

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 persist¹⁻³. Despite evidence that BEF relationships
30 can be scale-dependent⁴⁻⁷, 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^{4,6,8}.

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 humans⁹, yet even our basic knowledge of BEF in these systems lags
38 behind^{3,10}. For example, on coral reefs, a recent review found only ten studies have explicitly
39 tested the effects of biodiversity on ecosystem functioning¹¹, 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 species¹²⁻¹⁵. 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 effects¹⁶. 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 events¹⁷. Extensive coral loss following climate-induced
55 bleaching events often results in reductions in fish abundance and diversity¹⁸, 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 seabirds¹⁹. 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 fishes²⁰. 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 Ocean²¹ and one of the most remote coral reef areas in the world²². 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-Pacific¹⁷, including within the Chagos
74 Archipelago²³. 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^{20,24}.

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^{25,26}. Productivity has long been a key
81 metric of function in terrestrial studies²⁷, yet has rarely been used in BEF studies of coral-reef
82 fishes¹¹. 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 material²⁸.

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., $0 < \text{slope coefficient} < 1$)²⁹. However, the
99 non-saturating relationships observed here are in line with theoretical expectations for the
100 shape of BEF relationships in natural ecosystems³⁰. Moreover, the estimated slope is
101 extremely similar to that from a global analysis of coral-reef fish biomass³¹, demonstrating
102 remarkable consistency in BEF relationships across multiple spatial scales and functions in
103 natural systems³².

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 lost¹¹. 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 species³³, which can be key contributors to productivity despite their relatively minor
138 contribution to biomass^{34,35}. However, additional changes in coral-reef fish communities
139 occur over longer time scales following disturbance as reef structure continues to degrade³⁶.
140 For example, larger fish decline in abundance after more than 7 years following
141 disturbance³³, and altered patterns of coral-reef fish richness and biomass can persist for more
142 than 15 years³⁷. 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^{33,38}. For herbivorous
161 parrotfish, this population-level increase is preceded by a spike in individual growth rates,
162 likely fuelled by increased food availability³⁹. Considering the dominance of herbivorous
163 fishes on the studied reefs^{20,24}, and in the Chagos Archipelago as a whole⁴⁰, 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 increase¹⁷,
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 system²⁰.

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 column⁴¹, 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 scales⁴¹, a prediction that is supported by empirical studies of coral-reef fishes^{42,43}.
210 Indeed, on the reefs investigated here, herbivorous damselfish have faster growth rates
211 around islands with seabirds compared to islands with invasive rats²⁰. 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 worldwide⁴⁴. 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 scales⁴.

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^{4,27,45},
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^{21,22,46}, 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-free²⁰. 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^{17,23,47}. Ten of the islands in the Chagos Archipelago were re-visited in May

277 2018²⁴, 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^{23,47}, along
283 with the isolation of the study region from other stressors^{21,22,46}. The presence of invasive rats
284 did not modify the extent of coral bleaching on these reefs²⁴, 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^{48,49}.

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 individuals⁵⁰, 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^{51,52}. 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^{50,53–55}.

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 relationships⁵⁶. Productivity was calculated following the methods of^{34,35}. We first
312 determined the expected growth coefficient at the theoretical maximum species size (K_{\max})
313 for each species⁴¹. 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 possible⁴¹. 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 region⁴¹. Species traits were gathered from⁴¹, combined
318 with additional trait data from^{56–62}. We used a sea surface temperature of 28°C, which is the
319 typical mean sea surface temperature throughout the study region⁴⁶.

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 influence⁴¹. In the Chagos Archipelago, herbivorous damselfish
323 (*Plectroglyphidodon lacrymatus*) grow faster around islands with seabirds than islands with
324 invasive rats²⁰. 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 ⁶³, 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 ⁶⁴:

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

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 ³⁴:

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

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 islands⁶⁵. 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 (ε) 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^{29,31}. Furthermore, in log-log models the interpretation of β_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)³⁰. 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 MuMIn⁶⁶⁻⁷⁰.

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^{71,72}. 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 fit⁷³. 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)⁷³.

407

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- 573

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580 **Author Contributions** C.E.B. and N.A.J.G. conceived this study; C.E.B., N.A.J.G., and
581 S.K.W. collected the data; C.E.B. conducted the analyses; C.E.B. wrote the manuscript with
582 input from N.A.J.G. and S.K.W.

583 **Competing Interests** The authors declare no competing interests.

584

585

586 **Figure Legends**

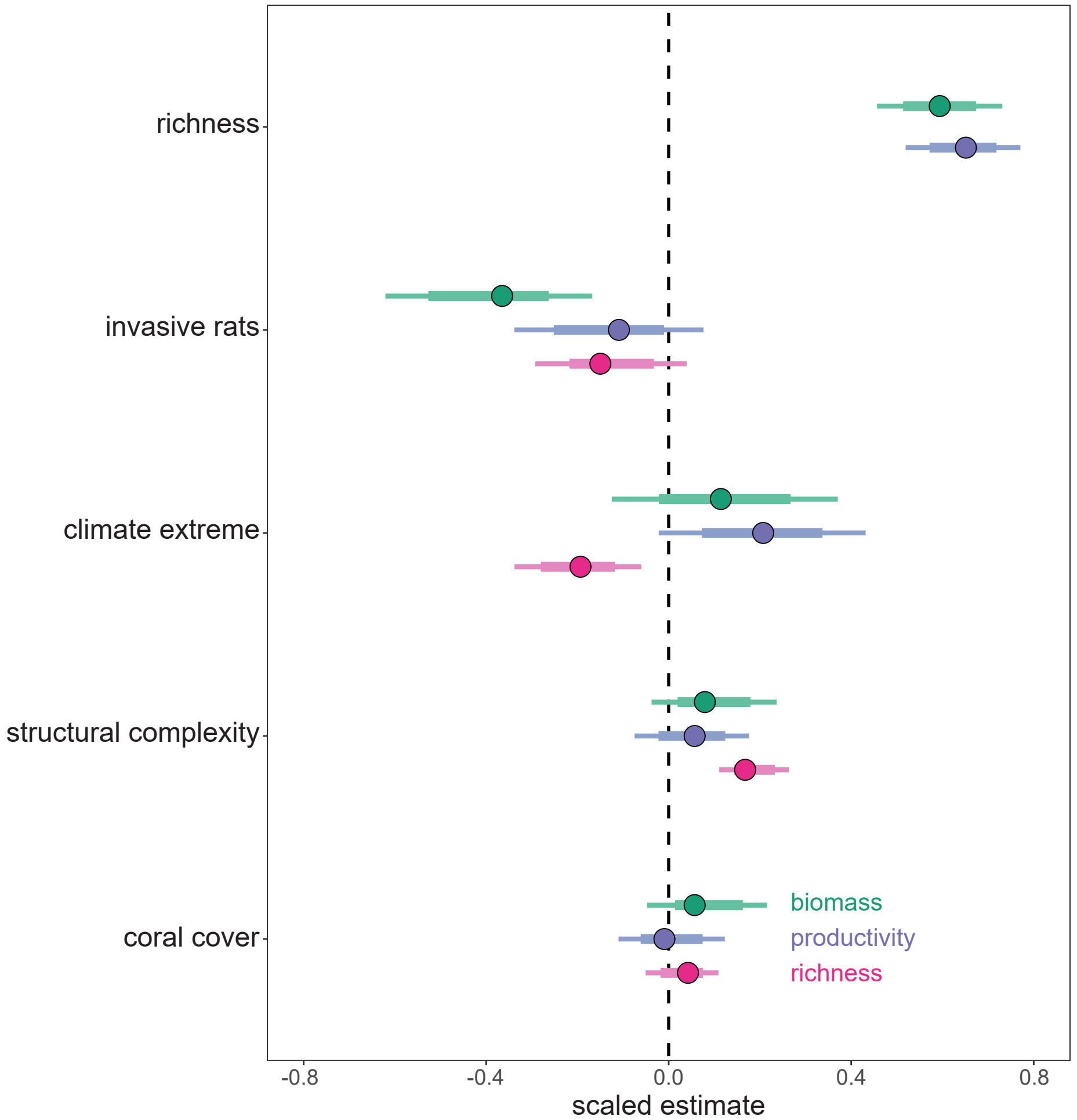
587 **Fig. 1 | Relationships between biodiversity, ecosystem function, and human disturbances**
588 **on remote coral reefs.** Points represent estimates from linear mixed-effects models testing
589 for an effect of each explanatory variable on coral-reef fish ecosystem function (biomass -
590 green, 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.

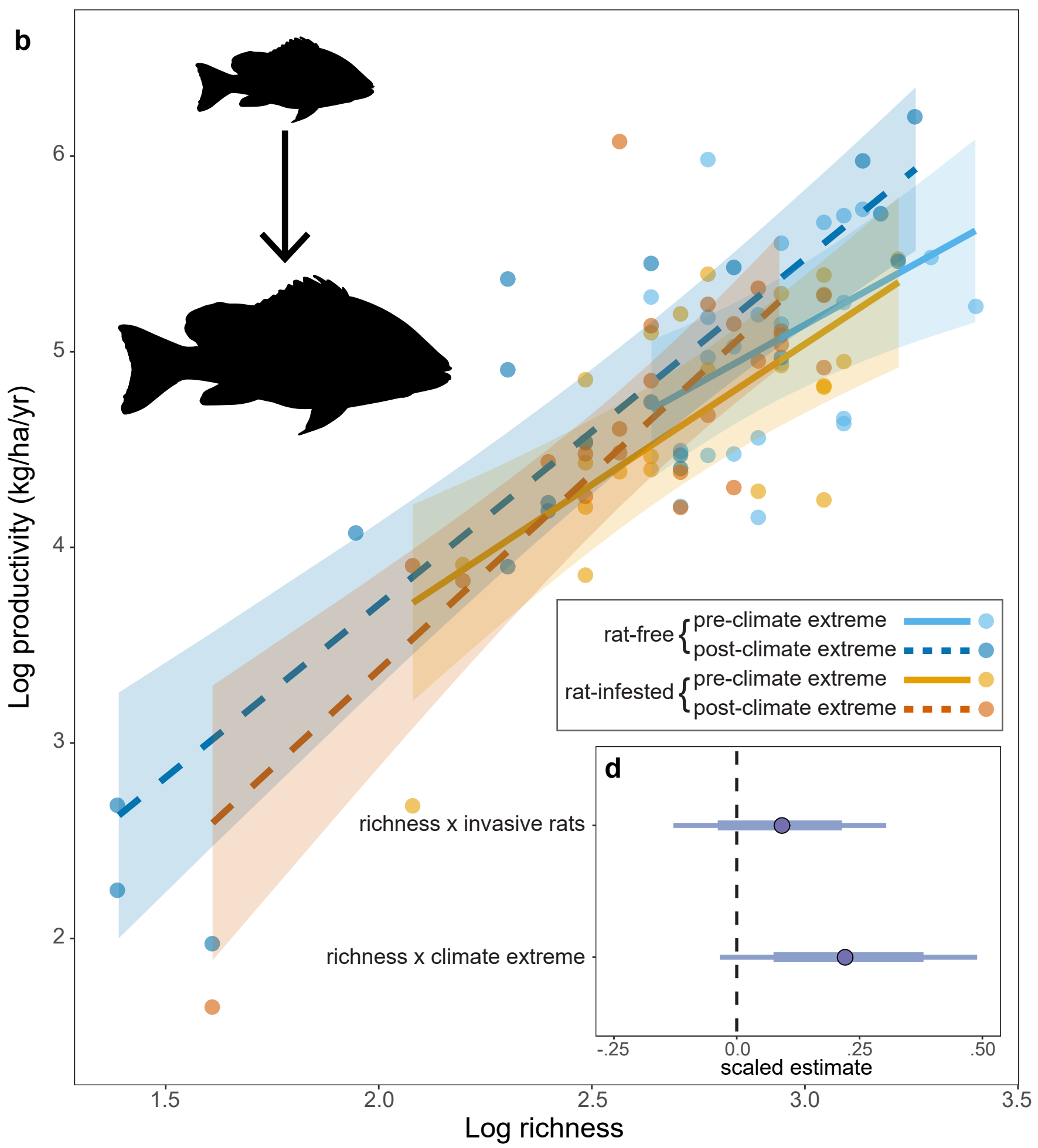
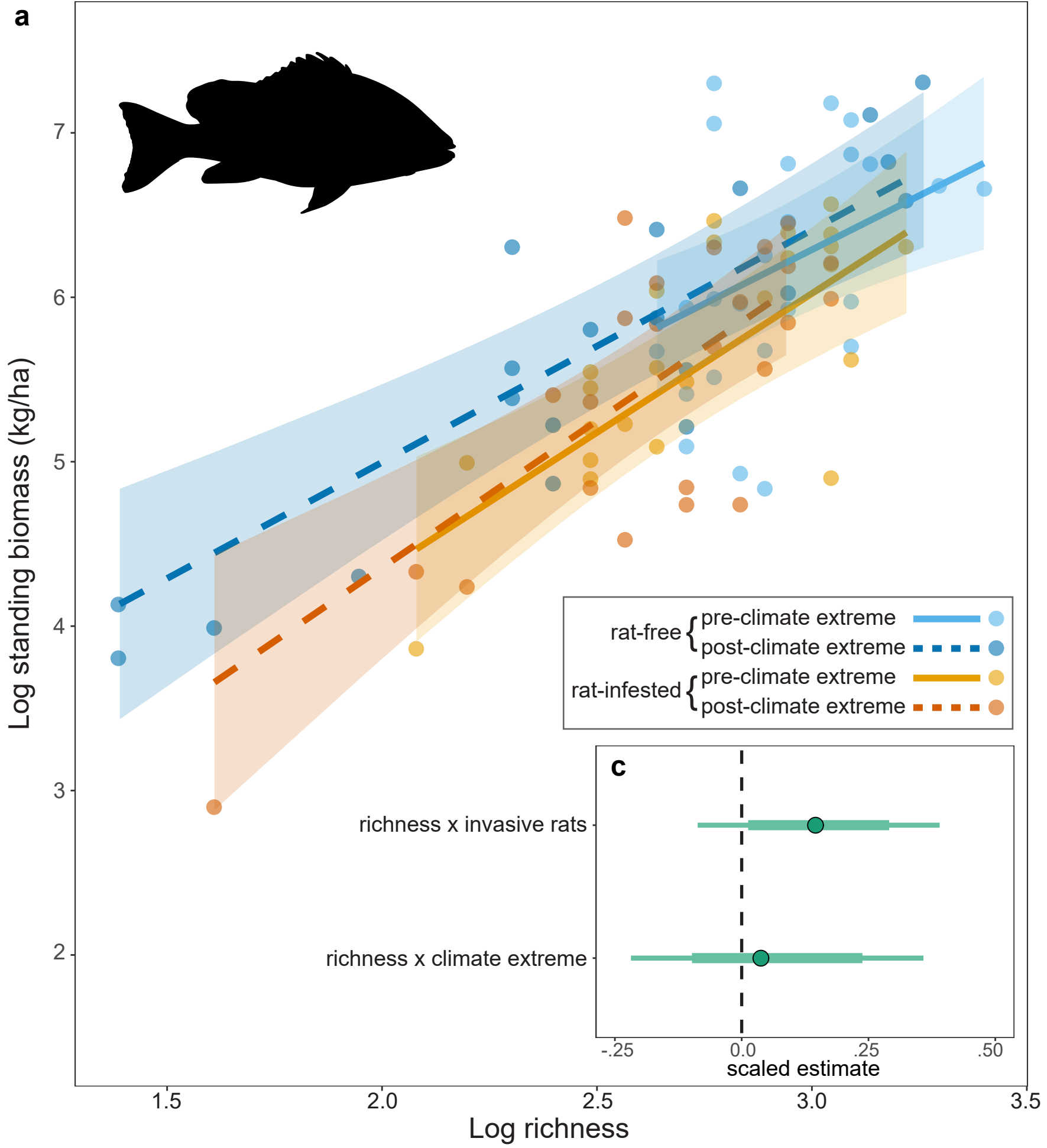
595 **Fig. 2 | Effect of human disturbances on biodiversity-ecosystem function relationships**
596 **on remote coral reefs.** Biomass (a) and productivity (b) of coral-reef fishes as a function of
597 species richness on reefs adjacent to islands that are free of invasive rats (“rat-free”, blue) or
598 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.

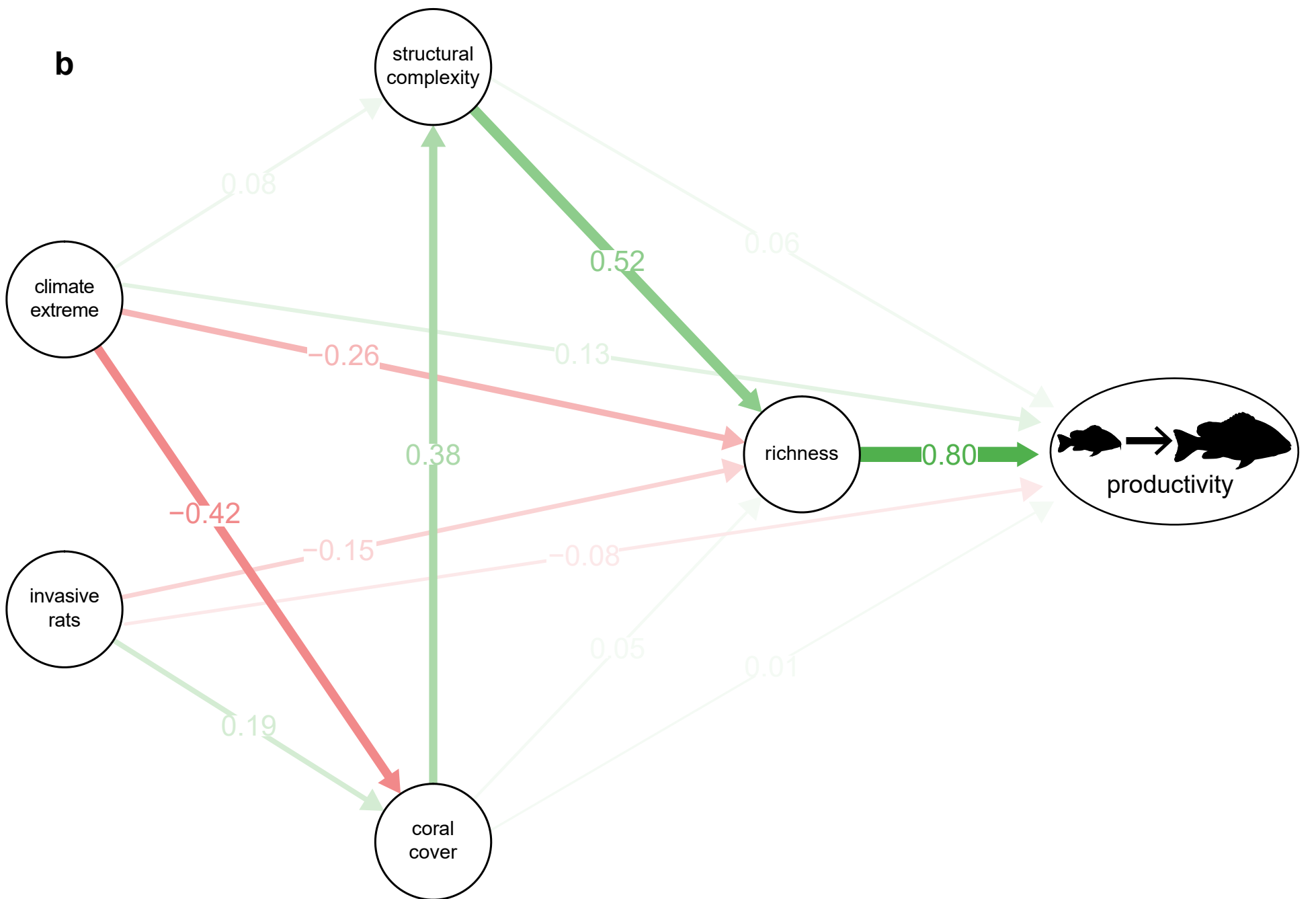
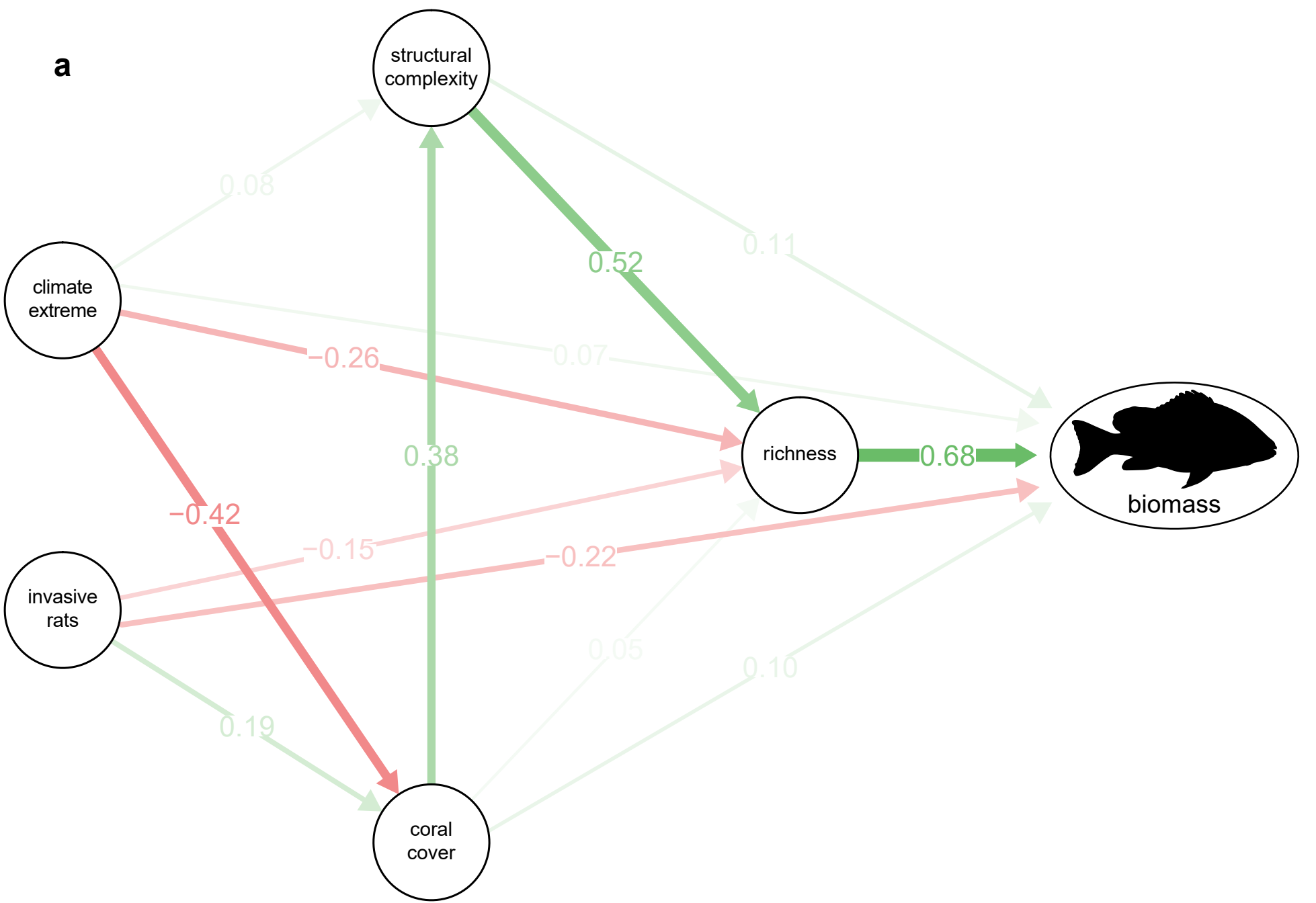
608 **Fig. 3 | Links between human-caused stressors, reef characteristics, biodiversity, and**
609 **ecosystem function.** Path analysis results for (a) biomass and (b) productivity. Green arrows

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).







human-caused stressors

reef characteristics

biodiversity

ecosystem function