

## Biological trade-offs underpin coral reef ecosystem functioning

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**Abstract :**

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

16 The flow of elements through biological communities fuels all ecosystems on earth<sup>1</sup>. Humans  
17 increasingly threaten biodiversity and ecosystem functioning<sup>2</sup>. Coral reefs are a prime  
18 example of an ecosystem severely impacted by anthropogenic activities. Drastic declines in  
19 habitat quality and fish biomass have evoked serious concerns about the persistence of coral  
20 reefs<sup>3,4</sup>. Maintaining ecosystem functions, defined as fluxes of elements, is a major goal for  
21 conservation of coral reefs<sup>5-7</sup>. However, past evaluations of functions on coral reefs have  
22 mostly relied on static proxies such as live coral cover, standing stock biomass of reef fishes,  
23 or measures of diversity<sup>8-10</sup>. These simplified proxies, although useful, may not properly  
24 represent ecological functions because the fluxes of elements can scale non-linearly with  
25 variables such as biomass<sup>11</sup>. Therefore, improving the quantification of ecological functions  
26 constitutes an important step towards the efficient management of coral reef ecosystem  
27 functioning<sup>7</sup>.

28 As a dominant group of consumers, coral reef fishes are essential vectors of carbon (C),  
29 nitrogen (N) and phosphorus (P)<sup>11-13</sup>. Ecosystem functions mediated by coral reef fishes  
30 include nutrient cycling, biomass production, herbivory, and piscivory (secondary  
31 consumption)<sup>7</sup>. While the high diversity of coral reef fishes has inspired many studies that  
32 focus on ecosystem functioning, only a handful of studies have attempted to quantify

33 functions as continuous fluxes<sup>7</sup>. Further, studies that have quantified functions as a flow of  
34 matter mostly focused on single functions (e.g. biomass production<sup>14,15</sup> or fish excretion<sup>13</sup>)  
35 and covered only a small number of species at local scales. Consequently, trade-offs among  
36 multiple functions, their drivers, and their vulnerability to anthropogenic stressors remain  
37 poorly understood in coral reef ecosystems across large spatial scales<sup>7</sup>.

38 Here, we integrate biogeochemistry and community ecology to advance our understanding of  
39 the elemental fluxes that underpin reef fish functioning. Using empirical species-specific data  
40 on basic organismal processes and Bayesian phylogenetic models, we parameterize  
41 individual-level bioenergetic models to estimate five key ecosystem functions: N excretion, P  
42 excretion, biomass production, herbivory, and piscivory for 1,100 species. We apply these  
43 bioenergetic models to 9,118 reef fish transects across 585 sites worldwide (Supplementary  
44 Table 1) to: (1) quantify community-level reef fish functions and their trade-offs, (2) extract  
45 the community- and species-level effects on these functions, and (3) gauge the vulnerability  
46 of reef fish functioning in the Anthropocene.

## 47 **Results**

48 We quantified five key ecosystem functions mediated by coral reef fishes across the globe  
49 (Fig. 1). Functions across localities show a similar geographical pattern. However, at the  
50 global scale we could not find a single location with high levels of functioning across all  
51 functions. A measure of multifunctionality thus does not appropriately represent the state of  
52 all functions assessed independently.

53 Biomass is the most commonly employed indicator of coral reef functioning<sup>7,8</sup>, and we  
54 demonstrate a predictably strong relationship between fish biomass and all five functions  
55 (Fig. 1). Specifically, in a multivariate mixed effects Bayesian model, the slopes of the log-  
56 transformed biomass were 0.932 (95%CI: 0.929, 0.934) for N excretion, 1.051 (1.047, 1.056)  
57 for P excretion, 0.771 (0.764, 0.780) for production, 0.940 (0.923, 0.957) for herbivory, and  
58 0.668 (0.635, 0.702) for piscivory. These slopes indicate that the relationships between  
59 biomass and functions are all non-linear, which demonstrates that biomass is not an  
60 appropriate proxy for function. We also incorporated sea surface temperature (SST) because  
61 it affects the metabolic and growth rates of fishes, which scales up to the community<sup>16</sup>. We  
62 found positive effects of SST on N excretion, production, and herbivory, and no effects of  
63 SST on P excretion and piscivory (Supplementary Table 3).

64 Our multivariate model allowed us to estimate the correlations between functions,  
65 independent of the effects of biomass and SST. In particular, we estimated correlations  
66 between functions on three levels: the locality effects, site effects, and residual variations  
67 (Fig. 2, Fig. S1). The correlations displayed comparable patterns on each level. We found  
68 strong negative trade-offs between P excretion and N excretion as well as P excretion and  
69 biomass production. Further, we found slightly weaker negative correlations between  
70 piscivory and N excretion as well as piscivory and herbivory. Thus, a reef fish community  
71 does not simultaneously display high values of functioning across all investigated functions.

72 To explore what drives the variation and trade-offs of functions beyond the effects of biomass  
73 and SST, we ran a multivariate Bayesian mixed effects model by adding ten variables that  
74 describe the structure of each fish assemblage: species richness and the median, lower, and  
75 upper 95% quantiles of size, immaturity, and trophic level of individuals inside a community.  
76 Each of these components have non-zero effects on at least one of the five functions,  
77 suggesting that the observed trade-offs may be, at least in part, rooted in the structure of the  
78 focal community (Fig. 3, Supplementary Table 4). Some associations such as the negative  
79 and positive effects of trophic level on herbivory and piscivory, respectively, are expected  
80 from first principles, whereas others, such as the positive effect of immaturity on biomass  
81 production and negative on P excretion, are not immediately obvious (Fig. 3).

82 Beyond community structure, we examined whether functions are driven by particular  
83 species across sites. We quantified the degree of dominance inside each community at the  
84 site-level and found that, on average, functions are dominated by a small fraction of the  
85 species in each community (Fig. 4a). We also calculated the proportion of species that is  
86 dominant in at least one transect (i.e. species with a disproportionately high contribution as  
87 compared to a community in which all species contribute equally), and many species play a  
88 dominant role somewhere in the surveyed locations. In particular, 49% of all species  
89 contributed disproportionately to a function in at least one surveyed community (Fig. 4b). Yet,  
90 very few species are dominant throughout their range (Fig. 4c). Thus, functions within  
91 communities tend to be driven by few dominant species, and the identity of those dominant  
92 species varies across sites.

## 93 **Discussion**

94 By quantifying five key processes mediated by coral reef fishes, we demonstrate that coral  
95 reef ecosystem functioning is shaped by biological trade-offs, local community structure, and

96 species identity. Standing biomass is one of the most commonly employed indicators of coral  
97 reef functioning<sup>7,8</sup>, and our analyses confirm the pervasive influence of biomass on all other  
98 processes. Yet, our results also show non-linear relationships between functions and biomass  
99 and suggest that biomass alone does not sufficiently characterize functioning; strong trade-  
100 offs occurred among the five functions independent of biomass. Using biomass as a proxy  
101 might, therefore, mask fundamental differences in community-level functioning.  
102 Furthermore, for a given value of biomass, no reef can yield above average values across all  
103 five functions. While a reef may stand out as a hotspot for one function, no reef can  
104 maximize all functions simultaneously.

105 The observed trade-offs among functions are driven by fish community structure and the  
106 organismal physiology and life-history traits of its constituents<sup>17,18</sup>. For example, we observed  
107 a clear trade-off between P excretion and biomass production which is mostly driven by the  
108 age and trophic structure (Fig. 3). Communities dominated by fishes with high trophic levels  
109 are characterized high P excretion rates because predatory fishes have a P-rich diet<sup>13</sup>. In  
110 contrast, biomass production is high in communities dominated by fishes that occupy low  
111 trophic levels because herbivores tend to exhibit higher growth rates<sup>19</sup> and less energy is lost  
112 with each step up the food chain ('trophic transfer efficiency'; ref). Moreover, P is retained  
113 for skeletal growth in young fishes, thus limiting P excretion rates<sup>17,20</sup>. Furthermore,  
114 metabolic theory predicts that small-bodied individuals have higher mass-specific metabolic  
115 rates, leading to elevated consumption rates and disproportionate contributions to functions  
116 that rely on rapid energetic turnover such as herbivory, piscivory, production, and N  
117 excretion<sup>15,21,22</sup>.

118 Our results also reveal that functions consistently rely on a few dominant species, but the  
119 identities of local, dominant species strongly vary across sites<sup>23</sup>. Locally, a small number of  
120 high-performing taxa may disproportionately impact rates of functioning at the community  
121 level due to high biomass or abundance<sup>24</sup>, which may have led to their designation as  
122 functionally-dominant "key species" in various locations<sup>25</sup>. However, our results revealed  
123 that no species dominated throughout their geographical range, and more than half of all  
124 species contributed disproportionately to a specific function at a at least one site. Thus, there  
125 are no widespread key species to target for coral reef conservation aimed at preserving these  
126 five functions; rather, local species dominance across functions can guide local conservation  
127 efforts, and the preservation of regional reef fish biodiversity should be prioritized in broad-  
128 scale policy.

129 Our global analysis of multiple functions suggests pathways in which human-induced shifts  
130 in reef fish community structure may impact coral reef ecosystems (Fig. 5). Fishing and  
131 climate-induced coral loss have caused declines in reef fish biomass and shifts in community  
132 structure<sup>26,27</sup>, and we suggest that these changes will differentially affect ecosystem  
133 functioning. Intensive fishing and associated reductions in the biomass of large fishes, for  
134 example, alters the size, age, and trophic structure of fish communities<sup>27</sup>. When accounting  
135 for the effect of biomass, these community shifts can enhance N excretion and production  
136 (e.g. <sup>15</sup>) but they will negatively impact P excretion, herbivory, and piscivory. Further,  
137 declines in coral cover related to climate change, and warming seas at higher latitude coral  
138 reefs are often associated with shifts toward herbivores<sup>28</sup>. Herbivores generally contribute  
139 little to P excretion<sup>13,17</sup>, so a shift to herbivore dominance and the subsequent decline of  
140 community-level P excretion may change the balance of nutrient cycling on coral reefs,  
141 potentially favoring algal growth over corals<sup>29</sup>.

142 Sustaining biomass, diversity, and ecosystem functioning are important objectives of most  
143 conservation initiatives<sup>8</sup>. While safeguarding fish biomass enhances functioning, the trade-  
144 offs between key functions reveal a critical challenge for coral reef conservation, where  
145 actions to enhance one function may negatively impact another. For example, the  
146 establishment of marine protected areas, which are one of the primary conservation strategies  
147 for coral reefs<sup>30</sup>, may protect herbivorous species. However, marine protected areas do not  
148 protect reefs from the pervasive effects of climate change<sup>30</sup>, and community shifts towards  
149 herbivore domination may result in the decline of P excretion. Thus, measuring conservation  
150 success with biomass or solely one function (e.g. herbivory) can mask the collapse of other  
151 essential functions. It is necessary to gauge the state of reef ecosystems based on multiple,  
152 complementary, process-based functions. Yet, our comprehension of process-based  
153 functioning or the definition a “functional” coral reef is still poorly understood<sup>7</sup>. Establishing  
154 functional baselines for global coral reefs is a critical challenge for future studies. Until then,  
155 our results suggest that coral reef fish functions can be managed by enhancing standing stock  
156 biomass, protecting local key species and vulnerable constituents of the community  
157 (e.g. large carnivores), and promoting regional biodiversity.

158 We demonstrate that the variability in processes that govern the elemental cycling in complex  
159 ecosystems such as tropical coral reefs represents an unrecognized challenge for protecting  
160 ecosystem functioning. Management strategies that call for the enhancement of ecosystem  
161 functioning via an economic mindset (i.e. where higher functioning is better) are not feasible.

162 Instead, conserving coral reef ecosystem functioning will require a more nuanced approach  
163 that considers processes that vary beyond the effect of standing stock biomass and are subject  
164 to local trade-offs, drivers, and anthropogenic threats.

165



## 166 **Methods**

### 167 **1. Underwater visual census database**

168 We used a published global database of reef fish abundances and sizes collected along belt  
169 transects<sup>16</sup>. This database encompasses 9,118 transects across 585 sites (within 98 localities)  
170 in the Central Indo-Pacific, Central Pacific, Eastern Pacific, Western Indian, Eastern Atlantic,  
171 and Western Atlantic Oceans. Sites are defined as small islands or stretches of continuous  
172 reefs in larger coastlines and localities encompass sites that belong to the same biogeographic  
173 sub-provinces<sup>16</sup>. The database only includes transects on the outer reef slope and with a hard  
174 reef bottom. Transects were carried out at a constant depth, parallel to the reef crest. We  
175 discarded the species inside families for which we did not have body stoichiometry data,  
176 individuals that were smaller than 7cm (to minimize the bias related to the identification of  
177 small individuals), and rare species for which less than 20 individuals were recorded across  
178 all transects. The dataset then included 1,110 species belonging to 25 families (Acanthuridae,  
179 Balistidae, Bothidae, Chaetodontidae, Cirrhitidae, Fistulariidae, Haemulidae, Holocentridae,  
180 Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mugilidae, Mullidae,  
181 Ostraciidae, Pempheridae, Pomacanthidae, Pomacentridae, Sciaenidae, Scorpaenidae,  
182 Serranidae, Siganidae, Tetraodontidae, Zanclidae). Sea surface temperature (SST) for each  
183 site was obtained from daily time-series data from the National Oceanic and Atmospheric  
184 Administration (NOAA) covering a 5-year period (°C; 0.25° resolution) (available from  
185 <https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html>)<sup>31</sup>; . Further, for  
186 each transect, we calculated species richness and estimated total standing stock biomass of  
187 fishes by using Bayesian length-weight relationships available from Fishbase<sup>32</sup>. All data  
188 processing and analyses were performed in the software program R (version 4.0.2; R core  
189 team 2020).

### 190 **2. Quantification of functions**

191 For each transect, we estimated five key process-based functions mediated by fishes: nitrogen  
192 excretion rate ( $\text{gN m}^{-2} \text{day}^{-1}$ ), phosphorus excretion rate ( $\text{gP m}^{-2} \text{day}^{-1}$ ), production of biomass  
193 through growth ( $\text{gC m}^{-2} \text{day}^{-1}$ ), herbivory, (i.e. ingestion rate of macrophytes ( $\text{gC m}^{-2} \text{day}^{-1}$ )),  
194 and piscivory (i.e. ingestion rate of fishes ( $\text{m}^{-2} \text{day}^{-1}$ ))<sup>7</sup>. These five functions were estimated  
195 for each transect using individual-based bioenergetic models predicting fluxes of carbon (C),  
196 nitrogen (N), and phosphorus (P) (e.g. daily C intake rates, N and P excretion rates, and  
197 growth rates)<sup>17</sup>. This bioenergetic model framework integrates elements of metabolic theory,

198 stoichiometry, and flexible elemental limitation.<sup>17</sup> We quantified the input parameters,  
199 including elements of metabolism, growth, and diet and body stoichiometry, for all 1110  
200 species through the integration of empirical data, data synthesis, and Bayesian phylogenetic  
201 models (see supplementary methods). We then ran a unique bioenergetic model for each  
202 combination of species identity, body size, and sea surface temperature ( $n = 30668$ ) to obtain  
203 the contribution of each individual to each function in each transect. Finally, we summarized  
204 functions at the community level by summing up all individual contributions inside a transect  
205 and dividing the sum by the surface area. Each function is thus expressed as dry mass (of C,  
206 N, or P) per day per square meter. We note that N excretion, P excretion, and biomass  
207 production include contributions of all fishes, whereas herbivory and piscivory are carried out  
208 by a subset of the community, with respect to their trophic guild as defined by<sup>33</sup>. To reduce  
209 the occurrence of misclassification of herbivores and piscivores, we categorized a species as a  
210 herbivore or piscivore if it had both the highest probability to be classified in that trophic  
211 group and this probability was more than 0.5, based on the probability scores of trophic  
212 guilds presented by Parravicini et al. (2020)<sup>33</sup>. Further, as a comparison, we quantified  
213 herbivory and piscivory rates using two alternative trophic guild classifications based on  
214 Expert opinion (Extended Data Fig. 3)<sup>9,33</sup>. Both the herbivory and piscivory rates match the  
215 Expert opinion trophic guild classifications. Finally, we estimated multifunction, i.e. one  
216 measure that combines all five functions by taking the geometric average of the five functions  
217 (normalized to a range between zero and 100). We used the geometric mean because  
218 functions are dependent on each other and vary by several orders of magnitude.

### 219 **3. Community structure variables**

220 We quantified a set of variables that characterize fish community structure. These variables  
221 describe the size, age, and trophic distribution of the community, as these may all affect  
222 functions<sup>17</sup>. Specifically, we calculated the 2.5%, 50%, and 97.5% quantiles of the total  
223 length, immaturity, and trophic level of all individuals per transect. The total length is based  
224 on visual estimations by divers. The immaturity is quantified using the following formula:

$$225 \text{immaturity}_i = \kappa(l_\infty - l_i),$$

226 where  $\kappa$  is the species-specific growth rate parameter and  $l_\infty$  is the species-specific  
227 asymptotic adult length, and  $l_i$  is the total length of individual  $i$ . Essentially, this is the  
228 derivative of the Von Bertalanffy growth model for a certain length, and the higher this value  
229 is, the younger the individual. Finally, trophic level was extracted from Fishbase<sup>34</sup>.

## 230 4. Multivariate regression models

231 We fitted three multivariate Bayesian models with all five functions to (1) predict functions  
 232 on the locality level to create a maps of functions, (2) investigate the effects of biomass and  
 233 SST, and the correlations among functions independent of biomass and SST, and (3) estimate  
 234 the effects of the community structure on each function. For each model, functions were log-  
 235 transformed to ensure the normal distribution of residuals and an allometric relationship with  
 236 biomass, which is hypothesized by metabolic theory<sup>35</sup>. In the underwater visual transect  
 237 database, 291 transects (3%) did not contain herbivores and 4467 transects (49%) did not  
 238 contain piscivores yielding zeros for herbivory and piscivory, respectively. We considered  
 239 that these absence of herbivores or piscivores are likely an underestimation of their actual  
 240 abundance at the surveyed reef site, as all reefs typically host a few herbivores and piscivores  
 241 (i.e. they are likely false-zeros). To avoid removing all transects with missing values for  
 242 herbivory or piscivory (n = 4,620) from our database when running multivariate analyses, we  
 243 imputed these zeros as missing values, and they were eventually set as parameters in the  
 244 multivariate models.

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

$$248 \begin{bmatrix} y_{E_N,i} \\ y_{E_P,i} \\ y_{B,i} \\ y_{H,i} \\ y_{P,i} \end{bmatrix} \sim MVNormal \left( \begin{bmatrix} \mu_{E_N,i} \\ \mu_{E_P,i} \\ \mu_{B,i} \\ \mu_{H,i} \\ \mu_{P,i} \end{bmatrix}, S \right),$$

$$\mu_{E_N,i} = (\beta 0_{E_N} + \delta_{E_N,loc} + \delta_{E_N,site})$$

$$\mu_{E_P,i} = (\beta 0_{E_P} + \delta_{E_P,loc} + \delta_{E_P,site})$$

$$249 \mu_{B,i} = (\beta 0_B + \delta_{B,loc} + \delta_{B,site})$$

$$\mu_{H,i} = (\beta 0_H + \delta_{H,loc} + \delta_{H,site})$$

$$\mu_{P,i} = (\beta 0_P + \delta_{P,loc} + \delta_{P,site}),$$

$$250 S = \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix} R \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix},$$

251 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  
252 excretion rate,  $y_{B,i}$  is the biomass production rate,  $y_{H,i}$  is the herbivory rate,  $y_{E_N,i}$  is the  
253 piscivory rate,  $\sigma$  represents the residual error of each function ( $E_N$ ,  $E_P$ ,  $B$ ,  $H$ , and  $P$ ),  $R$  is the  
254 correlation matrix of the residuals. Locality- and site-level effects are also structured  
255 including covariation among functions. There are thus three correlation matrices in total,  
256 meaning that the model will estimate the correlation between functions (independent of  
257 biomass and SST) on three levels: locality, site, and transect.  
258 We used non-centered parameterization for site and location effects and all standard  
259 deviations had the following prior:  $\sigma \sim student(3,0,2.5)$ . We used a prior ( $lkj\_corr$ ) for  
260 each of the three correlation matrices ( $R \sim lkj\_corr(1)$ ).

261 Second, we ran a mixed-effect model to investigate the effects of biomass and SST on all  
262 functions and the correlations among functions (independent of biomass and SST). The  
263 standing stock biomass of communities is positively related to all functions because of the  
264 additive nature of the quantification and metabolic theory<sup>35</sup>. Furthermore, because of the  
265 known relationship between temperature and parameters related to growth and respiration  
266 (see supplementary methods), functions are expected to be affected by temperature. We thus  
267 fitted a multivariate Bayesian mixed-effect model using transect-level log-transformed  
268 functions that included random effects for sites and localities:

$$269 \begin{bmatrix} y_{E_N,i} \\ y_{E_P,i} \\ y_{B,i} \\ y_{H,i} \\ y_{P,i} \end{bmatrix} \sim MVNormal \left( \begin{bmatrix} \mu_{E_N,i} \\ \mu_{E_P,i} \\ \mu_{B,i} \\ \mu_{H,i} \\ \mu_{P,i} \end{bmatrix}, S \right),$$

$$270 S = \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix} R \begin{bmatrix} \sigma_{E_N} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{E_P} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{B,i} & 0 & 0 \\ 0 & 0 & 0 & \sigma_H & 0 \\ 0 & 0 & 0 & 0 & \sigma_P \end{bmatrix}$$

$$271 \begin{aligned} \mu_{E_N,i} &= (\beta 0_{E_N} + \delta_{E_N,loc} + \delta_{E_N,site}) + \beta 1_{E_N} \log(biomass), i + \beta 2_{E_N} SST, i \\ \mu_{E_P,i} &= (\beta 0_{E_P} + \delta_{E_P,loc} + \delta_{E_P,site}) + \beta 1_{E_P} \log(biomass), i + \beta 2_{E_P} SST, i \\ \mu_{B,i} &= (\beta 0_B + \delta_{B,loc} + \delta_{B,site}) + \beta 1_B \log(biomass), i + \beta 2_B SST, i \\ \mu_{H,i} &= (\beta 0_H + \delta_{H,loc} + \delta_{H,site}) + \beta 1_H \log(biomass), i + \beta 2_H SST, i \\ \mu_{P,i} &= (\beta 0_P + \delta_{P,loc} + \delta_{P,site}) + \beta 1_P \log(biomass), i + \beta 2_P SST, i \end{aligned}$$

272 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  
 273  $\beta_{2_{E_N}}, \beta_{2_{E_P}}, \beta_{2_B}, \beta_{2_H}, \beta_{2_P}$  are the fixed effects of SST. Locality- and site-level effects are  
 274 thus structured including covariation among functions, independent of biomass and SST.  
 275 Similarly, the residual variation of functions incorporates the correlations between functions,  
 276 without the effect of biomass and SST. We used similar priors as described above, and we  
 277 used weakly-informative normal priors for the model slopes ( $\beta_1 \sim normal(1,1)$ ,  $\beta_2 \sim$   
 278  $normal(0,1)$ ).

279 Finally, to investigate the effect of community structure while still accounting for the effects  
 280 of standing biomass and SST, we fitted a mixed effect multivariate model similar to the  
 281 model specified above, but adding all community structure variables:

$$282 \mu_{function,i} = \beta_{0_{function}} + \beta_{1_{function}} \log(biomass), i + \beta_{2_{function}} SST, i + \beta_{3_{function}} richness, i + \beta_{4_{function}}$$

283 where *richness* is the species richness, *size* is the total length, *troph* is the trophic level,  
 284 *imm* is the immaturity, and *m*, 2.5%, and 97.5% represent the 50%, 2.5%, and 97.5%  
 285 quantiles across the fish community, respectively. For these models, we used weakly  
 286 informative priors for the fixed effect parameters ( $\beta_3 - \beta_{12} \sim normal(0,1)$ ) and the same  
 287 priors as described above for other parameters.

288 All Bayesian models were fitted using the R package *brms*<sup>36</sup>, which uses Stan, a C++ package  
 289 to perform full Bayesian inference<sup>37</sup>. The posterior distributions of model parameters were  
 290 estimated using Hamiltonian Monte Carlo (HMC) methods by using four chains of 2,000  
 291 samples, including 1,000 samples as a warm-up. Thus, a total of 4,000 draws were used to  
 292 estimate posterior distributions. The convergence and fit of the models were verified by  
 293 examining the Rhat, parameter trace plots, and posterior prediction plots (Extended Data Fig.  
 294 2).

## 295 **5. Species dominance and contributions to functions**

296 We quantified the relative contribution of each species to each function for all sites as  
 297 follows:

$$298 \text{contribution}_{f,i,j} = \frac{F_{f,i,j}}{\sum F_{f,j}}$$

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

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

$$305 \quad DD = \frac{A - A_{min}}{A_{max} - A_{min}},$$

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

$$309 \quad A_{min} = \frac{R^2 - 1}{2R},$$

310

$$311 \quad A_{max} = R - 1,$$

312

$$313 \quad A = \sum_{i=2}^R \frac{C_i + C_{i-1}}{2},$$

314

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

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

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425 ([https://github.com/nschiett/global\\_proc](https://github.com/nschiett/global_proc)) and figshare  
426 (<https://figshare.com/s/f789aec2c20492c4f0f9>). All data on individual empirical  
427 measurements are available from the corresponding author upon request.

428

## 429 **Figure legends**

430 **Fig. 1: Maps of the five key ecosystem functions, multifunctionality, and the**  
431 **relationships between the functions and biomass.** Left: Dots indicate localities of field  
432 surveys, with dot sizes representing the ranked values of the locality-level predictions of  
433 functions, and color scales showing categorical assignments (black = < 25%, grey = 25-75%,  
434 color = >75%). Black outlines highlight the five localities with the highest values of each  
435 function. Multifunctionality represents the weighted average of the five standardized  
436 functions. Right: The predicted values for functions and multifunctionality with increasing  
437 biomass. The lines represent the average modeled relationship and the shaded areas show the  
438 95% credible intervals of the predictions.

439 **Fig. 2: Correlations of the five functions, accounting for biomass and sea surface**  
440 **temperature.** a: Modeled correlation coefficients of residual errors. Dots represent the  
441 average and lines represent the 95%CI. b-k: Scatter plots of the mean residual errors of the  
442 functions.

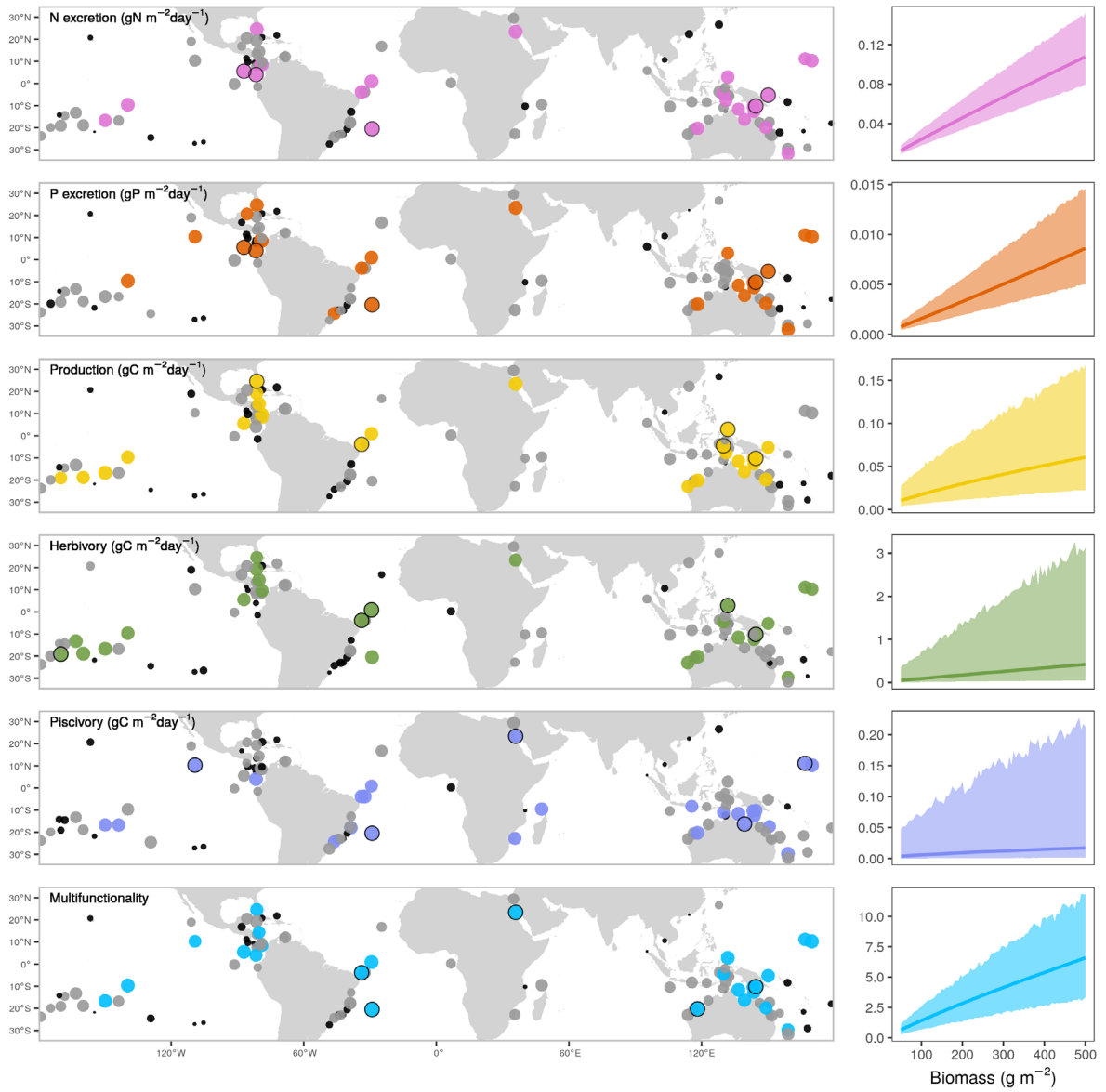
443 **Fig. 3. Effects of ecological community variables on the five functions.** Dots indicate fixed  
444 effect values from Bayesian linear regressions that examine the effects of species richness,  
445 trophic level, size, and immaturity of fishes. To represent both the median and spread of  
446 trophic level, size, and immaturity across individuals within a community, we included lower  
447 and upper 95% quantile values of these three traits as community variables. All data were  
448 log-transformed and standardized to compare across functions and variables (see  
449 Supplementary Table 2 for parameter values on non-standardized data). Dots represent the  
450 average effect size estimate, and horizontal lines indicate the 95% credible interval.  
451 Immaturity is defined as the derivative of the von Bertalanffy growth model for a given size;  
452 thus, the higher this value, the younger the individual.

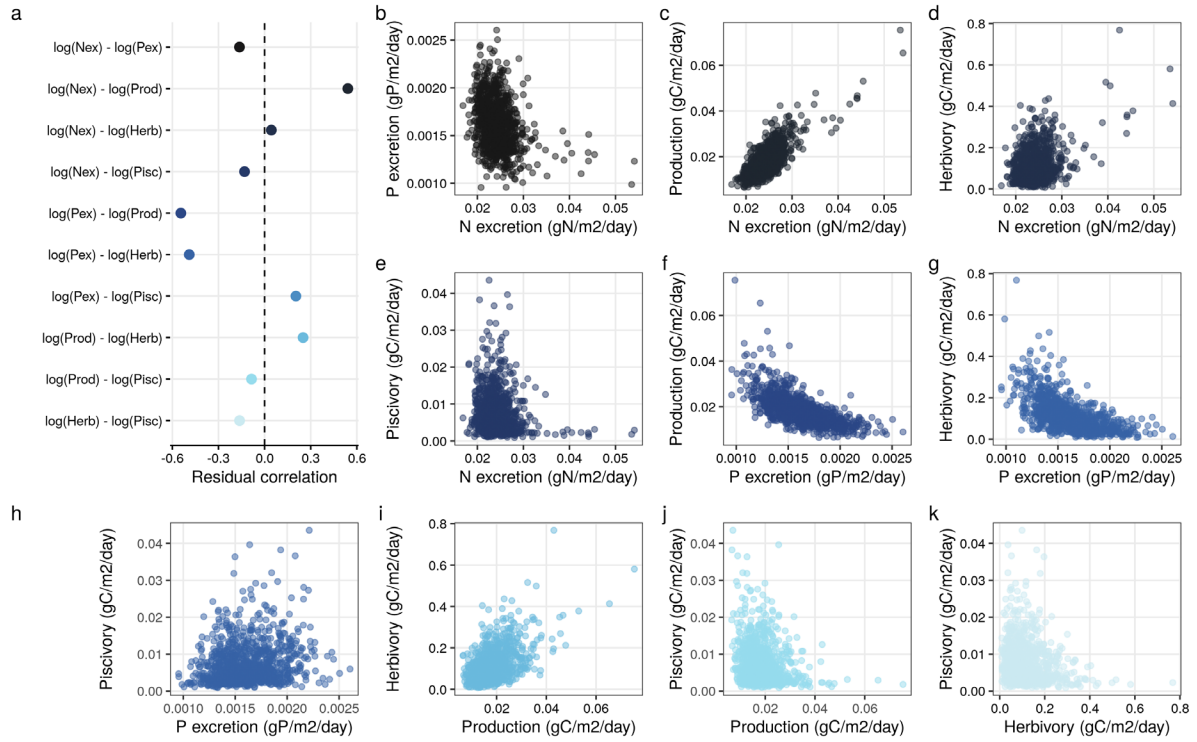
453 **Fig. 4: Local dominance in species contributions to five ecosystem functions on coral**  
454 **reefs.** a: The degree of dominance for each function at the site level. The degree of  
455 dominance of a community ranges between zero (all species contribute equally to the  
456 function) and one (a single species is the sole contributor to a given function). Colored dots  
457 represent the raw values, and the black dots and lines display the mean and 95% credible  
458 intervals of degree of dominance among all sites. In some cases, the credible interval was too  
459 small to be visible. The vertical dashed line shows the average degree of dominance of 1,000  
460 randomly simulated communities. b: Bar plot of the proportion of species that are dominant

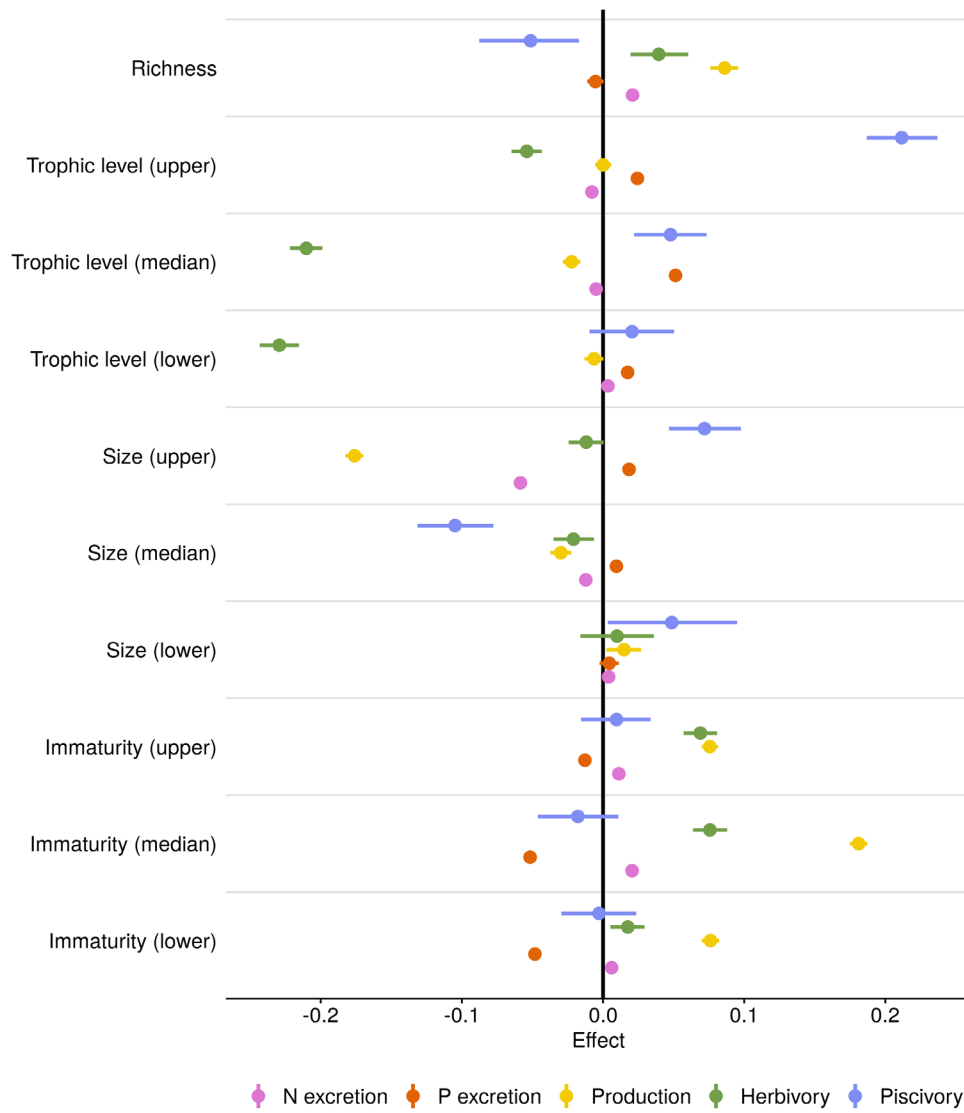
461 in at least one site relative to the total number of species, or, for herbivory and piscivory, the  
462 total number of herbivores and piscivores, respectively. c: Species-specific frequencies of  
463 dominance in each function across all sites, ranging from zero (species are never dominant)  
464 to one (dominant wherever present). A species is categorized as dominant in a community if  
465 its contribution to a function is higher than a scenario in which all species are equal (i.e. one  
466 divided by the number of species that contribute to the function).

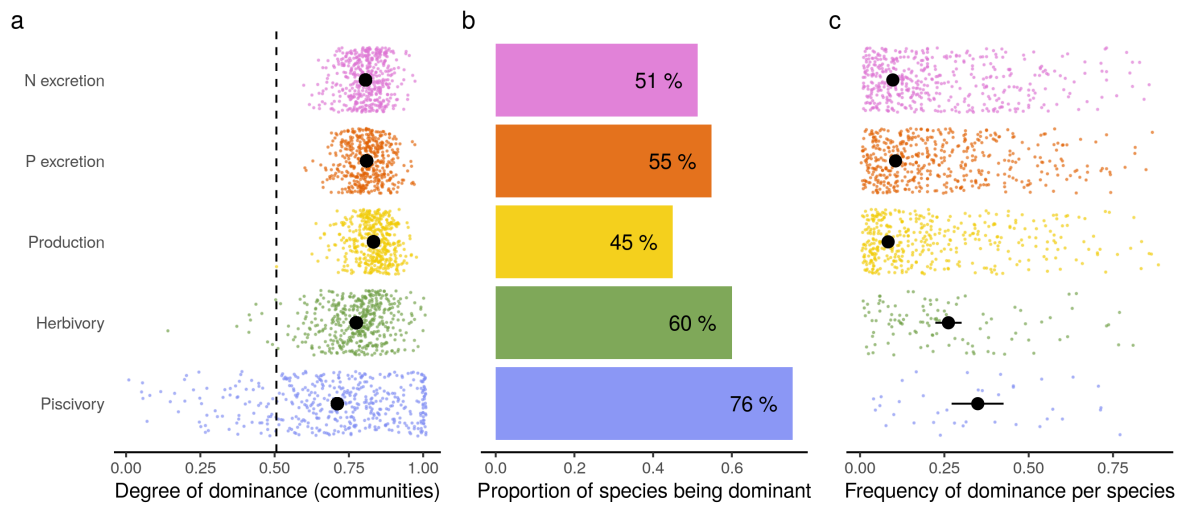
467 **Fig. 5. Vulnerability of the five functions to fishing and climate change-induced coral**  
468 **loss.** Conceptual schematic of the potential ways in which fishing and climate change can  
469 affect functions through their known effects on biomass and community structure.

470 **Figures**

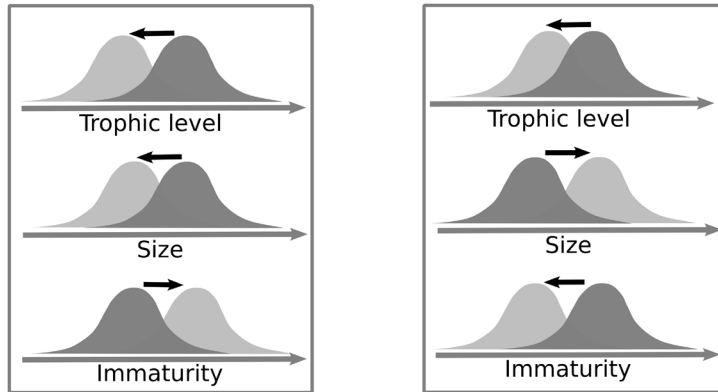
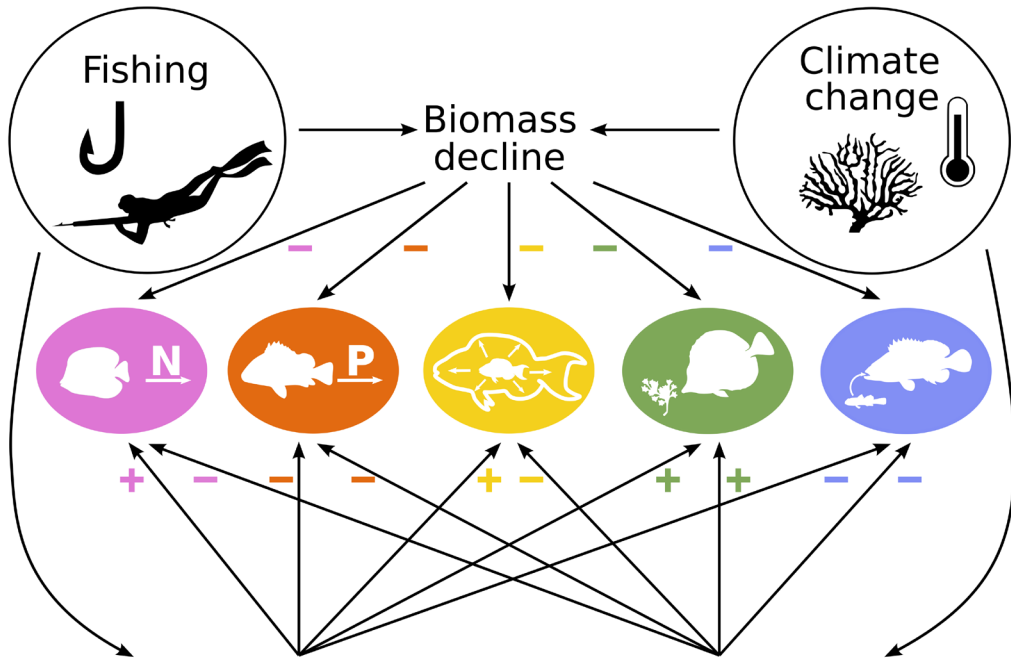






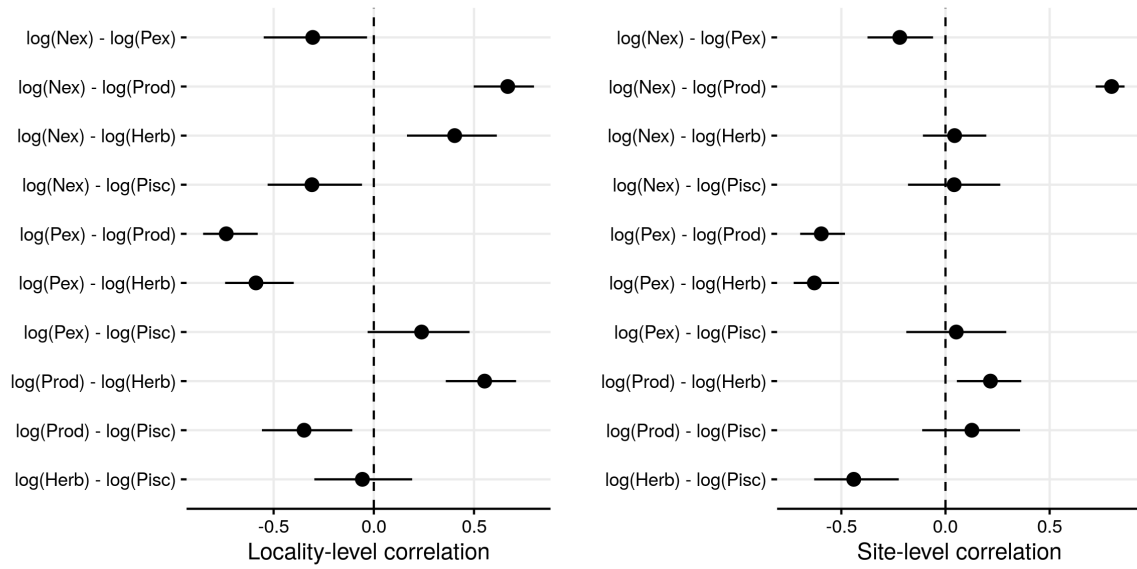






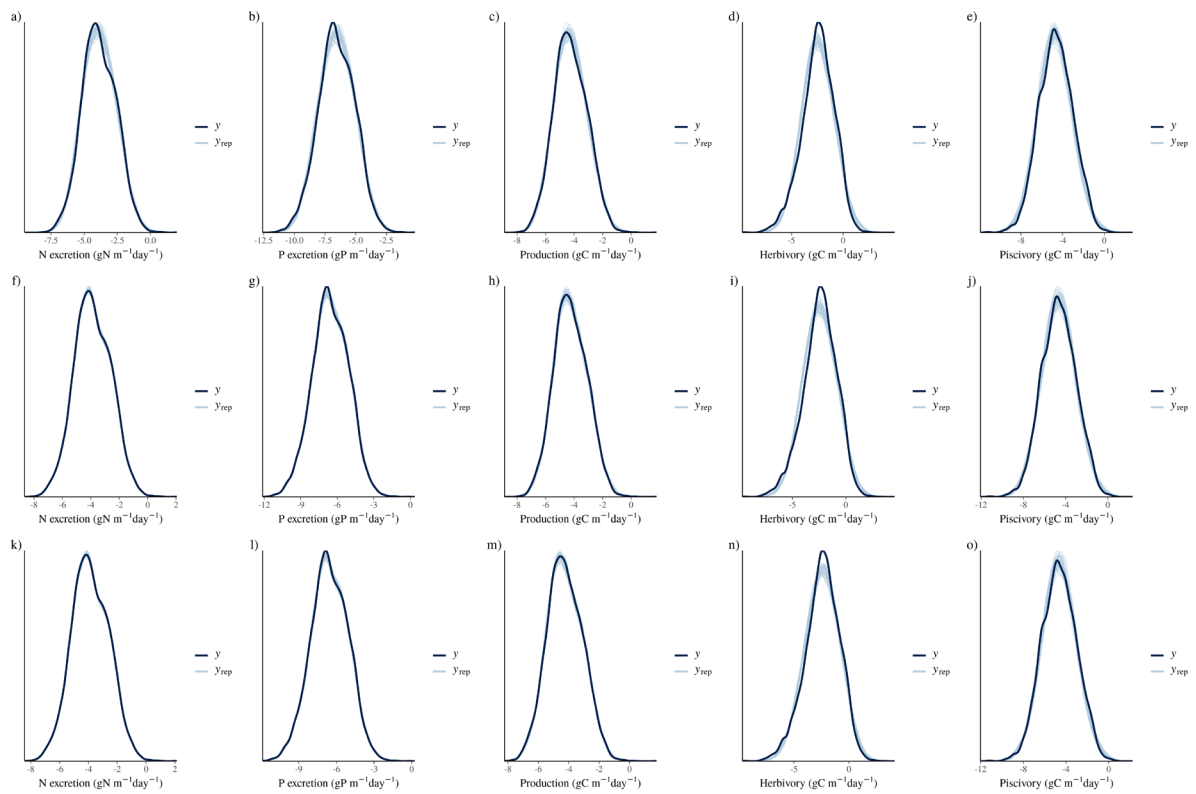
Community shift

477 **Extended data figures**



478

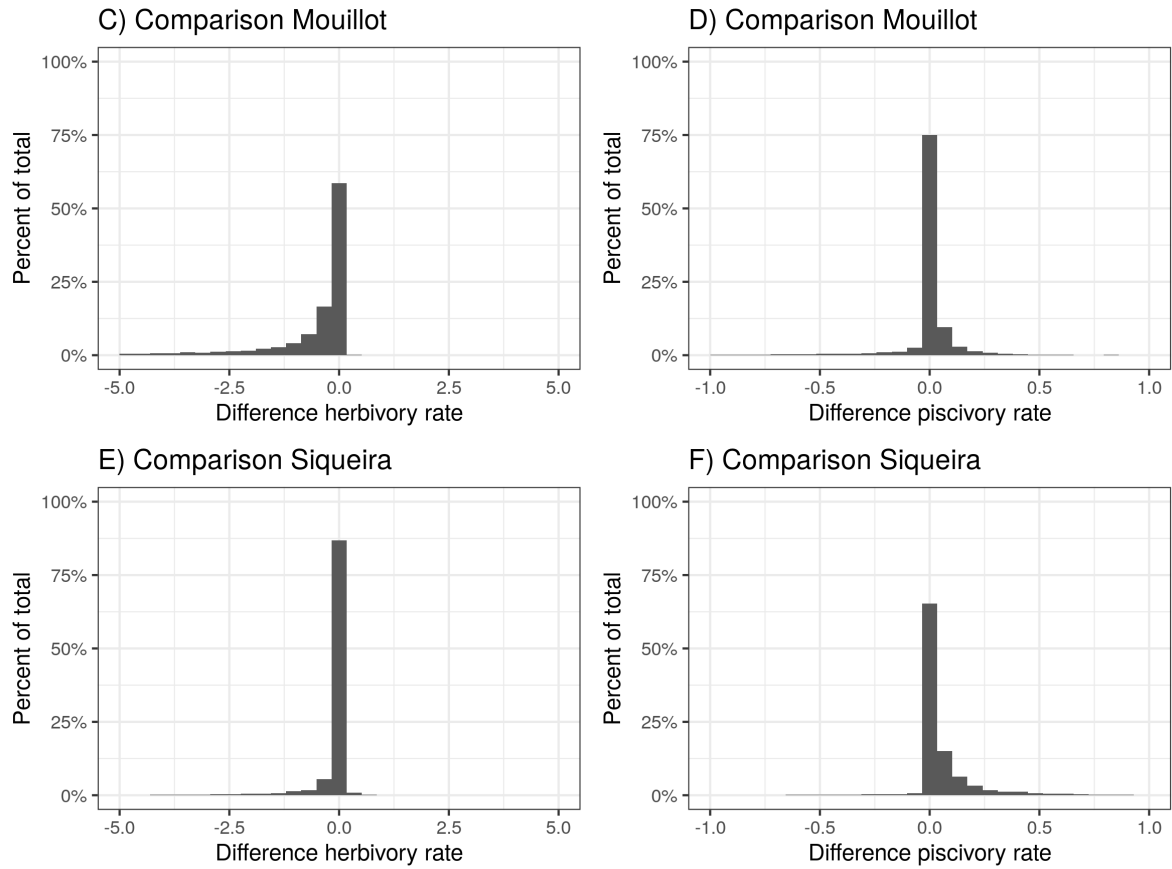
479 Extended Data Fig. 1. Correlations among functions, independent of biomass and sea surface  
480 temperature, on the locality and site level.



482

483 Extended Data Fig. 2. Posterior predictive checks of multivariate models. a-e: Intercept-only  
 484 model, f-j: model with biomass and sea surface temperature, k-o: model with all community  
 485 variables.

486



487

488 Extended Data Fig. 3: Comparison herbivory and piscivory rates when using alternative diet  
 489 classifications from Mouillot et al. (2014) and Siqueira et al. (2020).

490