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

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Abstract

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 to 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 sparing of nature, towards more favorable and sustainable ecological and social futures.

Introduction

Humans are profoundly impacting the Earth by altering 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', '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 bio-cultural values.[3–5] Although these three perspectives may be seen along continuums 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

77   myriad of key contributions to people from seafood and micronutrient production[14,15] to cultural and

78   recreational benefits[16,17]. In this context, it remains unclear whether tropical fish communities can

79   simultaneously provide benefits relevant to each of the three NFF perspectives, or if specific

80   management strategies can optimize them, in a 'one-size-fits-all' approach. This uncertainty is

81   compounded by the absence of a quantitative framework that integrates the multiple contributions

82   provided by reef fish communities. If the 'one-size-fits-all' hypothesis is rejected (i.e., there are more

83   trade-offs than co-benefits among NFF perspectives), a subsequent question is how the different NFF

84   perspectives are globally distributed across tropical reefs, i.e., among countries and management

85   types.

86

87   An important knowledge shortfall in applying the NFF framework to tropical reef fish communities is

88   the positioning and quantification of the 'Nature-as-Culture' perspective globally. Tropical reefs

89   provide various non-economic and non-material contributions that could be considered as cultural

90   benefits, such as identity, attachment, and other forms of satisfaction,[18,19] yet these contributions

91   remain difficult to estimate consistently worldwide. In addition, some would argue that contributions

92   to human cultures are intimately intertwined with several contributions to society. For example, in

93   addition to seafood supply, fishing has a significant traditional value in many coastal societies.[20,21] The

94   aesthetic value of reef fish communities creates an emotional attachment to nature[16] but is also a

95   source of lucrative activities through tourism.[22] As both 'Nature-for-Society' and 'Nature-as-Culture'

96   perspectives support human well-being and livelihoods, we merged them into a single perspective,

97   referred to hereafter as 'Nature-for-People', although the latter is skewed towards society's

98   contributions due to a lack of data on cultural aspects. We then distinguish fish contributions that

99   primarily sustain people's well-being from those that primarily benefit to ecosystem state and

100   processes (Table 1) - although recognizing that some contributions are in between, since people

101   depend on ecosystem functioning,[23,24] while biodiversity conservation may depend on people's

102   attachment to nature or cultural management[25].

103

104   Here, we present a global quantitative assessment of 29 potential contributions to both people and

105   nature provided by reef fish communities in tropical regions. Our main objective is to assess

106   covariations between contributions provided by fish communities to "Nature-for-Nature" (NN) and

107   'Nature-for-People' (NP) perspectives, and the extent to which these potential contributions are

108   spatially distributed across tropical reefs. To do so, we took advantage of the largest fish survey on

109   tropical shallow reefs worldwide, in which standardized visual assessments were undertaken at 1,237

110   sites in 37 countries, providing 112,000 quantitative biomass observations of 1,024 species. Then, we

111   (i*) defined and quantified 29 relevant indicators of NN and NP perspectives, (i*i*) determined the

112   dimensionality of these 29 contributions owing to trade-offs and co-benefits to test the one-size-fits-

113   all hypothesis, (i*ii*) proposed a typology of reef fish communities based on their balance between the

114   two NFF perspectives, (i*v*) mapped the global distribution of NN- vs. NP-oriented fish community

115   contributions across tropical reefs, and (v*) discussed future management options to eventually re-

116   balance NFF perspectives. We found that while many of the NN contributions were positively

117   correlated with total fish biomass, many others were largely independent and few were antagonistic,

118   indicating that overall reef fish communities can simultaneously provide a high level of different

119   contributions. Spatial autocorrelation among contributions occurred at local scale, but not at the global

120   scale, suggesting the predominance of local or regional factors underpinning the level of fish

121   contributions rather than major biogeographical constraints. Such studies can provide guidance for

122   building management plans with achievable targets, and enable us to imagine desirable futures for

123   both people and nature.

124

125

126   **Results**

127   **Methods summary**

128   We used biomass data from 1,024 ray-finned fishes and presence data from 60 elasmobranch species

129   in 1,237 tropical reefs, collected by the standardized underwater visual protocol of the Reef Life

130   Survey initiative.[26,27] For each reef, we estimated 29 contributions that the observed tropical fish

131   communities can potentially provide either to local people or to nature; see Table 1 for a full

132   description of NN and NP contributions. To assess covariations among these contributions at a global

133   scale, we performed a Principal Component Analysis (PCA) and determined the dimensionality of

134   fish contributions to nature and people on tropical reefs. We then introduced a heuristic framework

135   classifying reef fish communities according to the "Nature-for-Nature" and 'Nature-for-People'

136   perspectives[4,23] using two averaged synthetic NN and NP scores. We finally studied the global

137   distribution of NN and NP scores, their spatial autocorrelation estimated by the Moran index, and

138   their links with protection status.

139

140

141   **Table 1: Nature contributions used in this study.** We divided the 29 fish-based contributions into

142   two categories: Nature contribution for Nature (NN) and for People (NP). All metrics were calculated

143   at the reef fish community level using data from standardized reef fish surveys. We assumed that the

144   values of each contribution scale positively with its benefit to people or nature. *Contributions*

145   *identified by (*) have been log-transformed to limit the effect of asymmetric and high-magnitude*

146   *distributions* (see table S1 for calculation details and data sources).

	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	37
		Trait distinctiveness	Mean of species functional trait distinctiveness at the reef level	94
		Evolutionary distinctiveness	Mean of species evolutionary distinctiveness at the reef level	95
	Biomass distribution	Biomass per trophic guild* (3 trophic groups)	Total biomass of reef fish split into herbivores, invertivores and piscivores trophic guilds	96
		Functional entropy	Functional distance between species, weighted by their relative biomass in the reef	97
		Phylogenetic entropy	Phylogenetic distances between species, weighted by their relative biomass in the reef	98
	Biogeochemical flows	Nitrogen*	Total nitrogen excreted by reef fish	99
		Phosphorus*	Total phosphorus excreted by reef fish	99
		Carbonates* (5 polymorphs)	For each polymorph: total carbonates excreted by reef fish	100
	Food web stability	Trophic web robustness	Allometric coefficient between the number of trophic interactions and species richness, as a proxy of trophic robustness to local extirpations	101
		Mean trophic level	Species trophic level inferred in each local trophic web, weighted by their relative biomass.	87
Nature-for-People (NP) contributions	**Food availability**	Available biomass*	Total biomass of reef fish belonging to fishable families (expert opinion)	39
		Turnover of available biomass	Biomass turnover of fishable species in the reef	15
	Nutrient quality of fish	Available nutrients in fish flesh *(Calcium, Iron, Omega 3, Selenium, Vitamin A, Zinc)*	Nutrient quantities contained in an average 100g portion of fish on the reef (i.e. nutritive quality relative to the fishing effort)	28
	Cultural value	Aesthetic value	Aesthetic value of reef fish community	16, 102
		Public interest	Public interest (online) of reef fish community	103

148 **Correlations between contributions**

149 We initially examined whether reefs tend to show high values of several contributions simultaneously,

150 by measuring the linear correlation between contributions. The pairwise correlations between the 29

151 contributions provided by fish communities in 1,237 tropical reefs ranged from -0.70 to 0.93, with a

152 median of the absolute values of 0.21. Although some contributions were antagonistic or strongly

153 congruent, the majority of them showed correlations close to 0. Among the 406 pairwise correlations,

154 half showed minimal dependence ($r \in$ [-0.2; 0.2]), while 155 (38%) pairs were positively correlated

155 ($r > 0.2$), and 51 (13%) were negatively correlated ($r < -0.2$; Fig. S1). Nitrogen and phosphorus

156 recycling, as well as available biomass and phosphorus recycling, were the most strongly correlated

157 contributions ($r = 0.93$ for each pair). Fish communities with high phosphorus recycling also tended

158 to have high nitrogen recycling and more available biomass (i.e., biomass of fish families caught for

159 human consumption). Conversely, endemism and aesthetic value, and endemism and taxonomic

160 richness, were the most negatively correlated pairs of contributions ($r = -0.7$ for each), with high

161 endemism being associated with low taxonomic richness and aesthetic value. Between these two

162 extremes, many contributions were roughly independent. For example, for a given level of endemism,

163 we may found communities with very different invertivore biomass ($r = -0.001$; Fig. 1 and S2).

164

165 As the tropical regions were not equally sampled (700 reefs in Australia out of 1,237 in total), we

166 tested the robustness of the Pearson pairwise correlations between contributions to this unbalanced

167 sampling design. To achieve this, we compared the correlations among all pairs of contributions in

168 Australia (n = 702) and the rest of the world (n = 535). A Mantel test showed that these two

169 correlation matrices were fairly similar (r = 0.84, p = 0.001; Fig. S5). This implies that correlations

170 among contributions were robust to geographic overrepresentation and suggests an absence of

171 distinction between Australia and other regions in terms of contribution covariations.

172

173 **Dimensionality of contributions**

174 To better visualize covariations among all contributions, we studied this multidimensional space using

175 a PCA on the 29 contributions. We applied a weighted PCA to ensure that each contribution category

176   (e.g., 'Food web stability', see Table 1) had the same importance, regardless of the number of

177   contributions. The first four axes explained 64% of the total variance among the fish communities,

178   with PC1 and PC2 explaining 26% and 21%, respectively. PC1 was shaped by NN contributions, such

179   as nitrogen, phosphorus, or carbonate recycling, which depend on reef fish biomass. Hence, PC1

180   distinguished fish communities with low versus high total fish biomass (correlation between fish

181   community biomass and PC1 coordinates was high: r = 0.86; Fig. 1A). Taxonomic richness was also

182   positively correlated with biomass, notably due to reef fish communities in the Coral Triangle,

183   characterized by high values in both taxonomic richness and biomass. Thus, more than one third of

184   the contributions (11 out of 29) appeared to be closely associated with total fish biomass (Fig. S6) and

185   taxonomic richness. In contrast, Caribbean fish communities tended to show low values of biomass

186   but hosted many endemic species, so endemism was the only NN contribution negatively correlated

187   with PC1. Among NN contributions, PC2 was shaped by endemism and trait distinctiveness, which

188   were mostly related to ecological originality and mean trophic level (Fig. 1A and 1C). Taxonomic

189   richness was negatively correlated to PC2 (r = -0.40) since species-rich Indo-Pacific communities had

190   fewer distinct species and covered a large homogeneous biogeographic area.

191

192   In contrast to NN contributions, which were broadly positively correlated with fish biomass (Fig. S6)

193   and therefore had relatively low dimensionality, NP contributions showed more diverse covariations

194   (Fig. 1B). Some NP contributions were positively (e.g., Iron and Calcium: r = 0.61) and negatively

195   correlated (e.g., Biomass Turnover and Available Biomass: r = -0.36), whereas others were

196   independent (e.g., Aesthetic and Vitamin A: r = -0.17). Consequently, we could not summarize these

197   contributions along a single gradient. Since most reef fishes were consumed in at least some locations

198   and could be classified as harvested when considered at the global scale, the available biomass was

199   correlated to total fish biomass (r = 0.94) and was thus well represented by PC1. The cultural aspects

200   of NP contributions were instead better represented by PC2, with a strong public interest and aesthetic

201   value for fish communities with high biodiversity like in the Coral Triangle.

202

203 Although the first two axes of the PCA accounted for an important proportion of the total variance

204 (47% of the variance of the 29 dimensions summarized in two axes), more axes were needed to

205 accurately describe covariations among contributions. Biomass turnover, for example, was mainly

206 related to the third axis, while elasmobranch diversity and trait distinctiveness aligned with the 9th

207 and 8th axes, respectively (Fig. 1C). As a result, the elbow method, which selects the best trade-off

208 explaining a maximum total variance in contributions with a minimal number of PCA axes, suggested

209 that nine dimensions were required to adequately describe the overall covariations among the 29 fish-

210 based contributions on tropical reefs, capturing 84% of the total variance (see insert Fig. 1A). In

211 comparison, when the 29 contributions were randomized (i.e., when contributions were uncorrelated),

212 the elbow method selected 14 dimensions, explaining 55% of the variance.

213

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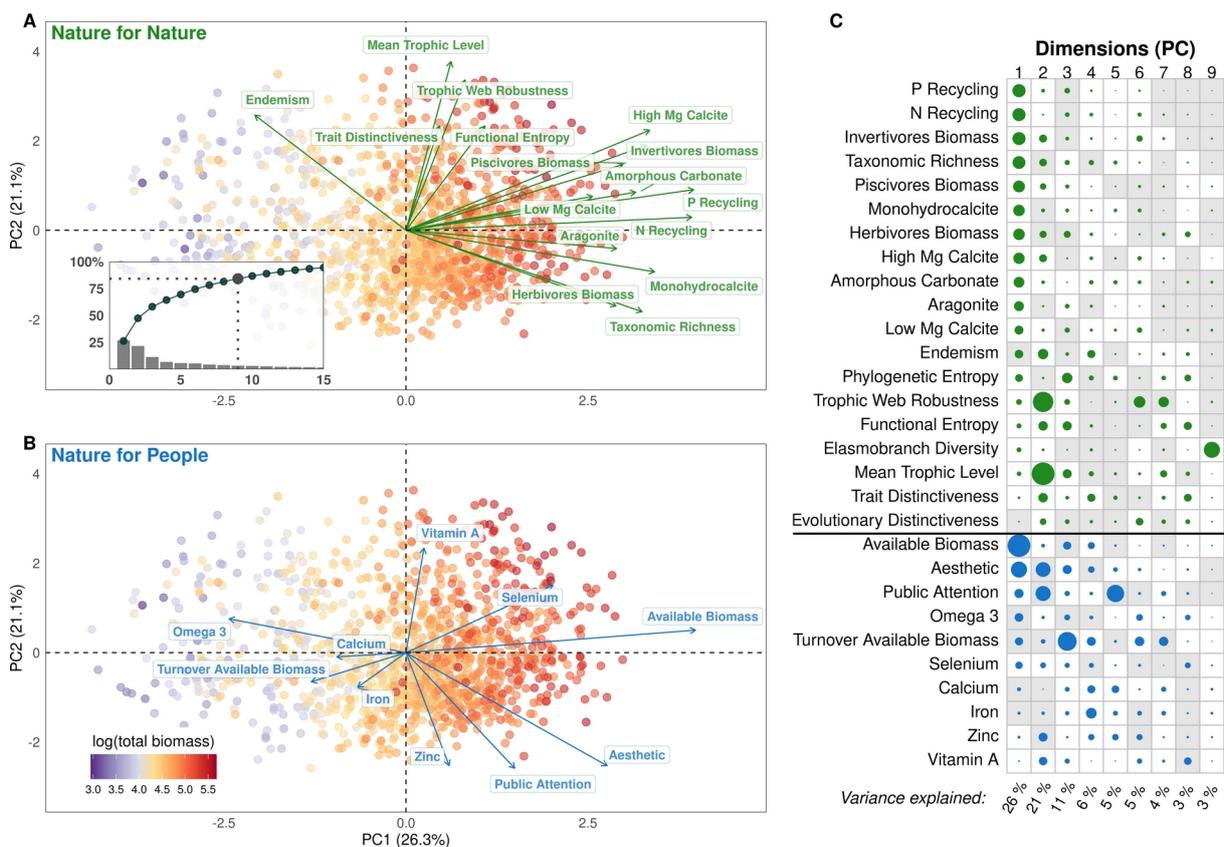
216 *Figure 1: Covariations and dimensionality of twenty-nine fish-based contributions to Nature*

217 *(green) and People (blue) on tropical reefs worldwide.*

218 *The covariations of contributions are represented in the two first PCA axes (Mg = Magnesium, N =*

219 *Nitrogen, P = Phosphorus). Total fish biomass, reported by color gradient, increases with the first*

220 *dimension of the PCA (A and B).* **(A)** *and* **(B)** *represent the same PCA, yet contributions are*

221 *highlighted in color according to their classification: either Nature-for-Nature (A), or Nature-for-*

222 *People (B).* **(A)** *Only well-represented contributions are displayed (cos² > 0.25): phylogenetic*

223 *entropy, evolutionary distinctiveness and elasmobranch diversity are not represented. The inset*

224 *displays eigenvalues of PCA axis in percent, and the cumulative curve of variance explained. The*

225 *black dot represents the dimensionality required to parsimoniously describe covariations of*

226 *contributions according to the elbow method (9 dimensions, 84% of variance explained; see Fig. S3).*

227 **(B)** *All contributions are represented.* **(C)** *Dot sizes are proportional to the importance of a*

228 *contribution in the total variance for a given PCA axis. Gray background indicates negative*

229 *correlation with the dimension, white background indicates positive correlation. The importance of*

230 *PCA dimensions in the total variance is reported as a percentage below. To see the PCA-biplot with*

231 *all contributions and color-blind friendly colors, refer to Fig. S4.*

232

233

234

235 **NN and NP scores are weakly correlated globally**

236 To reduce this multidimensional space in two dimensions, we calculated the mean of the contributions

237 according to the NN and NP perspectives.[24] More precisely, we scaled the contributions (mean of 0

238 and standard deviation of 1) and performed a weighted arithmetic mean of the NN and NP

239 contributions, using the same weights as for the PCA. This resulted in NN and NP scores for each reef

240 fish community that were normally distributed, zero-centered, and ranged between [-1.8; 1.4] and [-

241 2.0; 1.7], respectively. Across the 1,237 studied fish communities, we found a weak, albeit significant,

242 positive relationship between NN and NP scores ($R^2 = 0.06$, $p < 0.01$; Fig. 2A). This weak

243 relationship was influenced by some high latitude reefs included in the dataset showing both low NN

244 and NP values. Considering only locations with minimum monthly sea surface temperature (SST) >

245 20°C (n = 1,030, instead of the 1,237 reefs warmer than 17°C), the R-squared value was reduced to

246 0.01 ($p < 0.01$; Fig. S8). Consequently, reef fish communities could be represented across a two-

247 dimensional space made of NN and NP scores, where the number of communities in each of the four

248 portions was similar (Fig. 2-A).

249

NN and NP scores are weakly related to protection

251 We further classified the 1,237 reef fish communities into three management categories based on

252 protection status: 403 were fished, 601 had restrictions on fishing activities, and 233 reefs were in

253 effective no-take MPAs. Using a chi-square test, we showed that the number of fish communities in

254 each of the four parts of the NN-NP space was significantly influenced by the three management

255 categories (Chisq = 28.2, df = 6, p-value < 0.01). More precisely, we observed that the proportion of

256 fished communities was highest where both NN and NP scores were negative, and lowest where both

257 scores were positive (Fig. 2-B). However, we found that the protection status had little influence on

258 the distribution of fish communities in the NN-NP space (effect size measured by the V index of

259 Cramer: V = 0.11, df = 6). This was consistent with the roughly equivalent proportions of restricted

260 MPAs in dark and bright spot communities (Fig 2-B), defined as those having both low NN and low

261 NP scores vs. high NN and high NP scores.

262

**High NN and NP scores are widespread across the tropics**

264 We then investigated the global spatial distribution of these NN and NP scores across the tropics. For

265 each score, we calculated the Moran's index separately to measure the spatial autocorrelation for

266 increasing distance classes. The Moran indices allowed us to determine the distance at which the

267 scores were no longer autocorrelated (i.e., nearby reef communities no longer had similar scores

268 relative to a random spatial distribution; Moran index close to 0). We observed that the spatial

269 autocorrelations of NN and NP scores became negligible beyond distances over 1,348 km and 263

270 km, respectively (Fig. S9). This suggests that although NN scores were correlated at regional scales

271 and NP scores at a more local scale, these associations were not consistent across larger

272 biogeographic gradients or clustered within large areas or oceans.

273

274 In line with the absence of geographic clustering of contributions observed in the PCA, high scores

275 were widespread across tropical reefs (Fig. S10). Although the top 5% 'outlier' fish communities

276 (most extreme values) in each of the four NN x NP categories occurred in almost all oceans (Fig. 2-

277   C), we examined a few archetypal situations to illustrate where high scores could occur. For example,

278   NP-only outliers emerged, among other regions, in the Caribbean and the south-western Pacific

279   Islands. While Caribbean fish communities were characterized by high values of public interest, iron

280   concentration, and available biomass, reef fishes in SW Pacific islands tended to support remarkably

281   high aesthetic and nutrient (iron and calcium) contributions. In contrast, the NN-only outliers were

282   mostly present in the Galapagos archipelago due to a combination of high biomass, endemism,

283   evolutionary distinctiveness, and mean trophic level. Dark spot (both negative NN and NP scores)

284   outliers were mostly located at high absolute latitudes, as these fish communities had low aesthetic,

285   biomass, or mean trophic level values. These dark spot outliers, i.e., Canary (Spain) and Lord Howe

286   (Australia) islands, were more rocky sub-tropical reefs rather than tropical coral reefs, and tended to

287   experience colder temperatures (minimum SST ranging from 17°C to 20°C). In contrast, French

288   Polynesia was an outlier example among the bright spots (both positive NN and NP scores). This

289   archipelago concentrated important values of reef fish biomass, a high mean trophic level, a high

290   biodiversity, significant concentration of selenium, and fishes of high aesthetic value. Central

291   America was a region with outliers from both NN-only and NP-only categories. The Pacific side of

292   Central America hosted NN-only and bright spot outliers, due to high values of mean trophic level,

293   nutrient recycling, and evolutionary distinctiveness, whereas the Caribbean side was characterized by

294   NP-only fish communities with high biomass turnover and public interest. In the same way, Western

295   Australia and the southern Pacific islands hosted fish communities with high values in the four

296   corners of the NN-NP spectrum within the same geographic area (Fig. 2-C and S11).

297
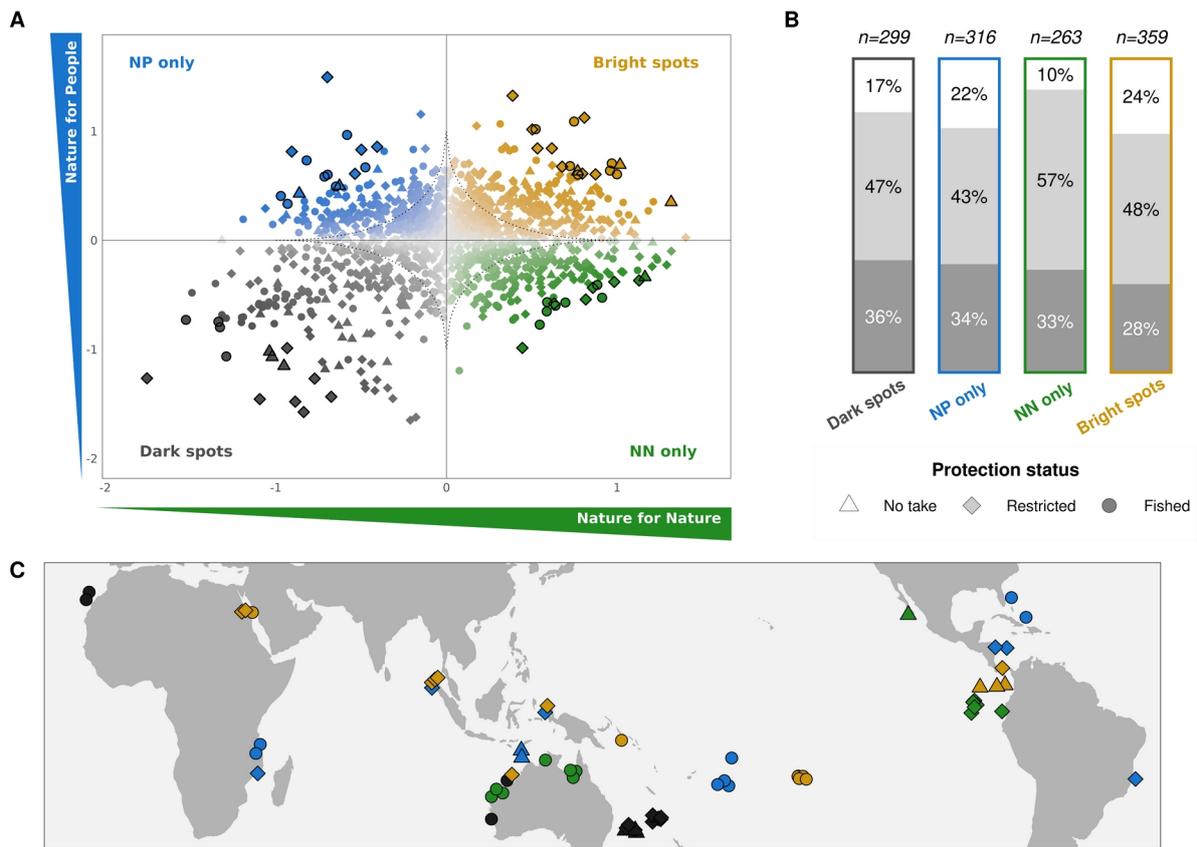
Figure 2: The four corners of the NN vs. NP spectrum and management strategies.

(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 NNxNS 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 Fig. S7 for details of outliers). (B) Protection status (No take reserves, restricted areas, fished area) does not strongly influence reefs categories in the NN - NP space (Chisq = 28.2, df = 6, p-value < 0.01, Cramer's V = 0.11) (C) Geographic distribution of the 5% reefs outliers in each NN-NP category and their management status.

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 'Nature-for-Nature' and 'Nature-for-People'

314   contributions, we found that these two perspectives are relatively independent, with high and low

315   values distributed globally across tropical fish communities. So, sustaining nature while promoting

316   human well-being seems achievable over larger scales, rather than representing mutually exclusive

317   options. Trade-offs may be more common at smaller scales, however (Fig. 2). This relative

318   independence of NN and NP scores is explained by the high dimensionality of fish community

319   contributions to nature and people, where nine dimensions, from 29 initial contributions, are needed to

320   describe the diversity of reef fish contributions. We show that trade-offs or negative correlations

321   among contributions are not the rule, so reef fish communities can provide high levels of several

322   different contributions, as observed in French Polynesia.

323

324   We also highlight synergies with many NN contributions being positively correlated with fish

325   biomass, since many NN and NP contributions are intrinsically linked to the amount of fish, such as

326   recycling capacities and available biomass for fisheries. In this sense, despite the central role of total

327   biomass in several NN contributions, we divided this biomass into different categories (i.e.,

328   herbivores, invertivores, piscivores and available biomass) to disentangle the different aspects of

329   ecosystem functioning and people's needs. However, the weights given to these categories in the PCA

330   analysis and the average scores, ensure that biomass remains equally important relative to other

331   contributions. Some contributions, such as nutrient concentrations, are independent of fish biomass,

332   since we chose to measure these contributions relative to human consumption (per 100g portion of

333   fish) and not by stock size (total biomass underwater). By considering catchable biomass and average

334   nutritive quality of fish, we take into account both important and complementary aspects of fisheries.[28]

335   Some other contributions are also largely independent from others, such as elasmobranch diversity,

336   which can provide an early warning signal of human impact before the collapse of other

337   contributions.[29] In addition, tropical reefs also include contributions to nature and people not based on

338   fish and not estimated here (e.g., shoreline protection[30], or coral growth[31]), which might be less related

339   to fish presence and biomass. Importantly, our study globally quantifies relative contributions of non-

340   material values provided by tropical reef fishes, such as aesthetics and public interest, and how these

341   compare to more economically-oriented contributions.[1,32] Regarding the NP perspective, we refer to

342   these as *potential* contributions because we only evaluate them underwater, but to become *realized*

343   contributions, they need to be accessed by people, which is influenced by a range of institutional

344   conditions as well as cultural, economic, and health dimensions not measured in our study.[33–35]

345

346   Covariations among all contributions seemed consistent across the geographical regions sampled

347   (e.g., similar covariations within and outside Australia) and climatic outliers (reefs with minimal SST

348   between 17°C and 20°C). This illustrates that, except for some contributions such as endemism and

349   evolutionary distinctiveness, fish-based contributions are more likely to be driven by local or regional

350   factors rather than by broad-scale geography or environmental gradients. As exceptions, endemism

351   and evolutionary distinctiveness are stronger in Central America than in Indo-Pacific reef

352   communities, because the former is a smaller region and has been isolated for longer than the

353   latter.[36,37] Fish communities valuable for both nature and people are widespread across the tropics

354   (especially for the NP scores), and we can reject the hypothesis that fish-based contributions are

355   simply driven by global geographic gradients, such as ocean basins or mean SST. Spatial

356   autocorrelation demonstrates that NN and NP values remain spatially correlated within the regional

357   scale only. While NN scores are no more similar to one another than expected by chance alone

358   beyond a distance of ~1,350 km, the spatial correlation between NP scores is significant only at a few

359   hundred kilometers. This suggests that NN values are more driven by regional environmental

360   conditions or fish life-history traits[38] while NP values depend on more local conditions such as

361   ecosystem uses, human impacts, management strategies, or habitat characteristics.[39]

362

363   Confronted with the challenge of reducing the dimensional space to adequately summarize the

364   distribution of all contributions across reef fish communities, we averaged the contributions along two

365   dimensions representing reef potentials for nature and people. Although averaging induces a loss of

366   natural complexity, we consider this heuristic framework necessary to visualize the global patterns

367   and trends of all estimated contributions, and to offer a broad view of fish community contributions in

368   line with the Nature Future Framework (NFF). In our approach, we weighted each contribution

369   category equally, yet several studies show that perceptions of Nature's contributions can differ across

370   populations and within populations.[40–42] Weighting human contributions in accordance with

371   indigenous perception and local knowledge[43] - or even according to local group perceptions[44] - would

372   be a critical step towards a finer and inclusive consideration of nature's contributions to people[45]. This

373   would require extensive socio-cultural information, but might lead to important, potentially different,

374   insights into covariations between contributions and management priorities. Despite this simplified

375   framework, we found that NN and NP values succeeded in capturing well-known outstanding reefs

376   supporting the highest scores. For example, the Galapagos Islands are "Nature-for-Nature" positive

377   outliers, due to their high endemism, elasmobranch diversity and well-preserved marine resources in

378   general.[46] Caribbean reefs are highly valuable for people, given the presence of commercial fishes and

379   the large human coastal population close to the reefs (e.g., attachment, recreational diving).[47] Finally,

380   the Coral Triangle is identified here as outstanding for both nature and people in some remote or well-

381   managed reefs.[48,49]

382   On the other hand, reefs with the lowest scores are mainly located at high latitudes where reefs tend to

383   provide reduced levels of contributions compared to near-equatorial reefs. The predominance of dark-

384   spots in subtropical reefs may be due to the fact that these 'marginal reefs' are often located in

385   conditions that are sub-optimal for foundational species such as corals.[50,51] However, it is worth noting

386   that the standardization of contributions, required to aggregate them, ensures that the average is zero.

387   Negative scores therefore only reflect reefs with below-average contributions. In addition, dark spots

388   were also found in tropical coral reefs such as in the nearshore of the Great Barrier Reef, and

389   conversely, above-average contributions were also observed in higher-latitude reefs as in Red Sea,

390   Florida or southern French Polynesia (Fig. S8 and S11). This suggests that all reefs may show any

391   contribution level regardless of their position along the latitudinal gradient. The inclusion of marginal

392   sub-tropical reefs in our analysis allowed us to describe a large gradient of ecological conditions. This

393   is important, especially considering that marginal reefs are often considered as natural laboratories to

394   understand the potential future state of coral reefs under growing human impact and warming

395   conditions.[51] Moreover, several tropical species are moving toward higher latitudes following climate

396   change.[52] This tropicalization may induce shifts in fish trait diversity[38,52] and thus a shift in provision

397   of some contributions to both nature and people that remains to be quantified.

398

399   We separated NN and NP contributions in our analyses for consistency within the NFF framework[4],

400   considering that contributions are valuable for people first or nature first. However, we recognize that

401   overlap exists for some contributions as people also indirectly benefit from NN contributions.[53] For

402   example, the capacity of an ecosystem to recycle nutrients or stabilize biomass through a high mean

403   trophic level would have obvious positive feedback on fisheries contributions to people. In this sense,

404   as contributions are sometimes interconnected, it would be interesting to investigate the relationships

405   between them in greater depth. For example, Antunes et al. (2024)[54] recently suggested using network

406   analysis to examine the diversity of contributions, allowing the modeling of links between

407   contributions and the measurement of energy flows that support material contributions. Thus, it would

408   be possible to express some NP contributions (e.g., available biomass) as a function of other NN

409   contributions (e.g., piscivore biomass and others), which might provide additional, potentially

410   different, insights into the strength of relationships between contributions, and could be valuable for

411   explanatory or predictive purposes.

412   Moreover, we have combined the 'Nature-to-Society' and 'Nature-as-Culture' contributions into

413   'Nature-for-People' contributions to visualize reefs within a 2-dimensional space and because many

414   NCs are difficult to estimate globally, but some NC and NS contributions may be largely independent.

415   For example, cultural and immaterial values, as symbolic or spiritual meanings of particular species,

416   might be unrelated to their material or economic value and are best studied independently. Although

417   29 different contributions were considered, the two cultural contributions that we were able to extract

418   from fish community data represent a third of the Nature-for-People dimensions, biasing this

419   perspective towards an utilitarian value. Introducing additional bio-cultural contributions, ideally on a

420   finer scale, such as heritage or symbolic species, would potentially highlight new and more complex

421   relationships between reef contributions and people,[55] and better represent the diversity of links

422   between people and nature. Further studies of reef cultural importance are an important next step if we

423   are to better account for the diversity of bio-cultural systems and progress our understanding of the

424   interplay between the three NFF dimensions. More generally, future inclusion of overlooked or

425   underrepresented contributions may modify the structure and dimensionality of the NN-NP space but

426 may also add redundant information given the broad range of fish roles and functions that we

427 considered in this most comprehensive database available to date.

428

429 We did not find clear associations between reef protection status and the NN and NP scores of reef

430 fish communities (Chisq = 28.2, df = 6, p-value < 0.01, Cramer's V = 0.11). As many countries or

431 bioregions have valuable reefs that significantly contribute to both NN and NP scores, one might

432 question whether the absence of any effect of protection status on NN and NP scores may result from

433 the placement of MPAs relative to socio-environmental constraints[47] or from a limited effect of MPAs

434 on most NN and NP contributions.[56] In this sense, we suggest that although multiple synergies exist

435 and some sites are valuable for many NN and NP contributions at once, the relatively high

436 dimensionality of fish community contributions to nature and people implies that this is not the rule.

437 Making "one-size-fits-all" areas is challenging and not always feasible, therefore the 'win-win'

438 paradigm of MPAs should probably evolve towards more specific and context-dependent

439 objectives.[57,58] This NN-NP space based on tropical reefs worldwide can be used in more local studies

440 to quantitatively characterize a reef, track its temporal trend, or facilitate comparative analyses among

441 others. With this heuristic framework, we can more explicitly quantify specific objectives of

442 protection and sustainable use of tropical reefs, and better allow narratives of success and positive

443 outcomes to be backed by data, rather than unsubstantiated claims.

444

445 As proposed by the Nature Futures Framework, our approach may indeed provide an exploration of

446 different conceptions we have regarding tropical reefs to shape our ecological and social futures.[5,6,53]

447 The NN axis raises awareness of the need to preserve ecosystem integrity and intrinsic values of

448 nature, independently of anthropic interests. On the other hand, the NP axis, and especially its

449 economic component, illustrates the emerging societal priority: whether the growth or post-growth

450 economic paradigm is preferable, and what relationship do we want with nature (see Fig. 3).[5]

451 Together, these two dimensions capture the ongoing debate on conservation and human future. Should

452 we better integrate people into nature ('land sharing') or spatially separate places of use and

453 protection ('land sparing')?[59,60] Would conservation benefit more from a total "half earth" protection,

454   i.e. fully protect half of the planet and use the other half, or a "whole earth" management including

455   people, i.e. maintain healthy ecosystems through the sustainable use of natural resources across the

456   whole earth?[61,62] While bright spots, valuable for both nature and people, would fit well with the land

457   sharing and whole earth management visions, the one-sided value of NN-only and NP-only reefs

458   would fit better with the land sparing and half earth perspectives. This mental space (Fig. 3) provides

459   an opportunity to quantitatively explore a gradient of narratives proposed by the Nature Future

460   Framework, between "Arcology" (people concentrated in dense, futuristic, self-sufficient cities,

461   surrounded by totally pristine nature, i.e "NN only") and "Optimizing nature / Innovative commons"

462   through a bio-cultural and social world that exploits whatever is necessary for human well-being as

463   long as it is sustainable.[5,6]

464
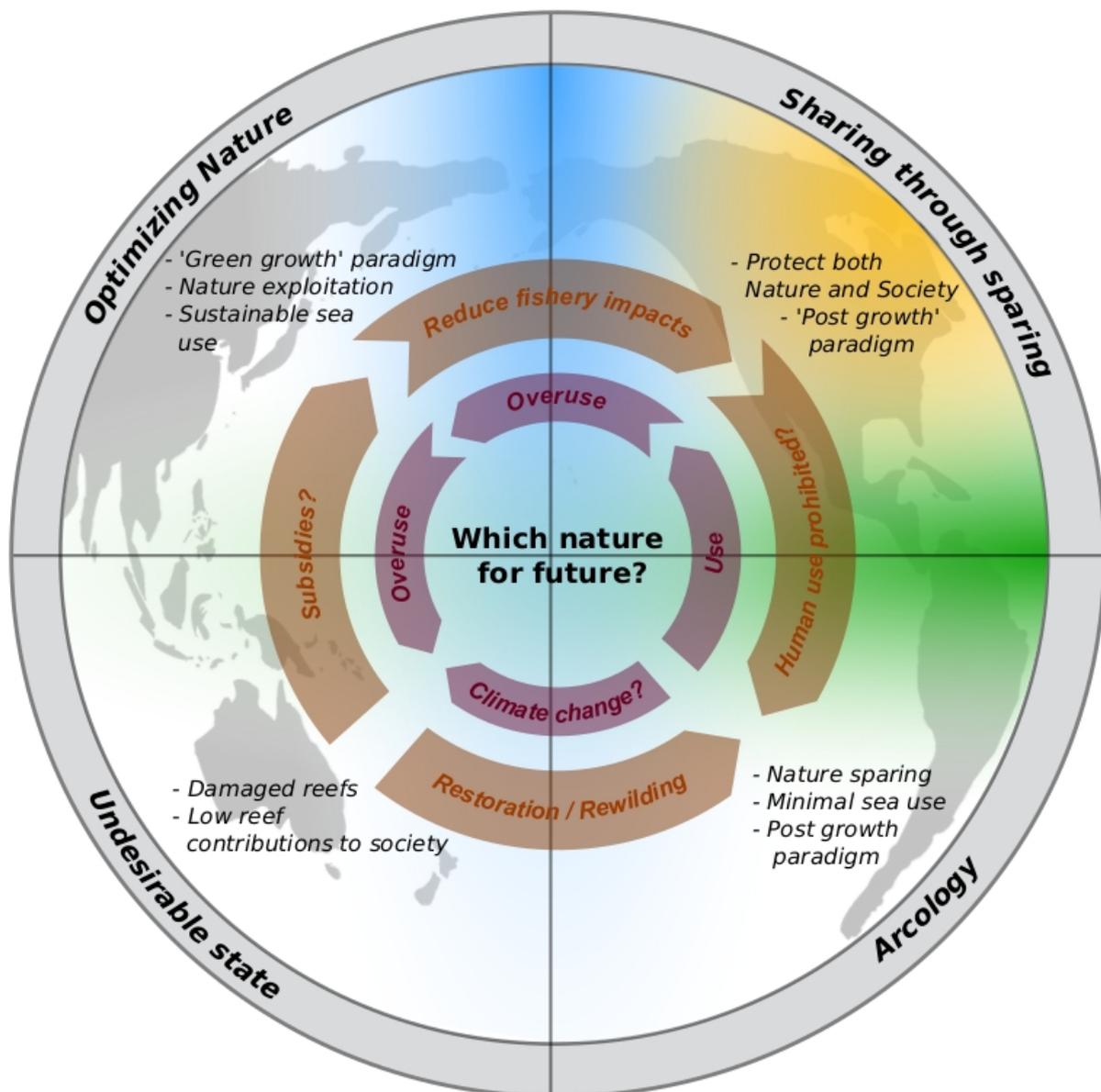
465   **Figure 3: Human well-being in Nature: which future for tropical reefs?**

466   *The four parts defined by the gradient of Nature protection and exploitation illustrate different*

467   *possible futures, exposed by the NFF.[6] "Optimizing nature for humans / Innovative commons"*

468   *proposes a bio-cultural and social future where societies exploit whatever is necessary for human*

469   *well-being as long as it is sustainable. "Arcology" calls for a future where people are concentrated in*

470   *dense, futuristic, self-sufficient cities, surrounded by totally pristine nature. Between both, "Sharing*

471   *through sparing" depicts a future where people exploit as little of nature as possible for their well-*

472   *being and safeguards the remainder. Possible dynamics are highlighted in orange and red.*

473

474

475   ## Conclusion

476   This study provides a global snapshot of fish community contributions but does not explicitly

477   examine whether these contributions are robust or resilient to human uses and ecological disturbances.

478   Determining the temporal dynamics of fish community scores in this NN-NP space is thus critical.

479   We also need to better understand the conditions of protection, habitat and climate under which

480   tropical reefs can remain in favorable states over time or instead shift towards less favorable states for

481   nature or people. From a management point of view, the goal is to determine how to enhance both NN

482   or NP scores on a given tropical reef under different protection rules. Although these concerns

483   challenge scientists and managers, they also resonate with societal choices: is it preferable to protect

484   NN-only reefs to maintain their status or try to increase their NP score and move towards a "nature-

485   based inclusive prosperity" [4] scenario? While prohibiting human uses in ecological bright spots would

486   maintain the last reef refugia in a valuable state for nature ("Arcology"), their use by people, even if

487   partial or regulated, would expose them to a risk of rapid exploitation leading to a sharp decrease in

488   NN score, particularly due to fish biomass decline[63,64] and top predator extirpation.[47,65] Likewise, the

489   priority may be to shift dark spot reefs towards more desirable states through restoration and/or

490   rewilding activities[66,67] to target either Nature-for-Nature contributions or to shape these reefs for

491   populations by supporting local Nature-for-People contributions like marine biomass turnover through

492   subsidies (e.g. aquaculture) and facilitating other uses (e.g. ecotourism). This kind of management

493   could be guided by multi-action planning tools which identify, on a given territory, an optimal

494 combination of management actions to achieve a set of recovery targets while minimizing

495 costs.[68,69]Such actions could be integrated into this NN-NP framework as people's contributions to

496 nature, influencing current reef status either negatively through overfishing and habitat degradation or

497 positively through effective ecosystem stewardship (Fig. 3).[70]

498

499 Overall, understanding which reefs are in which categories, using NN and NP scores and how to

500 enhance them, will be crucial to develop "living in harmony with Nature" scenarios.[6,71] By

501 quantitatively exploring the question of nature use into the NFF framework, we illustrate that these

502 two dimensions are not necessarily antagonistic but rarely met. In this context, protected areas may

503 play complementary roles since their objectives have increasingly shifted from a primary focus on

504 regulating or prohibiting human activities to preserve biodiversity and maintain ecosystem

505 functioning, to more balanced approaches that address the needs of both people and nature.[33] A more

506 realistic and operational option than seeking the "one-size-fits-all" management is to build networks

507 of protected areas varying in their priority values regarding NCPs and wildlife conservation.[72]

508 Towards this objective and given the third target of the CBD-COP15 to protect at least 30% of both

509 land and sea before 2030, managing co-benefits and trade-offs within but also among protected areas

510 is a priority.[73] The NN-NP quantitative framework we propose is a step forward in this objective.

511 Ultimately, this study offers insights into how nature conservation and human well-being can coexist

512 across tropical regions, highlighting potential synergies. It underscores the need for nuanced, context-

513 specific approaches to reef management for a sustainable desirable future.

514

515

516 **Experimental procedures**

517

518 **Reef fish data**

519 We compiled data from the Reef Life Survey (RLS) database containing the abundance and size

520 distribution of fish species collected through standardized surveys of tropical reefs worldwide.[27,75]

521 These underwater visual assessments, conducted between September 2006 and May 2019, consist of

522 50-meter-long transects with two 5 m wide (by 5 m high) belts surveyed, one on each side of the line.

523 Global sampling effort in RLS has been heterogeneous, more intensive around Australia, so we

524 explicitly considered the Australian oversampling in our global analyses (see section 'Correlation and

525 dimensionality of contributions' for more details).

526

527 We focused on sites with a minimum monthly sea surface temperature (SST) above 17°C. This

528 broader definition of "tropical reefs", including some sub-tropical reefs with no corals, has previously

529 been used to consider all reefs where tropical species are present.[15,49] We excluded anguilliforms

530 (Congridae, Muraenidae, Ophichthidae) and cryptobenthic families[76] because they remain difficult to

531 visually quantify consistently with daytime diver observations. Fish abundance counts and size

532 estimates were converted to biomass per species per transect using length–weight relationships

533 (https://fishbase.mnhn.fr/). Since diver perception of fish size can be biased in underwater surveys,[77,78]

534 we corrected fish size estimates according to Edgar et al. (2004).[79] To minimize the bias related to

535 juvenile identification, we excluded individuals < 3.75 cm for species with a maximum body size < 25

536 cm, and individuals < 6.25 cm for species with a maximum body size $\geq$ 25 cm.[80] Since the count and

537 biomass estimation of many elasmobranchs can be biased using underwater visual surveys,[81,82] we

538 only considered their species diversity not their abundance within each transect. To avoid over-

539 estimating fish abundance due to temporary fish aggregations or large roaming schools, we excluded

540 surveys with a total biomass over 500 kg/500m² or an abundance exceeding 10,000 individuals.

541

542 We classified reefs according to their protection status. Reefs within no-take Marine Protected Areas

543 (MPAs) or MPAs with multiple no-take zones, combined with high enforcement (expert opinion)[39]

544 were classified as "No-take", while reefs located in other MPAs were qualified as "Restricted", and

545 those without any documented MPAs were considered as "Fished" (Fig. S12).

546

547 **Assessment of contributions to nature and people**

548 We calculated 29 fish-based nature contributions in each tropical reef, split into NN and NP

549 categories (Table 1, see Table S1 for calculation details). These contributions were primarily

550 identified by an expert panel from the REEF-FUTURES consortium and co-authors of this study (UF,

551   DM, CA, SB, JC, GE, MG, FL, NL, AM, EM, MM, VP, LP, NS, RS, SV, and NM). Nitrogen and

552   phosphate recycling, carbonates excretion, biomass turnover, nutrient quality of fish, public attention

553   and fish aesthetics have all been measured on RLS data and published by the REEF-FUTURES group

554   (see Table 1 and S1 for references). Additionally, we considered facets of biodiversity such as species

555   richness, functional and phylogenetic diversity and trophic interactions, which determine ecosystem

556   functioning and stability.[32,83,84] Estimates of diversity, biomass, and biogeochemical fluxes, which are

557   crucial to ecological processes on tropical reefs,[76] were compared with more human-centered

558   contributions, through material or non-material bonds between Nature and People.[85] Based on the

559   literature and the expert panel of co-authors, contributions related to biodiversity or ecosystem

560   functioning were considered primarily valuable for nature (NN contributions).[5,32,76,83,84] On the other

561   hand, contributions that reflect opportunities for food supplies and cultural benefits were more related

562   to human well-being and livelihood (NP contributions).[5,23,85,86] We considered that these 29

563   contributions together capture the essence of fish roles and functions on tropical reefs with available

564   data on more than 1,000 species. We assumed that values of each contribution scale positively with its

565   benefit to people or nature. For example, a higher 'mean trophic level' is assumed to promote the

566   stability of the overall fish biomass.[87]

567

568   To compare the different contributions among reefs, we only considered species for which we could

569   estimate all contributions (others than elasmobranchs; leaving 1,024 out of the 1,679 observed species

570   in final dataset) and we selected transects with more than 80% of biomass and more than 80% of

571   abundance represented by these species. Ultimately, we conducted our study on 1,809 transects

572   corresponding to 1,237 sampling sites, distributed over 37 countries, and based on 1,024 teleost

573   species, and 60 elasmobranch species. In this global study, we refer to 'reef' as a single coordinate

574   location (called 'site' in the RLS protocol[75]). Each fish community contribution was calculated as the

575   average of the fish contributions across all the transects at this given reef. Despite the dissimilarity in

576   sample size among reefs, we consider that averaging the values limits the over-sampling bias of more

577   studied reefs by giving equal weight to all of them.

578

579   **Correlation and dimensionality of contributions**

580   To assess relationships among contributions while avoiding the influence of extreme values, we log-

581   transformed contributions with at least one order of magnitude between the median and the highest

582   value (see Table 1).

583

584   All contributions were centered (mean of 0) and reduced (standard deviation of 1) to study their

585   covariation in a linear multidimensional space. We performed a weighted Principal Component

586   Analysis (PCA) on the dataset comprising 1,237 reefs described by 29 contributions. The weighting

587   coefficients were chosen to fix the same weight for each category of contributions (e.g., 'Food web

588   stability', see table 1) in the PCA. This way, we gave equal importance to all the categories of nature

589   contributions whatever their number of contributions. For example, despite the large number of

590   carbonate polymorphs measured, their contributions had no greater influence on the PCA than the

591   contributions relating to food web stability, which allows us to be more flexible in the contributions

592   used. We extracted the eigenvalues of each PCA dimension to evaluate the percentage of the total

593   variance explained by each axis. The number of dimensions required to best represent all

594   contributions across reefs was determined using the elbow method,[88] selecting the best trade-off to

595   explain a maximum of the initial variance in contributions with as few PCA dimensions as possible. If

596   most fish community contributions are highly correlated, the majority of variance could be

597   summarized with a few PCA dimensions with high eigenvalues. Conversely, if most contributions are

598   independent, all PCA dimensions would have similar importance in explaining the total variance

599   (eigenvalues equal to 1). When randomizing contribution values among reefs, i.e. offsetting all

600   potential pairwise correlations between contributions, the elbow method indicated that the best trade-

601   off in terms of PCA dimensions for capturing initial variance was about half the number of

602   contributions. The weighted PCA was conducted in R with the 'FactomineR' package *v.2.8*.[89]

603

604   As the tropical regions have not been equally sampled (700 reefs in Australia out of 1,237 in total),

605   we also tested the robustness of the Pearson pairwise correlations between contributions to this

606   unbalanced sampling design. To achieve this, we measured the correlations among all contributions in

607   Australia and the rest of the world, and assessed the similarity of these two correlation matrices by

608   computing the Mantel index on R with the 'vegan' package *v.2.6-4*.[90]

609

Aggregation into a two-dimensional framework

611   To reduce the multidimensional space in two dimensions we aggregated all log-transformed, centered,

612   and scaled contributions into two synthetic scores according to two categories: NN and NP

613   contributions. To estimate these NN and NP scores per reef, we used a weighted arithmetic mean of

614   NN and NP contributions.[24] The same weighting coefficients were used as for the PCA. To ensure that

615   the way we aggregate contributions into composite indicators is not inducing bias in the analyses, we

616   compared the NN and NP scores obtained by seven different aggregation methods (see Table S2). All

617   NN (and respectively NP) scores were highly positively correlated to the weighted arithmetic mean,

618   with Pearson correlation coefficients above 0.96 and 0.74 for NN and NP scores, respectively (see

619   Fig. S13). As all aggregation methods were consistent, we pursued the analysis with the weighted

620   arithmetic mean, as it was the most parsimonious, using the same weights as in the PCA.

621

622   Since we averaged and centered all contributions, the means of NN and NP scores across all reefs are

623   zero. Thus, a negative score for a fish community implies that it has a lower value than the average of

624   all sampled sites, and conversely for positive values. We qualified sites with both positive NN and NP

625   scores as "bright spots" (i.e. reefs with valuable contributions both to people and nature), while those

626   with both negative scores were coined as "dark spots".

627

Spatial distribution and protection status

629   To test for spatial effects in the global distribution of scores on tropical reefs, we compared the spatial

630   autocorrelation (measured by the Moran index) of the NN and NP scores to a null model with the R

631   package 'ncf' and estimated the spatial extent of possible correlations with the interpolate "x-

632   intercept" of Epperson (1993).[91]

633

634   We also investigated whether NN and NP fish community scores could be related to their protection

635   status. The dispersion around zero of both scores as a function of the protection status was assessed

636 using a chi-square test, while the effect size of this relationship was estimated using the V index of

637 Cramer.[92,93]

638

639 All analyses and figures (except Fig. 3) were carried out on R v.4.1.2 (R Core Team 2021). All

640 relevant codes and data are available in a GitHub repository (see sections Data and materials

641 availability).

642

643 **Resource availability**

644 **Lead contact**

645 Requests for further information and resources should be directed to and will be fulfilled by the lead

646 contact, Ulysse Flandrin (ulysse.flandrin@gmail.com).

647 **Materials availability**

648 This study generated no new materials. The original Reef Life Survey data used in this study are

649 available online (https://reeflifesurvey.com/).

650 **Data and code availability**

651 All data and codes necessary to reproduce analyses and figures are available online at

652 https://doi.org/10.5281/zenodo.13753006.[74]

653

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658

Statement of authorship

Conceptualization: U.F., D.M., N.M. Methodology: All authors. Data Curation: All authors. Data analyses: U.F., N.L., D.M., N.M. Visualization: U.F. & NM. Writing – original draft: U.F. Writing – review & editing: All authors.

Competing Interest Statement

The authors declare that they have no competing interests.

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Supplemental materials

Table S1: Assessment method of the twenty-nine fish-based contributions on tropical reefs. All metrics were calculated at the reef level using data from standardized reef fish surveys (visual census). *Contributions identified by (*) have been log-transformed (log10(x+1) for contributions including some zeroes and log10(x) for the others) to limit the effect of asymmetric and high-magnitude distributions.*

Contributions	Assessment	Unit	Impact	References and data sources
Biomass*: Herbivores biomass Invertivores biomass Piscivores biomass Available biomass	Visual census in Reef Life Survey protocol. Fish abundance counts and size estimates were converted to biomass per species per survey using length–weight relationships presented for each species in Fishbase (https://fishbase.mnhn.fr/). Total biomass is the sum of each individual weight in each reef. Total biomass was divided into 3 trophic guilds, according to species diet inferred by Parravicini et al. (2020) ("Herbivores" = herbivores + microvores + detritivores, "Invertivores" = corallivores + invertivores + planktivores, and "Piscivores" = piscivores). Available biomass is assessed as the biomass of catchable families (expert opinion): Acanthuridae, Bothidae, Caesionidae, Carangidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Mugilidae, Mullidae, Nemipteridae, Scaridae, Sciaenidae, Scombridae, Scorpaenidae, Serranidae, Siganidae, Sparidae, Sphyraenidae, and species bigger than 20cm for the families: Balistidae, Holocentridae, Pomacanthidae, and Priacanthidae.	kg / 500m²	Biomass involved in nature processes. Many contributions are inherently biomass-dependent, with different ecological roles for different trophic guilds. The available biomass is the stock of catchable fish at a given time. It represents part of the fisheries potential.	RLS data: https://www.reeflifesurvey.com RLS method: 1 Trophic guild data: 2 Fishable families: *3, expert opinion*
Taxonomic richness	Number of teleost species in a reef (only non-cryptobenthic and non-anguiliforms teleosteii)	teleosteii species /reef(500m²)	component of teleostean biodiversity	
Elasmobranch diversity	Number of elasmobranch species detected in a reef (no additional filter)	elasmobranch species	component of elasmobranch biodiversity.	

Contributions	Assessment	Unit	Impact	References and data sources
		/reef(500m²)	Presence of rare/endangered species	
Endemism	Mean of endemism of species present in a reef. Species endemism = [max(range of each species) - specific range] / [max(range of each species) - min(range of each species)]. This way, the most ubiquitous species has an endemism of 0, while the species with the smallest living area has an endemism of 1. Range maps of species were extracted from Duhamet et al. (2023)[4], based on the method of Albouy et al. (2019)[5] with occurrence data from OBIS (https://obis.org/).		presence of species with narrow geographic range. Potential sensitivity of species to anthropogenic pressures, from a biodiversity protection perspective.	6 Range map data: 4 , method from 5
Functional and phylogenetic entropy	Reef functional entropy: sum of pairwise functional distance weighted by relative biomass of species inside each reef (mFD package). Reef phylogenetic entropy: phylogenetic distance weighted by relative biomass of species inside each reef (Entropart package).		complementarity in functional niches	Functional entropy from R package mFD v1.0.5 [7] (https://cran.r-project.org/web/packages/mFD/index.html) Phylogenetic tree from 8 9; Phylogenetic entropy calculated with R package Entropart v1.6-13 [10] (https://cran.r-project.org/web/packages/entropart/index.html)
Traits and Evolutionary distinctiveness	Functional distance between each species in a Diet x Size x Water position x Activity trait space (mFD package). Mean of species distinctiveness at the reef level. Mean of species evolutionary distinctiveness at the reef level (Picante package).		Importance of evolutionary history of communities in the adaptability of ecosystems.	7 Trait distinctiveness from R package mFD v1.0.5 (https://cran.r-project.org/web/packages/mFD/index.html) Phylogenetic tree from 8 Computation with R package Picante v1.8.2

Contributions	Assessment	Unit	Impact	References and data sources
				(https://cran.r-project.org/web/packages/picante/index.html)
Nitrogen and Phosphorus Recycling*	Individual phosphorus and nitrogen excretion estimated with the bioenergetics modeling described in Schiettekatte et al (2020)[11], using the fishflux R package (https://nschiett.github.io/fishflux/index.html). Sum up all individual excretions at reef scale.	$g_{nutrients} \cdot m^{-2}.d^{-1}$	Inorganic nutrients released by fishes in the ecosystem enhance growth of primary producers	Methods for bioenergetics modeling from 11
Carbonates excretion* Low Mg Calcite High Mg Calcite Aragonite Monohydrocalcite Amorphous carbonate	Individual carbonate excretion estimated using recently published models (Ghilardi et al., 2023)[12]. Sum up all individual contributions at the reef scale.	$\mu mol. m^{-2}.d^{-1}$	Release of carbonate in the ecosystem = enhance inorganic carbon cycling	Assessment model: 12 Data from: 13
Trophic web robustness	We constructed a trophic metaweb from trophic interaction probabilities between species by applying a body size niche model described by Albouy et al. (2019)[5]. We extracted local trophic webs of each reef to assess their robustness to secondary extinction (Rob0.5), with the allometric coefficient linking the number of links and species: L=(S/2)^b => b = log2(L) / (log2(S) - 1) (Carpentier et al., 2021).		robustness of an ecosystem to local species extirpations[14]	Trophic web model: 5 Trophic web analysis: 14
Mean Trophic Level	In each reef, we weighted species trophic level inferred in each local trophic web (see above), by the relative biomass of each species.		Proxy of the biomass stability through time in empirical food web[15]	Trophic web model: 5 Trophic web analysis: 15
Turnover of Available	Individual biomass turnover assessed with rfishprod package. Reef turnover	$\%.d^{-1}$	Biomass turnover of	16, 17 Data from 18

Contributions	Assessment	Unit	Impact	References and data sources
Biomass	is determined as the proportion of biomass produced per day (total production per day / total biomass).		targeted species in ecosystems. Proxy of the rate at which humans can harvest a given portion	
Available nutrients: Calcium Iron Zinc Selenium Vitamin A Omega 3	Nutrient quantities are determined from the nutrient concentration (Calcium, Iron, Omega 3, Selenium, Vitamin A, Zinc) in each species and their biomass in each reef. Nutrient availability is considered as the total nutrient quantities present in a 100-g food portion (wet weight) of fishable species at the reef scale.	calcium, iron, zinc: mg/100 g of fish Selenium, Vitamin A: µg/100 g of fish Omega 3: g/100g of fish	Availability of essential nutrients for local populations. Nutrient concentrations are independent of the available biomass and so focus on the nutritional quality of fish relative to fishing effort.	Data from 19
Aesthetic value	Estimation of species aesthetic value at the reef level, by accounting for species composition (individual species aesthetic values) and richness.		potential for the development of tourism activities, and emotional links to coral reef biodiversity	Methods from 20 and 21; data from 22
Public interest	Public interest of species is obtained by combining the number of views of wikipedia articles, photos on Flickr and mention on twitter. Reef public interests is the 3rd quartile of species public interest of the reef fish.		Public concern and cultural importance of reef fish biodiversity.	Data from 22

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683 **Table S2: Methods for aggregating multiple contributions into a composite indicator.** We
684 present here different methods to reduce complex information from different variables into an easier-
685 to-use composite indicator. The comparison of these composite indicators for reef NN and NP scores
686 is presented in figure S13.
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Composite indicator	Method of aggregation	Interest of the method	Reference
Arithmetic unweighted mean	Arithmetic mean of reef contribution values. Each contribution is previously centered (mean of 0) and scaled (standard deviation of 1)	Takes into account the quantitative values of contributions, avoiding subjective choice of contribution weights	
Arithmetic weighted mean	Same as above, but with a weighting coefficient. The weighting coefficients have been chosen to give equal importance to each contribution category (e.g. "food web stability", see Table 1)	Gives equal importance to the different facets of contributions	
Estimator in Dependant Sample (EDS)	Arithmetic mean of centered and scaled contributions, weighted by their degree of independence	Avoids the over-influence of highly correlated contributions that repeatedly provide identical information, by giving more weight to independent contributions	24
Rank mean	Mean reef ranks across all contributions	Robust to outlier values	
Geometric aggregation	Weighted geometric mean of the contributions values of a reef. Each contribution is scaled between 1 and 2.	Geometric mean is less compensatory than additive methods (as arithmetic mean).	
Technique for Order Preference by Similarity to an Ideal Solution (TOPSIS)	Proximity index (Euclidean distance) to a theoretical ideal reef (maximum values for each contribution). Each contribution is centered (mean of 0) and scaled (standard deviation of 1).	Scales explicitly the reefs between worst-case and best-case scenarios.	25
Mazziotta-Pareto Index (MPI)	Non-compensatory composite index which, based on linear aggregation, introduces a penalty for reefs with unbalanced contributions.	Assumes imperfect substitutability between various dimensions. The MPI favors reefs with balanced contributions.	Concept: 26, Package used: 27
Factor analysis	By performing a principal component analysis (PCA), the composite indicator is based on the reef coordinates in each PCA axis, multiplied by the proportion of variance explained in each axis.	Cannot be used to estimate NN and NP scores, as PCA axes do not conserve the directionality of contributions when they are negatively correlated.	27

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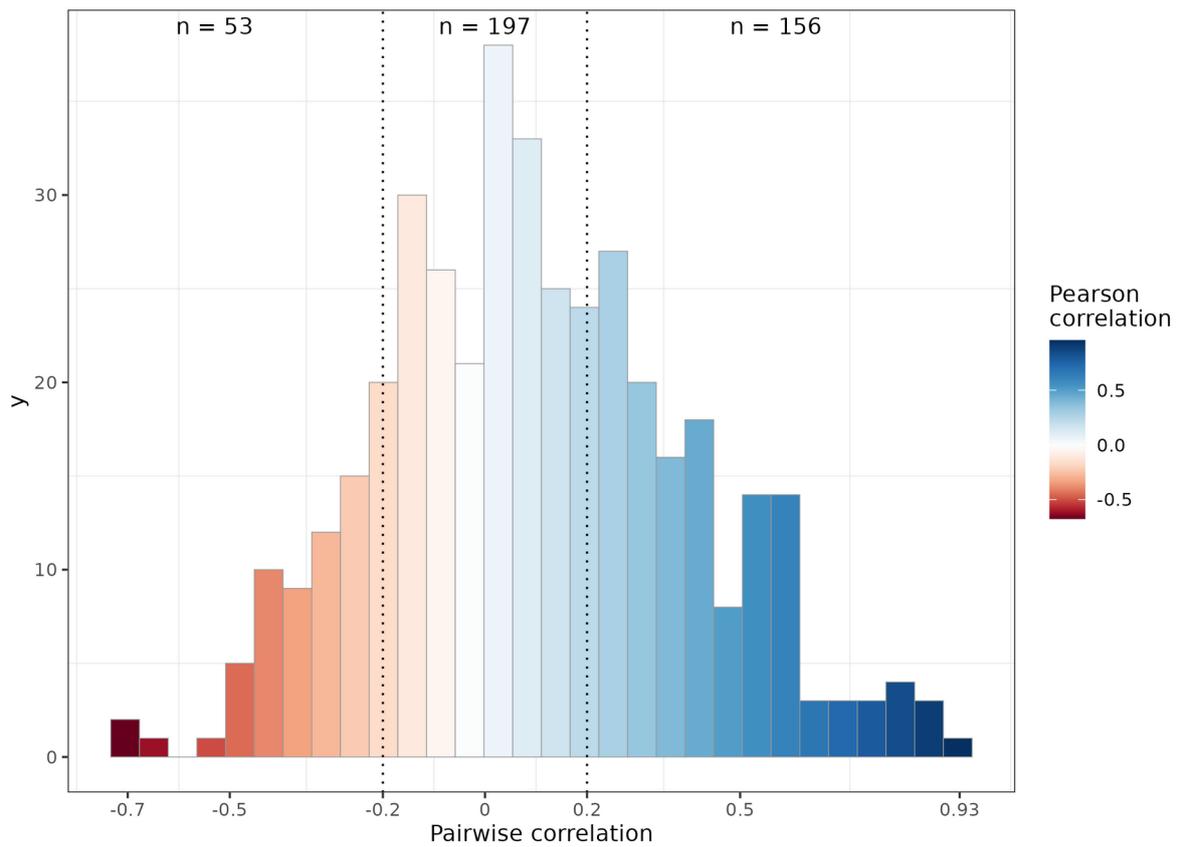
Figure S1: Distribution of pairwise correlation coefficients between all contributions. We measured the Pearson pairwise correlations between the 29 contributions provided by fishes in 1,237 tropical reefs. Within the 406 pairwise correlations, half show minimal dependence ($r \in$ [-0.2; 0.2]; bounded by the dotted lines), 156 (38%) pairs are positively correlated ($r > 0.2$) and 53 (13%) are negatively correlated ($r < -0.2$). All correlations with $|r| > 0.07$ are significant (p-value < 0.01) and the median of $|r|$ is 0.21.
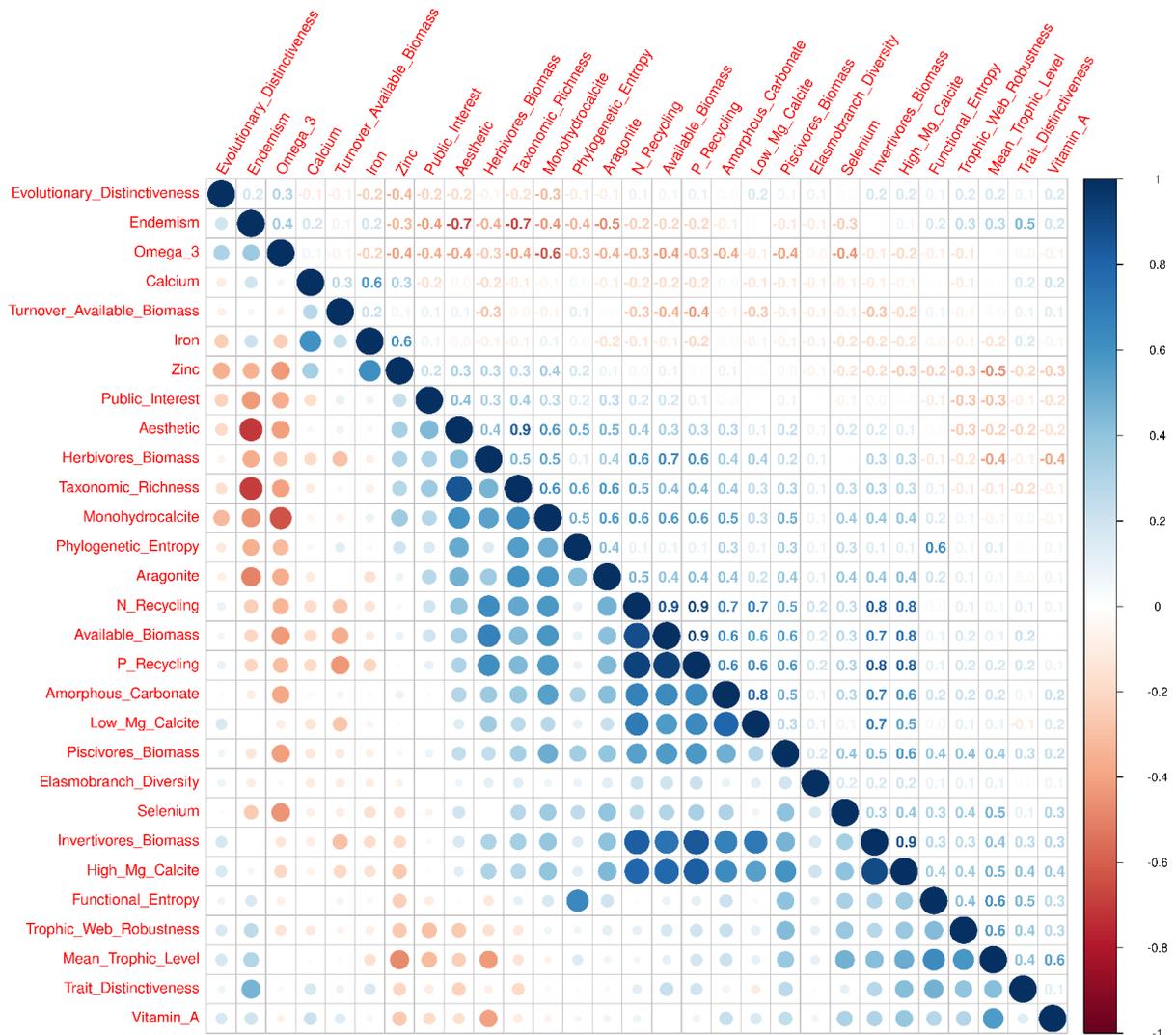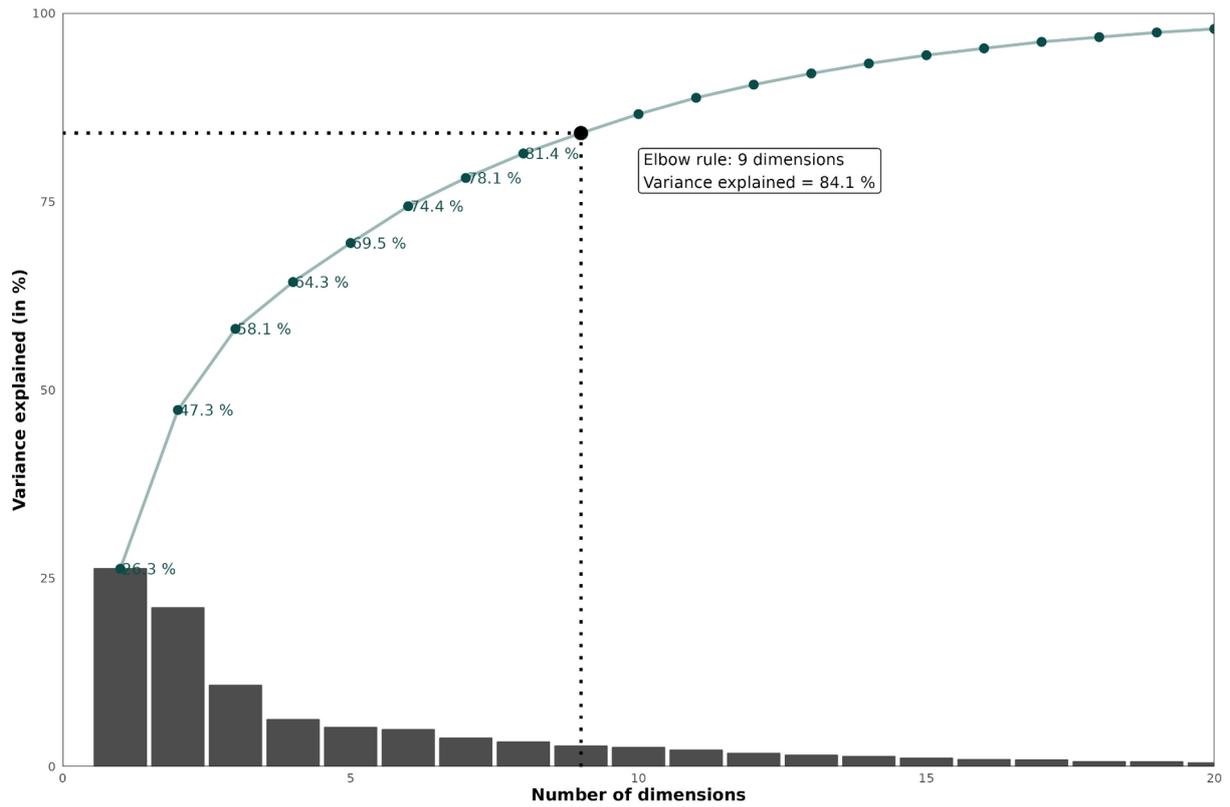
Figure S2: Correlogram of Pearson coefficient correlation between the 29 fish community contributions. Colors illustrate the value of the r coefficient of the correlation, with blue colors indicating positive correlations and red colors indicating negative correlations. The upper triangle precises each r coefficient.

Figure S3: Principal components, eigenvalues (in %), and explained variance from principal component analysis (PCA) performed at the global scale: 9 dimensions are worth describing the variability of reefs in a 29 contribution space. Gray bars indicate the eigenvalue of each PCA dimension, the blue line represents the cumulative curve of the variance explained, the last 9 dimensions of the PCA are not displayed. *The black dot represents the dimensionality required to parsimoniously describe covariations of contributions according to the elbow method (9 dimensions, 84% of variance explained).*
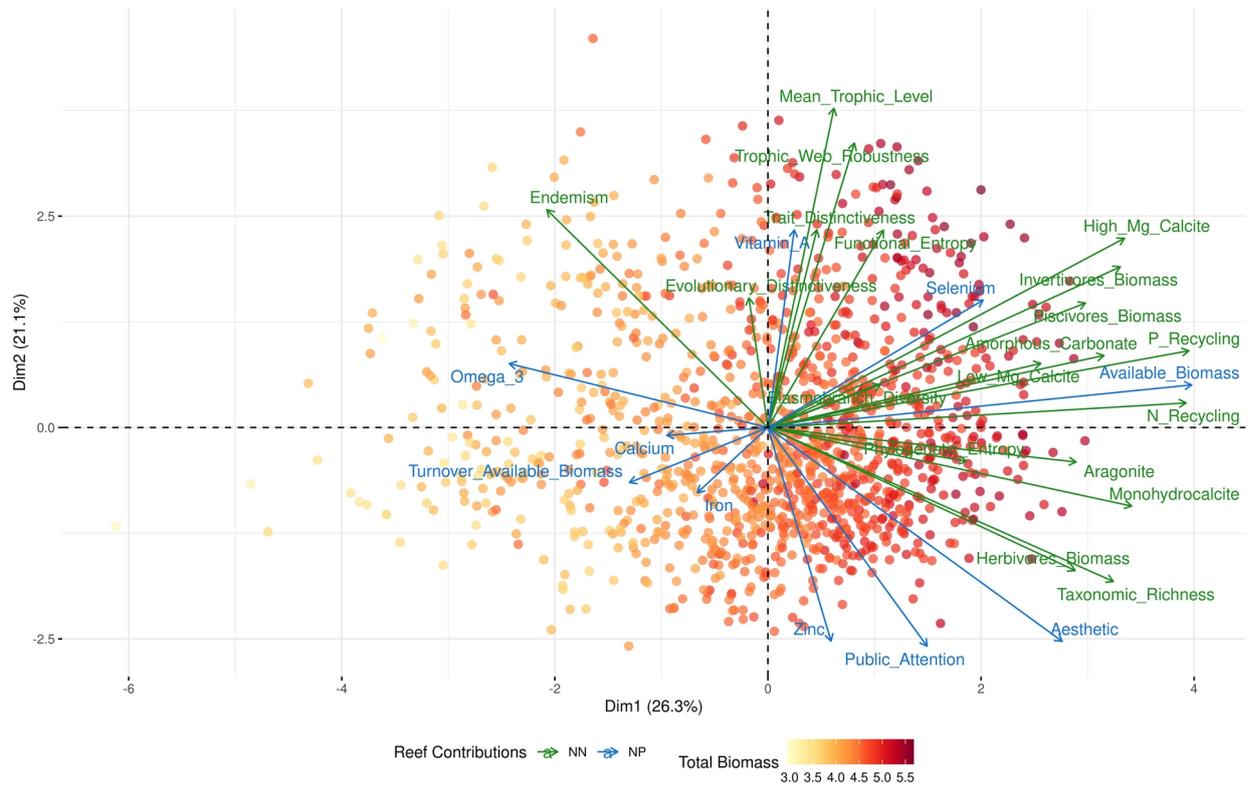
Figure S4: PCA biplot of all contributions used in this study. Color of variables indicates if contributions are relative to Nature (green) or People (blue). Points colors illustrate the total biomass in the reef. Many Nature-for-Nature contributions are positively correlated to the biomass, whereas Nature-for-people contributions are more scattered.
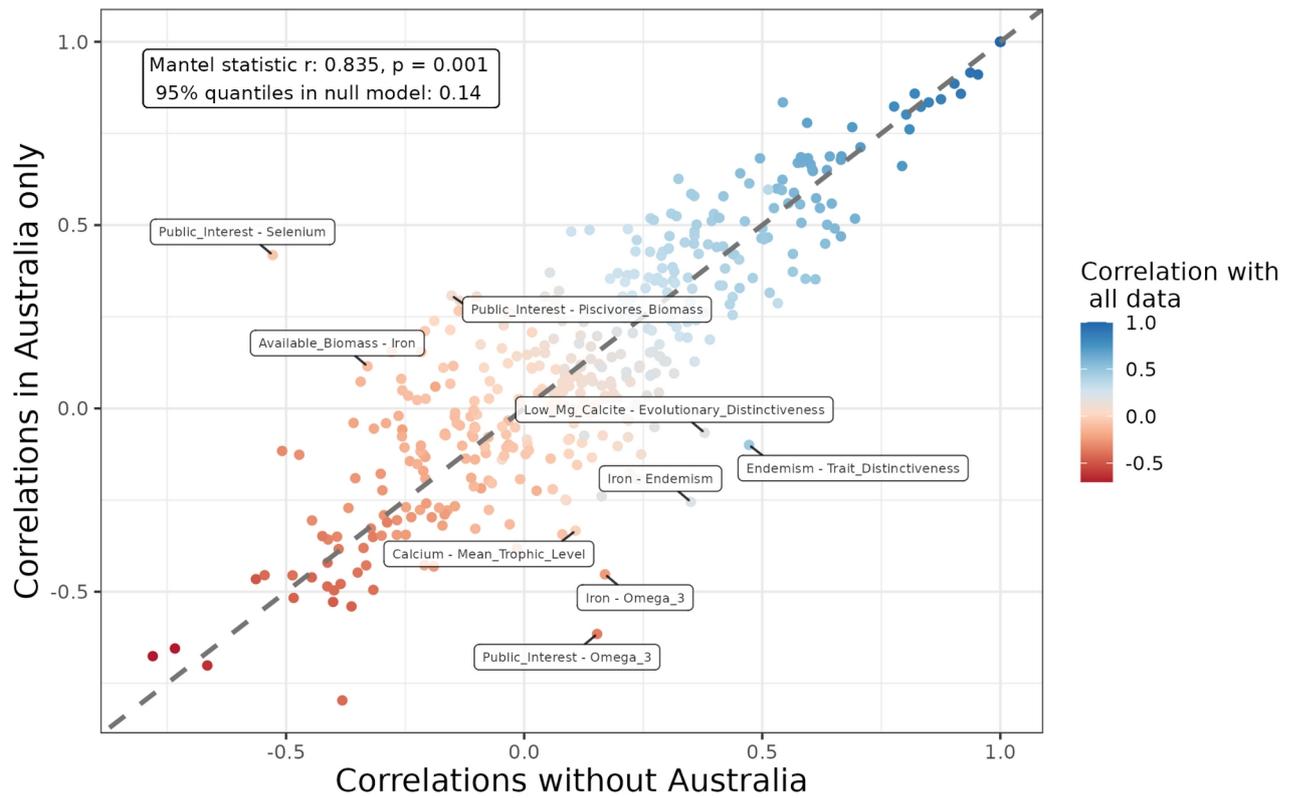
Figure S5: Robustness of pairwise correlations between contributions to the sampled region. We measured the Pearson pairwise correlations between the 29 contributions in reefs of Australia (n=702) and in reefs out of Australia (n=535). This plot compares the 406 pairwise correlations between these two sampled regions. The dashed line illustrates the 1:1 relationship. By comparing the correlation matrix of contributions between Australian reefs (n = 702 reefs) and tropical reefs in the rest of the world (n = 535 reefs), the Mantel test shows that these two correlograms are fairly similar (r = 0.835, p = 0.001).
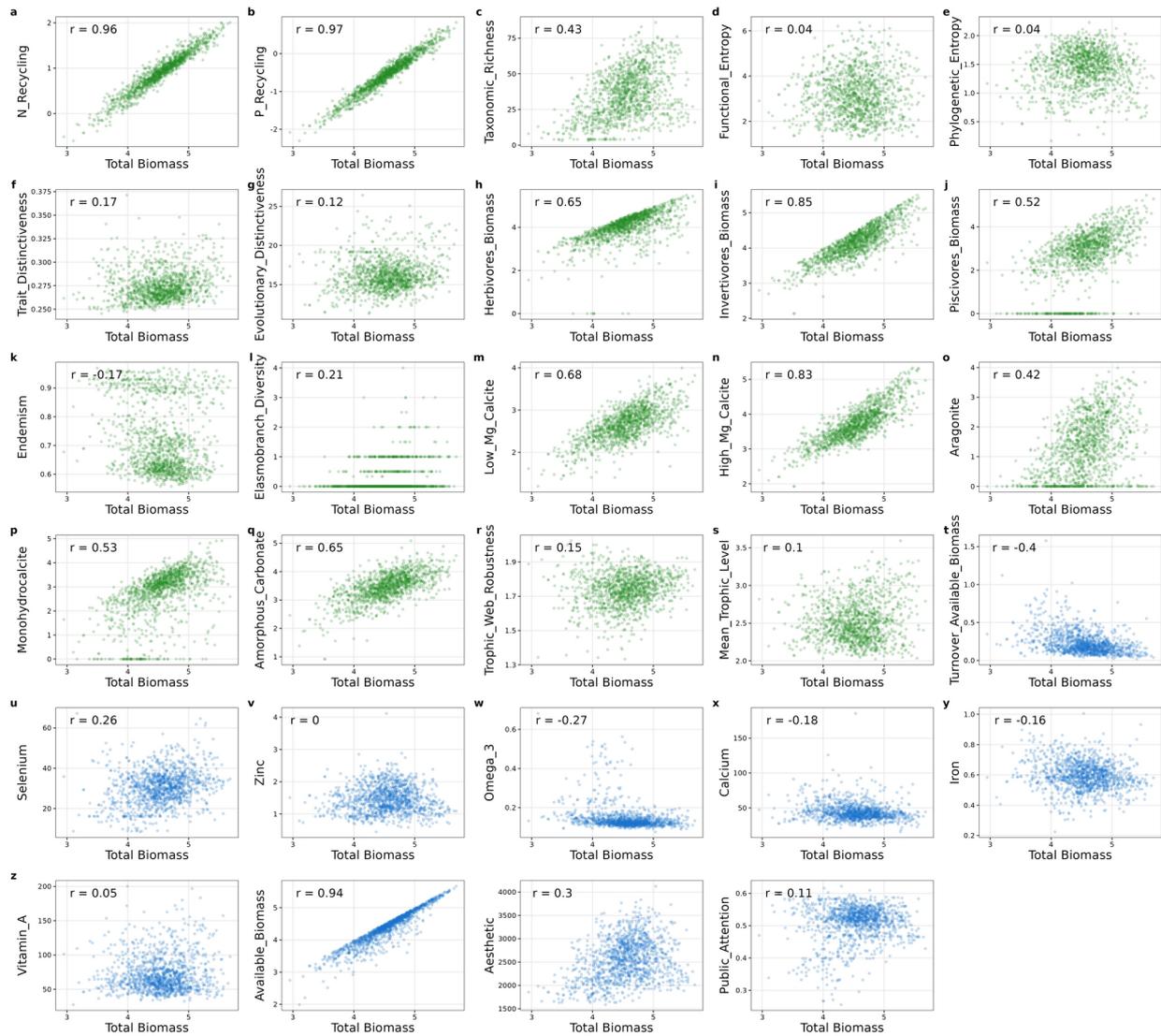
Figure S6: Relationship between Nature's Contributions and total biomass in coral reefs. At the global scale, we can see that many of Nature-for-Nature contributions (green) are positively correlated to the total biomass of the reef (r pearson correlation: median = 0.43, 1st quartile = 0.13, 3rd quartile = 0.67), whereas Nature-for-people contributions (blue) are more independent (r pearson correlation: median = 0.03, 1st quartile = -0.17, 3rd quartile = 0.22), except for available biomass (r = 0.94).

Figure S7: The position of reefs in the NNxNP space. For each reef, we average all contributions according to their category (NN or NP). In each quarter, the 5% outliers are named and highlighted in black (each name is preceded by a unique ID called 'SiteCode' in the RLS protocol).
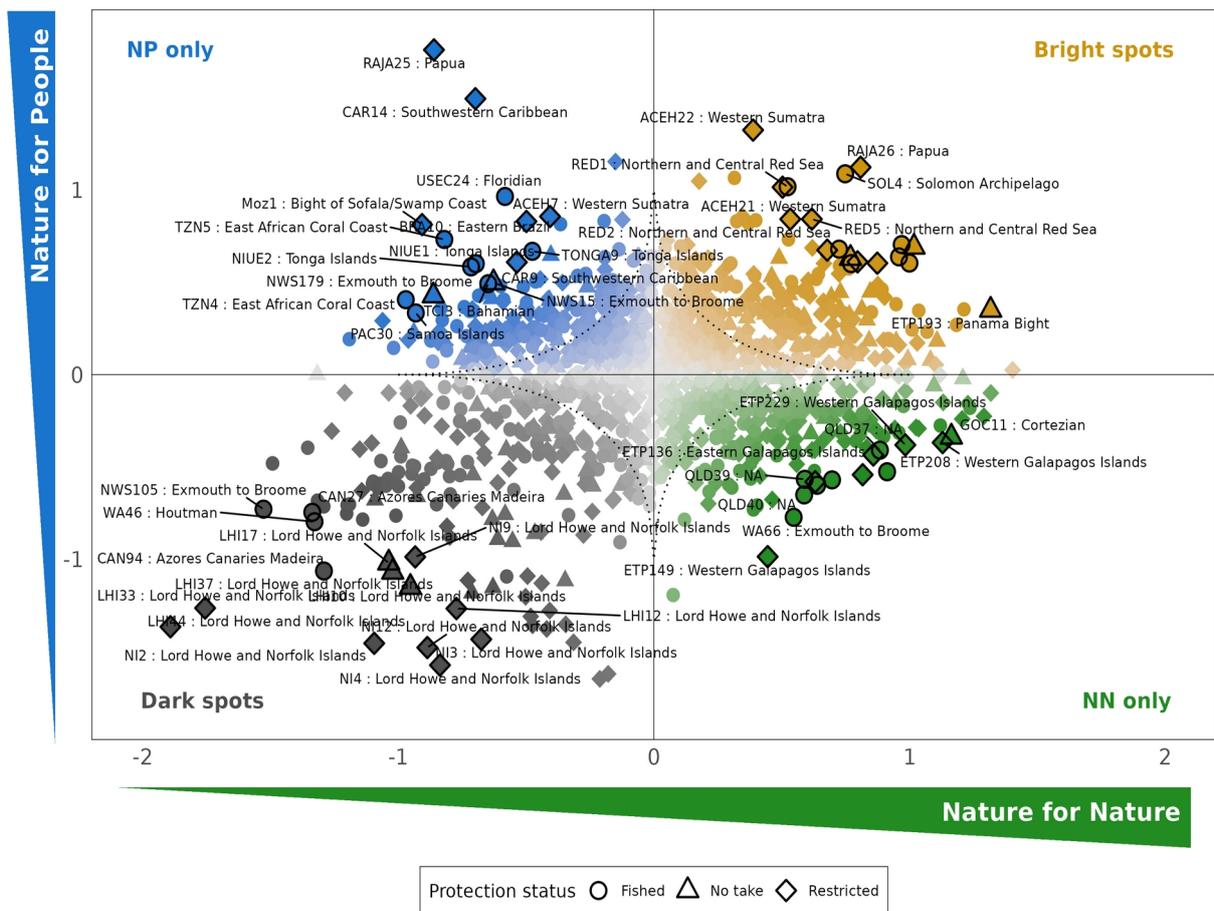
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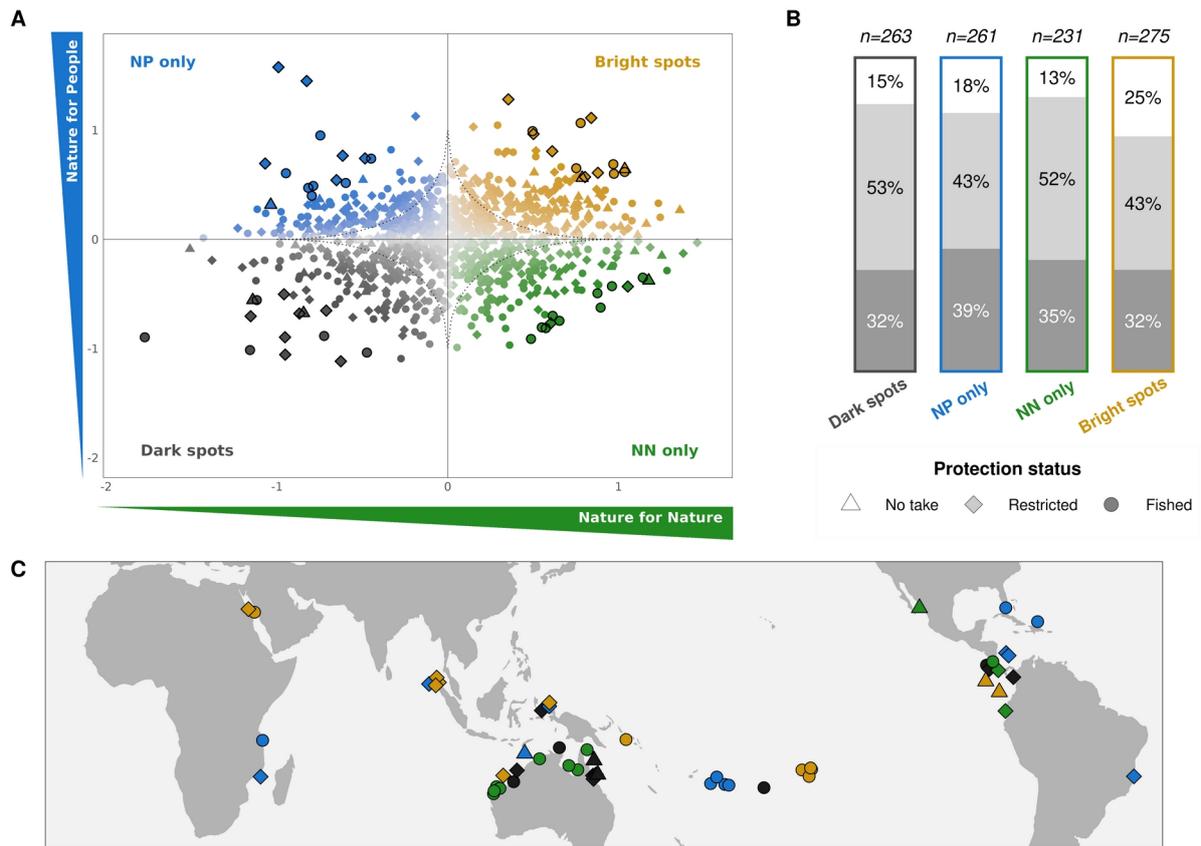
Figure S8: Sensitivity analysis: the four corners of the NN vs. NP spectrum and management strategies in tropical reefs only. *This figure has been constructed in the same way as figure 2, but considering only tropical reefs (minimum monthly sea surface temperature (SST) ≥ 20°C). We can note that the trends are largely conserved with figure 2, and that the reefs highlighted in (C) can be found in figure S11.*

(A) Relationship between NN and NP scores of tropical reefs. At the global scale, NN and NP scores are weakly correlated (r = 0.12, p < 0.001). The dashed lines indicate for each color the 50% quantile of the NNxNS 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. (B) Proportion of reefs under the different protection status (No take reserves, restricted areas, fished area). (C) Geographic distribution of the 5% tropical reefs outliers in each NN-NP category and their management status.

**A** Nature for Nature
Increment = 100 km, permutations = 99 , x intercept = 1347.9 km

B Nature for People
Increment = 100 km, permutations = 99 , x intercept = 263.3 km
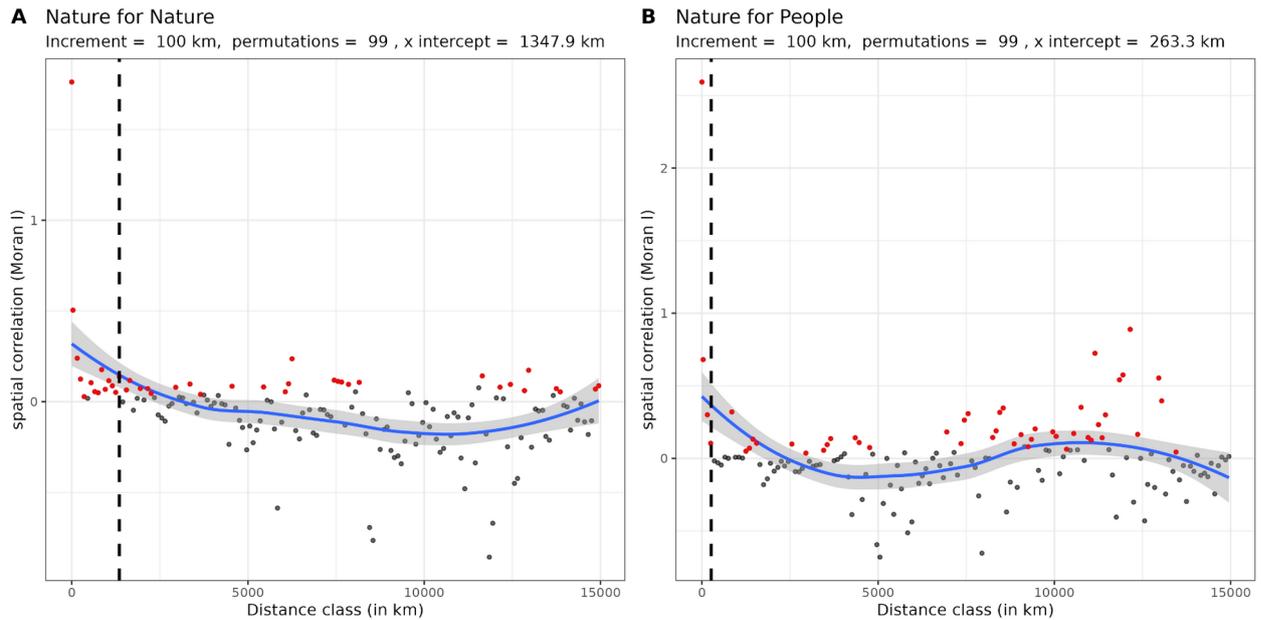
Figure S9: Spatial autocorrelation of NN and NP scores. Moran indices estimate the spatial dependence of scores at discrete distance classes (increment of 100 km). A Moran index measures the spatial autocorrelation of scores separately, e.g. by estimating whether nearby reef communities have closer scores than expected by chance. Moran indices significantly different from 0 are reported in red dots (p-value <0.01). Significant Moran index means that scores at this distance are more correlated than in a random spatial distribution of reefs. The Epperson x-intercept, highlighted by the dashed line, is the distance at which the reefs can be considered to be no more similar than expected by-chance-alone across the map (compared with 99 random models, i.e when the effect size of autocorrelation is close to 0). Reefs nearer than 1348 km have NN scores closer than expected by chance, while only reefs nearer than 263 km have close NP scores.
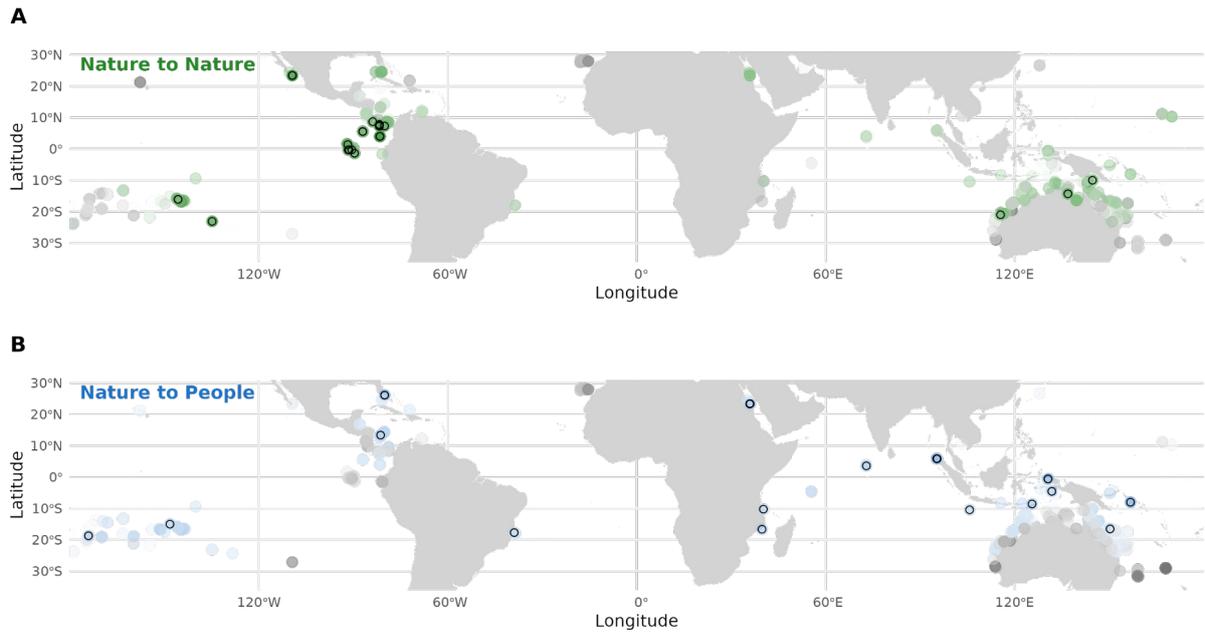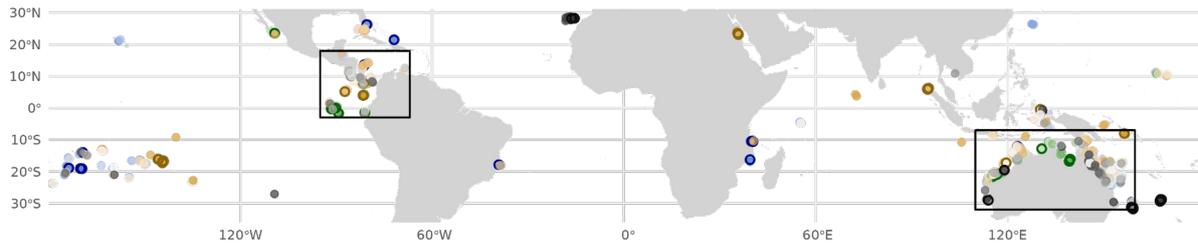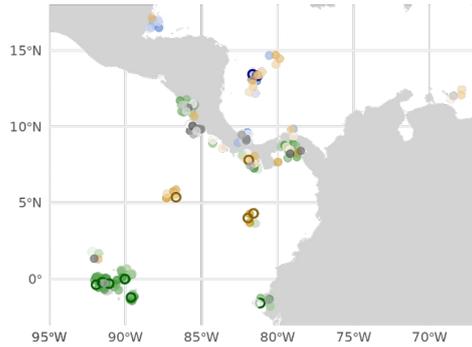
Figure S10: Global distribution of NN and NP scores. In each reef, we average all contributions according to their category (NN or NP). The intensity of green and blue represents the value of the scores of NN and NP respectively. The 2% highest scores are highlighted by black circles.
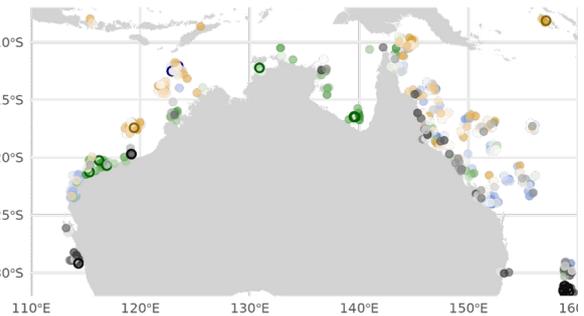
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807 **Figure S11: Geographic distribution of the tropical reefs according to their contribution to**
808 **Nature and People.** Colors of reefs are displayed according to their position in the NNxNP space (see
809 Fig. S7), reefs in the corner NN-only are in green, NP-only in blue, dark spots in grey and bright spots
810 in yellow. The brightness of colors hints at the level of contributions and the 5% outliers of each
811 corner are highlighted with a bold circle (see Fig. S7). Figures (B) and (C) are zooms on Central
812 America and Australia (black rectangles in (A)).
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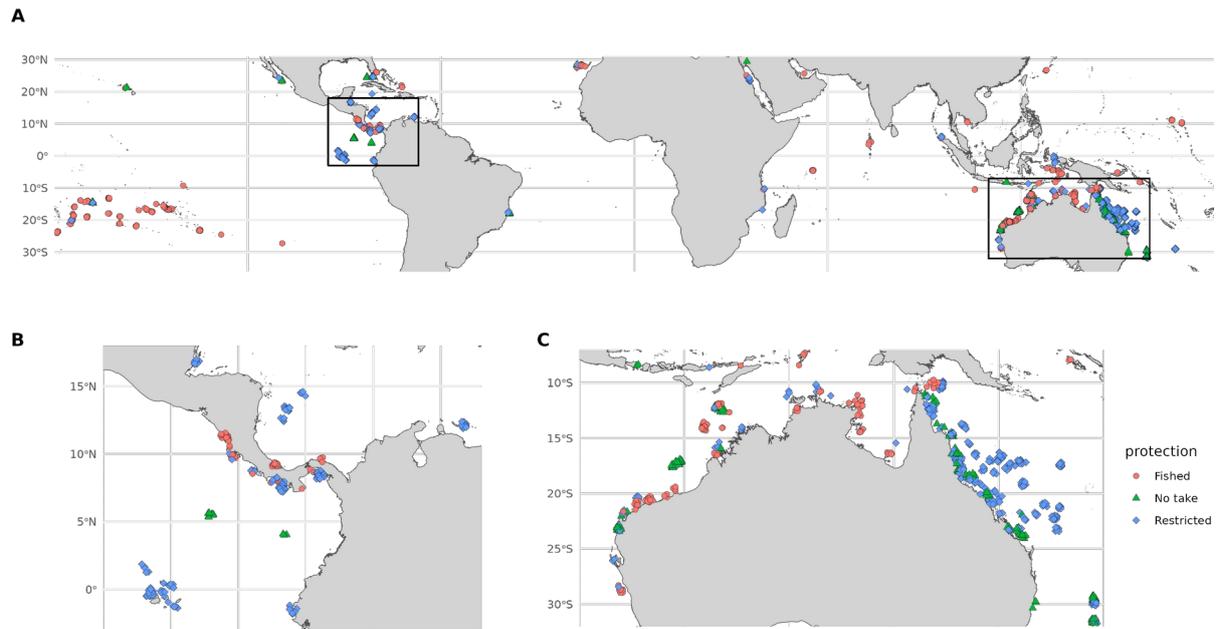
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823 **Figure S12: Reef life surveys used in this study and their protection status.** *Reefs within no-take*
824 *Marine Protected Areas (MPAs) or MPAs with multiple no-take zones, combined with high*
825 *enforcement (expert opinion; Cinner et al. 2020) were classified as "No-take", while reefs located in*
826 *other MPAs were qualified as "Restricted", and those without any documented MPAs were considered*
827 *as "Fished".* Figures (B) and (C) are zooms on Central America and Australia (black rectangles in
828 (A)).
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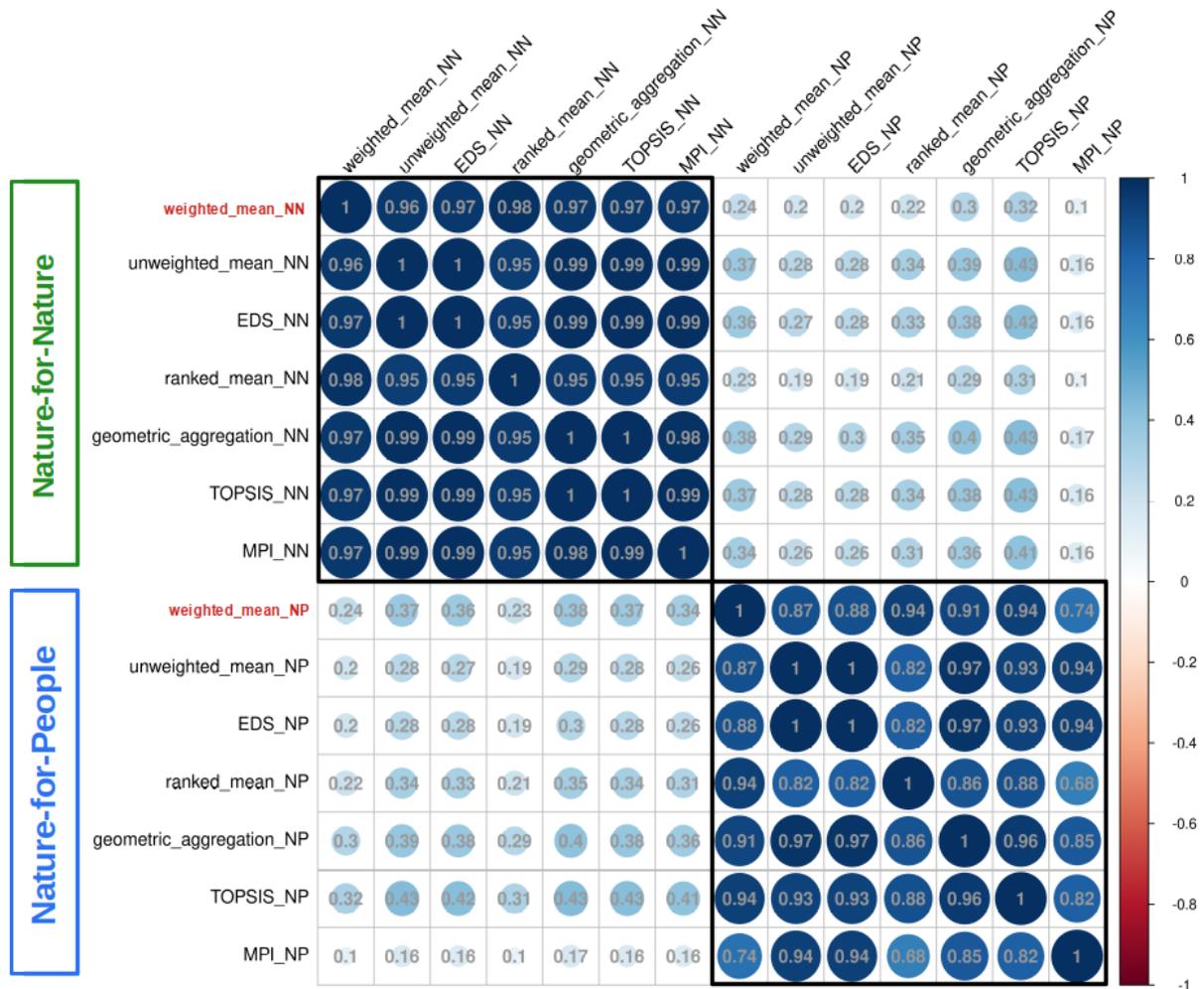
Figure S13: Correlogram of Pearson coefficient correlation between Nature-for-Nature (NN) and Nature-for-People (NP) scores estimated using different methods for calculating composite indicators. Colors illustrate the value of the pearson r coefficient of the correlation, with blue colors indicating positive correlations and red colors indicating negative correlations. The value of each r coefficient is specified for each pair in gray. All NN (and respectively NP) scores are highly positively correlated with the weighted arithmetic mean (highlighted in red), with Pearson correlation coefficients above 0.96 and 0.74 for NN and NP scores, respectively.

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