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Biological trade-offs underpin coral reef ecosystem functioning

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1 Title:

2 **Biological trade-offs underpin coral reef ecosystem**
3 **functioning**

4
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55

56 Abstract:

57

58 **Human impact increasingly alters global ecosystems, often reducing biodiversity and disrupting**
59 **the provision of essential ecosystem services to humanity. Therefore, preserving ecosystem**
60 **functioning is a critical challenge of the 21st century. Coral reefs are declining worldwide due to**
61 **the pervasive effects of climate change and intensive fishing, and while research on coral reef**
62 **ecosystem functioning has gained momentum, most studies rely on simplified proxies such as**
63 **fish biomass. This lack of quantitative assessments of multiple process-based ecosystem**
64 **functions hinders local and regional conservation efforts. Here, we combine global coral reef**
65 **fish community surveys and bioenergetic models to quantify five key ecosystem functions**
66 **mediated by coral reef fishes. We show that functions exhibit critical trade-offs driven by**
67 **varying community structures, such that no community can maximize all functions. Further,**
68 **functions are locally dominated by few species, but the identity of dominant species**
69 **substantially varies at the global scale. In fact, half of the 1,110 species in our dataset are**
70 **functionally dominant in at least one location. Our results reinforce the need for a nuanced,**
71 **locally tailored approach to coral reef conservation that considers multiple ecological functions**
72 **beyond the effect of standing stock biomass.**

73

74 Main text:

75

76 The flow of elements through biological communities fuels all ecosystems on earth, and
77 humans are increasingly threatening biodiversity and the persistence of these fluxes^{1,2}. Coral
78 reefs are a prime example of an ecosystem that is severely impacted by anthropogenic
79 activities, and drastic declines in habitat quality and fish biomass have evoked serious
80 concerns about the persistence of coral reefs^{3,4}. Maintaining ecosystem functions, defined as
81 fluxes of elements, is a major goal for coral reef conservation⁵⁻⁷. However, past evaluations of
82 functions on coral reefs have mostly relied on static proxies such as live coral cover, standing
83 stock biomass of reef fishes, or measures of diversity⁸⁻¹⁰. These simplified proxies, although
84 useful, may not properly represent ecological functions because fluxes of elements can scale
85 non-linearly with variables such as biomass¹¹. Therefore, improving the quantification of
86 ecological functions constitutes an important step toward the efficient management of coral
87 reef ecosystem functioning⁷.

88 As a dominant group of consumers, coral reef fishes are essential vectors of carbon (C),

89 nitrogen (N), and phosphorus (P)¹¹⁻¹³. Ecosystem functions mediated by coral reef fishes

90 include nutrient cycling, biomass production, herbivory, and piscivory (secondary
91 consumption)⁷. While the high diversity of coral reef fishes has inspired many studies that
92 focus on ecosystem functioning, only a handful of studies have attempted to quantify
93 functions as continuous fluxes⁷. Further, studies that have quantified functions as a flow of
94 energy and nutrients have mostly focused on single functions (e.g., biomass production^{14,15} or
95 fish excretion¹³), covering only a small number of species at local scales. Consequently,
96 trade-offs among multiple functions, their drivers, and their vulnerability to anthropogenic
97 stressors remain poorly understood in coral reef ecosystems across large spatial scales⁷.

98 Here, we integrate biogeochemistry and community ecology to advance our understanding of
99 the elemental fluxes that underpin reef fish functioning. Using empirical species-specific data
100 on basic organismal processes and extrapolation using Bayesian phylogenetic models, we
101 parameterize individual-level bioenergetic models to estimate five key ecosystem functions:
102 N excretion, P excretion, biomass production, herbivory, and piscivory for 1,100 species. We
103 apply these bioenergetic models to 9,118 reef fish transects across 585 sites at 98 localities
104 (i.e., regions encompassing sites that belong to the same biogeographic sub-province)
105 worldwide (Supplementary Table 1) to: (1) quantify community-level reef fish functions, (2)
106 investigate trade-offs among functions, and (3) extract the community and species-level
107 effects on these functions.

108 **Results**

109 We estimated five key ecosystem functions mediated by coral reef fishes across the globe
110 (Fig. 1). Across localities, all five functions show similar geographical patterns with on
111 average higher values around the equator. However, at the global scale, no location displayed
112 high levels (i.e. top 5%) of functioning across all functions. Therefore, multifunctionality
113 (i.e., the geometric mean of the five normalized functions) does not appropriately represent
114 the state of all functions assessed independently. For example, although the northern Coral
115 Sea had the highest multifunctionality value, piscivory in this location is 40% less than its
116 global maximum value.

117 Biomass is the most commonly employed indicator of coral reef functioning^{7,8}, and we
118 demonstrate a predictably strong relationship between fish biomass and all five functions
119 (Fig. 1). Specifically, in a multivariate mixed effects Bayesian model, the slopes of log-
120 transformed biomass were 0.932 (95%CI: 0.929, 0.934) for N excretion, 1.051 (1.047, 1.056)
121 for P excretion, 0.771 (0.764, 0.780) for production, 0.940 (0.923, 0.957) for herbivory, and

122 0.668 (0.635, 0.702) for piscivory. These slopes indicate that the relationships between
123 biomass and functions are all allometric, which demonstrates that biomass is not an
124 appropriate proxy for functioning. We also incorporated sea surface temperature (SST) due to
125 its impact on the metabolism and growth of individual fishes, which scales up to the
126 community¹⁶. We found positive effects of SST on N excretion, production, and herbivory
127 but no effects of SST on P excretion and piscivory (Supplementary Table 3).

128 Our multivariate model also allowed us to estimate the correlations between functions,
129 independent of the effects of biomass and SST. In particular, we estimated correlations
130 between functions on three levels: the locality effects, site effects, and residual variation (Fig.
131 2, Extended Data Fig. 1). The correlations displayed comparable patterns on each level. We
132 found negative trade-offs between P excretion and N excretion as well as P excretion and
133 biomass production. Further, we found slightly weaker negative correlations between
134 piscivory and N excretion as well as piscivory and herbivory. Thus, a reef fish community
135 cannot simultaneously display high values of functioning across all investigated functions.

136 To determine how community structure affects the variation and trade-offs of functions
137 beyond the effects of biomass and SST, we ran a multivariate Bayesian mixed effects model
138 with ten variables that describe the structure of each fish assemblage: species richness and the
139 median, lower, and upper 95% quantiles of size, immaturity (i.e., a measure combining
140 relative size and growth rate; see methods), and trophic level of individuals in a community.
141 Each of these variables has non-zero effects on at least one of the five functions, suggesting
142 that the observed trade-offs may be, at least in part, rooted in the structure of the focal
143 community (Fig. 3; Supplementary Table 4). Some associations, such as the negative and
144 positive effects of trophic level on herbivory and piscivory, respectively, are intuitive,
145 whereas others, such as the negative effect of immaturity on P excretion, are not immediately
146 obvious (Fig. 3).

147 Beyond community structure, we examined whether functions are driven by particular
148 species across sites. We quantified the degree of functional dominance (i.e.,
149 disproportionately large contributions by species to a given function) inside each community
150 at the site-level and found that, on average, functions are dominated by a small fraction of
151 species in each community (Fig. 4a). We also calculated the proportion of species that is
152 dominant in at least one site (i.e., species with a disproportionately high contribution as
153 compared to a community in which all species contribute equally), and we found that 49% of

154 all species contributed disproportionately to a function in at least one surveyed site (Fig. 4b).
155 Yet, very few species are dominant throughout their range (Fig. 4c). Thus, functions within
156 communities tend to be driven by few dominant species, but the identity of those dominant
157 species varies across sites.

158 **Discussion**

159 By quantifying five key processes mediated by coral reef fishes, we demonstrate that coral
160 reef ecosystem functioning is shaped by biological trade-offs, local community structure, and
161 species identity. Standing biomass is one of the most commonly employed indicators of coral
162 reef functioning^{7,8}, and our analyses confirm the strong influence of biomass on all other
163 processes. Yet, our results also show non-linear relationships between functions and biomass
164 and illustrate a high degree of residual variation, unexplained by biomass. This suggests that
165 biomass alone does not sufficiently characterize functioning; strong trade-offs occurred
166 among the five functions independent of biomass. Thus, using biomass as a proxy may mask
167 differences in community-level functioning. Furthermore, for a given value of biomass, no
168 reef can yield above average values across all five functions. While a reef may stand out as a
169 hotspot for one function, no reef can simultaneously maximize all functions.

170 The observed trade-offs among functions are driven by fish community structure and the
171 organismal physiology and life-history traits of its constituents^{17,18}. For example, we observed
172 a clear trade-off between P excretion and biomass production, which is mostly driven by
173 community age and trophic structure (Fig. 3). Communities dominated by fishes with high
174 trophic levels are characterized by high P excretion rates because predatory fishes have a P-
175 rich diet¹³. In contrast, biomass production is high in communities dominated by fishes that
176 occupy low trophic levels because herbivores tend to exhibit higher growth rates¹⁹. Moreover,
177 P is retained for skeletal growth in young fishes, thus limiting P excretion rates^{17,20}. Metabolic
178 theory predicts that small-bodied individuals have higher mass-specific metabolic rates,
179 leading to elevated consumption rates and disproportionate contributions to functions that
180 rely on rapid energetic turnover such as herbivory, piscivory, production, and N
181 excretion^{15,21,22}.

182 Our results reveal that functions consistently rely on a few dominant species, but the
183 identities of local, dominant species strongly vary across sites²³. Locally, a small number of
184 high-performing taxa may disproportionately impact rates of functioning at the community

185 level due to high biomass or abundance²⁴, which may have led to their designation as
186 functionally-dominant “key species” in various locations²⁵. However, our results also reveal
187 that no species dominated throughout its geographical range, and half of all species
188 contributed disproportionately to a specific function in at least one site. Thus, it is not
189 possible to pinpoint widespread key species that dominate functioning throughout their range
190 and can be placed at the center of conservation guidelines; rather, identifying local species
191 dominance across functions may be the best approach for small-scale conservation efforts,
192 and the preservation of regional reef fish biodiversity should be prioritized based on broad
193 scale policy.

194 Our global analysis of multiple functions suggests pathways by which human-induced shifts
195 in reef fish community structure may impact coral reef ecosystems. Fishing and climate-
196 induced coral loss have caused declines in reef fish biomass and shifts in community
197 structure^{26,27}, and we suggest that these changes will differentially affect ecosystem
198 functioning. Intensive fishing and associated reductions in the biomass of large fishes, for
199 example, alters the size, age, and trophic structure of fish communities²⁷. When accounting
200 for the effect of biomass, these community shifts can enhance N excretion and production¹⁵,
201 but they will negatively impact P excretion, herbivory, and piscivory. Further, declines in
202 coral cover related to climate change and warming seas are often associated with shifts
203 toward herbivores^{28,29}. Herbivores generally contribute little to P excretion^{13,17}, so a shift to
204 herbivore dominance and the subsequent decline of community-level P excretion may change
205 the balance of nutrient cycling on coral reefs, potentially favoring algal growth over corals³⁰.

206 Sustaining biomass, diversity, and ecosystem functioning are central objectives of most
207 conservation initiatives⁸. While safeguarding fish biomass enhances functioning, the trade-
208 offs between key functions reveal a critical challenge for coral reef conservation, where
209 actions to enhance one function may negatively impact another. For example, the
210 establishment of marine protected areas, which are one of the primary conservation strategies
211 for coral reefs³¹, may protect herbivorous species. However, marine protected areas do not
212 protect reefs from the pervasive effects of climate change³¹, and community shifts towards
213 herbivore domination may result in the decline of P excretion. Thus, measuring conservation
214 success with biomass or solely one function (e.g., herbivory) can mask the collapse of other
215 essential functions. It is necessary to gauge the state of reef ecosystems based on multiple,
216 complementary, process-based functions. Yet, we still lack understanding of process-based
217 functioning or the definition of a “functional” coral reef⁷. Establishing functional baselines

218 for global coral reefs is a critical challenge for future studies. Until then, our results suggest
219 that coral reef fish functions can be managed by enhancing standing stock biomass,
220 protecting local key species and vulnerable constituents of the community (e.g., large
221 carnivores), and promoting regional biodiversity.

222 We demonstrate that the variability in processes that govern elemental cycling in complex
223 ecosystems such as tropical coral reefs represents an unrecognized challenge for protecting
224 ecosystem functioning. Management strategies that call for the enhancement of ecosystem
225 functioning via an economic mindset (i.e., where higher functioning is better) are not
226 feasible. Instead, conserving coral reef ecosystem functioning will require a more nuanced
227 approach that considers processes that vary beyond the effect of standing stock biomass and
228 are subject to local trade-offs, drivers, and anthropogenic threats.

229 **Methods**

230 **1. Underwater visual census database**

231 We used a published global database of reef fish abundances and sizes collected along belt
232 transects¹⁶. This database encompasses 9,118 transects across 585 sites (within 98 localities)
233 in the Central Indo-Pacific, Central Pacific, Eastern Pacific, Western Indian, Eastern Atlantic,
234 and Western Atlantic Oceans. Sites are defined as small islands or stretches of continuous
235 reefs in larger coastlines and localities encompass sites that belong to the same biogeographic
236 sub-provinces¹⁶. The database only includes transects on the outer reef slope and with a hard
237 reef bottom. Transects were carried out at a constant depth, parallel to the reef crest. We
238 discarded the species inside families for which we did not have body stoichiometry data,
239 individuals that were smaller than 7cm (to minimize the bias related to the identification of
240 small individuals), and rare species for which less than 20 individuals were recorded across
241 all transects. The dataset then included 1,110 species belonging to 25 families (Acanthuridae,
242 Balistidae, Bothidae, Chaetodontidae, Cirrhitidae, Fistulariidae, Haemulidae, Holocentridae,
243 Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mugilidae, Mullidae,
244 Ostraciidae, Pempheridae, Pomacanthidae, Pomacentridae, Sciaenidae, Scorpaenidae,
245 Serranidae, Siganidae, Tetraodontidae, and Zanclidae). Sea surface temperature (SST) for
246 each site was obtained from daily time-series data from the National Oceanic and
247 Atmospheric Administration (NOAA) covering a 5-year period (°C; 0.25° resolution) ^{(32;}
248 available from <https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html>).
249 Further, for each transect, we calculated species richness and estimated total standing stock

250 biomass of fishes by using Bayesian length-weight relationships available from FishBase³³.
251 All data processing and analyses were performed in the software program R (version 4.0.2; R
252 core team 2020).

253 **2. Quantification of functions**

254 For each transect, we estimated five key process-based functions mediated by fishes: nitrogen
255 excretion rate ($\text{gN m}^{-2} \text{day}^{-1}$), phosphorus excretion rate ($\text{gP m}^{-2} \text{day}^{-1}$), production of biomass
256 through growth ($\text{gC m}^{-2} \text{day}^{-1}$), herbivory, (i.e., ingestion rate of macrophytes ($\text{gC m}^{-2} \text{day}^{-1}$)),
257 and piscivory (i.e., ingestion rate of fishes ($\text{gC m}^{-2} \text{day}^{-1}$))⁷. These five functions were
258 estimated for each transect using individual-based bioenergetic models predicting fluxes of
259 carbon (C), nitrogen (N), and phosphorus (P) (e.g., daily C intake rates, N and P excretion
260 rates, and growth rates)¹⁷. This bioenergetic model framework integrates elements of
261 metabolic theory, stoichiometry, and flexible elemental limitation¹⁷. We estimated the input
262 parameters, including elements of metabolism, growth, and diet and body stoichiometry, for
263 all 1,110 species through the integration of empirical data, data synthesis, and extrapolation
264 based on Bayesian phylogenetic models (see supplementary methods). We then ran a unique
265 bioenergetic model for each combination of species identity, body size, and sea surface
266 temperature ($n = 30,668$) to obtain the contribution of each individual to each function in
267 each transect. Finally, we summarized functions at the community level by summing up all
268 individual contributions inside a transect and dividing the sum by the surface area. Each
269 function is thus expressed as dry mass (of C, N, or P) per day per square meter. We note that
270 N excretion, P excretion, and biomass production include contributions of all fishes, whereas
271 herbivory and piscivory are carried out by a subset of the community, with respect to their
272 trophic guild as defined by³⁴. To reduce the occurrence of misclassification of herbivores and
273 piscivores, we categorized a species as herbivorous or piscivorous if it had both the highest
274 probability to be classified in that trophic group and this probability was more than 0.5, based
275 on the probability scores of trophic guilds presented by Parravicini et al. (2020)³⁴. Further, as
276 a comparison, we estimated herbivory and piscivory rates using two alternative trophic guild
277 classifications based on expert opinion^{9,34} (Supplementary Data Fig. 3). Both the herbivory
278 and piscivory rates match the expert opinion trophic guild classifications. Finally, we
279 estimated multifunctionality, i.e., one measure that combines all five functions by taking the
280 geometric average of the five functions (normalized to a range between zero and 100). We
281 used the geometric mean because functions are dependent on each other and vary by several
282 orders of magnitude.

283 **3. Community structure variables**

284 We quantified a set of variables that characterize fish community structure. These variables
285 describe the size, age, and trophic distribution of the community, as these may all affect
286 functions¹⁷. Specifically, we calculated the 2.5%, 50%, and 97.5% quantiles of the total
287 length, immaturity, and trophic level of all individuals per transect. We included the 2.5%
288 and 97.5% quantiles to account for the spread of these traits within communities, while
289 avoiding the effect of outliers. The total length is based on visual estimations by divers. The
290 immaturity is quantified using the following formula:

$$291 \text{immaturity}_i = \kappa(l_\infty - l_i),$$

292 where κ is the species-specific growth rate parameter and l_∞ is the species-specific asymptotic
293 adult length, and l_i is the total length of individual i . Essentially, this is the derivative of the
294 von Bertalanffy growth model for a certain length, and the higher this value is, the younger
295 the individual. Finally, trophic level was extracted from FishBase³⁵.

296 **4. Multivariate regression models**

297 We fitted three multivariate Bayesian models with all five functions to (1) predict functions
298 on the locality level to create a map of functions, (2) investigate the effects of biomass and
299 SST as well as the correlations among functions independent of biomass and SST, and (3)
300 estimate the effects of the community structure on each function. For each model, functions
301 were log-transformed to ensure the normal distribution of residuals and an allometric
302 relationship with biomass, which is hypothesized by metabolic theory³⁶. In the underwater
303 visual transect database, 291 transects (3%) did not contain herbivores and 4,467 transects
304 (49%) did not contain piscivores yielding zeros for herbivory and piscivory, respectively. We
305 considered that these absences of herbivores or piscivores are likely an underestimation of
306 their actual abundance at the surveyed reef site, as all reefs typically host a few herbivores
307 and piscivores (i.e., they are likely false zeros). To avoid removing all transects with missing
308 values for herbivory or piscivory ($n = 4,620$) from our database when running multivariate
309 analyses, we imputed these zeros as missing values, and they were eventually set as
310 parameters in the multivariate models.

311 First, we performed a multivariate intercept-only regression model with the five log-
312 transformed functions to estimate the functions per locality. The model structure includes
313 random effects for localities and sites:

$$314 \begin{bmatrix} y_{E_N,i} \\ y_{E_P,i} \\ y_{B,i} \\ y_{H,i} \\ y_{P,i} \end{bmatrix} \sim MVNormal \left(\begin{bmatrix} \mu_{E_N,i} \\ \mu_{E_P,i} \\ \mu_{B,i} \\ \mu_{H,i} \\ \mu_{P,i} \end{bmatrix}, S \right),$$

$$315 \begin{aligned} \mu_{E_N,i} &= (\beta 0_{E_N} + \delta_{E_N,loc} + \delta_{E_N,site}) \\ \mu_{E_P,i} &= (\beta 0_{E_P} + \delta_{E_P,loc} + \delta_{E_P,site}) \\ \mu_{B,i} &= (\beta 0_B + \delta_{B,loc} + \delta_{B,site}) \\ \mu_{H,i} &= (\beta 0_H + \delta_{H,loc} + \delta_{H,site}) \\ \mu_{P,i} &= (\beta 0_P + \delta_{P,loc} + \delta_{P,site}), \end{aligned}$$

$$316 S = \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix} R = \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix},$$

317 where i is the index of the transect, $y_{E_N,i}$ is the N excretion rate of transect i , $y_{E_P,i}$ is the P
318 excretion rate, $y_{B,i}$ is the biomass production rate, $y_{H,i}$ is the herbivory rate, $y_{E_N,i}$ is the
319 piscivory rate, σ represents the residual error of each function (E_N , E_P , B , H , and P), R is the
320 correlation matrix of the residuals, and $\delta_{function,loc}$ and $\delta_{function,site}$ represent the random effects of
321 locality and sites, respectively. Locality- and site-level effects are also structured including
322 covariation among functions. There are thus three correlation matrices in total, meaning that
323 the model will estimate the correlation between functions on three levels: locality, site, and
324 transect.

325 We used non-centered parameterization for site and location effects and all standard
326 deviations had the following prior: $\sigma \sim student(3,0,2.5)$. We used a prior (lkj_corr) for each
327 of the three correlation matrices ($R \sim lkj_corr(1)$).

328 Second, we ran a mixed-effect model to investigate the effects of biomass and SST on all
329 functions and the correlations among functions (independent of biomass and SST). The
330 standing stock biomass of communities is positively related to all functions because of the
331 additive nature of the quantification and metabolic theory³⁶. Furthermore, because of the
332 known relationship between temperature and parameters related to growth and respiration
333 (see supplementary methods), functions are expected to be affected by temperature. We thus

334 fitted a multivariate Bayesian mixed-effect model using transect-level log-transformed
 335 functions that included random effects for sites and localities:

$$336 \begin{bmatrix} y_{E_N,i} \\ y_{E_p,i} \\ y_{B,i} \\ y_{H,i} \\ y_{P,i} \end{bmatrix} \sim MVNormal \left(\begin{bmatrix} \mu_{E_N,i} \\ \mu_{E_p,i} \\ \mu_{B,i} \\ \mu_{H,i} \\ \mu_{P,i} \end{bmatrix}, S \right),$$

$$337 S = \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_p} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix} R \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_p} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix}$$

$$338 \begin{aligned} \mu_{E_N,i} &= (\beta 0_{E_N} + \delta_{E_N,loc} + \delta_{E_N,site}) + \beta 1_{E_N} \log(biomass), i + \beta 2_{E_N} SST, i \\ \mu_{E_p,i} &= (\beta 0_{E_p} + \delta_{E_p,loc} + \delta_{E_p,site}) + \beta 1_{E_p} \log(biomass), i + \beta 2_{E_p} SST, i \\ \mu_{B,i} &= (\beta 0_B + \delta_{B,loc} + \delta_{B,site}) + \beta 1_B \log(biomass), i + \beta 2_B SST, i \\ \mu_{H,i} &= (\beta 0_H + \delta_{H,loc} + \delta_{H,site}) + \beta 1_H \log(biomass), i + \beta 2_H SST, i \\ \mu_{P,i} &= (\beta 0_P + \delta_{P,loc} + \delta_{P,site}) + \beta 1_P \log(biomass), i + \beta 2_P SST, i \end{aligned}$$

339 where $\beta 1_{E_N}, \beta 1_{E_p}, \beta 1_B, \beta 1_H, \beta 1_P$ are the fixed effects of the log-transformed biomass, and

340 $\beta 2_{E_N}, \beta 2_{E_p}, \beta 2_B, \beta 2_H, \beta 2_P$ are the fixed effects of SST. Locality- and site-level effects are

341 thus structured including covariation among functions, independent of biomass and SST.

342 Similarly, the residual variation of functions incorporates the correlations between functions,

343 without the effect of biomass and SST. We used similar priors as described above, and we

344 used weakly-informative normal priors for the model slopes ($\beta 1 \sim normal(1,1)$,

345 $\beta 2 \sim normal(0,1)$).

346 Finally, to investigate the effect of community structure while still accounting for the effects

347 of standing biomass and SST, we fitted a mixed effect multivariate model similar to the

348 model specified above, but we added all community structure variables:

$$349 \mu_{function,i} = \beta 0_{function} + \beta 1_{function} \log(biomass), i + \beta 2_{function} SST, i + \beta 3_{function} richness, i + \beta 4_{function} size_m, i + \beta 5_{function} size_{97.5}, i$$

350 where *richness* is the species richness, *size* is the total length, *troph* is the trophic level, *imm* is

351 the immaturity, and *m*, 2.5%, and 97.5% represent the 50%, 2.5%, and 97.5% quantiles

352 across the fish community, respectively. For these models, we used weakly informative priors

353 for the fixed effect parameters ($\beta_3 - \beta_{12} \sim normal(0,1)$) and the same priors as described
354 above for other parameters.

355 All Bayesian models were fitted using the R package *brms*³⁷, which uses Stan, a C++ package
356 to perform full Bayesian inference³⁸. The posterior distributions of model parameters were
357 estimated using Hamiltonian Monte Carlo (HMC) methods by using four chains of 2,000
358 samples, including 1,000 samples as a warm-up. Thus, a total of 4,000 draws were used to
359 estimate posterior distributions. The convergence and fit of the models were verified by
360 examining the Rhat, parameter trace plots, and posterior prediction plots (Extended Data Fig.
361 2).

362 5. Species dominance and contributions to functions

363 We estimated the relative contribution of each species to each function for all sites as
364 follows:

$$365 \text{ contribution}_{f,i,j} = \frac{F_{f,i,j}}{\sum F_{f,j}},$$

366 where i is a certain species, j is a site, and F is the value of function f .

367 Then, we quantified the degree of species dominance per function for each site. We first
368 ranked species according to their contribution to function, then we quantified the cumulative
369 contributions of species to functions. Finally, we used the area under the species
370 accumulation curve as a measure for the degree of dominance. Specifically, the degree of
371 dominance (DD) for a function performed by R species was calculated as follows:

$$372 DD = \frac{A - A_{min}}{A_{max} - A_{min}},$$

373 where A is the area under the curve, A_{min} is the theoretical area under the curve where each
374 species has an equal contribution to a certain function, and A_{max} is the theoretical area under
375 the curve where one species performs the entire function. They are quantified as:

$$376 A_{min} = \frac{R^2 - 1}{2R},$$

$$377 A_{max} = R - 1,$$

$$378 A = \sum_{i=2}^R \frac{C_i + C_{i-1}}{2},$$

379 where C_i is the contribution of a certain species and R equals the species richness in the case
380 of N excretion, P excretion, and production. For herbivory and piscivory, R represents the
381 number of herbivores and piscivores, respectively. The degree of dominance thus ranges
382 between 0 and 1, where 0 means that each species contributes equally and 1 means that a
383 single species performs the entire function.

384 Finally, we quantified the frequency of dominance per species (i.e., the number of sites in
385 which a species is dominant for a given function divided by the total number of sites in which
386 that species is observed). A species is considered dominant for a certain function in a given
387 site if its contribution is higher than $1/R$ (i.e., they contribute more than the situation in which
388 each species contributes equally to a certain function).

389

390 **Data availability**

391 All data needed to reproduce the figures are available on GitHub
392 (https://github.com/nschiett/global_proc) and figshare
393 (<https://doi.org/10.6084/m9.figshare.13285901.v1>). All empirical data that were used to
394 estimate parameters for bioenergetic modeling (see supplemental materials) will be available
395 on figshare (<https://doi.org/10.6084/m9.figshare.19134446.v1>) following a 2 year embargo.

396 **Code availability**

397 All code to reproduce the figures are available on GitHub
398 (https://github.com/nschiett/global_proc) and figshare
399 (<https://doi.org/10.6084/m9.figshare.13285901.v1>).

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413 **Author contributions**

414 N.M.D.S and V.P. conceived the idea and N.M.D.S, V.P., S.J.B., J.M.C., and S.V. designed
415 methodology; N.M.D.S., J.M.C., S.J.B., A.M., F.M., V.P., K.S.M., J.E.A. and D.E.B.
416 collected the data; N.A.J.G., D.R.B., D.E.B., J.E.A., J.E.A.-G., G.J.E., C.E.L.F., S.R.F.,
417 A.M.F., A.L.G., M.K., Y. L., O.J.L., F.M., E.L.R., F.A.R.-Z., R.D.S.-S., and L.V. shared
418 existing data. N.M.D.S. analyzed the data and led the writing of the manuscript. All authors
419 contributed significantly to the drafts and approved the final version for publication.

420 **Competing interests**

421 The authors declare no competing interests.

422

423 **Figure legends**

424

425 **Fig. 1: Maps of the five key ecosystem functions, multifunctionality, and the** 426 **relationships between the functions and biomass.**

427 Left: Dots indicate localities of field surveys, with dot sizes representing the ranked values of
428 the locality-level predictions of functions, and color scales showing categorical assignments
429 (black = < 25%, grey = 25-75%, color = >75%). Black outlines highlight the five localities
430 with the highest values of each function. Multifunctionality represents the geometric mean of
431 the five normalized functions. Right: The back-transformed predicted values for functions
432 and multifunctionality with increasing biomass. The lines represent the average modeled
433 relationship, and the shaded areas show the 95% credible intervals of the predictions. All
434 relationships between functions and biomass are non-linear.

435 **Fig. 2: Correlations of the five functions, accounting for biomass and sea surface** 436 **temperature.**

437 **a:** Modeled correlation coefficients of residual errors. Dots represent the average, and the
438 95% CI is too narrow to be shown. **b-k:** Scatter plots of the mean residual errors of the
439 functions.

440 **Fig. 3. Effects of ecological community variables on the five functions.**

441 Dots indicate fixed effect values from Bayesian linear regressions that examine the effects of
442 species richness, trophic level, size, and immaturity of fishes. To represent both the median
443 and spread of trophic level, size, and immaturity across individuals within a community, we
444 included lower and upper 95% quantile values of these three traits as community variables.
445 All data were log-transformed and standardized to compare across functions and variables
446 (see Supplementary Table 4 for parameter values on non-standardized data). Dots represent
447 the average effect size estimate, and horizontal lines indicate the 95% credible interval.
448 Immaturity is defined as the derivative of the von Bertalanffy growth model for a given size;
449 thus, the higher the value, the younger the individual.

450

451

452

453 **Fig. 4: Local dominance in species contributions to five ecosystem functions on coral**
454 **reefs.**

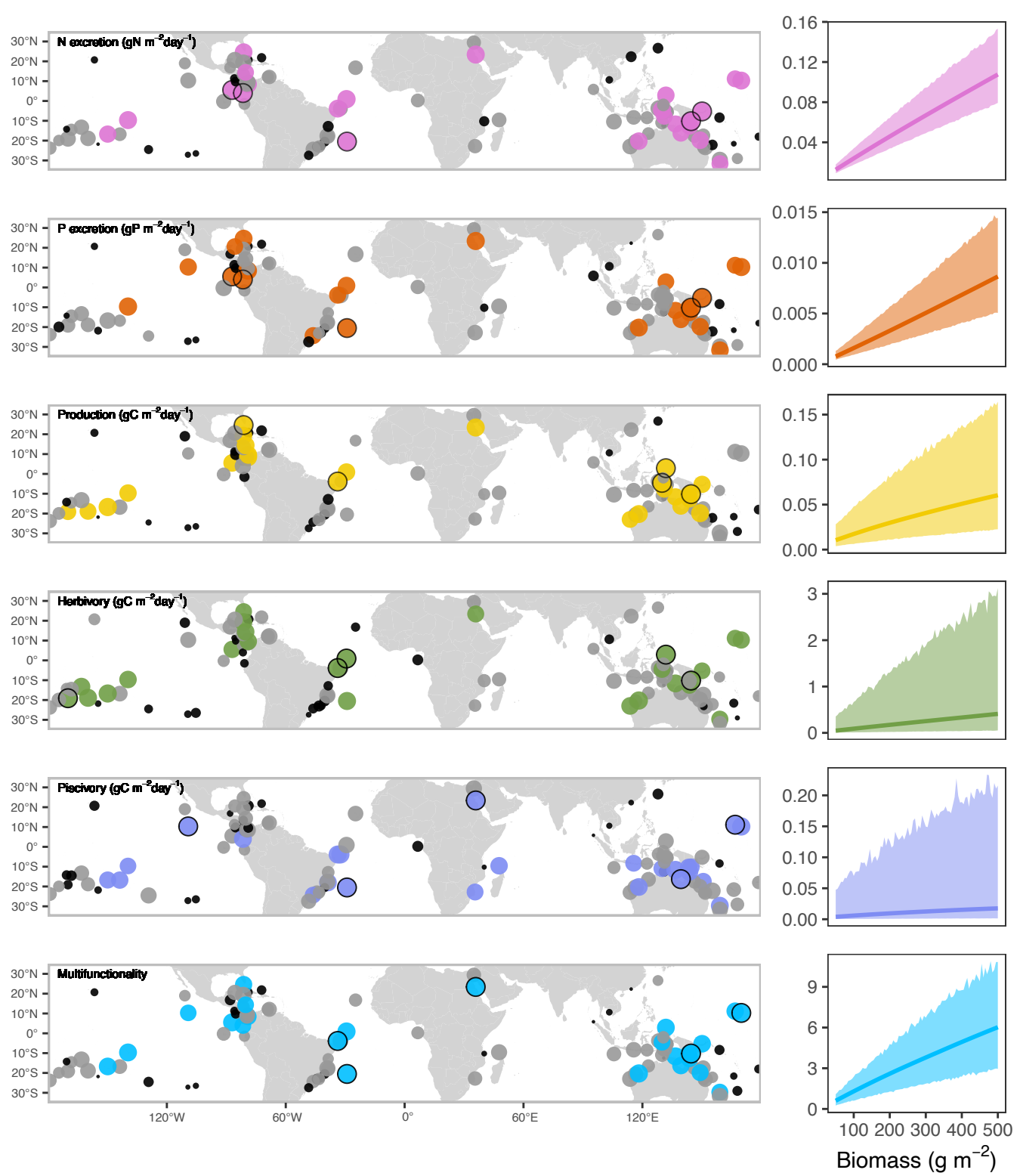
455 **a:** The degree of dominance for each function at the site level. The degree of dominance of a
456 community ranges between zero (all species contribute equally to the function) and one (a
457 single species is the sole contributor to a given function). Colored dots represent the raw
458 values, and the black dots and lines display the mean and 95% credible intervals of degree of
459 dominance among all sites. In some cases, the credible interval is too small to be visible. The
460 vertical dashed line shows the average degree of dominance of 1,000 randomly simulated
461 communities. **b:** Bar plot of the proportion of species that are dominant in at least one site
462 relative to the total number of species, or, for herbivory and piscivory, the total number of
463 herbivores and piscivores, respectively. **c:** Species-specific frequencies of dominance in each
464 function across all sites, ranging from zero (species are never dominant) to one (dominant
465 wherever present). The black dots and lines display the mean and 95% credible intervals of
466 the frequency of dominance among species. A species is categorized as dominant in a
467 community if its contribution to a function is higher than a scenario in which all species are
468 equal (i.e., one divided by the number of species that contribute to the function).

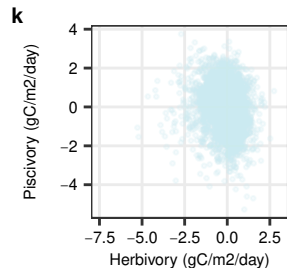
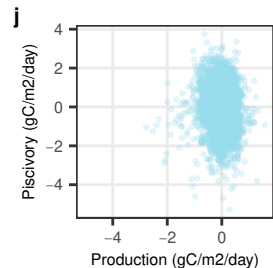
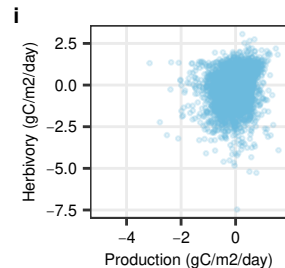
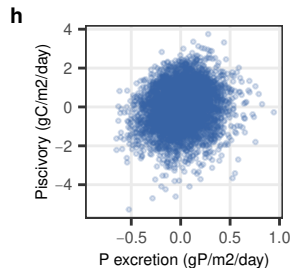
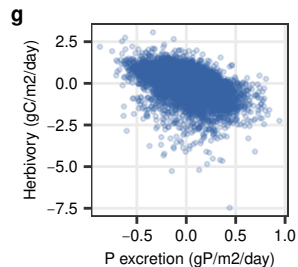
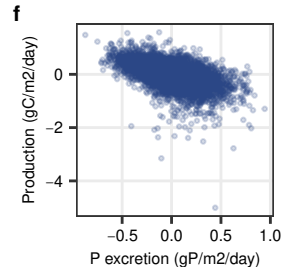
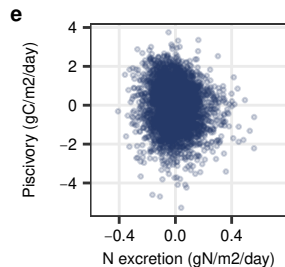
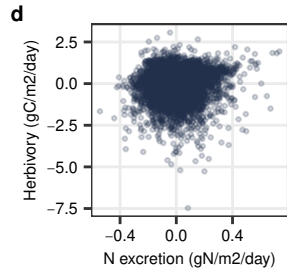
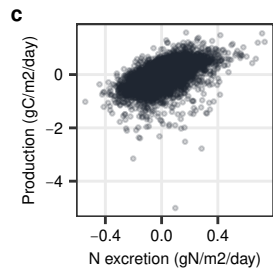
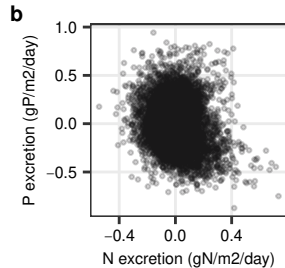
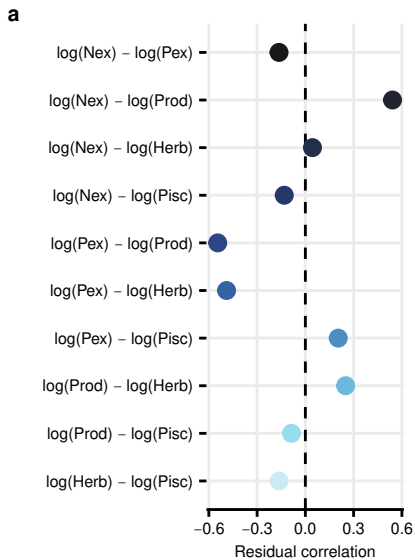
469 **References**

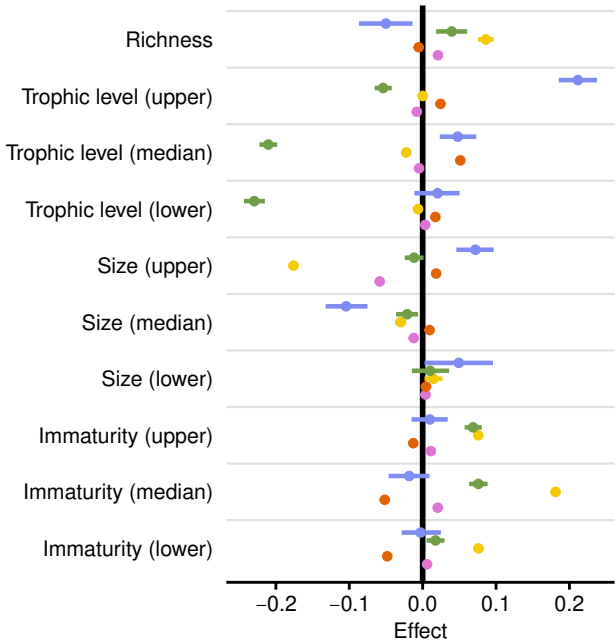
- 470 1. Welte, N. *et al.* Bridging food webs, ecosystem metabolism, and biogeochemistry
471 using ecological stoichiometry theory. *Frontiers in Microbiology* **8**, 1298 (2017).
- 472 2. Ceballos, G. *et al.* Accelerated modern human-induced species losses: Entering the
473 sixth mass extinction. *Science Advances* **1**, 1–5 (2015).
- 474 3. Hughes, T. P. *et al.* Global warming and recurrent mass bleaching of corals. *Nature*
475 **543**, 373–377 (2017).
- 476 4. Pauly, D. *et al.* Towards sustainability in world fisheries. vol. 418 689–695 (2002).
- 477 5. Bellwood, D. R., Streit, R. P., Brandl, S. J. & Tebbett, S. B. The meaning of the term
478 ‘function’ in ecology: A coral reef perspective. vol. 33 948–961 (2019).
- 479 6. Williams, G. J. *et al.* Coral reef ecology in the Anthropocene. *Functional Ecology* **33**,
480 1014–1022 (2019).
- 481 7. Brandl, S. J. *et al.* Coral reef ecosystem functioning: Eight core processes and the role
482 of biodiversity. *Frontiers in Ecology and the Environment* **17**, 445–454 (2019).
- 483 8. Cinner, J. E. *et al.* Meeting fisheries, ecosystem function, and biodiversity goals in a
484 human-dominated world. *Science* **368**, 307–311 (2020).
- 485 9. Mouillot, D. *et al.* Functional over-redundancy and high functional vulnerability in
486 global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the*
487 *United States of America* **111**, 13757–62 (2014).
- 488 10. Mora, C. *et al.* Global Human Footprint on the Linkage between Biodiversity and
489 Ecosystem Functioning in Reef Fishes. *PLoS Biology* **9**, e1000606 (2011).
- 490 11. Barneche, D. R. *et al.* Scaling metabolism from individuals to reef-fish communities
491 at broad spatial scales. *Ecology Letters* **17**, 1067–1076 (2014).
- 492 12. McIntyre, P. B. *et al.* Fish distributions and nutrient cycling in streams: can fish create
493 biogeochemical hotspots. *Ecology* **89**, 2335–2346 (2008).
- 494 13. Allgeier, J. E., Layman, C. A., Mumby, P. J. & Rosemond, A. D. Consistent nutrient
495 storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global*
496 *Change Biology* **20**, 2459–2472 (2014).
- 497 14. Morais, R. A. & Bellwood, D. R. Pelagic Subsidies Underpin Fish Productivity on a
498 Degraded Coral Reef. *Current Biology* **29**, 1521–1527.e6 (2019).
- 499 15. Morais, R. A., Connolly, S. R. & Bellwood, D. R. Human exploitation shapes
500 productivity–biomass relationships on coral reefs. *Global Change Biology* **26**, 1295–1305
501 (2020).

- 502 16. Barneche, D. R. *et al.* Body size, reef area and temperature predict global reef-fish
503 species richness across spatial scales. *Global Ecology and Biogeography* **28**, 315–327 (2019).
- 504 17. Schittekatte, N. M. D. *et al.* Nutrient limitation, bioenergetics and stoichiometry: A
505 new model to predict elemental fluxes mediated by fishes. *Functional Ecology* **34**, 1857–
506 1869 (2020).
- 507 18. Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M. & Brown, J. H. Metabolic
508 theory predicts whole-ecosystem properties. *Proceedings of the National Academy of*
509 *Sciences* **112**, 2617–2622 (2015).
- 510 19. Morais, R. A. & Bellwood, D. R. Global drivers of reef fish growth. *Fish and*
511 *Fisheries* **19**, 874–889 (2018).
- 512 20. Hood, J. M., Vanni, M. J. & Flecker, A. S. Nutrient recycling by two phosphorus-rich
513 grazing catfish: The potential for phosphorus-limitation of fish growth. *Oecologia* **146**, 247–
514 257 (2005).
- 515 21. Barneche, D. R. & Allen, A. P. The energetics of fish growth and how it constrains
516 food-web trophic structure. *Ecology Letters* **21**, 836–844 (2018).
- 517 22. Brandl, S. J. *et al.* Demographic dynamics of the smallest marine vertebrates fuel
518 coral reef ecosystem functioning. *Science* **364**, 1189–1192 (2019).
- 519 23. Lefcheck, J. S. *et al.* Tropical fish diversity enhances coral reef functioning across
520 multiple scales. *Science Advances* **5**, (2019).
- 521 24. Topor, Z. M., Rasher, D. B., Duffy, J. E. & Brandl, S. J. Marine protected areas
522 enhance coral reef functioning by promoting fish biodiversity. *Conservation Letters* **12**,
523 e12638 (2019).
- 524 25. Bellwood, D. R., Hughes, T. P. & Hoey, A. S. Sleeping Functional Group Drives
525 Coral-Reef Recovery. *Current Biology* **16**, 2434–2439 (2006).
- 526 26. Darling, E. S. & D’agata, S. Coral Reefs: Fishing for Sustainability. vol. 27 R65–R68
527 (2017).
- 528 27. Graham, N. A. J. *et al.* Human Disruption of Coral Reef Trophic Structure. *Current*
529 *Biology* **27**, 231–236 (2017).
- 530 28. Graham, N. A. J. *et al.* Dynamic fragility of oceanic coral reef ecosystems.
531 *Proceedings of the National Academy of Sciences of the United States of America* **103**, 8425–
532 8429 (2006).
- 533 29. Stuart-Smith, R. D., Brown, C. J., Ceccarelli, D. M. & Edgar, G. J. Ecosystem
534 restructuring along the great barrier reef following mass coral bleaching. *Nature* **560**, (2018).

- 535 30. Burkepile, D. E. *et al.* Nutrient supply from fishes facilitates macroalgae and
536 suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports* **3**, 1493 (2013).
- 537 31. Graham, N. A. J. *et al.* Changing role of coral reef marine reserves in a warming
538 climate. *Nature Communications* **11**, 1–8 (2020).
- 539 32. Reynolds, R. W. *et al.* Daily High-Resolution-Blended Analyses for Sea Surface
540 Temperature. *J. Climate*, **20**, 5473–5496. (2007).
- 541 33. Froese, R., Thorson, J. T. & Reyes, R. B. A Bayesian approach for estimating length-
542 weight relationships in fishes. *Journal of Applied Ichthyology* **30**, 78–85 (2014).
- 543 34. Parravicini, V. *et al.* Delineating reef fish trophic guilds with global gut content data
544 synthesis and phylogeny. *PLoS Biology* **18**, e3000702 (2020).
- 545 35. Froese, R. & Pauly, D. FishBase. *World Wide Web electronic publication*. (2018).
- 546 36. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a
547 metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
- 548 37. Bürkner, P.-C. brms : An R Package for Bayesian Multilevel Models using Stan.
549 *Journal of Statistical Software* **80**, 1–28 (2017).
- 550 38. Carpenter, B. *et al.* Stan : A Probabilistic Programming Language. *Journal of*
551 *Statistical Software* **76**, 1–31 (2017).







● N excretion
 ● P excretion
 ● Production
 ● Herbivory
 ● Piscivory

