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Functional rarity of coral reef fishes at the global scale: Hotspots and challenges for conservation

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ABSTRACT

Characterizing functional diversity has become central in ecological research and for biodiversity assessment. Understanding the role of species with rare traits, i.e. functionally rare species, in community assembly, ecosystem dynamics and functioning has recently gained momentum. However, functional rarity is still ignored in conservation strategies.

Here, we quantified global functional and evolutionary rarity for 2073 species of coral reef fishes and compared the rarity values to IUCN Red List status. Most species were functionally common but geographically rare. However, we found very weak correlation between functional rarity and evolutionary rarity. Functional rarity was highest for species classified as not evaluated or threatened by the IUCN Red List. The location of functional rarity hotspots (Tropical Eastern Pacific) did not match hotspots of species richness and evolutionary distinctiveness (Indo-Australian Archipelago), nor the currently protected areas. We argue that functional rarity should be acknowledged for both species and site prioritization in conservation strategies.

1. Introduction

Current conservation plans and policy decisions largely rely on the evaluation of taxonomic diversity, at both local and large scales (Davies et al., 2017; Hidasi-Neto et al., 2013; Rosenfeld, 2002; Thuiller et al., 2015). For example, current protected areas mostly match with biodiversity hotspots defined by species number for a given area (Brum et al., 2017; Davies et al., 2017; Devictor et al., 2010; Pollock et al., 2017). At the species level, one major conservation tool is the Red List of the International Union for Conservation of Nature (IUCN) (Rodrigues et al., 2006), which still ignores the diversity of biological attributes (traits and genes) supported by species (Vié et al., 2009). However, assessing the diversity of organismal evolutionary history has become central to biodiversity monitoring and analysis (Cadotte et al., 2013), as well as accounting for organismal traits that are linked to species performance and niche axes (Díaz and Cabido, 2001; Stuart-Smith et al., 2013; Violle et al., 2007; Violle and Jiang, 2009), so to species coexistence and ecosystem dynamics (McGill et al., 2006; Violle et al., 2007) but also to species functional distinctiveness or uniqueness (Chase, 2013; Godet et al., 2015; Jain et al., 2014; Mouillot et al., 2013; Murray et al., 2002; Pavoine et al., 2005; Violle et al., 2017b). In this context, it appears urgent to bring organismal functions – e.g., using functional traits as proxies (Díaz and Cabido, 2001; Violle et al., 2007) – into the global conservation agenda (Cadotte et al., 2011; Naeem et al., 2012; Pollock et al., 2017).

Conservation efforts usually focus on subsets of emblematic or threatened species and habitats due to limited resources (Arponen, 2012). With the ongoing extinction crisis (Ceballos et al., 2017), much emphasis has been put on prioritizing the protection of rare species and their habitat (Cofre and Marquet, 1999). Species' population size, geographical range and habitat breadth together define several forms of rarity reflecting the potential vulnerability of species to demographic extinctions and habitat alteration (Rabinowitz, 1981). More recently, phylogenetic relationships have been included in species rarity assessment (Isaac et al., 2007; Redding et al., 2010). In the same vein, Violle et al. (2017b) have recently proposed a framework to define functional rarity, accounting for both distinctiveness of species trait values and species geographical range size. After considering a pool of species and a spatial scale, the functional rarity of a species can be quantified based on both the distinctiveness of its trait values compared to the other

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species of the pool and its geographical range compared to the geographic extent of the study. In this framework, a species can be geographically rare because of its small range size, but at the same time common in terms of its traits. Conversely, a species can be geographically common with a large range size, but rare in terms of traits. The same framework can also apply to define phylogenetic rarity which is already included in species rarity assessment (Isaac et al., 2007; Redding et al., 2010). Functional rarity as defined by Violle and colleagues mirrors the concept of functional redundancy (Ricotta et al., 2016; Yachi and Loreau, 1999). Functional redundancy is the fact that a group of individuals (or species) at a given site share similar functions, thus being redundant. While, functional redundancy focuses at the site-level on shared functions, functional rarity concentrates on unshared functions at the species-level.

Previous works only examined the amount of phylogenetic rarity in biodiversity hotspots covered by protected areas (Mouillot et al., 2016), as it represents a crucial evolutionary heritage and potential for adaptation (Forest et al., 2007), but ignored functional rarity. When they did include functional rarity, phylogenetic and functional rarity did not necessarily match between species (Violle et al., 2017b; Winter et al., 2013). For example, carnivores at a global scale have concordant functional and phylogenetic rarity values (Dalerum, 2013), allowing consistent strategies to conserve both dimensions. Yet, other studies have reported a decoupling of taxonomic, phylogenetic and functional rarities across space (Gonçalves-Souza et al., 2014; Hidasi-Neto et al., 2013, 2015). If a decoupling between the different dimensions of rarity emerges at a global scale, we need to reassess whether current conservation practices, and especially protected areas, cover the hotspots of functional, phylogenetic and taxonomic rarity (Pollock et al., 2017). In addition to local and regional conservation initiatives, a global species-based assessment of functional rarity can pinpoint areas or taxa that need further protection (Mouillot et al., 2016; Pollock et al., 2017).

Coral reef ecosystems are the most diverse marine systems, containing about 30% of all multicellular marine species (Fisher et al., 2015). They provide important ecosystems functions and services, including nitrogen cycling and larvae nurseries, as well as fisheries and shoreline protection (Harborne et al., 2006; Moberg and Folke, 1999). Coral reef ecosystems are currently facing multiple threats (Bellwood et al., 2004; Hoegh-Guldberg et al., 2007; Hughes et al., 2018). They notably experience massive, rapid and repeated coral bleaching events (Hughes et al., 2018; van Hooidonk et al., 2014; Wilson et al., 2006). These disturbances lead to a decrease in fish diversity and abundance potentially leading to a loss of key ecosystem functions and services (Pratchett et al., 2011; Rogers et al., 2018). Indeed, some fish species have unique combinations of traits (Mouillot et al., 2013) or perform unique functions on reefs (Bellwood et al., 2006), and as such deserve conservation attention. Furthermore, coral reef fishes show high functional vulnerability (Mouillot et al., 2014; Parravicini et al., 2014), because many combinations of functional traits are supported by only few species. However, the global geographic distribution of functional rarity is virtually unknown for coral reef fishes. The density of functionally rare species may simply match with species richness hotspots, such as the Coral Triangle, owing to a sampling effect, or it may peak in other areas where coral reef fishes have an original evolutionary history. Here we examined the global distribution of functional rarity in coral reef fishes and how it relates to their evolutionary rarity, to IUCN Red List Status and conservation efforts.

2. Material and methods

2.1. Fish occurrences

We used a worldwide database of reef fish presence-absence across tropical oceans (Parravicini et al., 2013), aggregated from almost 500 references (Kulbicki et al., 2013). The initial data contained both tropical and coral reefs, however, we limited our study to locations containing coral reefs for easier comparison between sites, ending with 259 cells of 5° by 5° (corresponding to ~555 km by 555 km at the Equator, see Fig. A1 for details on data selection). We selected 2073 species (over 6300 reported coral reef fish species) for which functional trait information and the position on a phylogenetic tree were available. These species belong to 19 fish families (over 169 occurring on coral reefs) that are dominant on coral reefs (Kulbicki et al., 2013). Our sub-sampling of species compared to the full range of species did not change the relative species richness across cells (see Fig. A2, Spearman's rho = 0.99, $p < 0.001$).

2.2. Trait data

We considered six categorical functional traits representing the ability of tropical-reef fish species to forage resources and to reproduce (Mouillot et al., 2014; Villéger et al., 2017, see Appendix B for detailed links between traits and functions). Fish size (total body length) was 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 of body length. Mobility was coded using three ordered categories: sedentary (including territorial species), mobile within a reef, and mobile between reefs. The 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 (> 50 individuals) groups. Vertical position in the water column was coded using three ordered categories: benthic, bentho-pelagic, and pelagic. We defined seven trophic categories based on the main items consumed by each species: herbivorous-detritivorous (i.e., fish feeding on turf or filamentous algae and/or undefined organic material), macro-algal herbivorous (i.e., fish 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), planktivorous (i.e., fish eating small organisms in the water column), piscivorous (including fish and cephalopods), and omnivorous (i.e., fish for which both vegetal and animal material are important in their diet).

2.3. Fish IUCN status

We used the `taxize` package v.0.7.8 (Chamberlain et al., 2016; Chamberlain and Szöcs, 2013) to retrieve up-to-date IUCN status for fishes (IUCN, 2017). For easier interpretation, we grouped species into four categories depending on their threat level: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) species as “Threatened” (n = 56); Least Concern (LC) and Near Threatened (NT) species as “Not Threatened” (n = 1011); Data Deficient (DF) species as “Data Deficient” (n = 120) and species without known status as “Not Evaluated” species (n = 886). We found no difference (p = 0.11, Fisher's exact test for count data) in the proportion of species in each threat group between our subset of 2073 species and the 6300 known species of coral reef fishes (Fig. A3). The proportions of species in each status differed between the Atlantic and Indo-Pacific realms ($\chi^2 = 121$, d.f. = 3, $p < 0.001$) (Fig. A4).

2.4. Functional rarity components

We computed Gower's pairwise distances between species because we had both ordinal and nominal traits (Gower, 1971). We used the `dist.ktab()` function in `ade4` v.1.7-6 to compute the distances (Dray and Dufour, 2007; Pavoine et al., 2009). We computed rarity components based on the framework of Violle et al. (2017b) and the `funrar` package v.1.2.0 (Grenié et al., 2017; Violle et al., 2017a). We estimated functional distinctiveness D_i of species i using functional dissimilarities, representing how rare the traits of a given species are compared to all the other species globally as:

$$D_i = \frac{\sum_{j=1,j\neq i}^{N} d_{ij}}{N-1}, \quad (1)$$

where d_{ij} was the functional distance between species i and j and N the total number of species in the species pool. The functional distances d_{ij} were scaled between 0 and 1. D_i captured how different are the traits, on average, of a given species compared to the rest of the species pool. D_i was equal to one when species i was maximally different to the other species. We tested the influence of the species pool definition from which functional distinctiveness was extracted. To this aim, we split the cells into two realms—Atlantic and Pacific—and estimated species distinctiveness values separately in each realm. There was a strong correlation between realm-specific and global distinctiveness values (see Fig. A5; Spearman's rho = 0.82, $p < 0.001$ for Atlantic; Spearman's rho = 1, $p < 0.001$ for Indo-Pacific).

We performed a sensitivity analysis to check whether specific traits had strong influences on functional distinctiveness values: we left out each trait one by one and recomputed functional distinctiveness values using the five remaining traits. The recomputed functional distinctiveness values correlated strongly with functional distinctiveness obtained from all the traits (Fig. A6, Spearman's rho > 0.86 for all the combinations).

We defined geographical restrictedness of species i, R_i, as:

$$R_i = 1 - \frac{K_i}{K_{tot}}, \quad (2)$$

where K_i was the number of cells where species i was present and K_{tot} the total number of cells. R_i was close to one for a species present at a single site only, and was equal to zero for a species present in all sites over the whole geographic range considered (here all coral reefs cells). Because each cell did not contain the same habitat area, we also computed restrictedness acknowledging relative reef area, i.e., K_i was then the cumulated habitat area in all the cells where species i was present and K_{tot} the sum of habitat area in all cells. The correlation between geographic restrictedness estimated on coral reefs and on coral plus tropical reefs was high (Fig. A7, Spearman's rho = 0.98, $p < 0.001$). Estimating the range of species based on coral reef cells only marginally changed the estimate of relative range size between species.

We combined the two indices into a synthetic index of functional rarity (FR), to rank the functionally rarest species:

$$FR_i = \frac{D_{i,sc} + R_{i,sc}}{2}, \quad (3)$$

where $D_{i,sc}$ was the functional distinctiveness of species i scaled between zero and one and $R_{i,sc}$ the restrictedness of species scaled between zero and one. FR_i weighs equally species with very distinct traits (high D_i) and species present in a few cells (high R_i). A species with FR_i close to one was both very restricted in geographic distribution (high $R_{i,sc}$) and had very distinct traits compared to the rest of the species pool (high D_i).

2.5. Evolutionary distinctiveness

We used the supertree of coral reef fish taxa provided by Leprieur et al. (2016). Even though this tree comprises a large number of polytomies, it is one of the most exhaustive phylogenetic tree available for coral reef fishes, and as such, is well-suited to study global patterns of fish functional rarity. Based on the phylogenetic relationships among taxa, we computed their Evolutionary Distinctiveness (Isaac et al., 2007). The Evolutionary Distinctiveness of species i, ED_i, is high when the species has a long unshared branch length with all the other species. The more “isolated” a species is in a phylogenetic tree, the higher its evolutionary distinctiveness. We computed ED using the `picante` package (Kembel et al., 2010) v.1.6-2 and the fair proportion option following Isaac et al. (2007).

We computed an evolutionary equivalent of FR_i for species i, denoted as Evolutionary Rarity ER_i:

$$ER_{\mathrm{i}} = \frac{ED_{i,sc} + R_{i,sc}}{2}, \quad (4)$$

where $ED_{i,sc}$ was the scaled evolutionary distinctiveness between zero and one of species i, and $R_{i,sc}$ the scaled geographic restrictedness between zero and one of species i. ER_i weighs equally species that are highly evolutionary distinct (high ED_i) and species present in a small number of cells (high R_i). A species with ER_i close to one was both very restricted in geographic distribution (high $R_{i,sc}$) and very distinct in phylogenetic history, having a very long branch length separating it from the rest of the species pool (high $ED_{i,sc}$). A species with intermediate values of both ED_i and R_i could also have a high ER_i value.

2.6. Statistical analyses and maps

All analyses were carried out using R (R Core Team, 2017) v.3.4.1.

A Principal Coordinates Analysis (PCoA) identified orthogonal dimensions determining the variation in functional distances (`pcoa()` function in the `ape` package v.4.1, Paradis et al., 2004). We assessed the contribution of the elementary traits to these dimensions, and represented how the functional rarity components varied along the dimensions. The axes were selected as their explained variance was greater to the null expectation of a broken stick model (Legendre and Legendre, 2012). We found no systematic bias in terms of occupation of the total functional trait space between our subset of species and the global set of 6316 tropical reef species (see Fig. A8, Spearman's = 0.98, $p < 0.001$).

To illustrate rarity hotspots and coldspots on the map we ranked all the species according to each above-mentioned index, and we counted the number of species per cell that were in the global top 10% (highest 10%) for each index. Because choosing a 10% threshold is still arbitrary, we also performed the analyses with 5% and 15% thresholds, but it did not change the results qualitatively (see Fig. A9). The number of top 10% evolutionary rare species at a site can be related to phylogenetic endemism (PE) as defined by Rosauer et al. (2009). We did find a strong correlation between this number of top 10% ER species and PE (see Fig. A11).

In order to assess to what extent the differences in the number of top-ranked species were primarily driven by species richness differences between cells we used null models (Gotelli and Graves, 1996). We used the curveball algorithm (Strona et al., 2014) from the `nullmodel()` function in the `vegan` package v.2.5-2 (Oksanen et al., 2018). The curveball algorithm randomizes the presences of species across cells while keeping the same species richness at each cell, and the same number of occurrences for each species. We computed 2000 permutations and for each of them we counted the number of top 10% species at each cell. For each cell we then compared the observed values to the randomized ones using the Standard Effect Size score (SES) computed as the difference between the observed value and the mean of predicted values by the null model, divided by the standard deviation of predicted values:

$$SES_j(I) = \frac{I_{j,Obs} - \hat{I}_{j,Pred}}{sd(I_{j,Pred})} \quad (5)$$

where j is the cell, I the index of interest, $I_{j,Obs}$ the observed index at cell j, $\hat{I}_{j,\ Pred}$ the average of predicted indices at cell j and $sd(I_{j,\ Pred})$ the standard deviation of the predicted indices. The SES score measures how much the observed value is far from the values predicted by the null model accounting for species richness. If the number of top species in the cell was driven by species richness only, SES scores should be close to 0. On the contrary, an SES score with a great absolute value means that this null hypothesis is less probable (Gotelli and Graves, 1996).

We compared the obtained maps using a modified version of the *t*-

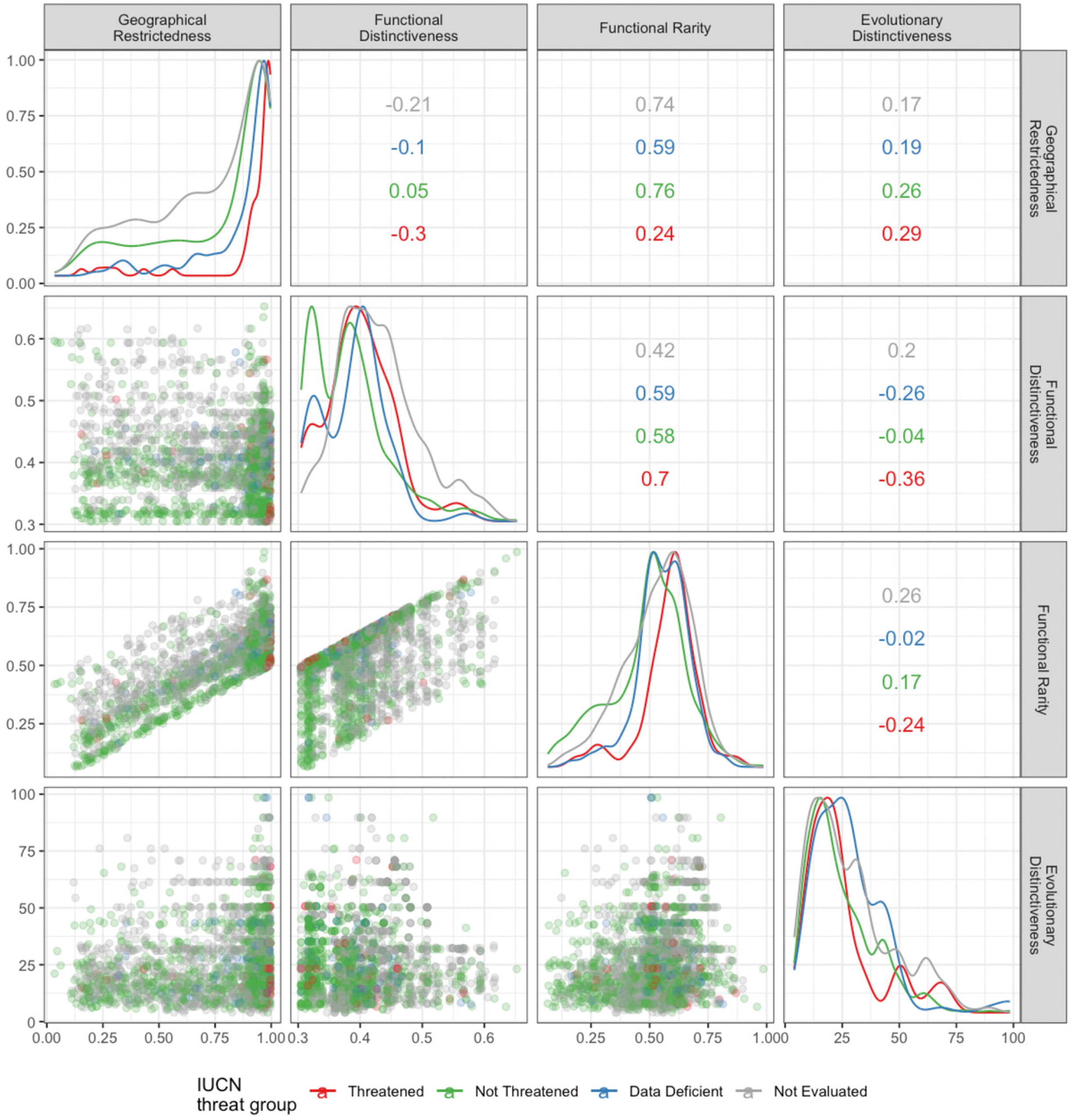

Fig. 1. Biplots showing the relationships between the various components of species rarity by IUCN status. The plots in the upper right triangle above the diagonal indicates the Spearman correlation between components for each IUCN threat group. The diagonal shows the density plot for each component per IUCN threat group. Plots in the lower left triangle under the diagonal are scatterplots linking two components with each dot representing a single species with color representing its IUCN threat group.

test to account for spatial autocorrelation (Dutilleul et al., 1993). We used the `SpatialPack` package v.0.2-3 (Osorio and Vallejos, 2014).

We performed a multiple comparison Kruskal-Wallis rank-sum test to compare rarity components across IUCN groups. We used the `kruskal()` function of the `agricolae` package v.1.2-6 (de Mendiburu, 2017). We also performed post-hoc tests using Fisher's least significant difference to differentiate between groups.

We calculated the Pagel's λ value of phylogenetic signal of species rarity components, using the `fitContinuous()` function in the `geiger` package v.2.0.6 (Harmon et al., 2008). Because Pagel's λ works only on binary trees, we resolved the polytomies randomly 30 times using the `multi2di()` function in the `ape` package v.4.1 (Paradis et al., 2004): the different λ values changed only by $< 0.1\%$.

3. Results

The distributions of functional distinctiveness and restrictedness were highly skewed (Fig. 1, panels on the diagonal), with most species being functionally common and geographically restricted, while evolutionary rarity showed a more symmetrical distribution. Functional distinctiveness was significantly but weakly correlated with both geographic restrictedness (Spearman's $\rho = -0.09$, $p < 0.001$) and evolutionary distinctiveness (Spearman's $\rho = -0.08$, $p < 0.001$). Geographic restrictedness showed the strongest correlation with evolutionary distinctiveness (Spearman's $\rho = 0.21$, $p < 0.001$).

The first two axes of the functional space explained 51.6% of trait variance among fishes (Fig. 2). The first axis differentiated big, large schooling and planktivorous species from small, solitary and

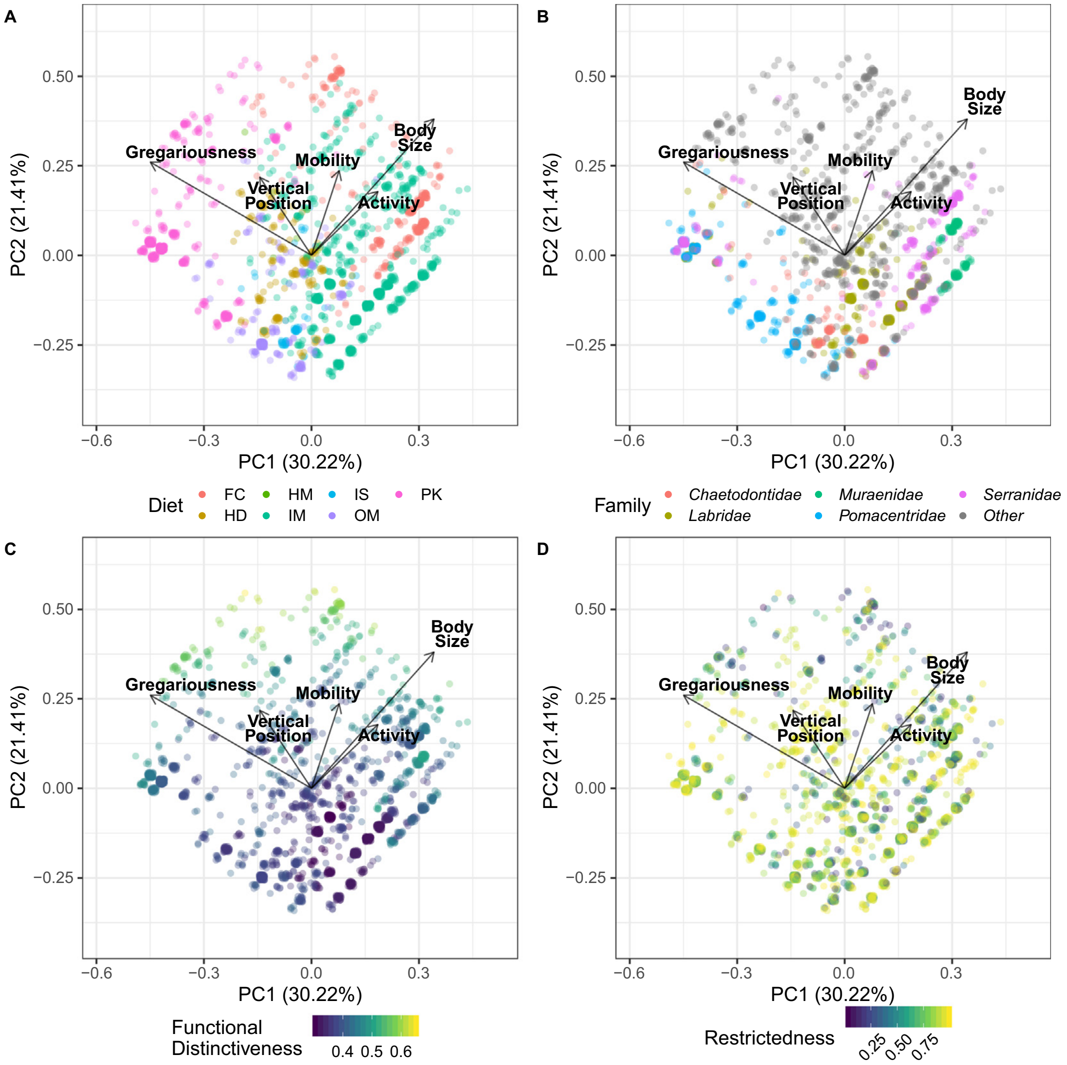

Fig. 2. Principal Coordinates Analysis (PCoA) representing the functional space of coral reef fishes based on their traits. The first two axes explain 51.6% of the variance in the distance matrix. (A) Colored by diet: FC, piscivorous; HM, macroalgal herbivorous; IS, invertivorous on sessile organisms; HD, herbivorous invertivorous; IM, invertivorous on mobile organism; OM, omnivorous; PK, planktivores (B) Colored with the five most numerous families (C) Colored by functional distinctiveness (D) Colored by geographical restrictedness.

omnivorous species. The second axis differentiated mobile species with highly specialized diet (planktivorous or piscivorous) from sedentary generalist (invertivorous, omnivorous) species (correlations between traits and axes in Table A1). We mapped the scores of the five most species-rich families on these axes (Fig. 2B). Because most species of these families were sedentary and benthic, they were located in the lower half of the functional space. Functional distinctiveness was correlated with the second axis (Fig. 2C) (Spearman's $\rho = 0.71$, $p < 0.001$), but not with the first axis (Spearman's $\rho = -0.02$, $p > 0.1$), i.e., species with large schools and large body size were functionally more distinct. Geographic restrictedness was weakly correlated with the two axes (Fig. 2D) (Axis 1: Spearman's $\rho = -0.05$, $p = 0.03$; Axis 2: Spearman's $\rho = -0.10$, $p < 0.001$), while functional rarity was weakly correlated with the first axis but more strongly with the second one (Axis 1: Spearman's $\rho = -0.09$, $p < 0.001$; Axis 2: Spearman's $\rho = -0.36$, $p < 0.001$). Evolutionary distinctiveness was weakly correlated with the first axis (Axis 1: Spearman's $\rho = 0.15$, $p < 0.001$; Axis 2: Spearman's $\rho = 0.03$, $p = 0.11$), while evolutionary rarity was correlated with neither axis (Axis 1: Spearman's $\rho = 0.01$, $p = 0.68$; Axis 2: Spearman's $\rho = -0.07$, $p = 0.002$).

Across IUCN threat groups, functional distinctiveness was the highest for Not Evaluated species, followed by Threatened and Data Deficient species (Fig. 3A) (Kruskal-Wallis $\chi^2 = 262$, d.f. = 3, $p < 0.001$). Not Threatened species had lowest functional distinctiveness on average. Geographic restrictedness was the highest for Threatened species (Fig. 3B), followed by Data Deficient species, Not Threatened species and finally Not Evaluated species (Kruskal-Wallis $\chi^2 = 93$, d.f. = 3, $p < 0.001$). This was expected as geographic restrictedness is directly related to species range size which is a criterion for the IUCN assessment. Functional rarity (Fig. 3C) was the highest for Threatened and Data Deficient species (Kruskal-Wallis $\chi^2 = 58.9$, d.f. = 3, $p < 0.001$). Not Threatened species had the lowest functional rarity. Evolutionary distinctiveness was the highest for Data Deficient and Not Evaluated species (Kruskal-Wallis $\chi^2 = 18$, d.f. = 3, $p < 0.001$). Evolutionary rarity (Fig. 3D) was the highest for Threatened and Data Deficient species and the lowest for Not Threatened and Not Evaluated species (Kruskal-Wallis $\chi^2 = 18$, d.f. = 3, $p < 0.001$).

Bivariate relationships between rarity components showed very contrasted correlation coefficients between IUCN threat groups (Fig. 1). Functional distinctiveness and evolutionary distinctiveness were negatively correlated for Threatened and Data Deficient groups (Spearman's $\rho = -0.36$, $p = 0.006$; and Spearman's $\rho = -0.26$, $p = 0.004$ respectively), while this correlation was positive for Not Evaluated species (Spearman's $\rho = 0.2$, $p < 0.001$) and Not Threatened species showed

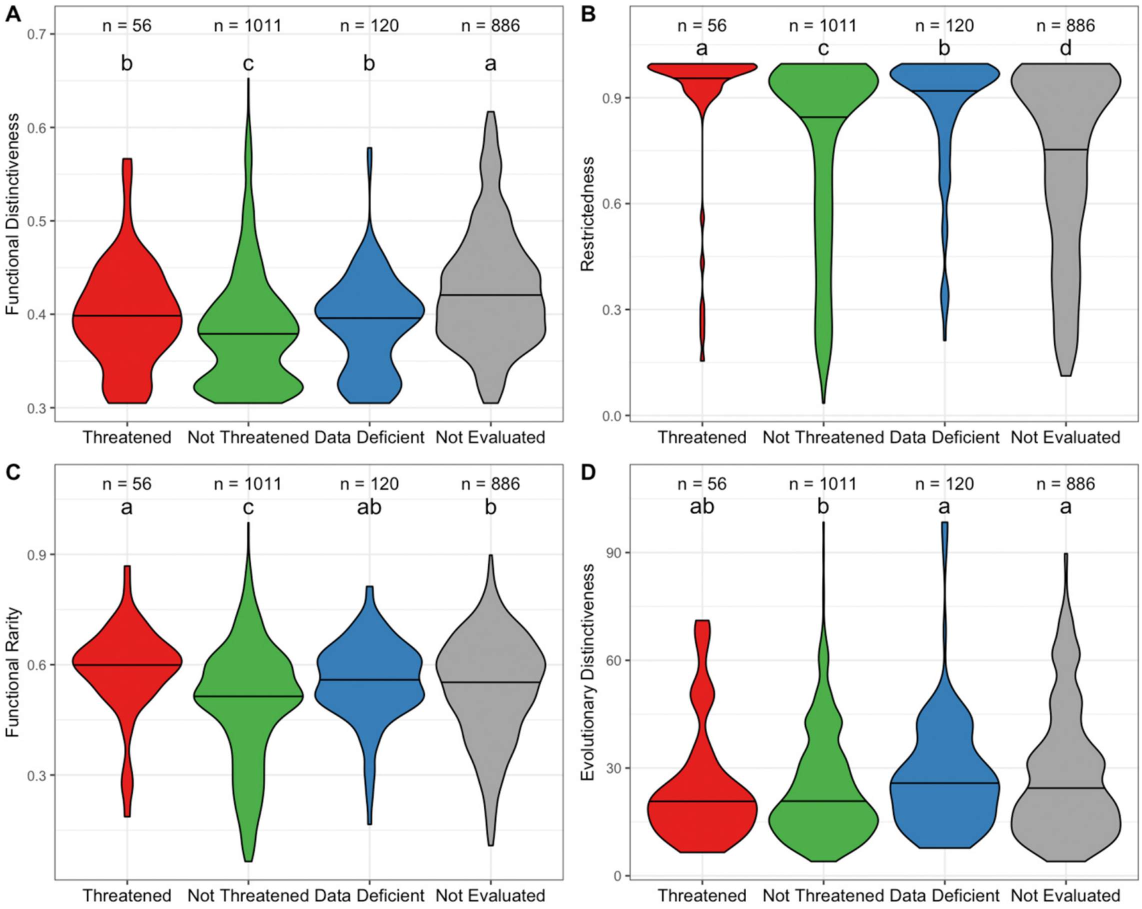

Fig. 3. Violin plots showing the smoothed distribution of species rarity components within each IUCN threat group: (A) Functional distinctiveness (B) Restrictedness (C) Functional rarity (D) Evolutionary distinctiveness. The solid line indicates the group median value. Letters indicate statistical sub-groups from a Kruskal-Wallis rank-sum test. Two groups that are significantly different have two different lower-case letters. Numbers above the violins indicate the number of species in each IUCN threat group.

no correlation (Spearman's $\rho = -0.04$, $p = 0.27$). Functional distinctiveness and geographic restrictedness also exhibited different correlation coefficients between groups: Threatened and Not Evaluated species had a moderate negative correlation (Spearman's $\rho = -0.30$, $p = 0.03$; Spearman's $\rho = -0.21$, $p < 0.001$), while Data Deficient and Not Evaluated species had no clear correlation (Spearman's $\rho = -0.10$, $p = 0.27$; Spearman's $\rho = 0.05$, $p = 0.11$).

Functional distinctiveness had a higher Pagel's λ value ($\lambda = 0.85$) than functional rarity and restrictedness ($\lambda = 0.70$ and $\lambda = 0.68$, respectively), while the phylogenetic structuring did not depart from a Brownian model of trait evolution. The randomly resolved polytomies had little effect on λ values. The two families with the highest functional rarity value were the *Caesionidae* and the *Carangidae*. *Caesionidae* had a mean functional rarity of 0.66, while other families had a mean of 0.4 (see Fig. 4). These families were functionally rare because most of their species live in large schools, have specialized diets (*Carangidae* are piscivores, while *Caesionidae* are planktivores), and are very mobile across reefs.

We counted the number of top 10% rare species in each 5° by 5° cell and examined the spatial congruence of rarity hotspots. Functional rarity hotspots poorly matched with evolutionary distinctiveness hotspots (Corrected Pearson's $\rho = 0.19$, $F = 1.18$, $p = 0.29$, see all tests in Table A2). The Indo-Australian Archipelago (IAA), as well as Eastern Africa, showed the highest number of top 10% functionally distinctive species (Fig. 5A), while the top 10% evolutionary distinctive species (Fig. 5E) were concentrated in the IAA. However, the highest number of top 10% functionally rare species was located in the Tropical Eastern Pacific (Fig. 5C). The number of most evolutionarily rare species peaked in the Caribbean as well as East China Sea and the South of Japan (Fig. 5G). When using null models, the IAA had a lower than expected number of top 10% functionally and evolutionarily rare species while reefs in the Tropical Eastern Pacific or along the East African coast host more top rarest species than expected given the number of species. The Arabic Peninsula, as well as the Tropical Eastern Pacific exhibited SES values over 3 for all indices, i.*e*, higher number of top 10% species than expected from the null models, while the Caribbean had SES values under −3 only for functional distinctiveness and around 3 for all the other indices.

There was a negative relationship between the protection percentage on a grid cell (using strict protection definition, see Mouillot et al., 2016) and the number of top 10% functionally distinct species (corrected Pearson's $\rho = -0.20$, $F = 7.86$, $p = 0.006$). Grid cells with the highest number of top 10% functionally distinct species were in areas with low protection coverage, such as the Tropical Eastern Pacific. Furthermore, there was no relation between protection coverage and functional rarity at the grid cell scale (corrected Pearson's $\rho = 0.02$, $F = 0.05$, $p = 0.83$).

4. Discussion

We used a global dataset on coral reef fishes to assess the geographic distribution of their functional and phylogenetic rarity, and the degree to which rarest species were under IUCN conservation status. Functional rarity correlates with specific trait values such as large body size and large schools (> 50 individuals). Functional rarity also reveals novel hotspots in areas that are less speciose and far from the Indo-

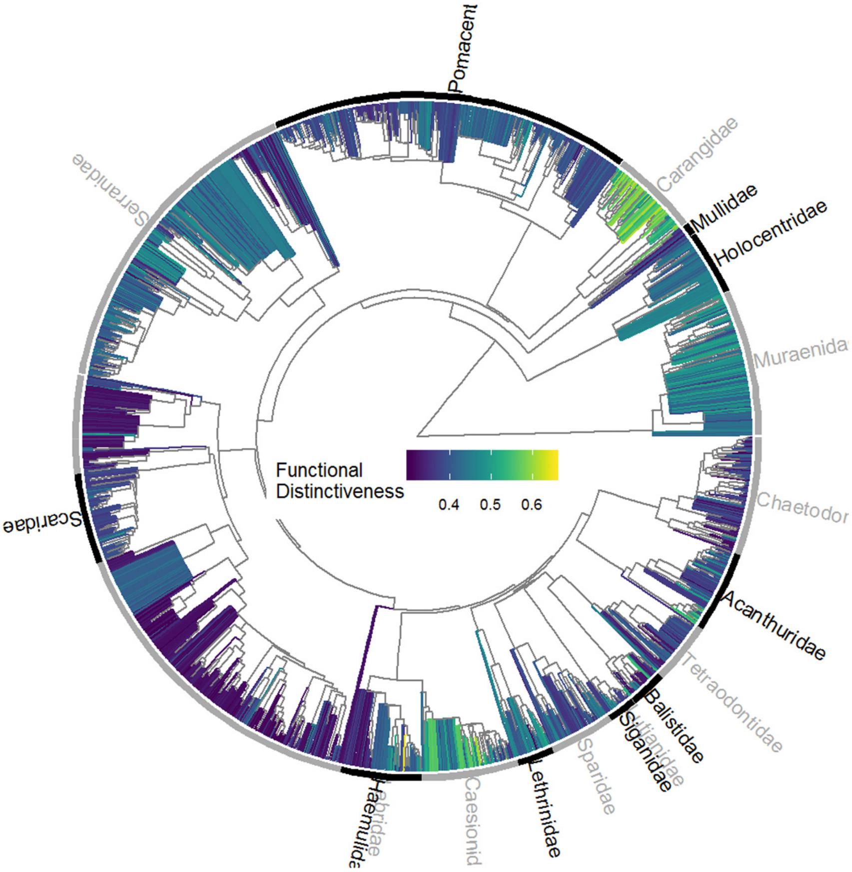

Fig. 4. Phylogenetic tree of coral reef fishes with functional distinctiveness values on terminal branches representing species. Family names are indicated on the outside ring. The colors of the families are only a visual cue to read the phylogenetic tree, they have no meaning per se. Grey and black labels may overlap because of non-monophyletic families. The extent of families is indicated by the colored rings. *Caesionidae* and *Carangidae* both have a higher mean functional distinctiveness than other families.

Australian Archipelago.

4.1. Functional and evolutionary rarity hotspots

Functional rarity hotspots are mainly located in the Tropical Eastern Pacific region and in the Caribbean, while evolutionary rarity hotspots are concentrated in the Indo-Australian Archipelago. The rarity hotspots, are consistent with what has already been shown according to the history of coral reef fish diversification and the influence of connectivity among regions (Cowman and Bellwood, 2013). Indeed, highly connected regions, such as the Indo-Australian Archipelago, host species that are less restricted in their distribution (low restrictedness) and thus exhibit lower functional rarity value. On the contrary, less connected regions, such as the Tropical Eastern Pacific or the Atlantic, have been isolated for longer (Pellissier et al., 2014). In addition, the extinction process in isolated regions is not balanced by colonization and induces lower diversity (Pellissier et al., 2014). Assuming random extinctions among all species, this lower diversity tends to increase functional distinctiveness, with less species having the same functional traits. All these combined factors make functional rarity to be higher in less connected regions, as in the Eastern Pacific. We must also take into account the isolation from coral reef Quaternary refugia, which explains patterns of diversification in the IAA (Pellissier et al., 2014). This refugia is located near the IAA, region exhibiting the highest species diversity, and thus lower overall functional differentiation, because of hosting more species in a similar trait space. Functional rarity hotspots could thus be explained by the history and biogeography of coral reef fishes.

4.2. Evolutionarily and functionally distinct species

Functional and evolutionary distinctiveness are correlated differently depending on the IUCN threat group. Furthermore, functional rarity does not depart from a Brownian model of trait evolution across the phylogeny, which suggests that closely related species share a more similar functional rarity value than distantly related species.

The relationship between evolutionary (ED) and functional distinctiveness depends on the mode of trait evolution, the rates of speciation and extinction in a clade, and the interaction between these processes (Thuiller et al., 2015). *S*pecies lacking close relatives are likely to exhibit more distinct combinations of traits due to some unique evolutionary history. However, this is far from being a strict rule, as highlighted by the presence of both quite functionally ordinary (e.g. Omilteme rabbit) and quite distinct (e.g. northern hairynosed wombat) species on the mammal EDGE list (Isaac et al., 2007). Particular traits can impact evolutionary distinctiveness if they affect diversification rates. For example, some traits have been identified as driving higher extinction rates, making surviving taxa to be evolutionarily more distinct. For example, body size is often correlated with extinction risk (Davies et al., 2008; Lee and Jetz, 2011). Trait values can also be associated with differences in speciation rates between clades – for example, body size was found to be positively correlated with speciation rates in fishes (Rabosky et al., 2013). The influence of factors such as convergent evolution and niche conservatism on the relationship between ED and functional distinctiveness is still poorly explored. A comprehensive perspective on how functional and evolutionary distinctiveness relate across different taxa is necessary to guide conservation prioritization.

We used a recently published super-tree comprising over 2000 species of coral reef fishes (Leprieur et al., 2016) to assess ED. However, because this super-tree contains many polytomies at the genus level, the estimation of evolutionary distinctiveness may be biased. Indeed, polytomies induce high long terminal branches at the genus level, giving high ED scores to the sub-tending species. Fully resolved phylogenies would provide a better estimation of the link between functional and evolutionary distinctiveness but are not yet available.

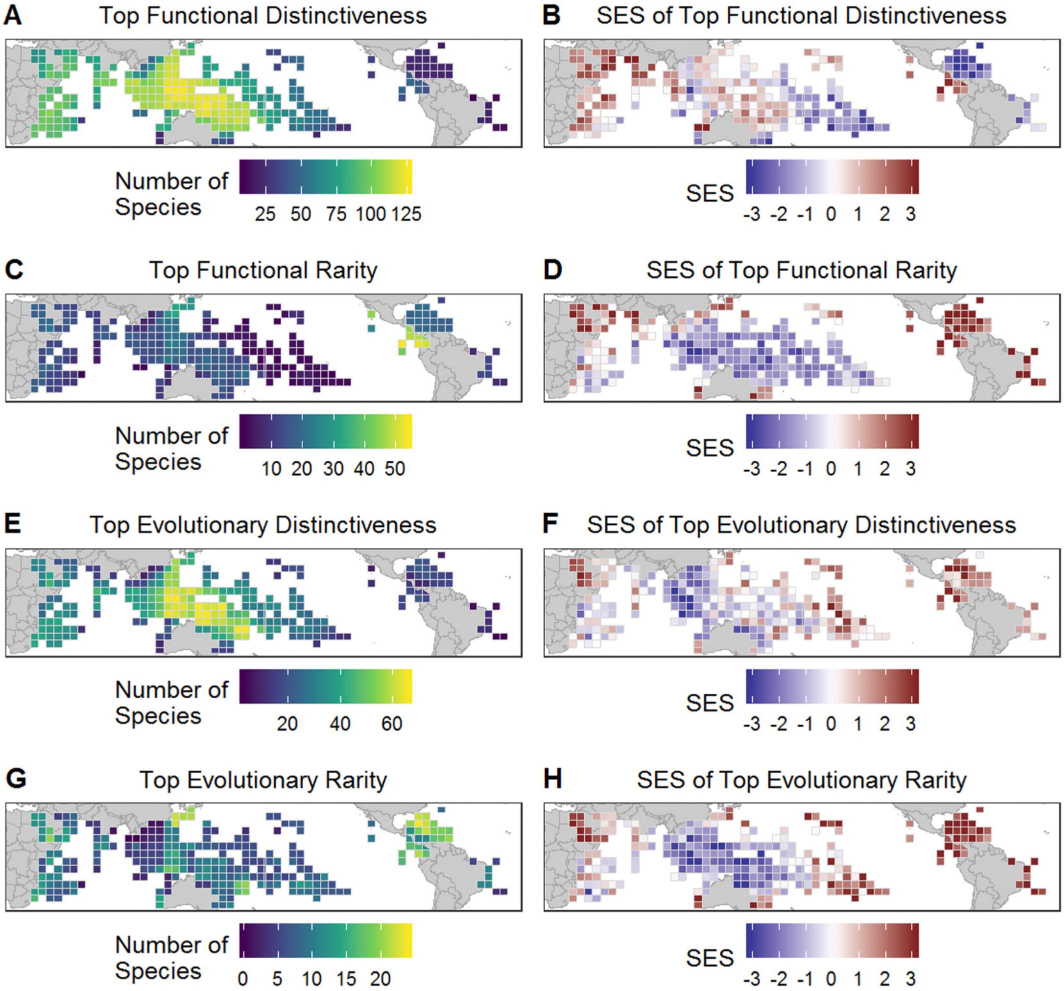

Fig. 5. Maps showing the global distribution of the number of top 10% coral reef fishes per cell for each species rarity component and the corresponding Standard Effect Size (SES) from a null model correcting for species richness. (A) Functional distinctiveness, (B) SES for functional distinctiveness; (C) Functional rarity, (D) SES for functional rarity; (E) Evolutionary distinctiveness sensu Isaac et al., 2007, (F) SES for evolutionary distinctiveness; (G) Evolutionary rarity, (H) SES for evolutionary rarity. For the number of species in the top 10% (left column) for each component color scales linearly with the values and independently in each panel while color scale for SES values similarly across panels (right column).

4.3. Do we currently protect the functional rarity of coral reef fishes?

Geographic restrictedness is logically highest for Threatened species and lowest for Not Evaluated taxa. It confirms the importance of the Extent Of Occurrence (EOO) criteria when defining the threat status in the IUCN Red list. However, we also show that species not yet Evaluated by IUCN have higher Functional Rarity than species listed as "Not Threatened", while Not Evaluated taxa have higher Distinctiveness than other categories. In addition, Data Deficient species is the second functionally rarest group (see Fig. 3). Since functionally rare species differ in traits compared to other species (low redundancy), they may support rare ecosystem functions that would not be supported by other species (Mouillot et al., 2013). Then some species among the Not Evaluated and Data Deficient groups are certainly ecologically unique in their roles while being ignored in conservation strategies. Functional rarity could then become a future prioritization criterion for IUCN within these groups (Arponen, 2012), see for example the top 20 functionally rarest species that are Data Deficient (Table 2).

Not Threatened species consistently show lower values of all considered rarity components than Threatened and Data Deficient species. However, there are several outlier taxa in the Not Threatened group. Eleven out of twenty species with the highest functional rarity come from the Not Threatened group (Table 1), and would deserve particular conservation attention because of their low functional redundancy and possibly specific role. This finding validates the use of functional rarity as a new facet to identify species that are not threatened in terms of demography and geographic distribution but are still likely to support unique functions on coral reefs.

Threatened species tend to exhibit high functional rarity values, although it is not yet a conservation criterion. Furthermore, we find a negative relationship between the protection percentage on a given grid cell (using strict protection definition, see Mouillot et al., 2016) and the number of top 10% functionally distinct species present in that cell. Altogether these results suggest a spatial mismatch between conservation efforts and functional rarity. For instance, current conservation efforts cannot efficiently protect some of the functionally rarest coral reef fish families such as *Carangidae* or *Caesionidae*, since being highly mobile predators (D'agata et al., 2016a). Therefore these families would need alternative specific conservation measures like giant protected areas (e.g. Chagos), quotas or gear restrictions (Graham et al., 2017; Singleton and Roberts, 2014).

Functional rarity is an appealing concept to study both applied and theoretical ecology but its computation must be handled with care. The significance of functional rarity critically depends on the traits and the spatial scale (Violle et al., 2017a). We selected functional traits representing key ecological strategies of coral reef fishes (Mouillot et al., 2014; see Appendix B1 for trait-function details). We used a distance

Table 1
Top 20 species with highest functional rarity value. "–" means the species has no IUCN status.

Species	Functional rarity	Functional distinctiveness	Geographic restrictedness	IUCN threat group	IUCN status
Xenistius californiensis	0.986	0.652	0.969	Not Threatened	LC
Lutjanus peru	0.959	0.635	0.965	Not Threatened	LC
Caranx hippos	0.904	0.616	0.911	Not Threatened	LC
Carangoides bartholomaei	0.898	0.616	0.900	Not Evaluated	–
Seriola quinqueradiata	0.897	0.593	0.961	Not Evaluated	–
Trachurus trachurus	0.868	0.566	0.981	Threatened	VU
Seriola peruana	0.862	0.566	0.969	Not Threatened	LC
Carangoides ruber	0.859	0.589	0.900	Not Evaluated	–
Caranx crysos	0.859	0.589	0.900	Not Threatened	LC
Pseudocaranx wrighti	0.858	0.566	0.961	Not Evaluated	–
Seriola hippos	0.857	0.593	0.884	Not Evaluated	–
Caesio suevica	0.856	0.562	0.969	Not Evaluated	–
Lutjanus novemfasciatus	0.854	0.562	0.965	Not Threatened	LC
Lutjanus viridis	0.853	0.563	0.961	Not Threatened	LC
Chloroscombrus chrysurus	0.852	0.580	0.911	Not Threatened	LC
Caranx caballus	0.850	0.566	0.946	Not Threatened	LC
Caesio striata	0.848	0.558	0.965	Not Evaluated	–
Decapterus punctatus	0.842	0.562	0.942	Not Threatened	LC
Pseudocaranx dinjerra	0.841	0.544	0.988	Not Evaluated	–
Caranx latus	0.837	0.571	0.907	Not Threatened	LC

metric (Gower) to scale ordinal traits appropriately, functional dissimilarities–used to compute functional rarity indices–should be adapted to the nature of traits used (Pavoine et al., 2009). Also, the estimation of functional rarity depends on the spatial scale considered, here, the functional dissimilarities were considered only at global scale (but see Fig. A5), but finer scales (realms, regions or local) could be used and as such affect the results.

Furthermore, we studied coral reef fishes using presence-absence data, but if available, functional rarity components could be computed with abundance data (Violle et al., 2017a, 2017b). We also did a sensitivity analysis to ensure that the patterns of functional rarity we observed were not the result of a single trait driving the entire signal (see Fig. A6). Whether functional rarity is used in species assessments for conservation planning or for investigating fish biodiversity dynamics, the number and the nature of selected traits should be justified.

4.4. Functional rarity and insurance

Our study extends previous works on the lack of functional insurance in species-poor areas (Bender et al., 2017). Functional insurance describes the potential resilience in ecosystem functions that results from redundancy, the fact that several species share the same characteristics in a given area and in the functional composition of a given ecosystem (Yachi and Loreau, 1999). Functional redundancy is a key component of functional insurance (Nyström, 2006). Functional redundancy is directly linked to functional distinctiveness in a community, because the higher the functional redundancy the lower the community-level functional distinctiveness (Ricotta et al., 2016). The most functionally distinct specie are the least functionally redundant compared to the species pool. Thus sites harboring a high number of functionally distinct species may show the least functional redundancy such as in the Tropical Eastern Pacific. The functional groups with the least number of species may support non-redundant ecosystem functions across the Indo-Pacific region (D'agata et al., 2016b). Furthermore, vulnerability of fish species depends on their specific combination of traits; for example, large fishes are more susceptible to human impact (Mellin et al., 2016), or they can be more targeted by fishing depending on their trophic status, diet or size (Micheli et al., 2014). The vulnerability of ecosystem functions could also suffer from an ecological "inactivation threshold" under which, if a species has a lower abundance than the threshold, the function is not supported or active anymore (Soliveres et al., 2016). Non-linear effects between functional

Table 2
Top 20 Data Deficient species with the highest functional rarity value.

Species	Functional rarity	Functional distinctiveness	Geographic restrictedness	IUCN threat group	IUCN status
Naso tuberosus	0.813	0.578	0.842	Data Deficient	DD
Naso reticulatus	0.800	0.562	0.861	Data Deficient	DD
Liopropoma longilepis	0.737	0.471	0.992	Data Deficient	DD
Orthopristis forbesi	0.722	0.460	0.992	Data Deficient	DD
Orthopristis cantharinus	0.718	0.460	0.985	Data Deficient	DD
Prionurus scalprum	0.717	0.467	0.965	Data Deficient	DD
Orthopristis lethopristis	0.715	0.456	0.992	Data Deficient	DD
Myripristis formosa	0.713	0.458	0.981	Data Deficient	DD
Boops lineatus	0.690	0.451	0.958	Data Deficient	DD
Gymnothorax serratidens	0.686	0.436	0.992	Data Deficient	DD
Uropterygius polystictus	0.686	0.436	0.992	Data Deficient	DD
Sparisoma griseorubrum	0.682	0.431	0.996	Data Deficient	DD
Epinephelus posteli	0.678	0.446	0.950	Data Deficient	DD
Cirrhilabrus brunneus	0.671	0.438	0.958	Data Deficient	DD
Paralabrax auroguttatus	0.664	0.419	0.996	Data Deficient	DD
Semicossyphus reticulatus	0.660	0.427	0.965	Data Deficient	DD
Stegastes otophorus	0.658	0.420	0.981	Data Deficient	DD
Canthigaster flavoreticulata	0.658	0.417	0.988	Data Deficient	DD
Paralabrax humeralis	0.657	0.419	0.985	Data Deficient	DD
Argyrops megalommatus	0.655	0.422	0.969	Data Deficient	DD

rarity and ecosystem function are likely (Soliveres et al., 2016) and further research on the relationship between functional rarity and functional insurance is thus required. The functional redundancy literature could be revisited to highlight results on functional rarity instead.

4.5. Concluding remarks – Functionally rare coral reef fishes: rare birds or red herrings?

We highlight that functional rarity hotspots are spatially distinct from other previously known species richness or rarity hotspots. Adding functional rarity to the other classical biodiversity facets should offer a more integrated view for conservation prioritization (Davies and Cadotte, 2011; Pollock et al., 2017). Here we show that functional rarity hotspots spatially mismatch with evolutionary rarity hotspots. If we include different biodiversity facets to prioritize which areas we should protect first, then we should go beyond protecting the Coral Triangle area. The Tropical Eastern Pacific, for instance, hosts a high number of functionally rare species, and would deserve more protection coverage. However, given the fact that different biodiversity facets (taxonomic, phylogenetic or functional richness or rarities) provide different messages and highlight different areas to protect (Guilhaumon et al., 2015), choosing the “best” set of candidate areas is not a trivial issue. Our results suggest protecting areas everywhere, but as the resources are limited, i.e. we are facing an “agony of choice” (Vane-Wright et al., 1991), it underlines the limits of a hotspot-based strategy integrating multiple facets (Schmitt, 2011). As recently applied to birds and mammals (Pollock et al., 2017), functional rarity could be included as a maximization criterion: choosing protected areas that maximize representativeness of functionally rare species. This maximization should also take into account high connectivity between protected areas to allow better population persistence (Andrello et al., 2015), while also taking social and economic costs into account (Andrello et al., 2017).

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Appendices. Supplementary data

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