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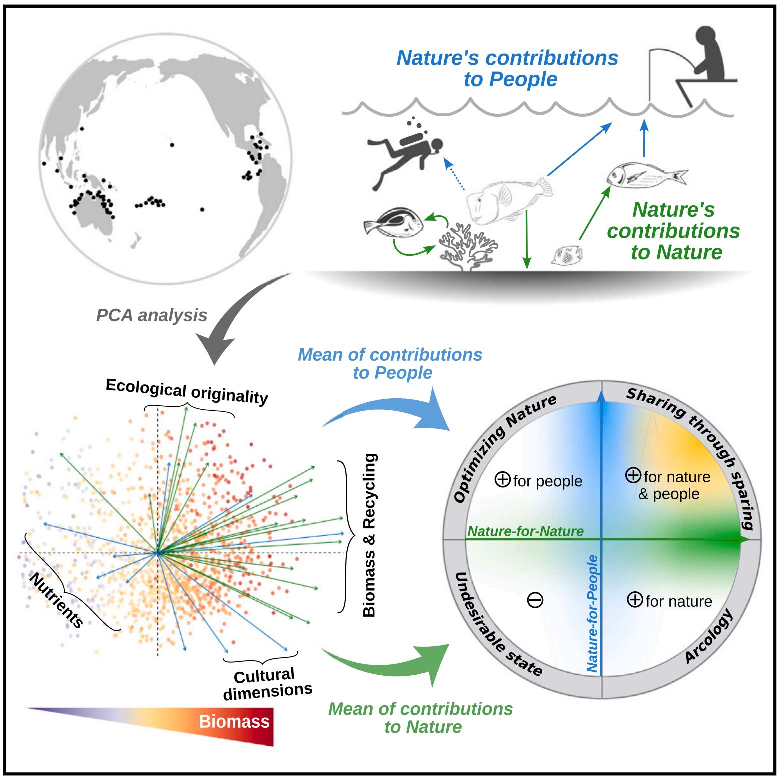
Fish communities can simultaneously contribute to nature and people across the world's tropical reefs

Graphical abstract



Highlights

- Contributions to nature and people are often linked to fish biomass on tropical reefs
- Tropical fish contributions, and notably those to people, show a high dimensionality
- Tropical reef fish communities can support both ecological and societal benefits
- Tropical reef management should achieve sustainable futures for both nature and people

Authors

Ulysse Flandrin, David Mouillot,
Camille Albouy, ...,
Rick D. Stuart-Smith,
Sébastien Villéger, Nicolas Mouquet

Correspondence

ulysse.flandrin@gmail.com

In brief

Anthropogenic pressures are damaging tropical reefs, threatening their biodiversity and key contributions to both people's well-being and nature itself. We analyzed 29 contributions from 1,237 tropical reef fish communities, revealing that, despite inherent trade-offs, these contributions can coexist locally. We distinguished fish community contributions primarily benefiting nature or people, highlighting the presence of reefs valuable to both perspectives all over the tropical regions. This finding paves the way toward tropical reef management strategies that integrate these two dimensions to simultaneously improve ecological processes and human well-being, offering more desirable and sustainable futures.

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Fish communities can simultaneously contribute to nature and people across the world's tropical reefs

Ulysse Flandrin,[1,14,*] David Mouillot,[1] Camille Albouy,[2,3] Sonia Bejarano,[4] Nicolas Casajus,[5] Joshua Cinner,[6] Graham Edgar,[7] Mattia Ghilardi,[4,8] Fabien Leprieur,[1] Nicolas Loiseau,[1] Aaron MacNeil,[9] Eva Maire,[1,10] Matthew McLean,[11] Valeriano Parravicini,[5,8,12] Loïc Pellissier,[2,3] Nina Schiettekatte,[8,13] Rick D. Stuart-Smith,[7] Sébastien Villéger,[1] and Nicolas Mouquet[1,5]
[1]MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France
[2]Ecosystems and Landscape Evolution, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland
[3]Unit of Land Change Science, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
[4]Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstraße 6, 28359 Bremen, Germany
[5]FRB-CESAB, Montpellier, France
[6]Thriving Oceans Research Hub, School of Geosciences, University of Sydney, Camperdown, NSW, 2006, Australia
[7]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia
[8]PSL Université Paris, UAR 3278 CRIOBE–EPHE-UPVD-CNRS, 52 Avenue Paul Alduy, 66000 Perpignan, France
[9]Ocean Frontier Institute, Department of Biology, Dalhousie University, Halifax, NS B3H 4R2, Canada
[10]Lancaster Environment Centre, Lancaster University, Lancaster, UK
[11]Department of Biology and Marine Biology, Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC 28403, USA
[12]Laboratoire d'Excellence "CORAIL," Paris, France
[13]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, HI, USA
[14]Lead contact
*Correspondence: ulysse.flandrin@gmail.com
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SCIENCE FOR SOCIETY Tropical reef fishes provide critical contributions to human well-being and nature sustainability, yet they are increasingly threatened by human activities. Protecting reef fish communities requires significant actions by policymakers and strong support from local people. However, a limited understanding of how contributions to nature and people are related complicates efforts to support both simultaneously and hinders the exploration of desirable futures for nature and people.

We show that reef fish communities can be ecologically healthy while providing significant benefits to people, challenging the classical view that conservation must favor one over the other. This paves the way for transdisciplinary approaches, involving ecologists, social scientists, policymakers, and local people. By refining management strategies, we can better address local people's needs while achieving conservation goals. This inclusive effort helps us build a desirable future where nature and society thrive together in balance.

SUMMARY

Anthropogenic activities are eroding biodiversity and its contributions to nature and people worldwide. Yet, the dual imperative to protect nature and sustain human well-being raises potential trade-offs that remain to be quantified. Using standardized fish surveys across 1,237 tropical reefs worldwide, we converted the presence and abundance data of 1,024 species into 29 fish community contributions that primarily benefit either nature or people. We show that "nature-for-nature" contributions are mostly positively correlated with total fish biomass, while "nature-for-people" contributions are more independent. Trade-offs among contributions are not the rule, with some tropical fish communities simultaneously providing high levels of different contributions. High mean contributions have been found in all tropical oceans, so sustaining healthy tropical reefs while promoting human well-being seems achievable within most countries, rather than mutually exclusive. Our framework offers an opportunity to explore different management strategies and pathways on tropical reefs between the use and the sparing of nature toward more favorable and sustainable ecological and social futures.

INTRODUCTION

Humans are profoundly impacting the earth by altering the climate and overexploiting natural living resources. The impact of anthropogenic activities on biodiversity is so pervasive that the ability of impoverished ecosystems to sustain themselves and continue to support human well-being and livelihoods is increasingly questioned.[1,2] Thus, the conservation and sustainable management of ecosystems and their biodiversity, which provide nature's contributions to people (NCP), are a prime concern among government policies and stakeholder strategies. The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) was formed to consider the dual imperative to conserve biodiversity and sustain human well-being. One step further, IPBES recently developed the Nature Futures Framework (NFF) to achieve this goal. This heuristic tool separately considers the three different management perspectives of ‘‘nature-for-nature’’ (NN), ‘‘nature-for-society,’’ and ‘‘nature-as-culture,’’ which respectively promote an ecocentric vision protecting nature's intrinsic value, an optimization of nature to meet human material needs, and the preservation of biocultural values.[3–5] Although these three perspectives may be seen along continua with blurred boundaries, recognizing these three poles helps to account for a wide diversity of links between nature and people and to navigate the different associated management pathways.[5,6] With this tool, IPBES calls for imagining new ‘‘positive futures’’ for both nature and people,[7] breaking away from the pervasive economic growth and gross domestic product paradigm.[8] Yet, the extent of potential trade-offs between the dual imperatives of protecting nature and maintaining human well-being remains to be quantified.

Tropical shallow reefs cover less than 1% of our oceans but support about one-third of global marine biodiversity[9] and provide essential cultural and food contributions to over a billion people.[10] However, this biodiversity and its associated contributions to ecosystem functioning and human well-being are threatened by climate change and overexploitation.[7,11] Together, these stressors degrade habitats and deplete fish populations, leading to local species extirpation[12] and loss of traditional resources.[13] Fishes are the main links between shallow reefs and human societies in the tropics, supporting a myriad of key contributions to people, from seafood and micronutrient production[14,15] to cultural and recreational benefits.[16,17] In this context, it remains unclear whether tropical fish communities can simultaneously provide benefits relevant to each of the three NFF perspectives or if specific management strategies can optimize them in a ‘‘one-size-fits-all’’ approach. This uncertainty is compounded by the absence of a quantitative framework that integrates the multiple contributions provided by reef fish communities. If the one-size-fits-all hypothesis is rejected (i.e., there are more trade-offs than cobenefits among NFF perspectives), a subsequent question is how the different NFF perspectives are globally distributed across tropical reefs, i.e., among countries and management types.

An important knowledge shortfall in applying the NFF framework to tropical reef fish communities is the positioning and quantification of the Nature-as-Culture perspective globally. Tropical reefs provide various non-economic and non-material contributions that could be considered as cultural benefits, such as identity, attachment, and other forms of satisfaction,[18,19] yet these contributions remain difficult to estimate consistently worldwide. In addition, some would argue that contributions to human cultures are intimately intertwined with several contributions to society. For example, in addition to seafood supply, fishing has a significant traditional value in many coastal societies.[20,21] The esthetic value of reef fish communities creates an emotional attachment to nature[16] but is also a source of lucrative activities through tourism.[22] As both Nature-for-Society and Nature-as-Culture perspectives support human well-being and livelihoods, we merged them into a single perspective, referred to hereafter as ‘‘nature-for-people’’ (NP), although this is skewed toward society's contributions due to a lack of data on cultural aspects. We then distinguish fish contributions that primarily sustain people's well-being from those that primarily benefit the ecosystem state and processes (Table 1)—although we recognize that some contributions are in between, since people depend on ecosystem functioning,[23,24] while biodiversity conservation may depend on people's attachment to nature or cultural management.[25]

Here, we present a global quantitative assessment of 29 potential contributions to both people and nature provided by reef fish communities in tropical regions. Our main objective is to assess covariations between contributions provided by fish communities to NN and NP perspectives and the extent to which these potential contributions are spatially distributed across tropical reefs. To do so, we took advantage of the largest fish survey on tropical shallow reefs worldwide, in which standardized visual assessments were undertaken at 1,237 sites in 37 countries, providing 112,000 quantitative biomass observations of 1,024 species. Then, we (1) defined and quantified 29 relevant indicators of NN and NP perspectives, (2) determined the dimensionality of these 29 contributions owing to trade-offs and cobenefits to test the one-size-fits-all hypothesis, (3) proposed a typology of reef fish communities based on their balance between the two NFF perspectives, (4) mapped the global distribution of NN- vs. NP-oriented fish community contributions across tropical reefs, and (5) discussed future management options to eventually rebalance NFF perspectives. We found that, while many of the NN contributions were positively correlated with total fish biomass, many others were largely independent, and few were antagonistic, indicating that overall, reef fish communities can simultaneously provide high levels of different contributions. Spatial autocorrelation among contributions occurred at the local scale, but not at the global scale, suggesting the predominance of local or regional factors underpinning the level of fish contributions rather than major biogeographical constraints. Such studies can provide guidance for building management plans with achievable targets and enable us to imagine desirable futures for both people and nature.

RESULTS

Methods summary

We used biomass data from 1,024 ray-finned fishes and presence data from 60 elasmobranch species in 1,237 tropical reefs collected by the standardized underwater visual protocol of the

Table 1. Nature contributions used in this study

	Category	Contribution	Description	Reference
Nature-for-Nature (NN) contributions	biodiversity	taxonomic richness of Teleostei	number of teleost species per reef	–
		taxonomic richness of Elasmobranchii	number of elasmobranch species per reef	–
		endemism	mean of endemism of species; endemism is assessed from species geographic range	Kulbicki et al.[26]
		trait distinctiveness	mean of species functional trait distinctiveness at the reef level	Cornwell et al.[27]
		evolutionary distinctiveness	mean of species evolutionary distinctiveness at the reef level	Kembel et al.[28]
	biomass distribution	biomass per trophic guild[a] (three trophic groups)	total biomass of reef fish split into herbivores, invertivores, and piscivores trophic guilds	Parravicini et al.[29]
		functional entropy	functional distance between species, weighted by their relative biomass in the reef	Mason et al.[30]
		phylogenetic entropy	phylogenetic distances between species, weighted by their relative biomass in the reef	Marcon and Hérault[31]
	biogeochemical flows	nitrogen[a]	total nitrogen excreted by reef fish	Schiettekatte et al.[32]
		phosphorus[a]	total phosphorus excreted by reef fish	Schiettekatte et al.[32]
		carbonates[a] (five polymorphs)	for each polymorph: total carbonates excreted by reef fish	Ghilardi[33]
	food web stability	trophic web robustness	allometric coefficient between the number of trophic interactions and the species richness as a proxy of trophic robustness to local extirpations	Carpentier et al.[34]
		mean trophic level	species trophic level inferred in each local trophic web weighted by its relative biomass	Danet et al.[35]
Nature-for-People (NP) contributions	food availability	available biomass[a]	total biomass of reef fish belonging to fishable families (expert opinion)	Cinner et al.[36]
		turnover of available biomass	biomass turnover of fishable species in the reef	Seguin et al.[15]
	nutrient quality of fish	available nutrients in fish flesh (calcium, iron, omega 3, selenium, vitamin A, zinc)	nutrient quantities contained in an average 100 g portion of fish on the reef (i.e., nutritive quality relative to the fishing effort)	Maire et al.[37]
	cultural value	esthetic value	esthetic value of reef fish community	Langlois et al.[16]; Tribot et al.[38]
		public interest	public interest (online) in reef fish community	Mouquet et al.[39]

We divided the 29 fish-based contributions into two categories: Nature-for-Nature (NN) and Nature-for-People (NP) contributions. All metrics were calculated at the reef fish community level using data from standardized reef fish surveys. We assumed that the values of each contribution scale positively with its benefit to people or nature.

[a] Contribution was log transformed to limit the effect of asymmetric and high-magnitude distributions (see Table S1 for calculation details and data sources).

Reef Life Survey (RLS) initiative.[40,41] For each reef, we estimated 29 contributions that the observed tropical fish communities can potentially provide either to local people or to nature; see Table 1 for a full description of NN and NP contributions. To assess covariations among these contributions at a global scale, we performed a principal-component analysis (PCA) and determined the dimensionality of fish contributions to nature and people on tropical reefs. We then introduced a heuristic framework classifying reef fish communities according to the NN and NP perspectives[4,23] using two averaged synthetic NN and NP scores. We finally studied the global distribution of NN and NP scores, their spatial autocorrelation estimated by the Moran index, and their links with protection status.

Correlations between contributions

We initially examined whether reefs tend to show high values of several contributions simultaneously by measuring the linear correlation between contributions. The pairwise correlations between the 29 contributions provided by fish communities in 1,237 tropical reefs ranged from -0.70 to 0.93, with a median of the absolute values of 0.21. Although some contributions were antagonistic or strongly congruent, the majority of them showed correlations close to 0. Among the 406 pairwise correlations, half showed minimal dependence ($r \in [-0.2; 0.2]$), while 155 (38%) pairs were positively correlated ($r > 0.2$), and 51 (13%) were negatively correlated ($r < -0.2$; Figure S1). Nitrogen and phosphorus recycling, as well as available biomass and

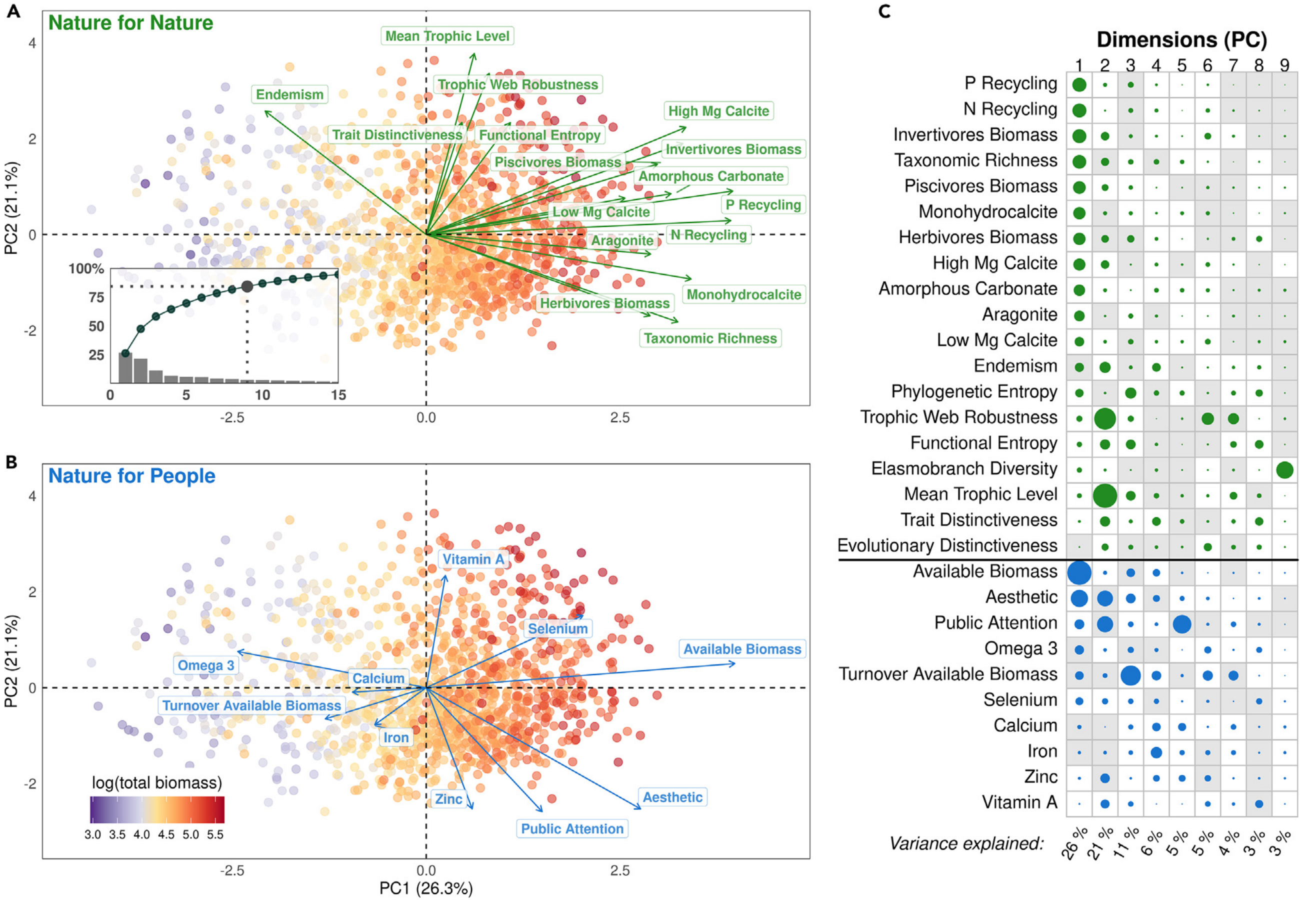

Figure 1. Covariations and dimensionality of 29 fish-based contributions to nature (green) and people (blue) on tropical reefs worldwide

(A and B) The covariations of contributions are represented in the two first PCA axes (Mg, magnesium; N, nitrogen; P, phosphorus). Total fish biomass, reported by color gradient, increases with the first dimension of the PCA (A and B). (A) and (B) represent the same PCA, yet contributions are highlighted in color according to their classification: either nature-for-nature (A) or nature-for-people (B). (A) Only well-represented contributions are displayed ($\cos^2 > 0.25$): phylogenetic entropy, evolutionary distinctiveness, and elasmobranch diversity are not represented. The inset displays eigenvalues of PCA axis in percentage and the cumulative curve of variance explained. The black dot represents the dimensionality required to parsimoniously describe covariations of contributions according to the elbow method (nine dimensions, 84% of variance explained; see Figure S3). (B) All contributions are represented.

(C) Dot sizes are proportional to the importance of a contribution in the total variance for a given PCA axis. Gray background indicates negative correlation with the dimension, white background indicates positive correlation. The importance of PCA dimensions in the total variance is reported as a percentage below. To see the PCA biplot with all contributions and color-blind-friendly colors, refer to Figure S4.

phosphorus recycling, were the most strongly correlated contributions ($r = 0.93$ for each pair). Fish communities with high phosphorus recycling also tended to have high nitrogen recycling and more available biomass (i.e., biomass of fish families caught for human consumption). Conversely, endemism and esthetic value, and endemism and taxonomic richness, were the most negatively correlated pairs of contributions ($r = -0.7$ for each), with high endemism being associated with low taxonomic richness and esthetic value. Between these two extremes, many contributions were roughly independent. For example, for a given level of endemism, we may find communities with very different invertivore biomass ($r = -0.001$; Figures 1 and S2).

As the tropical regions were not equally sampled (700 reefs in Australia of 1,237 in total), we tested the robustness of the Pearson pairwise correlations between contributions to this unbalanced sampling design. To achieve this, we compared the correlations among all pairs of contributions in Australia ($n = 702$) and the rest of the world ($n = 535$). A Mantel test showed that these two correlation matrices were fairly similar ($r = 0.84$, $p = 0.001$; Figure S5). This implies that correlations among contributions were robust to geographic overrepresentation and suggests an absence of distinction between Australia and other regions in terms of contribution covariations.

Dimensionality of contributions

To better visualize covariations among all contributions, we studied this multidimensional space using a PCA on the 29 contributions. We applied a weighted PCA to ensure that each contribution category (e.g., "food web stability," see Table 1) had the same importance, regardless of the number of contributions. The first four axes explained 64% of the total variance among the fish communities, with PC1 and PC2 explaining 26% and 21%, respectively. PC1 was shaped by NN contributions, such as nitrogen, phosphorus, or carbonate recycling, which depend on reef fish biomass. Hence, PC1 distinguished fish communities with low vs. high total fish biomass (correlation between fish community biomass and PC1 coordinates was high: $r = 0.86$; Figure 1A). Taxonomic richness was also positively correlated with biomass, notably due to reef fish communities in the Coral Triangle, characterized by high values in both taxonomic richness and biomass. Thus, more than one-third of the contributions (11 of 29) appeared to be closely associated with total fish biomass (Figure S6) and taxonomic richness. In contrast, Caribbean fish communities tended to show low values of biomass but hosted many endemic species, so endemism was the only NN contribution negatively correlated with PC1. Among NN contributions, PC2 was shaped by endemism and trait distinctiveness, which were mostly related to ecological originality and mean trophic level (Figures 1A and 1C). Taxonomic richness was negatively correlated to PC2 ($r = -0.40$) since species-rich Indo-Pacific communities had fewer distinct species and covered a large homogeneous biogeographic area.

In contrast to NN contributions, which were broadly positively correlated with fish biomass (Figure S6) and therefore had relatively low dimensionality, NP contributions showed more diverse covariations (Figure 1B). Some NP contributions were positively (e.g., iron and calcium: $r = 0.61$) and negatively correlated (e.g., biomass turnover and available biomass: $r = -0.36$), whereas others were independent (e.g., esthetic and vitamin A: $r = -0.17$). Consequently, we could not summarize these contributions along a single gradient. Since most reef fishes were consumed in at least some locations and could be classified as harvested when considered at the global scale, the available biomass was correlated to total fish biomass ($r = 0.94$) and was thus well represented by PC1. The cultural aspects of NP contributions were instead better represented by PC2, with a strong public interest and esthetic value for fish communities with high biodiversity, like in the Coral Triangle.

Although the first two axes of the PCA accounted for an important proportion of the total variance (47% of the variance of the 29 dimensions summarized in two axes), more axes were needed to accurately describe covariations among contributions. Biomass turnover, for example, was mainly related to the third axis, while elasmobranch diversity and trait distinctiveness aligned with the ninth and eighth axes, respectively (Figure 1C). As a result, the elbow method, which selects the best trade-off explaining a maximum total variance in contributions with a minimal number of PCA axes, suggested that nine dimensions were required to adequately describe the overall covariations among the 29 fish-based contributions on tropical reefs, capturing 84% of the total variance (see inset in Figure 1A). In comparison, when the 29 contributions were randomized (i.e., when contributions were uncorrelated), the elbow method selected 14 dimensions, explaining 55% of the variance.

NN and NP scores are weakly correlated globally

To reduce this multidimensional space in two dimensions, we calculated the mean of the contributions according to the NN and NP perspectives.[24] More precisely, we scaled the contributions (mean of 0 and standard deviation of 1) and performed a weighted arithmetic mean of the NN and NP contributions, using the same weights as for the PCA. This resulted in NN and NP scores for each reef fish community that were normally distributed, zero-centered, and ranged between [−1.8; 1.4] and [−2.0; 1.7], respectively. Across the 1,237 studied fish communities, we found a weak, albeit significant, positive relationship between NN and NP scores (R-squared = 0.06, $p < 0.01$; Figure 2A). This weak relationship was influenced by some high-latitude reefs included in the dataset showing both low NN and low NP values. Considering only locations with minimum monthly sea surface temperature (SST) > 20°C ($n = 1,030$, instead of the 1,237 reefs warmer than 17°C), the R-squared value was reduced to 0.01 ($p < 0.01$; Figure S8). Consequently, reef fish communities could be represented across a two-dimensional space made of NN and NP scores, where the numbers of communities in each of the four portions were similar (Figure 2A).

NN and NP scores are weakly related to protection

We further classified the 1,237 reef fish communities into three management categories based on protection status: 403 were fished, 601 had restrictions on fishing activities, and 233 were in effective no-take Marine Protected Areas (MPAs). Using a chi-squared test, we showed that the number of fish communities in each of the four parts of the NN-NP space was significantly influenced by the three management categories (chi-squared = 28.2, df = 6, $p < 0.01$). More precisely, we observed that the proportion of fished communities was highest where both NN and NP scores were negative and lowest where both scores were positive (Figure 2B). However, we found that the protection status had little influence on the distribution of fish communities in the NN-NP space (effect size measured by the V index of Cramer: V = 0.11, df = 6). This was consistent with the roughly equivalent proportions of restricted MPAs in dark- and bright-spot communities (Figure 2B), defined as those having both low NN and low NP scores vs. high NN and high NP scores.

High NN and NP scores are widespread across the tropics

We then investigated the global spatial distribution of these NN and NP scores across the tropics. For each score, we calculated the Moran index separately to measure the spatial autocorrelation for increasing distance classes. The Moran indices allowed us to determine the distance at which the scores were no longer autocorrelated (i.e., nearby reef communities no longer had similar scores relative to a random spatial distribution; Moran index close to 0). We observed that the spatial autocorrelations of NN and NP scores became negligible beyond distances over 1,348 and 263 km, respectively (Figure S9). This suggests that although NN scores were correlated at regional scales and NP scores at a more local scale, these associations were not consistent across larger biogeographic gradients or clustered within large areas or oceans.

In line with the absence of geographic clustering of contributions observed in the PCA, high scores were widespread across tropical reefs (Figure S10). Although the top 5% “outlier” fish communities (most extreme values) in each of the four NN × NP categories occurred in almost all oceans (Figure 2C), we examined a few archetypal situations to illustrate where high scores could occur. For example, NP-only outliers emerged, among other regions, in the Caribbean and the southwestern (SW) Pacific Islands. While Caribbean fish communities were characterized by high values of public interest, iron

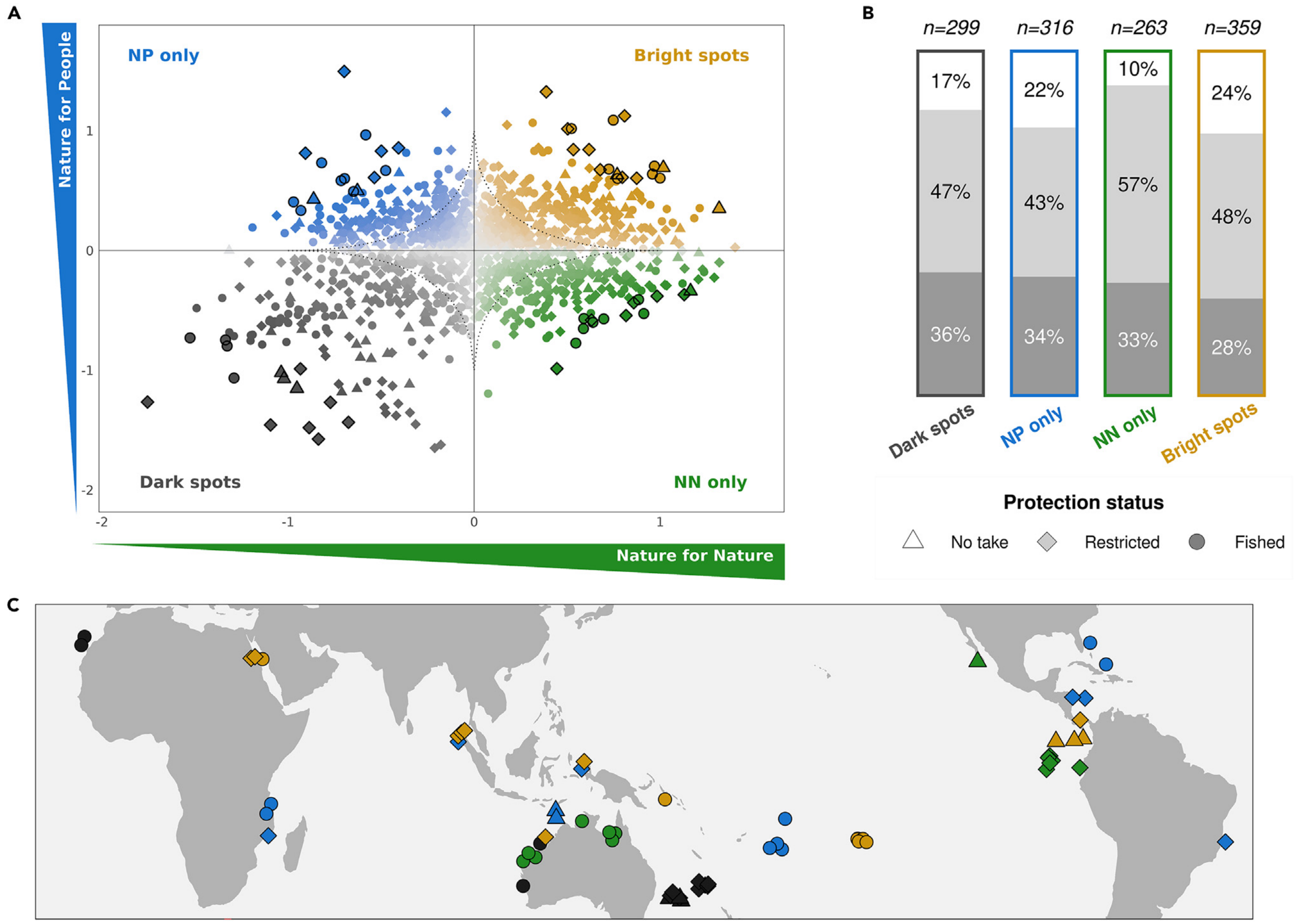

Figure 2. The four corners of the NN vs. NP spectrum and management strategies

(A) At the global scale, NN and NP scores are weakly correlated (r = 0.24, $p < 0.001$). The dashed lines indicate for each color the 50% quantile of the NN × NS gradient. Therefore, the dashed curved lines encompass 50% of the reefs. Symbols for reefs that are 5% outliers of each quarter are highlighted with black borders (see Figure S7 for details of outliers).

(B) Protection status (no-take reserves, restricted areas, fished areas) does not strongly influence reef categories in the NN-NP space (chi-squared = 28.2, df = 6, $p < 0.01$, Cramer's V = 0.11).

(C) Geographic distribution of the 5% of reef outliers in each NN-NP category and their management status.

concentration, and available biomass, reef fishes in the SW Pacific islands tended to support remarkably high esthetic and nutrient (iron and calcium) contributions. In contrast, the NN-only outliers were mostly present in the Galapagos archipelago due to a combination of high biomass, endemism, evolutionary distinctiveness, and mean trophic level. Dark-spot (both negative NN and negative NP scores) outliers were mostly located at high absolute latitudes, as these fish communities had low esthetic, biomass, or mean trophic level values. These dark-spot outliers, i.e., Canary (Spain) and Lord Howe (Australia) islands, were more rocky sub-tropical reefs rather than tropical coral reefs and tended to experience colder temperatures (minimum SST ranging from 17°C to 20°C). In contrast, French Polynesia was an outlier example among the bright spots (both positive NN and positive NP scores). This archipelago concentrated important values of reef fish biomass, high mean trophic level, high biodiversity, significant concentration of selenium, and fishes of high esthetic value. Central America was a region with outliers from both NN-only and NP-only categories. The Pacific side of Central America hosted NN-only and bright-spot outliers, due to high values of mean trophic level, nutrient recycling, and evolutionary distinctiveness, whereas the Caribbean side was characterized by NP-only fish communities with high biomass turnover and public interest. In the same way, Western Australia and the southern Pacific islands hosted fish communities with high values in the four corners of the NN-NP spectrum within the same geographic area (Figures 2C and S11).

DISCUSSION

Tropical fish communities provide a myriad of contributions to people and nature, yet little is known about whether these contributions can occur simultaneously or face inherent trade-offs. Using quantitative estimates of 29 fish-based potential NN and NP contributions, we found that these two perspectives are relatively independent, with high and low values distributed globally across tropical fish communities. So, sustaining nature while promoting human well-being seems achievable over larger scales, rather than representing mutually exclusive options. Trade-offs may be more common at smaller scales, however (Figure 2). This relative independence of NN and NP scores is explained by the high dimensionality of fish community contributions to nature and people, where 9 dimensions, from 29 initial contributions, are needed to describe the diversity of reef fish contributions. We show that trade-offs or negative correlations among contributions are not the rule, so reef fish communities can provide high levels of several different contributions, as observed in French Polynesia.

We also highlight synergies with many NN contributions being positively correlated with fish biomass, since many NN and NP contributions are intrinsically linked to the amount of fish, such as recycling capacities and available biomass for fisheries. In this sense, despite the central role of total biomass in several NN contributions, we divided this biomass into different categories (i.e., herbivores, invertivores, piscivores, and available biomass) to disentangle the different aspects of ecosystem functioning and people's needs. However, the weights given to these categories in the PCA and the average scores ensure that biomass remains equally important relative to other contributions. Some contributions, such as nutrient concentrations, are independent of fish biomass, since we chose to measure these contributions relative to human consumption (per 100 g portion of fish) and not by stock size (total biomass underwater). By considering catchable biomass and average nutritive quality of fish, we take into account both important and complementary aspects of fisheries.[37] Some other contributions are also largely independent of others, such as elasmobranch diversity, which can provide an early warning signal of human impact before the collapse of other contributions.[42] In addition, tropical reefs also include contributions to nature and people not based on fish and not estimated here (e.g., shoreline protection[43] or coral growth[44]), which might be less related to fish presence and biomass. Importantly, our study globally quantifies relative contributions of non-material values provided by tropical reef fishes, such as esthetics and public interest, and how these compare to more economically oriented contributions.[1,45] Regarding the NP perspective, we refer to these as *potential* contributions because we evaluate them only underwater, but to become *realized* contributions, they need to be accessed by people, which is influenced by a range of institutional conditions as well as cultural, economic, and health dimensions not measured in our study.[46–48]

Covariations among all contributions seemed consistent across the geographical regions sampled (e.g., similar covariations within and outside Australia) and climatic outliers (reefs with minimal SST between 17°C and 20°C). This illustrates that, except for some contributions such as endemism and evolutionary distinctiveness, fish-based contributions are more likely to be driven by local or regional factors rather than by broad-scale geography or environmental gradients. As exceptions, endemism and evolutionary distinctiveness are stronger in Central America than in Indo-Pacific reef communities, because the former is a smaller region and has been isolated for longer than the latter.[26,49] Fish communities valuable for both nature and people are widespread across the tropics (especially for the NP scores), and we can reject the hypothesis that fish-based contributions are simply driven by global geographic gradients, such as ocean basins or mean SST. Spatial autocorrelation demonstrates that NN and NP values remain spatially correlated within the regional scale only. While NN scores are no more similar to one another than expected by chance alone beyond a distance of $\sim$1,350 km, the spatial correlation between NP scores is significant only at a few hundred kilometers. This suggests that NN values are more driven by regional environmental conditions or fish life-history traits,[50] while NP values depend on more local conditions such as ecosystem uses, human impacts, management strategies, or habitat characteristics.[36]

Confronted with the challenge of reducing the dimensional space to adequately summarize the distribution of all contributions across reef fish communities, we averaged the contributions along two dimensions representing reef potentials for nature and people. Although averaging induces a loss of natural complexity, we consider this heuristic framework necessary to visualize the global patterns and trends of all estimated contributions and to offer a broad view of fish community contributions in line with the NFF. In our approach, we weighted each contribution category equally, yet several studies show that perceptions of nature's contributions can differ across populations and within populations.[51–53] Weighting human contributions in accordance with Indigenous perception and local knowledge[54]—or even according to local group perceptions[55]—would be a critical step toward a finer and inclusive consideration of NCP.[56] This would require extensive sociocultural information, but might lead to important, potentially different, insights into covariations between contributions and management priorities. Despite this simplified framework, we found that NN and NP values succeeded in capturing well-known outstanding reefs supporting the highest scores. For example, the Galapagos Islands are NN-positive outliers, due to their high endemism, elasmobranch diversity, and well-preserved marine resources in general.[57] Caribbean reefs are highly valuable for people, given the presence of commercial fishes and the large human coastal population close to the reefs (e.g., attachment, recreational diving).[58] Finally, the Coral Triangle is identified here as outstanding for both nature and people in some remote or well-managed reefs.[59,60]

On the other hand, reefs with the lowest scores are mainly located at high latitudes where reefs tend to provide reduced levels of contributions compared to near-equatorial reefs. The predominance of dark spots in sub-tropical reefs may be due to the fact that these "marginal reefs" are often located in conditions that are sub-optimal for foundational species such as corals.[61,62] However, it is worth noting that the standardization of contributions, required to aggregate them, ensures that the average is zero. Negative scores therefore reflect only reefs with below-average contributions. In addition, dark spots were also found in tropical coral reefs such as in the nearshore of the Great Barrier Reef, and conversely, above-average contributions were also observed in higher-latitude reefs as in the Red Sea or near Florida or southern French Polynesia (Figures S8 and S11). This suggests that all reefs may show any contribution level regardless of their position along the latitudinal gradient. The inclusion of marginal sub-tropical reefs in our analysis allowed us to describe a large gradient of ecological conditions. This is important, especially considering that marginal reefs are often considered as natural laboratories to understand the potential future state of coral reefs under growing human impact and warming conditions.[62] Moreover, several tropical species are moving toward higher latitudes following climate change.[63] This tropicalization may induce shifts in fish trait diversity[50,63] and thus a shift in provision of some contributions to both nature and people that remains to be quantified.

We separated NN and NP contributions in our analyses for consistency within the NFF,[4] considering that contributions are valuable for people first or nature first. However, we recognize that overlap exists for some contributions, as people also indirectly benefit from NN contributions.[64] For example, the capacity of an ecosystem to recycle nutrients or stabilize biomass through a high mean trophic level would have obvious positive feedback on fisheries contributions to people. In this sense, as contributions are sometimes interconnected, it would be interesting to investigate the relationships between them in greater depth. For example, Antunes et al.[65] recently suggested using network analysis to examine the diversity of contributions, allowing the modeling of links between contributions and the measurement of energy flows that support material contributions. Thus, it would be possible to express some NP contributions (e.g., available biomass) as a function of other NN contributions (e.g., piscivore biomass and others), which might provide additional, potentially different, insights into the strength of relationships between contributions and could be valuable for explanatory or predictive purposes.

Moreover, we have combined the Nature-for-Society (NS) and Nature-as-Culture (NC) contributions into NP contributions to visualize reefs within a two-dimensional space and because many NCs are difficult to estimate globally, but some NC and NS contributions may be largely independent. For example, cultural and immaterial values, as symbolic or spiritual meanings of particular species, might be unrelated to their material or economic value and are best studied independently. Although 29 different contributions were considered, the two cultural contributions that we were able to extract from fish community data represent a third of the NP dimensions, biasing this perspective toward a utilitarian value. Introducing additional biocultural contributions, ideally on a finer scale, such as heritage or symbolic species, would potentially highlight new and more complex relationships between reef contributions and people[66] and better represent the diversity of links between people and nature. Further studies of reef cultural importance are an important next step if we are to better account for the diversity of biocultural systems and progress our understanding of the interplay between the three NFF dimensions. More generally, future inclusion of overlooked or underrepresented contributions may modify the structure and dimensionality of the NN-NP space but may also add redundant information, given the broad range of fish roles and functions that we considered in this most comprehensive database available to date.

We did not find clear associations between reef protection status and the NN and NP scores of reef fish communities (chi-squared = 28.2, df = 6, $p < 0.01$, Cramer's V = 0.11). As many countries or bioregions have valuable reefs that significantly contribute to both NN and NP scores, one might question whether the absence of any effect of protection status on NN and NP scores may result from the placement of MPAs relative to socioenvironmental constraints[58] or from a limited effect of MPAs on most NN and NP contributions.[67] In this sense, we suggest that although multiple synergies exist and some sites are valuable for many NN and NP contributions at once, the relatively high dimensionality of fish community contributions to nature and people implies that this is not the rule. Making one-size-fits-all areas is challenging and not always feasible; therefore the ''win-win'' paradigm of MPAs should probably evolve toward more specific and context-dependent objectives.[68,69] This NN-NP space based on tropical reefs worldwide can be used in more local studies to quantitatively characterize a reef, track its temporal trend, or facilitate comparative analyses, among others. With this heuristic framework, we can more explicitly quantify specific objectives of protection and sustainable use of tropical reefs and better allow narratives of success and positive outcomes to be backed by data, rather than unsubstantiated claims.

As proposed by the NFF, our approach may indeed provide an exploration of different conceptions we have regarding tropical reefs to shape our ecological and social futures.[5,6,64] The NN axis raises awareness of the need to preserve ecosystem integrity and intrinsic values of nature, independent of anthropic interests. On the other hand, the NP axis, and especially its economic component, illustrates the emerging societal priority: whether the growth or post-growth economic paradigm is preferable, and what relationship do we want with nature (see Figure 3).[5] Together, these two dimensions capture the ongoing debate on conservation and human future. Should we better integrate people into nature (''land sharing'') or spatially separate places of use and protection (''land sparing'')?[70,71] Would conservation benefit more from a total ''half-earth'' protection, i.e., fully protect half of the planet and use the other half, or a ''whole-earth'' management including people, i.e., maintain healthy ecosystems through the sustainable use of natural resources across the whole earth?[72,73] While bright spots, valuable for both nature and people, would fit well with the land-sharing and whole-earth management visions, the one-sided value of NN-only and NP-only reefs would fit better with the land-sparing and half-earth perspectives. This mental space (Figure 3) provides an opportunity to quantitatively explore a gradient of narratives proposed by the NFF, between ''Arcology'' (people concentrated in dense, futuristic, self-sufficient cities, surrounded by totally pristine nature, i.e., ''NN only'') and ''Optimizing nature/innovative commons,'' through a biocultural and social world that exploits whatever is necessary for human well-being as long as it is sustainable.[5,6]

Conclusion

This study provides a global snapshot of fish community contributions but does not explicitly examine whether these contributions are robust or resilient to human uses and ecological disturbances. Determining the temporal dynamics of fish community scores in this NN-NP space is thus critical. We also need to better understand the conditions of protection, habitat, and climate under which tropical reefs can remain in favorable states over time or instead shift toward less favorable states for nature or people. From a management point of view, the goal is to

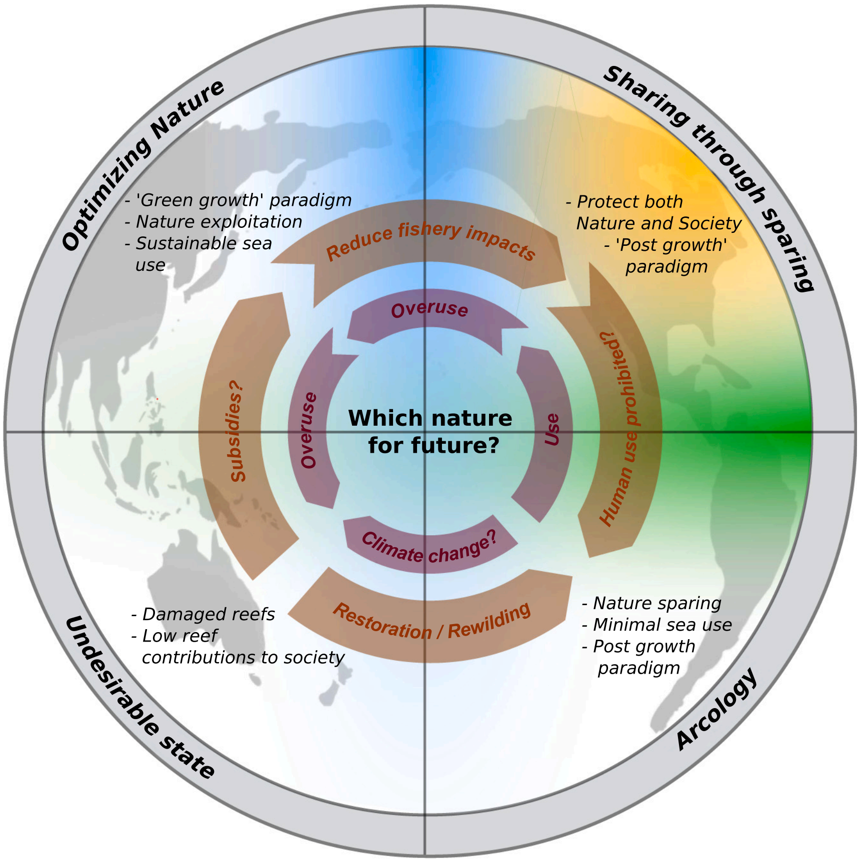

Figure 3. Human well-being in nature: which future for tropical reefs?

The four parts defined by the gradient of nature protection and exploitation illustrate different possible futures, exposed by the NFF.[6] "Optimizing nature for humans" (or "innovative commons" if we include cultural aspects) propose a biocultural and social future where societies exploit whatever is necessary for human well-being as long as it is sustainable. "Arcology" calls for a future where people are concentrated in dense, futuristic, self-sufficient cities, surrounded by totally pristine nature. Between both, "Sharing through sparing" depicts a future where people exploit as little of nature as possible for their well-being and safeguard the remainder. Possible dynamics are highlighted in orange and red.

determine how to enhance both NN and NP scores on a given tropical reef under different protection rules. Although these concerns challenge scientists and managers, they also resonate with societal choices: is it preferable to protect NN-only reefs to maintain their status or try to increase their NP score and move toward a "nature-based inclusive prosperity"[4] scenario? While prohibiting human uses in ecological bright spots would maintain the last reef refugia in a valuable state for nature (Arcology), their use by people, even if partial or regulated, would expose them to a risk of rapid exploitation leading to a sharp decrease in NN score, particularly due to fish biomass decline[74,75] and top predator extirpation.[58,76] Likewise, the priority may be to shift dark-spot reefs toward more desirable states through restoration and/or rewilding activities[77,78] to either target NN contributions or shape these reefs for populations by supporting local NP contributions like marine biomass turnover through subsidies (e.g., aquaculture) and facilitating other uses (e.g., ecotourism). This kind of management could be guided by multiaction planning tools that identify, on a given territory, an optimal combination of management actions to achieve a set of recovery targets while minimizing costs.[79,80] Such actions could be integrated into this NN-NP framework as people's contributions to nature, influencing current reef status either negatively through overfishing and habitat degradation or positively through effective ecosystem stewardship (Figure 3).[81]

Overall, understanding which reefs are in which categories, using NN and NP scores, and how to enhance them will be crucial to develop "living in harmony with nature" scenarios.[6,82]

By quantitatively exploring the question of nature use into the NFF, we illustrate that these two dimensions are not necessarily antagonistic but rarely met. In this context, protected areas may play complementary roles since their objectives have increasingly shifted from a primary focus on regulating or prohibiting human activities to preserve biodiversity and maintain ecosystem functioning to more balanced approaches that address the needs of both people and nature.[46] A more realistic and operational option than seeking the one-size-fits-all management is to build networks of protected areas varying in their priority values regarding NCPs and wildlife conservation.[83] Toward this objective and given the third target of the 15th Conference of the Parties to the Convention on Biological Diversity (CBD-COP15) to protect at least 30% of both land and sea before 2030, managing cobenefits and trade-offs within but also among protected areas is a priority.[84] The NN-NP quantitative framework we propose is a step forward in this objective. Ultimately, this study offers insights into how nature conservation and human well-being can coexist across tropical regions, highlighting potential synergies. It underscores the need for nuanced, context-specific approaches to reef management for a sustainable desirable future.

EXPERIMENTAL PROCEDURES

Reef fish data

We compiled data from the RLS database containing the abundance and size distribution of fish species collected through standardized surveys of tropical reefs worldwide.[41,85] These underwater visual assessments, conducted between September 2006 and May 2019, consist of 50-m-long transects with two 5 m wide (by 5 m high) belts surveyed, one on each side of the line. Global sampling effort in the RLS has been heterogeneous, more intensive around Australia, so we explicitly considered the Australian oversampling in our global analyses (see "Correlation and dimensionality of contributions" for more details).

We focused on sites with a minimum monthly SST above 17°C. This broader definition of "tropical reefs," including some sub-tropical reefs with no corals, has previously been used to consider all reefs where tropical species are present.[15,60] We excluded anguilliforms (Congridae, Muraenidae, Ophichthidae) and cryptobenthic families[86] because they remain difficult to visually quantify consistently with daytime diver observations. Fish abundance counts and size estimates were converted to biomass per species per transect using length-weight relationships (https://fishbase.mnhn.fr/). Since diver perception of fish size can be biased in underwater surveys,[87,88] we corrected fish size estimates according to Edgar et al..[89] To minimize the bias related to juvenile identification, we excluded individuals <3.75 cm for species with a maximum body size <25 cm and individuals <6.25 cm for species with a maximum body size ≥25 cm.[90] Since the count and biomass estimation of many elasmobranchs can be biased using underwater visual surveys,[91,92] we considered only their species diversity and not their abundance within each transect. To avoid overestimating fish abundance due to temporary fish aggregations or large roaming schools, we excluded surveys with a total biomass over 500 kg/500 m^2 or an abundance exceeding 10,000 individuals.

We classified reefs according to their protection status. Reefs within no-take MPAs or MPAs with multiple no-take zones, combined with high enforcement (expert opinion),[36] were classified as "no-take," while reefs located in other MPAs were qualified as "restricted," and those without any documented MPAs were considered as "fished" (Figure S12).

Assessment of contributions to nature and people

We calculated 29 fish-based nature contributions in each tropical reef, split into NN and NP categories (Table 1, see Table S1 for calculation details). These contributions were primarily identified by an expert panel from the REEF-FUTURES consortium and coauthors of this study (U.F., D.M., C.A., S.B., J.C., G.E., M.G., F.L., N.L., A.M., E.M., M.M., V.P., L.P., N.S., R.S.-S., S.V., and N.M.). Nitrogen and phosphate recycling, carbonate excretion, biomass turnover, nutrient quality of fish, public attention, and fish esthetics have all been measured on RLS data and published by the REEF-FUTURES group (see Tables 1 and S1 for references). In addition, we considered facets of biodiversity such as species richness, functional and phylogenetic diversity, and trophic interactions, which determine ecosystem functioning and stability.[45,93,94] Estimates of diversity, biomass, and biogeochemical fluxes, which are crucial to ecological processes on tropical reefs,[86] were compared with more human-centered contributions through material or non-material bonds between nature and people.[95] Based on the literature and the expert panel of coauthors, contributions related to biodiversity or ecosystem functioning were considered primarily valuable for nature (NN contributions).[5,45,86,93,94] On the other hand, contributions that reflect opportunities for food supplies and cultural benefits were more related to human well-being and livelihood (NP contributions).[5,23,95,96] We considered that these 29 contributions together capture the essence of fish roles and functions on tropical reefs with available data on more than 1,000 species. We assumed that the values of each contribution scale positively with its benefit to people or nature. For example, a higher "mean trophic level" is assumed to promote the stability of the overall fish biomass.[35]

To compare the different contributions among reefs, we considered only species for which we could estimate all contributions (other than elasmobranchs; leaving 1,024 of the 1,679 observed species in the final dataset), and we selected transects with more than 80% of biomass and more than 80% of abundance represented by these species. Ultimately, we conducted our study on 1,809 transects corresponding to 1,237 sampling sites, distributed over 37 countries, and based on 1,024 teleost species and 60 elasmobranch species. In this global study, we refer to "reef" as a single coordinate location (called "site" in the RLS protocol[85]). Each fish community contribution was calculated as the average of the fish contributions across all the transects at this given reef. Despite the dissimilarity in sample size among reefs, we consider that averaging the values limits the oversampling bias of more studied reefs by giving equal weight to all of them.

Correlation and dimensionality of contributions

To assess relationships among contributions while avoiding the influence of extreme values, we log-transformed contributions with at least one order of magnitude between the median and the highest value (see Table 1).

All contributions were centered (mean of 0) and reduced (standard deviation of 1) to study their covariation in a linear multidimensional space. We performed a weighted PCA on the dataset comprising 1,237 reefs described by 29 contributions. The weighting coefficients were chosen to fix the same weight for each category of contributions (e.g., "food web stability," see Table 1) in the PCA. This way, we gave equal importance to all the categories of nature contributions whatever their number of contributions. For example, despite the large number of carbonate polymorphs measured, their contributions had no greater influence on the PCA than the contributions relating to food web stability, which allowed us to be more flexible in the contributions used. We extracted the eigenvalues of each PCA dimension to evaluate the percentage of the total variance explained by each axis. The number of dimensions required to best represent all contributions across reefs was determined using the elbow method,[97] selecting the best trade-off to explain a maximum of the initial variance in contributions with as few PCA dimensions as possible. If most fish community contributions are highly correlated, the majority of variance could be summarized with a few PCA dimensions with high eigenvalues. Conversely, if most contributions are independent, all PCA dimensions would have similar importance in explaining the total variance (eigenvalues equal to 1). When randomizing contribution values among reefs, i.e., offsetting all potential pairwise correlations between contributions, the elbow method indicated that the best trade-off in terms of PCA dimensions for capturing initial variance was about half the number of contributions. The weighted PCA was conducted in R with the FactomineR package v.2.8.[98]

As the tropical regions have not been equally sampled (700 reefs in Australia out of 1,237 in total), we also tested the robustness of the Pearson pairwise correlations between contributions to this unbalanced sampling design. To achieve this, we measured the correlations among all contributions in Australia and the rest of the world and assessed the similarity of these two correlation matrices by computing the Mantel index on R with the vegan package v.2.6-4.[99]

Aggregation into a two-dimensional framework

To reduce the multidimensional space in two dimensions, we aggregated all log-transformed, centered, and scaled contributions into two synthetic scores according to two categories: NN and NP contributions. To estimate these NN and NP scores per reef, we used a weighted arithmetic mean of NN and NP contributions.[24] The same weighting coefficients were used as for the PCA. To ensure that the way we aggregate contributions into composite indicators is not inducing bias in the analyses, we compared the NN and NP scores obtained by seven different aggregation methods (see Table S2). All NN (and respectively NP) scores were highly positively correlated to the weighted arithmetic mean, with Pearson correlation coefficients above 0.96 and 0.74 for NN and NP scores, respectively (see Figure S13). As all aggregation methods were consistent, we pursued the analysis with the weighted arithmetic mean, as it was the most parsimonious, using the same weights as in the PCA.

Since we averaged and centered all contributions, the means of NN and NP scores across all reefs are zero. Thus, a negative score for a fish community implies that it has a lower value than the average of all sampled sites and conversely for positive values. We qualified sites with both positive NN and positive NP scores as bright spots (i.e., reefs with valuable contributions to both people and nature), while those with both negative scores were coined as dark spots.

Spatial distribution and protection status

To test for spatial effects in the global distribution of scores on tropical reefs, we compared the spatial autocorrelation (measured by the Moran index) of the NN and NP scores to a null model with the R package ncf and estimated the spatial extent of possible correlations with the interpolate "x-intercept" of Epperson.[100]

We also investigated whether NN and NP fish community scores could be related to their protection status. The dispersion around zero of both scores as a function of the protection status was assessed using a chi-squared test, while the effect size of this relationship was estimated using the V index of Cramer.[101,102]

All analyses and figures (except Figure 3) were carried out on R v.4.1.2 (R Core Team 2021). All relevant codes and data are available in a GitHub repository (see "Data and code availability").

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Ulysse Flandrin (ulysse.flandrin@gmail.com).

Materials availability

This study generated no new materials. The original RLS data used in this study are available online (https://reeflifesurvey.com/).

Data and code availability

All data and codes necessary to reproduce analyses and figures are available online at Zenodo: https://doi.org/10.5281/zenodo.13753006.[103]

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AUTHOR CONTRIBUTIONS

Conceptualization, U.F., D.M., and N.M.; methodology, all authors; data curation, all authors; data analyses, U.F., N.L., D.M., and N.M.; visualization, U.F. and N.M.; writing – original draft, U.F.; writing – review & editing, all authors.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

SUPPLEMENTAL INFORMATION

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