected degrees of freedom implemented in the program SAM v.4 (Rangel *et al.* 2010). Second, we calculated for each pair of variables, the spatial overlap between 10% of cells with the highest values for each variable, or 'hotspots' (Tittensor *et al.* 2010). Then, for each pair of variables, we calculated the observed overlap (O_o) as the number of cells being a hotspot for both variables. According to Mouillot *et al.* (2011), this can then be compared to the expected number of overlaps between two variables hotspots (O_e) defined as:

$$O_e = N_i \cdot N_j / N_t$$

where N_i is the number of hotspots for the variable i , N_j is the number of hotspots for the variable j and N_t is the total number of cells present in the grid. To test whether O_o was significantly different from O_e , the spatial position of hotspots was randomly permuted 9999 times and the difference between O_o and O_e calculated for each permutation. The absolute difference between O_o and O_e was then compared to its null distribution to test for differences between observed and expected values.

RESULTS

The analysis of the IUCN Red List revealed 47 endangered reef fishes. Their richness by cell peaks in the Indo-Australian Archipelago (with 11 species) and is closely related to the total richness of reef fishes (Fig. 2, Table 1). However, as the IUCN Red List has assessed only a few families, we also considered small-ranged species to represent a sensitive component of assemblages to threats. Overall we identified 779 small-ranged fishes corresponding to about 13% of the global pool. Contrary to endangered species, the richness of small-ranged species spatially mismatched with the total species richness (Fig. 2, Table 1). While hotspots of species richness are located at the Indo-Australian Archipelago and the Caribbean, hotspots of small-ranged species are found in peripheral zones in both the Indo-Pacific and the Atlantic. As a result, taxonomic sensitivity (i.e. the proportion of endangered or small-ranged species) was comparatively higher in peripheral areas and negatively related to total richness of fish species

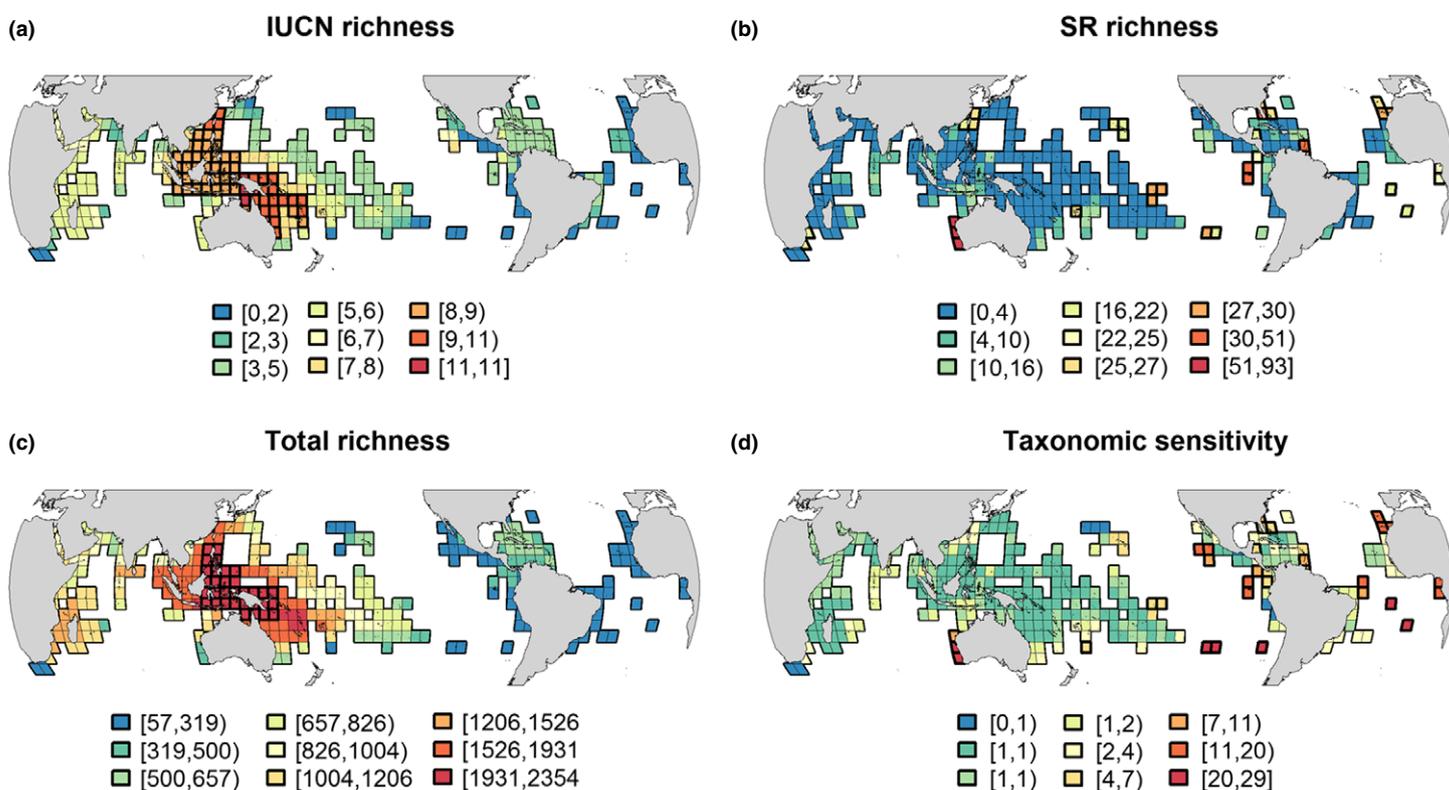


Figure 2 Global gradients of (a) IUCN species richness, (b) small-ranged species richness, (c) total species richness and (d) taxonomic sensitivity (defined as the proportion of IUCN and endemic species) for assemblages of tropical reef fishes. Black bordered cells represent hotspots.

(Fig. 2, Table 1). However, even in peripheral areas, taxonomic sensitivity was generally low, ranging from 0% to 29%, and seldom reaching values higher than 5%.

Functional richness, or the total number of FEs, was strongly related with species richness (Table 1). More than 350 FEs by cell are found in the Indo-Australian Archipelago while the functionally poorest locations were isolated islands such as Easter Island and Sala y Gomez, in the Pacific and almost the entire Eastern Atlantic (Fig. 3). The richness of sensitive FEs, or the number of FEs with only one species, was generally related to functional richness, although some hotspots of functional richness, such as the Western Indian Ocean, mismatched with the hotspots of sensitive functional richness (Fig. 3).

Functional sensitivity, or the proportion of sensitive FEs, was remarkably high ranging from 40% to 83% (Fig. 3). In other words, even extremely species-rich regions such as the Central Indo-Pacific have more than one-third of FEs represented by just one species. This pattern is not reproducible by a random assignation of species to FEs since the richness of sensitive functions is always higher than the values obtained under a null model (Table S1). Deviations from random expectations are remarkably correlated with species richness indicating that the richer the assemblage the more the richness of vulnerable functions deviates from what is expected by chance (Fig. S1).

Functional sensitivity was robust to the number of traits considered and was not driven by any particular trait (Fig. S2). Moreover, functional sensitivity remained remarkably high (between 5% and 67%) even when reducing the number of FEs by one order of magnitude (86 instead of 646,

Fig. S2). Regardless of the classification employed, hotspots of functional sensitivity were mainly found in the Eastern Tropical Pacific, isolated islands in the Atlantic Ocean and across the Eastern Atlantic. The levels of taxonomic and functional sensitivity were moderately positively related (Table 1). However, functional sensitivity always exceeds taxonomic sensitivity (Fig. S3).

Human threats were remarkably high across the China Sea and between Philippines and Japan, while management protection level was globally low, with notable exceptions such as Hawaii and the Great Barrier Reef (Fig. 4). Combining the spatial patterns of threats, sensitivity and protection into an integrated framework indicates vulnerability hotspots matching hotspots of small-ranged species like in peripheral regions of the Central Pacific and the Eastern Atlantic (Fig. 5). Taxonomic vulnerability was mainly driven by sensitivity while functional vulnerability was mainly due to a combination of sensitivity and exposure to threats (Fig. S4). In both cases, the extent of protection by MPAs had a minor role in determining assemblage vulnerability.

Vulnerability estimates were robust to the criteria employed for estimating protection effort (see Figs S5–S7). Functional vulnerability values were robust to the number of traits and the categorisation of functional traits (see Fig. S8). Geographical patterns of vulnerability were insensitive to the variable chosen to estimate exposure to human threats (cumulative impact score vs. human population density, Fig. S9). Moreover, using data from the 169 checklist locations instead of estimated range sizes provided similar results (Figs S10–S12).

Table 1 Spatial congruence between pairs of variables for global assemblages of tropical reef fishes

	Richness of small-ranged species	Endangered species richness	Functional richness	Richness of sensitive functional entities	Human threats	Protection	Taxonomic sensitivity	Functional sensitivity	Taxonomic vulnerability	Functional vulnerability
Species Richness	-0.24**	0.89**	0.94**	0.75*	-0.10 ^{ns}	-0.12 ^{ns}	-0.44*	-0.90**	-0.38*	-0.50*
Richness of small-ranged species		-0.19 ^{ns}	-0.26*	-0.23 ^{ns}	0.05 ^{ns}	0.17**	0.74***	0.26 ^{ns}	0.64**	0.16 ^{ns}
Endangered species richness			0.85**	0.69*	-0.15 ^{ns}	-0.09 ^{ns}	-0.37 ^{ns}	-0.52**	-0.28*	-0.52*
Functional richness				0.92*	-0.01 ^{ns}	-0.13 ^{ns}	-0.53*	-0.92**	-0.46*	-0.53*
Richness of sensitive functional entities					-0.05 ^{ns}	-0.11 ^{ns}	-0.55**	-0.77*	-0.47**	0.47*
Human threats						-0.01 ^{ns}	0.05 ^{ns}	0.11 ^{ns}	0.40**	0.72***
Protection							0.15 ^{ns}	0.10 ^{ns}	-0.21**	-0.36**
Taxonomic sensitivity								0.56**	0.90***	0.32**
Functional sensitivity									0.49**	0.49**
Taxonomic vulnerability										0.78**
Species Richness	0 (3.2)*	31 (6.2)***	27 (3.3)***	3 (3.1) ^{ns}	3 (3.1) ^{ns}	0 (3.1)*	0 (3.1)*	0 (3.1)*	0 (3.1)*	1 (3.1) ^{ns}
Richness of small-ranged species		2 (6.4) ^{ns}	2 (3.4) ^{ns}	5 (3.2) ^{ns}	3 (3.2) ^{ns}	4 (3.2) ^{ns}	16 (3.1)***	1 (3.2) ^{ns}	12 (3.2)***	3 (3.2) ^{ns}
Endangered species richness			33 (6.2)***	7 (6.2) ^{ns}	6 (6.2) ^{ns}	6 (6.2) ^{ns}	0 (6.2)**	0 (6.2)**	0 (6.2)**	1 (6.2)*
Functional richness				5 (3.3) ^{ns}	4 (3.3) ^{ns}	1 (3.3) ^{ns}	0 (3.3)*	0 (3.3)*	0 (3.3)*	1 (3.3) ^{ns}
Richness of sensitive functional entities					2 (3.1) ^{ns}	0 (3.1)*	0 (3.1)*	0 (3.1) ^{ns}	0 (3.1)*	1 (3.1) ^{ns}
Human threats						0 (3.1) ^{ns}	5 (3.1) ^{ns}	6 (3.1) ^{ns}	10 (3.1)***	21 (3.1)***
Protection							5 (3.1) ^{ns}	4 (3.1) ^{ns}	5 (3.1) ^{ns}	0 (3.1)*
Taxonomic sensitivity								12 (3.1)***	26 (3.1)***	12 (3.1)***
Functional sensitivity									13 (3.1)***	13 (3.1)***
Taxonomic vulnerability										17 (3.1)***

Top: pairwise spatial correlations between studied variables. Human threats derived from Halpern *et al.* (2008). ns: not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Bottom: pairwise spatial overlaps between hotspots (10% of highest values) of variables (in parentheses is the expected value under the null hypothesis) and significance after permutation test (ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Sample size consists of 310 grid cells.

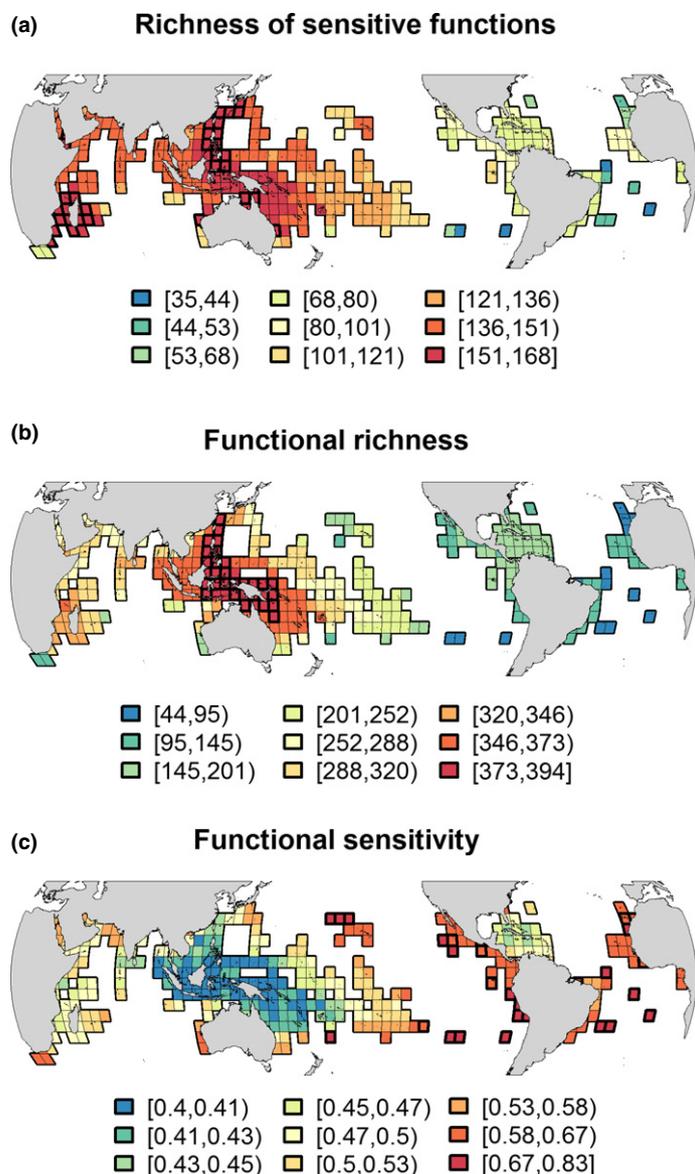


Figure 3 Global gradients of (a) the richness of sensitive functions (i.e. functional entities represented by just one species), (b) functional richness (i.e. the total richness of functional entities) and (c) functional sensitivity defined as the proportion of sensitive functions to total richness for assemblages of tropical reef fishes. Black bordered cells represent hotspots.

DISCUSSION

Vulnerability analysis is increasingly recognised as an important tool to identify the risks created by multiple pressures on systems (Turner *et al.* 2003; Allison *et al.* 2009; De Lange *et al.* 2010). While social evaluations of vulnerability are common for assessing responses of people to economic and environmental disturbances (Adger 2006), similar macroecological evaluations focused on species assemblages or ecosystem vulnerability are still scarce. This is partly due to the lack of an appropriate quantitative framework. We filled this gap by adapting the human vulnerability framework to ecological and social-ecological investigations at the macroecological scale (Hughes *et al.* 2012; Cinner *et al.* 2013b; McClanahan

et al. 2013). We provided novel metrics for a vulnerability assessment of taxonomic and functional components based on available global databases on threats (exposure) and protection (adaptive capacity) and by adding our global evaluation of reef fish assemblages (sensitivity).

Our findings suggest that hotspots of taxonomic and functional sensitivity and vulnerability of reef fish assemblages weakly match those of total species richness and small-ranged species richness and endangered species richness. While the mismatch between taxonomic sensitivity and species richness was expected as the uneven distribution of small- versus large-ranged species have been already documented (Gaston 2000; Hughes *et al.* 2002; Jetz & Rahbek 2002; Orme *et al.* 2005), incorporating functional information reveals new geographical gradients of sensitivity to threats. Surprisingly and despite the increasing interest in ecosystem functions, macroecological research has seldom considered the functional role performed by species and even less the vulnerability of this diversity component particularly on large spatial scales (Naeem *et al.* 2012; Tyler *et al.* 2012). The spatial mismatches reported here showed that species richness is not an umbrella for vulnerability of assemblages. Rather, richness is more likely to provide some buffer against vulnerability. When ecosystem function is of concern for management, it is lower diversity systems that require the most management efforts to avoid losses of function (Boyer & Jetz 2014). Nevertheless, Stuart-Smith *et al.* (2013) recently reported that species-poor temperate assemblages show higher functional diversity than several richer tropical areas, whereas D'agata *et al.* (2014) showed that fish richness is weakly eroded along a human pressure gradient but that many functions and phylogenetic lineages are lost.

Functional sensitivity, the proportion of FEs with no insurance in an assemblage, is extremely high in the Eastern Tropical Pacific and the Atlantic Ocean. This gradient of functional sensitivity is almost the reverse to that of species richness, since species-poor assemblages are weakly buffered against species extinction (Boyer & Jetz 2014). There is, however, a surprisingly large amount of functional sensitivity even in species-rich areas. Indeed, the minimum proportion of sensitive functions across the world is 36%, even in the Indo-Australian Archipelago where more than 2000 species are present and are expected to buffer FEs against species extinction due to high functional redundancy. Even when employing a coarse classification of traits, at least 5% of the 86 FEs present in the Indo-Australian Archipelago are highly sensitive, i.e. with one species only, despite the extraordinary high species richness in the area. Overall, this suggests that high species richness alone cannot guarantee a high level of redundancy for all functions and even extraordinarily rich systems are not functionally buffered against species loss.

The highest functional sensitivity is found at the St. Fernandez Archipelago (off the coast of Chile), where 83% of FEs were represented by just one species. Similar situations may be found in other isolated locations, such as Easter Island (77%) in the Pacific and St. Helena (80%) in the Atlantic. This high functional sensitivity can also characterise large portions of the ocean such as the entire Eastern Atlantic where functional sensitivity is 64% on average.

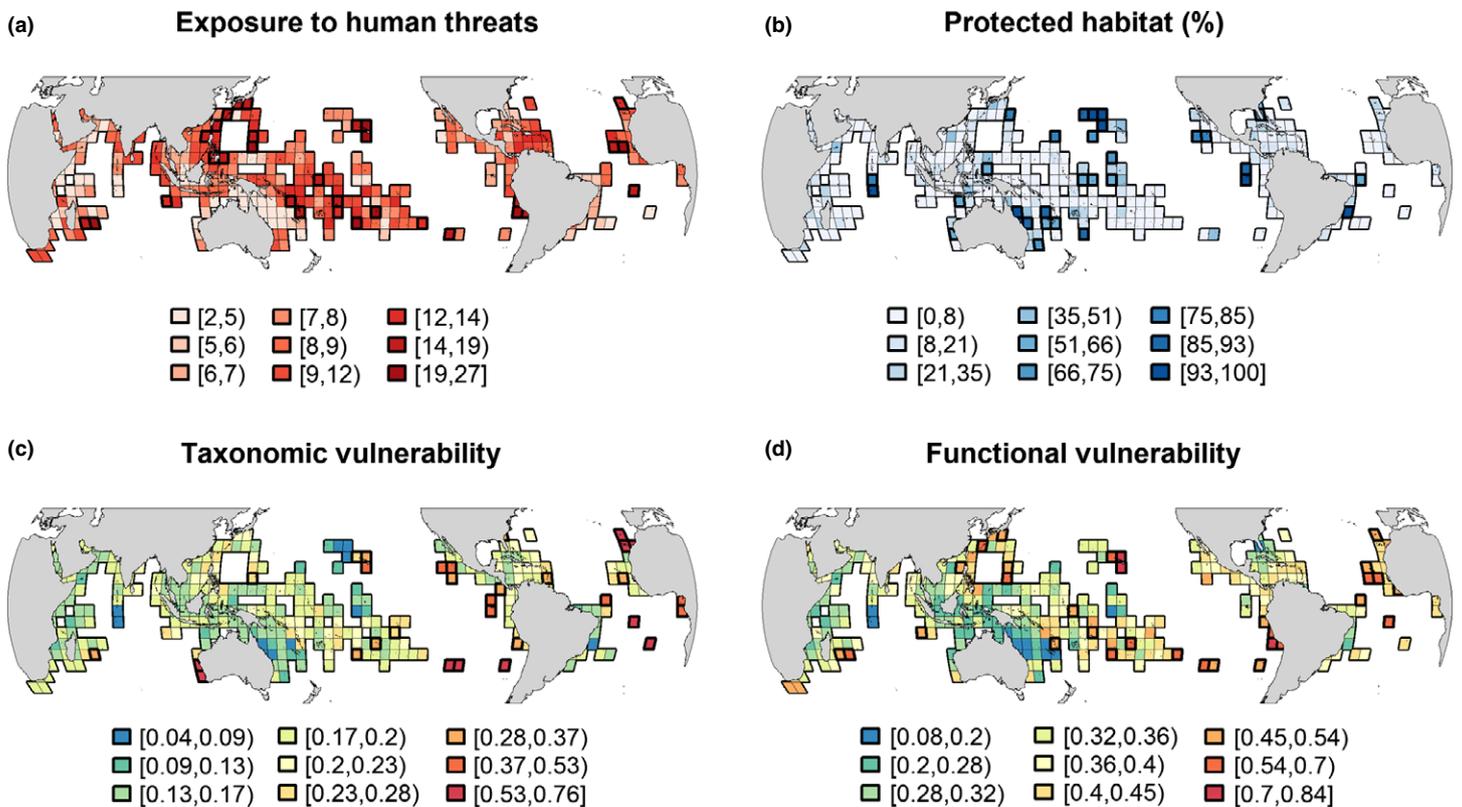


Figure 4 Global gradients of (a) human threat intensity derived from Halpern *et al.* (2008), (b) protection (i.e. the percentage of reef fish habitat within marine protected areas), (c) taxonomic vulnerability and (d) functional vulnerability (see main text) for assemblages of tropical reef fishes. Black bordered cells represent hotspots.

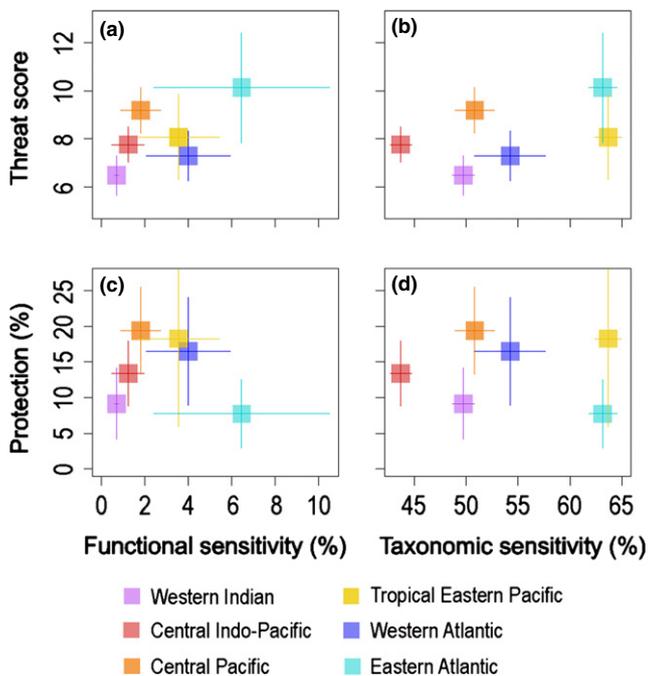


Figure 5 (a) Relationship between threat's score and functional sensitivity of the six major biogeographical regions for reef fishes according to Kulbicki *et al.* (2013); (b) relationship the threat's score and taxonomic sensitivity; (c) relationship between protection effort (% of protected habitat) and functional sensitivity; (d) relationship between protection effort and taxonomic sensitivity.

Combining our sensitivity estimates with protection effort and exposure to human threats into vulnerability scores allowed us to define areas where the probability of taxonomic or functional biodiversity loss is high. The distribution of MPAs does not match the hotspots of taxonomic and functional vulnerability. Considering an index of MPA effectiveness, Mora *et al.* (2006) showed that the global network of MPAs is largely inadequate for the protection of coral reefs. Our analyses reveal that only the large marine parks of the Great Barrier Reef and northern Hawaii have the potential to markedly reduce fish assemblage vulnerability. Our findings are in general agreement with previous evaluations that highlight the need for more extensive areas of protection for tropical reefs (Mora *et al.* 2006; Mora & Sale 2011). In this context, our framework provides new metrics and a functional perspective for assessing the large-scale efforts to protect tropical reef ecosystems.

In conclusion, using a new ecological vulnerability framework, we identified tropical reef areas that are critical for preventing the loss of fish taxonomic and functional biodiversity. These areas, such as the Western Indian Ocean, differ in important ways from the fish richness hotspots previously identified close to the Indo-Australian Archipelago. Such mismatches among properties of assemblages are common (Jetz & Rahbek 2002; Orme *et al.* 2005; Devictor *et al.* 2010; Mouillot *et al.* 2011; Stuart-Smith *et al.* 2013). However, decisions about what should be preserved: centres of richness,

endemism, functional diversity or functional sensitivity are now left to scientists, managers and policy makers (Hughes *et al.* 2002; Tittensor 2013). Of course, the ideal choice would be to protect all the above but this solution is inapplicable in a world of limited resources. Unfortunately, the present MPA network does not spatially match with the most vulnerable assemblages but the spatial match between taxonomic and functional vulnerability suggests a global conservation–ecosystem service win–win strategy if both taxonomically and functionally vulnerable reef fish assemblages are more protected.

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AUTHORSHIP

V.P., S.V., T.R.M., D.M., M.K. conceived the study and all authors contributed to the refinement of the framework. All authors participated to the collection of the data needed. V.P. and S.V. conducted the analyses. V.P., S.V., T.R.M., D.R.B., D.M. and M.K. wrote the first draft of the manuscript, and all the authors contributed substantially with comments and revisions.

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