

1 **Biodiversity increases ecosystem functions despite multiple stressors on coral reefs**

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11 **Positive relationships between biodiversity and ecosystem functioning (BEF)**  
12 **highlight the importance of conserving biodiversity to maintain key ecosystem functions**  
13 **and associated services. Although natural systems are rapidly losing biodiversity due to**  
14 **numerous human-caused stressors, our understanding of how multiple stressors**  
15 **influence BEF relationships comes largely from small, experimental studies. Here, using**  
16 **remote assemblages of coral-reef fishes, we demonstrate strong, non-saturating**  
17 **relationships of biodiversity with two ecosystem functions; biomass and productivity.**  
18 **These positive relationships were robust to both an extreme heatwave that triggered**  
19 **coral bleaching and to invasive rats which disrupt nutrient subsidies from native**  
20 **seabirds. Despite having only minor effects on BEF relationships, both stressors still**  
21 **decreased ecosystem functioning via other pathways. The extreme heatwave reduced**  
22 **biodiversity, which, due to the strong BEF relationships, ultimately diminished both**  
23 **ecosystem functions. Conversely, the loss of cross-system nutrient subsidies directly**  
24 **decreased biomass. These results demonstrate multiple ways by which human-caused**  
25 **stressors can reduce ecosystem functioning, despite robust BEF relationships, in natural**  
26 **high-diversity assemblages.**

27 By conducting studies of biodiversity and ecosystem functioning (BEF) at broader  
28 spatial and temporal scales, significant advances have been made in determining the contexts  
29 under which positive BEF relationships persist<sup>1-3</sup>. Despite evidence that BEF relationships  
30 can be scale-dependent<sup>4-7</sup>, however, testing the effects of different, simultaneous stressors on  
31 BEF has remained confined to small-scale studies, in part due to the difficulty in isolating the  
32 effects of specific stressors in natural systems. Thus, there remains a critical discrepancy  
33 between the scales at which we study multi-stressor impacts on BEF versus the scales at  
34 which both human disturbances and management actions influence ecosystems<sup>4,6,8</sup>.

35           The need to understand how multiple human-caused stressors influence BEF in  
36 hyperdiverse systems is even more urgent, as diverse tropical systems are among the most  
37 threatened by humans<sup>9</sup>, yet even our basic knowledge of BEF in these systems lags  
38 behind<sup>3,10</sup>. For example, on coral reefs, a recent review found only ten studies have explicitly  
39 tested the effects of biodiversity on ecosystem functioning<sup>11</sup>, none of which tested the  
40 influence of multiple stressors. Remote coral reefs provide a unique opportunity to fill these  
41 knowledge gaps, because while they are still exposed to some key stressors, they are free  
42 from many of the local pressures experienced by areas close to human population centres.  
43 Examining BEF relationships on remote reefs therefore enables a rigorous test of how  
44 multiple stressors influence biodiversity and ecosystem functioning in a hyperdiverse, natural  
45 system.

46           Here, we use a unique, large-scale natural experiment, allowing for a cross-factored  
47 design within a remote archipelago to test the response of ecosystem functioning in coral-reef  
48 fishes to two of the most pervasive drivers of biodiversity loss: climate change and invasive  
49 species<sup>12-15</sup>. Understanding the simultaneous influence of these two drivers on biodiversity  
50 and ecosystem function is particularly important because, unlike other key causes of  
51 biodiversity loss (e.g., exploitation, land use change), even remote ecosystems have not  
52 escaped their effects<sup>16</sup>. On coral reefs, the effects of climate change typically manifest as  
53 climate extremes (i.e., warm-water anomalies), which are triggering increasingly frequent and  
54 severe mass coral bleaching events<sup>17</sup>. Extensive coral loss following climate-induced  
55 bleaching events often results in reductions in fish abundance and diversity<sup>18</sup>, but the effects  
56 of bleaching on BEF relationships remain unknown. Invasive rats, which have been  
57 introduced to nearly all islands worldwide, cause severe declines and local extinctions of  
58 numerous species of island-dwelling plants and animals, including seabirds<sup>19</sup>. By depleting  
59 seabird populations, invasive rats disrupt the natural flow of nutrient subsidies (guano) to

60 coral reefs, thereby reducing the biomass of coral-reef fishes<sup>20</sup>. However, it is unknown how  
61 seabird nutrients influence biodiversity on coral reefs, and how this in turn influences  
62 multiple metrics of ecosystem function.

63         Because there are no prior studies examining BEF relationships on remote coral reefs,  
64 we first established whether biodiversity increases ecosystem functioning of coral-reef fishes  
65 in a remote area. Specifically, we conducted surveys of coral-reef fishes throughout the  
66 Chagos Archipelago, the largest uninhabited and unfished coral reef area in the Indian  
67 Ocean<sup>21</sup> and one of the most remote coral reef areas in the world<sup>22</sup>. We then determined: (1)  
68 Does a climate extreme and/or an invasive species alter BEF relationships? (2) What are the  
69 direct and biodiversity-mediated indirect pathways by which these human disturbances  
70 influence ecosystem functioning? To test the effect of a climate extreme on BEF relationships  
71 and ecosystem functioning, we conducted replicate surveys of coral-reef fishes immediately  
72 before and two to four years after the 2015/2016 marine heatwave, which caused extensive  
73 coral bleaching on reefs throughout the Indo-Pacific<sup>17</sup>, including within the Chagos  
74 Archipelago<sup>23</sup>. To test for an effect of invasive species, in each year we compared coral-reef  
75 fish biodiversity and ecosystem functioning around rat-free islands with abundant seabird  
76 populations to nearby islands with invasive rats, and thus few seabirds<sup>20,24</sup>.

77         For both questions, we used two metrics of ecosystem functioning: fish biomass and  
78 productivity. Standing biomass is one of the most commonly used metrics of ecosystem  
79 function, as it is related to the provision of ecosystem services, and serves as a useful proxy  
80 for functions including energy flux and nutrient cycling<sup>25,26</sup>. Productivity has long been a key  
81 metric of function in terrestrial studies<sup>27</sup>, yet has rarely been used in BEF studies of coral-reef  
82 fishes<sup>11</sup>. Combined, these two metrics complement each other to give a more complete  
83 picture of ecosystem function, as biomass provides a static measure of energy and material

84 storage, while productivity provides a dynamic measure of the movement of energy and  
85 material<sup>28</sup>.

## 86 Results and Discussion

### 87 *Biodiversity-ecosystem function (BEF) relationships on remote coral reefs*

88         There was a positive relationship between biodiversity and both measures of  
89 ecosystem function, with biodiversity exhibiting the strongest effect on ecosystem function  
90 relative to all other measured predictors (Fig 1). Both BEF relationships were non-saturating  
91 (concave-up), with estimated power coefficients of 1.53 for biomass and 1.67 for productivity  
92 (linear mixed-effects models [LMM] - biomass: 95% CI 1.17 to 1.88, 75% CI: 1.32 to 1.73;  
93 productivity: 95% CI 1.33 to 1.98, 75% CI 1.47 to 1.85; Supplementary Table 1). These  
94 estimates translate to a 15.8% increase in biomass and 17.3% increase in productivity for  
95 each 10% increase in species richness. The estimated slope for the relationship between log  
96 richness and log biomass was greater than that obtained in a majority of manipulative  
97 experiments in terrestrial and aquatic systems, which typically have slopes that are indicative  
98 of saturating (concave-down) relationships (i.e.,  $0 < \text{slope coefficient} < 1$ )<sup>29</sup>. However, the  
99 non-saturating relationships observed here are in line with theoretical expectations for the  
100 shape of BEF relationships in natural ecosystems<sup>30</sup>. Moreover, the estimated slope is  
101 extremely similar to that from a global analysis of coral-reef fish biomass<sup>31</sup>, demonstrating  
102 remarkable consistency in BEF relationships across multiple spatial scales and functions in  
103 natural systems<sup>32</sup>.

### 104 *Effects of human-caused stressors on BEF relationships*

105         Compared to the strong overall effects of biodiversity on ecosystem functions, the  
106 influences of a climate extreme and invasive species on the BEF relationships were minor,  
107 demonstrating that the BEF relationships for some functions may be resilient to even the

108 largest forms of disturbance. Despite both stressors, the positive relationships between  
109 biodiversity and ecosystem function persisted (Figs. 2a, 2b). However, there were trends  
110 suggesting that the slope of the relationship between biodiversity and biomass was steeper in  
111 the presence of invasive rats, while the slope for productivity was steeper after the climate  
112 extreme (Figs. 2c, 2d; Supplementary Figs. 1, 2).

113         The slope for the relationship between diversity and biomass was greater around  
114 islands with invasive rats than around rat-free islands, although this pattern was only apparent  
115 when using observed species richness and the 95% confidence interval overlapped zero,  
116 demonstrating that this difference was only marginal (Fig. 2c; Supplementary Table 2; LMM  
117 – estimate 0.37, 95% CI -0.22 to 1.00; 75% CI 0.03 to 0.74). This marginal difference was  
118 primarily driven by higher standing biomass around rat-free islands at low-levels of diversity,  
119 as demonstrated by a greater difference in the BEF slopes between rat-free and rat-infested  
120 islands at lower levels of richness, with the lines converging at high richness levels (Fig. 2a).  
121 This pattern suggests that nutrient subsidies provided by seabirds may help maintain  
122 ecosystem function, especially when biodiversity is lower. By contrast, there was no  
123 evidence that the climate extreme had any effect on the BEF relationship for biomass (Fig.  
124 2c; Supplementary Table 2; LMM - estimate 0.10, 95% CI -0.56 to 0.92; 75% CI -0.25 to  
125 0.61).

126         There was no evidence that the presence of invasive rats influenced the slope of the  
127 BEF relationship for productivity (Fig. 2d; Supplementary Table 2; LMM - estimate 0.24,  
128 95% CI -0.33 to 0.78; 75% CI -0.10 to 0.55). Instead, the slope of the BEF relationship was  
129 marginally greater after a climate-induced bleaching event compared to before the event, with  
130 a 95% confidence interval that barely overlapped zero when using either observed or  
131 estimated species richness (Fig. 2d; Supplementary Table 2; LMM - estimate 0.57; 95% CI -  
132 0.09 to 1.26, 75% CI 0.19 to 0.98). This finding is consistent with the notion that biodiversity

133 becomes more important following disturbance, as species vary in their response to stressors  
134 and functional redundancy is lost<sup>11</sup>. This extreme climatic event likely affected the BEF for  
135 productivity but not biomass because over the relatively short-time scale examined here (2-4  
136 years post-disturbance), coral bleaching typically causes the largest declines in small  
137 species<sup>33</sup>, which can be key contributors to productivity despite their relatively minor  
138 contribution to biomass<sup>34,35</sup>. However, additional changes in coral-reef fish communities  
139 occur over longer time scales following disturbance as reef structure continues to degrade<sup>36</sup>.  
140 For example, larger fish decline in abundance after more than 7 years following  
141 disturbance<sup>33</sup>, and altered patterns of coral-reef fish richness and biomass can persist for more  
142 than 15 years<sup>37</sup>. Consequently, the effects of climate-induced bleaching on BEF relationships  
143 for both biomass and productivity may accumulate over time, suggesting that the long-term  
144 influence of bleaching on BEF relationships could be an important avenue for future work.

145 *Effects of human-caused stressors on ecosystem functions via direct and diversity-mediated*  
146 *pathways*

147       Beyond their effects on the relationships between biodiversity and ecosystem  
148 function, human-caused stressors can also influence ecosystem functioning through direct  
149 and/or biodiversity-mediated indirect pathways. In these remote assemblages of coral-reef  
150 fishes, climate-induced bleaching had little direct effect on either ecosystem function (Fig. 3;  
151 structural equation model [SEM] - direct effect on biomass 0.07; direct effect on productivity  
152 0.13). Results from mixed-effects models corroborated this result and similarly suggested  
153 that, if anything, the climate extreme had a small, positive influence on ecosystem function,  
154 after accounting for all other variables (Fig. 1; Supplementary Table 1; LMM – biomass:  
155 estimate 0.11, 95% CI -0.12 to 0.37, 75% CI -0.02 to 0.27; productivity: estimate 0.21, 95%  
156 CI -0.02 to 0.43, 75% CI 0.07 to 0.34). This somewhat counter-intuitive result was likely  
157 driven by groups of coral-reef fish that benefit following bleaching events, at least in the

158 short-term. While small-bodied, coral-dependent species typically suffer reductions in density  
159 immediately following disturbance, larger-bodied groups including herbivores, piscivores,  
160 and mixed-diet feeders often exhibit temporary increases in abundance<sup>33,38</sup>. For herbivorous  
161 parrotfish, this population-level increase is preceded by a spike in individual growth rates,  
162 likely fuelled by increased food availability<sup>39</sup>. Considering the dominance of herbivorous  
163 fishes on the studied reefs<sup>20,24</sup>, and in the Chagos Archipelago as a whole<sup>40</sup>, it is reasonable  
164 that direct effects of the climate-induced bleaching were weakly positive in this region.

165         Importantly, however, the climate extreme had a large negative effect on diversity,  
166 which ultimately resulted in net negative effects on both ecosystem functions via a diversity-  
167 mediated pathway (Fig. 3; SEM – indirect effect on biomass via richness: -0.18; indirect  
168 effect on productivity via richness: -0.21). Indeed, there was an estimated 17.6% reduction in  
169 species richness 2-4 years after the climate extreme compared to immediately before the  
170 extreme heatwave (Fig 1; Supplementary Fig 3; Supplementary Table 2; LMM - 95% CI -  
171 28.7 to -5.8%, 75% CI -24.4 to -11.1%). Because diversity had the strongest direct effect on  
172 ecosystem function relative to all other measured variables (Fig. 3; SEM - direct effect of  
173 richness on biomass 0.68, direct effect of richness on productivity 0.80), the loss of diversity  
174 following the climate extreme, in turn, led to a net loss of ecosystem function. Combined  
175 with the fact that positive BEF relationships were maintained (and in the case of productivity,  
176 perhaps even strengthened) despite the climate extreme (Fig. 2), these results suggest that as  
177 the frequency and severity of climate-induced bleaching events continues to increase<sup>17</sup>,  
178 preserving biodiversity will remain important for maintaining ecosystem function but will be  
179 increasingly challenging as bleaching itself reduces biodiversity. More broadly, these results  
180 highlight the importance of considering multiple pathways through which human-caused  
181 stressors can influence ecosystem function.



182 Invasive rats also decreased biodiversity, but their effects on ecosystem function via  
183 this pathway were less severe than those caused by the climate extreme (Fig 3; SEM -  
184 indirect effect on biomass via richness -0.11; indirect effect on productivity via richness -  
185 0.12). Reefs adjacent to islands with rats had an estimated 13.9% fewer species than islands  
186 near abundant seabird populations, but this difference was only marginal (Fig 1; LMM - 95%  
187 CI -25.4 to 4.0%; 75% CI -19.6 to -3.2%). In contrast to the climate extreme, invasive rats  
188 had consistently negative effects on both ecosystem functions. Specifically, the loss of  
189 nutrient subsidies due to the presence of invasive rats had direct negative consequences for  
190 biomass, (Fig 3; SEM biomass: direct effect = -0.22;), which is consistent with other analyses  
191 in this study (Fig 1; LMM – estimate -0.36, 95% CI -0.62 to -0.17, 75% CI -0.53 to -0.26)  
192 and previous work in this system<sup>20</sup>.

193 For productivity, the estimated influence of invasive rats varied based on a number of  
194 assumptions. We first modelled reef-wide productivity assuming no systematic difference in  
195  $K_{\max}$  (a standardized measure of the fish growth coefficient  $K^{41}$ , see *Methods*) between reefs  
196 adjacent to rat-infested versus rat-free islands. This assumption is reasonable given that on a  
197 global scale, differences in primary productivity across sites, which presumably correlates  
198 with resource availability, explains almost no variation in  $K_{\max}^{41}$ . Under this scenario, there is  
199 little evidence that the loss of nutrient subsidies had a direct effect on productivity, although  
200 mixed-effects models revealed a trend towards a negative effect (Fig. 1; Fig. 3;  
201 Supplementary Table 1; SEM: productivity: direct effect: -0.08; coefficient estimate from  
202 LMM: -0.11; 95% CI -0.34 to 0.08, 75% CI -0.25 to -0.01). That there was even a trend  
203 towards a loss in productivity as a result of invasive rats under this most conservative  
204 scenario is noteworthy, and suggests that the functional traits of fish communities that drive  
205 community-wide productivity, including size, feeding group, and position in the water  
206 column<sup>41</sup>, differ between rat-infested compared to rat-free islands.

207           Although resource availability has little influence on  $K_{\max}$  at a global scale, it is  
208 expected to play a more prominent role in explaining differences in growth rates over small  
209 spatial scales<sup>41</sup>, a prediction that is supported by empirical studies of coral-reef fishes<sup>42,43</sup>.  
210 Indeed, on the reefs investigated here, herbivorous damselfish have faster growth rates  
211 around islands with seabirds compared to islands with invasive rats<sup>20</sup>. Therefore, we also  
212 modelled community-wide productivity under the assumption that seabird nutrient subsidies  
213 similarly enhance the growth rates, and thus the  $K_{\max}$ , of other species (see *Methods*). As  
214 expected, under the assumption of enhanced growth around islands with seabirds the negative  
215 effects of invasive rats on community-wide productivity are comparable to their effects on  
216 biomass (Supplementary Table 3; Supplementary Fig. 2). Despite the variation in effect size,  
217 the consistent negative influence of invasive rats on diversity and ecosystem function  
218 suggests that, in contrast to the climate-induced bleaching event, the disruption of nutrient  
219 subsidies negatively influences all species and ecosystem processes. This result is particularly  
220 concerning given that the capacity of animals to move nutrients has diminished across nearly  
221 all ecosystems worldwide<sup>44</sup>. If the loss of nutrient subsidies has similar effects on ecosystem  
222 functions in other systems, then restoring natural nutrient pathways should be a critical  
223 component of any management strategy.

## 224 *Conclusions*

225           Human-caused stressors can affect ecosystem functioning in several ways, three of  
226 which were investigated here: (1) indirect effects on ecosystem function by affecting  
227 biodiversity, (2) effects on the relationship between biodiversity and ecosystem function, and  
228 (3) direct effects on ecosystem function (Fig. 4). Importantly, these three mechanisms are not  
229 mutually exclusive, nor do they always work in tandem. Thus, to accurately predict whether  
230 ecosystem functions will be sustained in the face of rapid environmental change, it is

231 necessary to evaluate all the mechanisms by which disturbances can influence ecosystem  
232 function at management-relevant scales<sup>4</sup>.

233 Here, we demonstrate that non-saturating BEF relationships occur on remote coral  
234 reefs, thus adding to the growing body of evidence that the positive effects of biodiversity on  
235 ecosystem function may be one of the few general rules in ecology. That BEF relationships  
236 have been found regardless of ecosystem (terrestrial, aquatic, marine), trophic level (primary  
237 producers, consumers), and spatial scale (local, regional, global) is noteworthy in a discipline  
238 dominated by ‘context-dependent’ findings. Moreover, these positive relationships persisted  
239 despite two pressing causes of human-induced environmental change. Thus, BEF  
240 relationships in natural systems may withstand at least some of the multitude stressors to  
241 which they are exposed, at least in relatively pristine, hyperdiverse systems. These robust  
242 positive relationships between biodiversity and ecosystem function highlight the importance  
243 of conserving biodiversity to maintain ecosystem functions and their associated services<sup>4,27,45</sup>,  
244 and consequently suggest that biodiversity conservation should be a key management  
245 priority. Despite these persistent BEF relationships, however, human-caused stressors  
246 ultimately reduced ecosystem functions via multiple other pathways. Specifically, a climate  
247 extreme caused diversity-mediated declines in ecosystem function. Conversely, the loss of  
248 nutrient subsidies had more direct consequences, especially for biomass. Therefore, while  
249 biodiversity is clearly important to ecosystem function, biodiversity conservation alone may  
250 not sustain ecosystem functions if underlying stressors are not reduced.

251

252 **Methods**

253 *Study area*

254           This study was conducted in the Chagos Archipelago, Indian Ocean (5° 50'S, 72°  
255 00'E). Importantly, these coral reefs are isolated from the majority of direct human stressors,  
256 such as fishing and poor water quality<sup>21,22,46</sup>, which enabled us to investigate biodiversity-  
257 ecosystem function relationships in a relatively pristine, high-diversity system. At the same  
258 time, even these remote reefs are prone to the some of the same stressors that affect nearly all  
259 locations worldwide, namely climate change and invasive species. Therefore, we were able to  
260 simultaneously investigate how these major sources of human-caused environmental change  
261 influence ecosystem functioning and BEF relationships without the confounding influence of  
262 other local human stressors.

263           To investigate the effects of invasive species, we surveyed coral-reef fish  
264 communities around 12 islands, six of which have invasive rats and six of which are rat-free.  
265 Rats were introduced to some islands of the Chagos Archipelago hundreds of years ago,  
266 while other islands have never had rats. Islands that are rat-free are home to dense  
267 populations of nesting seabirds, with 10 internationally important bird areas designated. The  
268 high densities of seabirds on some islands provide natural nutrient subsidies to adjacent coral  
269 reefs. By contrast, islands that are rat-infested have few seabirds, which due to the resultant  
270 loss of their nutrient subsidies, results in lower coral-reef fish biomass compared to nearby  
271 islands that are rat-free<sup>20</sup>. Surveys were conducted around these reefs in March 2015.

272           To determine how climate change affects ecosystem function, we revisited eleven of  
273 the same islands (five rat-free and six rat-infested) 2-4 years after a major climate extreme.  
274 The reefs of the Chagos Archipelago were severely bleached as a result of warm-water  
275 anomalies during 2015-2016, which caused mass coral bleaching throughout the Indian and  
276 Pacific Oceans<sup>17,23,47</sup>. Ten of the islands in the Chagos Archipelago were re-visited in May

277 2018<sup>24</sup>, and one island was re-visited in March 2019, due to weather and logistical  
278 constraints. Due to the broad spatial scale of this marine heatwave, we were unable to test its  
279 effects by comparing an unaffected control area to an affected area. Instead, we compared the  
280 same reefs before versus after the heatwave under the assumption that any observed temporal  
281 changes were primarily caused by the heatwave. This assumption is reasonable given the  
282 extreme temperature anomalies in the region that occurred during this time period<sup>23,47</sup>, along  
283 with the isolation of the study region from other stressors<sup>21,22,46</sup>. The presence of invasive rats  
284 did not modify the extent of coral bleaching on these reefs<sup>24</sup>, so these two stressors were  
285 treated as independent.

#### 286 *Surveys of biodiversity and ecosystem function*

287 To quantify biodiversity and ecosystem function of coral-reef fishes, we censused all  
288 diurnal, non-cryptic fishes along four replicate 30-m transects, spaced 10 m apart, on the  
289 lagoonal side of each island (1-3 m depth). Large and mobile fishes were counted in a 5-m  
290 wide belt during a first pass along the transect, and damselfishes (Pomacentridae) were  
291 counted in a 2-m wide belt during a second pass along the same transect. For all individuals  
292 greater than 7 cm total length (TL), the species and size (TL, visually estimated to the nearest  
293 cm) were recorded. Because we necessarily excluded small and cryptic fishes in these  
294 surveys, if anything our results likely underestimate species diversity and the relationship  
295 between biodiversity and ecosystem functioning on these reefs. Along the same transects, we  
296 quantified percent coral cover using line and point-intercept methods and structural  
297 complexity using a standard visual scale, that is widely used in reef ecological studies<sup>48,49</sup>.

298 We used observed species richness and standardized species richness as our  
299 biodiversity metrics. Observed species richness was determined directly from the underwater  
300 visual surveys as the number of species per transect. Because species richness is positively

301 related to sample coverage and the observed number of individuals<sup>50</sup>, we also calculated a  
302 standardized measure of species richness. Here, sample coverage was equal across all  
303 locations, but locations differed in the total number of individuals present. Therefore, we  
304 calculated standardized species richness as the Chao index with abundance-based data using  
305 the R package iNEXT<sup>51,52</sup>. The Chao index, which is based on the rarefaction-extrapolation  
306 of Hill numbers, provides an unbiased estimate of asymptotic species richness and enables  
307 comparisons among communities with differing numbers of individuals or sampling  
308 effort<sup>50,53–55</sup>.

309 We measured ecosystem function as standing fish biomass and fish productivity. Fish  
310 counts were converted to biomass using published species-specific length-weight  
311 relationships<sup>56</sup>. Productivity was calculated following the methods of<sup>34,35</sup>. We first  
312 determined the expected growth coefficient at the theoretical maximum species size ( $K_{\max}$ )  
313 for each species<sup>41</sup>.  $K_{\max}$  has the advantage over the traditional Von Bertalanffy growth  
314 coefficient ( $K$ ) in that it is standardized to a constrained body length, making comparisons  
315 across populations and species possible<sup>41</sup>. We obtained  $K_{\max}$  from published estimates based  
316 on the maximum size, diet, and position in water column of each species, combined with the  
317 mean sea surface temperature in the region<sup>41</sup>. Species traits were gathered from<sup>41</sup>, combined  
318 with additional trait data from<sup>56–62</sup>. We used a sea surface temperature of 28°C, which is the  
319 typical mean sea surface temperature throughout the study region<sup>46</sup>.

320 Importantly, differences in primary productivity explain almost no variability in  $K_{\max}$   
321 at a global scale, but at smaller spatial scales differences in resource availability among sites  
322 are likely to have a greater influence<sup>41</sup>. In the Chagos Archipelago, herbivorous damselfish  
323 (*Plectroglyphidodon lacrymatus*) grow faster around islands with seabirds than islands with  
324 invasive rats<sup>20</sup>. Although *P. lacrymatus* is the only species for which such comparative data  
325 are published, these differences in growth likely apply at least to other herbivorous fishes,

326 and may also transfer up the food chain to higher trophic groups. Indeed, unpublished data  
 327 suggest that  $K$  for the parrotfish *Chlorurus sordidus* is 22% higher around islands with  
 328 seabirds compared to islands with rats in the same study area, which is extremely similar to  
 329 the mean estimated difference for *P. lacrymatus* of 25%. Therefore, we calculated  $K_{max}$ , and  
 330 subsequently productivity, under four possible scenarios: (1) no difference in  $K_{max}$  between  
 331 rat-free versus rat-infested islands, (2) 10% higher  $K_{max}$  around rat-free islands  
 332 (corresponding to the lower bound of the 95% posterior prediction interval for *P.*  
 333 *lacrymatus*), (3) 25% higher  $K_{max}$  around rat-free islands (corresponding to the estimated  
 334 mean difference for *P. lacrymatus*), and (4) 45% higher  $K_{max}$  around rat-free islands  
 335 (corresponding to the upper bound of the 95% posterior prediction interval for *P.*  
 336 *lacrymatus*). For all scenarios, the percent differences in  $K_{max}$  were applied to all species.  
 337 While none of these scenarios is completely realistic, they are useful in that they include a  
 338 reasonable range of likely possibilities. We present results from the most conservative model,  
 339 assuming no differences in  $K_{max}$ , in the main text and comparisons of all models in the  
 340 supplement.

341 Using a modified formula from <sup>63</sup>, we then used  $K_{max}$  to estimate the age ( $t$ ) of each  
 342 fish given its length:

343 
$$t = \frac{1}{K_{max}} \ln \left[ \frac{L_{max}}{\left(1 - \frac{L_{act}}{L_{max}}\right) L_{max}} \right]$$

344 where  $L_{max}$  is the maximum size (total length) from the literature as described above and  $L_{act}$   
 345 is the actual length of each individual from the field surveys. These estimated ages were  
 346 plugged into the Von Bertalanffy Growth Function to calculate daily growth of each fish over  
 347 the course of one year. We converted estimated growth in length to estimated growth in mass  
 348 using the same species-specific length-weight relationships used to calculate standing

349 biomass. The summed rates of biomass growth thus give an estimate of potential productivity  
350 ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ).

351 To obtain an estimate of productivity that accounts for mortality, we first calculated  
352 natural mortality rates (M) following the formula in <sup>64</sup>:

$$\log(M) = -0.0066 - 0.279 \log(L_{max}) + 0.6543 \log(K_{max}) + 0.4634 \log(T)$$

353 where T is the same temperature (28°C) used above to estimate  $K_{max}$ . Because the Chagos  
354 Archipelago is a remote Marine Protected Area, fishing mortality is expected to equal zero,  
355 and therefore total mortality (Z) is equal to natural mortality (M). We rescaled Z to a daily  
356 mortality estimate ( $Z_d$ ), and estimated the daily probability of survival for each fish following  
357 <sup>34</sup>:

$$P_{surv} = e^{-Z_d}$$

358 We simulated mortality by obtaining random samples from a Bernoulli distribution following  
359 a success probability of  $P_{surv}$ . We then multiplied this daily survival schedule by the daily  
360 growth rates and summed the values over the course of one year to obtain an estimate of  
361 yearly productivity after accounting for mortality. Finally, for biomass and productivity we  
362 summed species values for each transect to get community-wide estimates of these two  
363 functions.

#### 364 *Statistical analyses*

365 To test for an overall effect of biodiversity on ecosystem function, we modelled each  
366 ecosystem function using hierarchical mixed-effects models following Gaussian distributions.  
367 For both responses, island within atoll were included as random effects to account for our  
368 nested sampling including repeated surveys at the same islands<sup>65</sup>. In total, 48 transects  
369 conducted around 12 islands were included from 2015, and 44 transects from 11 islands were



370 included from 2018/2019 (4 transects/island/year). To test for an effect of biodiversity (S)  
371 while accounting for other factors that may influence ecosystem function (EF), we included  
372 coral cover (CC), structural complexity (SC), climate extreme (CE, pre or post), and invasive  
373 rats (IR, rat-free or rat-infested) as additional fixed effects:

$$\log(EF_{ij}) \sim \beta_0 + \beta_1 \times \log(S_{ij}) + \beta_2 \times \log(CC_{ij}) + \beta_3 \times SC_{ij} + \beta_4 \times CE_{ij} + \beta_5 \times IR_{ij} \\ + b_{1ij} + b_{2j} + \varepsilon_{ij}$$

374 where islands (*i*) are nested within atolls (*j*), and the residual error ( $\varepsilon$ ) is normally  
375 distributed. We modelled the relationship between ecosystem function and diversity on a log-  
376 log scale, as this specification has the most empirical support across many systems, including  
377 coral reefs<sup>29,31</sup>. Furthermore, in log-log models the interpretation of  $\beta_1$  is equivalent to the  
378 power coefficient, and thus enables a test of the shape of the relationship between ecosystem  
379 function and diversity ( $\beta < 1$  represents concave-down/saturating,  $\beta > 1$  represents concave-  
380 up/non-saturating)<sup>30</sup>. We ran all models using observed species richness and estimated  
381 asymptotic species richness. Visual analysis of residual plots revealed no departures from the  
382 assumptions of normality and homoscedasticity, and there was no evidence of  
383 multicollinearity among predictor variables (all VIF < 1.6). For both ecosystem functions, the  
384 estimated effect of richness on function was qualitatively similar regardless of whether  
385 observed or estimated species richness was used. Therefore, we present results from models  
386 using observed species richness in the main text and present comparisons of the models using  
387 estimated richness in the supplement (Supplementary Tables 1-4; Supplementary Fig. 1-3).

388 To determine whether human disturbances altered BEF relationships, we added  
389 interaction terms for climate extreme\*richness and invasive rats\*richness to the mixed-effects  
390 models and measured the estimated coefficients for these interactions. All models were

391 conducted in R version 3.6.0 with associated packages lme4, blme, jtools, ggeffects, and  
392 MuMIn<sup>66-70</sup>.

393 Finally, to examine the pathways by which ecosystem function is affected by  
394 biodiversity and human stressors, we conducted structural equation models using the R  
395 packages lavaan and semPlot<sup>71,72</sup>. As with the mixed-effects models, we included structural  
396 complexity and coral cover as additional factors in the path analyses, and ran all models using  
397 both observed and estimated species richness. We corroborated the estimated effect of each  
398 stressor on each ecosystem function determined from the structural equation models by  
399 comparing the results to those from the additive mixed-effects models described above. We  
400 also ran an additional mixed-effects model as described above, but with log(richness) as the  
401 response, to which we compared the estimated effects of each stressor on biodiversity from  
402 the structural equation model. We evaluated structural equation model fits using both a  
403 relative (Comparative Fit Index [CFI]) and absolute (Standardized Root Mean Residual  
404 [SRMR]) index of fit<sup>73</sup>. For our biomass model the CFI was 0.991 and SRMR was 0.044 and  
405 for our productivity model the CFI was 0.991 and SRMR was 0.042, all of which are beyond  
406 the generally-accepted thresholds for good model fits (CFI > 0.95 and SRMR < 0.08)<sup>73</sup>.

407

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581 S.K.W. collected the data; C.E.B. conducted the analyses; C.E.B. wrote the manuscript with  
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583 **Competing Interests** The authors declare no competing interests.

584

585

586 **Figure Legends**

587 **Fig. 1 | Relationships between biodiversity, ecosystem function, and human disturbances**  
588 **on remote coral reefs.** Points represent estimates from linear mixed-effects models testing  
589 for an effect of each explanatory variable on coral-reef fish ecosystem function (biomass -  
590 green, productivity - purple) or biodiversity (richness - pink). Thick lines represent 75%  
591 confidence intervals, and thin lines represent 95% CIs. All estimates and confidence intervals  
592 are scaled (mean-centered and scaled by one standard deviation) to facilitate comparisons of  
593 effect sizes among the explanatory variables. For non-scaled estimates, see the main text and  
594 Supplementary Table 1.

595 **Fig. 2 | Effect of human disturbances on biodiversity-ecosystem function relationships**  
596 **on remote coral reefs.** Biomass (a) and productivity (b) of coral-reef fishes as a function of  
597 species richness on reefs adjacent to islands that are free of invasive rats (“rat-free”, blue) or  
598 infested by invasive rats (“rat-infested”, orange), immediately before a climate extreme that  
599 resulted in mass coral bleaching (“pre-climate extreme”, lighter, solid lines) and 2-4 years  
600 after a climate extreme (“post-climate extreme”, darker, dashed lines). Each point represents  
601 the data for one transect, with 4 transects/island conducted around 12 islands in 2015 and 11  
602 islands in 2018/2019. Lines are predicted (fitted) values from linear mixed effects models  
603 after accounting for structural complexity and coral cover, and shaded areas represent 95%  
604 CIs. (c,d) Estimated coefficients for the interaction term between richness and each stressor  
605 from the same models. Points represent scaled estimates, thick lines represent 75%  
606 confidence intervals, thin lines represent 95% CIs. For non-scaled estimates, see the main text  
607 and Supplementary Table 2.

608 **Fig. 3 | Links between human-caused stressors, reef characteristics, biodiversity, and**  
609 **ecosystem function.** Path analysis results for (a) biomass and (b) productivity. Green arrows

610 indicate a positive effect and red arrows represent a negative effect. The shading and  
611 thickness of the lines correspond to the strength of the standardized path coefficients, which  
612 are also displayed.

613 **Fig. 4 | Hypothesized and observed effects of human-caused stressors on biodiversity**  
614 **and ecosystem function.** Stressors can influence ecosystem function by: (1) indirectly by  
615 affecting biodiversity, which does not alter the slope of the BEF relationship, but can reduce  
616 ecosystem function by reducing the range of values of biodiversity; (2) by affecting the  
617 relationship between biodiversity and ecosystem function, thus changing the slope of the BEF  
618 relationship; and/or (3) directly by affecting ecosystem function, which can lower ecosystem  
619 function despite similar levels of biodiversity. Importantly, although each scenario is depicted  
620 separately, these scenarios are not mutually exclusive (i.e., stressors can simultaneously  
621 influence biodiversity and ecosystem function in multiple ways, those causing multiple  
622 changes to the depicted lines). The primary mechanisms observed here were (1) and (3), as  
623 demonstrated with structural equation modelling and corroborated with linear mixed-effects  
624 models. Both stressors also had minor effects on the strength of the different BEF  
625 relationships (2), as demonstrated by marginal changes to BEF slopes in linear mixed-effects  
626 models. Symbols in each box represent the stressor that caused changes in ecosystem  
627 function via each mechanism (thermometer = climate extreme leading to coral bleaching; rat  
628 = invasive species leading to the loss of seabird nutrient subsidies).





