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1 **Linking key human-environment theories to inform the sustainability of coral reefs**

2  
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16  
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19 **Summary**

20 Effective solutions to the ongoing “coral reef crisis” will remain limited until the  
21 underlying drivers of coral reef degradation are better understood. Here, we conduct a  
22 global-scale study of how four key metrics of ecosystem states and processes on coral  
23 reefs (top predator presence, reef fish biomass, trait diversity, and parrotfish scraping  
24 potential) are explained by 11 indicators based on key human-environment theories from  
25 the social sciences. Our global analysis of >1,500 reefs reveals three key findings. First,  
26 the proximity of the nearest market has the strongest and most consistent relationships  
27 with these ecosystem metrics. This finding is in keeping with a body of terrestrial research  
28 on how market accessibility shapes agricultural practices, but the integration of these  
29 concepts in marine systems is nascent. Second, our global study shows that resource  
30 conditions tend to display a n-shaped relationship with socioeconomic development.  
31 Specifically, the probability of encountering a top predator, fish biomass, and fish trait  
32 diversity were highest where human development was moderate, but lower where  
33 development was either high or low. This finding contrasts with previous regional-scale  
34 research demonstrating an environmental Kuznets curve hypothesis (which predicts a U-  
35 shaped relationship between socioeconomic development and resource conditions).  
36 Third, together, our ecosystem metrics are best explained by the integration of different  
37 human-environment theories. Our best model includes interactions between indicators  
38 from different theoretical perspectives, revealing how marine reserves can have different  
39 outcomes depending on how far they are from markets and human settlements, as well  
40 as the size of surrounding human population.

41  
42 **Keywords:** social-ecological system, coral reef, fisheries, sustainability

43

44 **Introduction**

45

46 Coral reefs host an estimated 1,000,000 multicellular species and provide key goods and  
47 services to tens of millions of people in tropical countries<sup>1,2</sup>. Despite their biological and  
48 socioeconomic importance, many coral reefs are being severely degraded<sup>3-5</sup>. Efforts to  
49 understand and seek effective solutions to this degradation are hampered by a poor  
50 understanding of the underlying social and economic drivers of degradation on coral reefs  
51 (i.e. the drivers of change)<sup>6-10</sup>.

52 To date, the coral reef literature has been dominated by a neo-Malthusian  
53 perspective on human-environment interactions, which considers human population (size,  
54 growth rate, structure) as the primary driver of degradation on coral reefs<sup>4,11-15</sup>. This  
55 human-environment perspective dates back to the works of Reverend Thomas Malthus,  
56 who posited that human population would outpace agricultural production because the  
57 former increased exponentially, while the latter increased only linearly. In the late 1960s,  
58 concerns about population pressure resurfaced in an environmental context<sup>16,17</sup>, often  
59 referred to as neo-Malthusianism<sup>18</sup>. Modifications of this theory examine how population  
60 combines with affluence and technology to generate human impacts on the environment  
61 (the IPAT model)<sup>19</sup> and Ester Boserup's more nuanced theory of how population growth  
62 can spur technological innovation<sup>20</sup>. Although the importance of human population in  
63 shaping human-environment interactions is supported by theoretical and empirical work  
64 from a broad range of systems<sup>13,21-24</sup>, human population is only one of many potential  
65 drivers of change. There are also impacts from less visible social and economic processes  
66 that operate at larger spatial and temporal scales<sup>23,25,26</sup>. These are investigated in a range of  
67 alternative social theories regarding how humans impact the environment, including  
68 Agricultural Location Theory<sup>27</sup>, the Environmental Kuznets Curve<sup>28</sup>, and New Institutional  
69 Common Property Economics<sup>29</sup>, each of which emphasizes different drivers of change and  
70 associated policy levers.

71 The role of market proximity in shaping how terrestrial resources are used is  
72 captured by a body of work typically referred to as Agricultural Location Theory<sup>26,30</sup>.  
73 Originating with von Thünen's 1826 Isolated State<sup>31</sup>, the concept is based on a central place

74 hierarchy, which emphasizes how location affects resource use through the combined  
75 influence of environmental factors and transport costs on production and profitability<sup>26,32</sup>.  
76 This concept is central to much contemporary work in agricultural economics, land-use  
77 change, and economic geography<sup>23,26</sup>, though its adaptation to marine contexts has  
78 traditionally been limited to maritime transportation<sup>30</sup> and more recent applications in  
79 predicting the condition of coral reef fish biomass<sup>33-36</sup>, diversity<sup>37</sup>, and coral cover<sup>10</sup>. Key  
80 indicators used in adaptations of Agricultural Location Theory in a reef context include  
81 proximity to markets (often measured as the time it takes to travel between a reef and the  
82 nearest market<sup>38</sup>) and a modification which incorporates the population size of the market  
83 (referred to as ‘gravity’<sup>33,39</sup>). This modification essentially integrates agricultural location  
84 and neo-Malthusian perspectives.

85         The environmental Kuznets curve hypothesis suggests that economic growth drives  
86 environmental degradation until it reaches a tipping point at which further growth drives  
87 better environmental conditions<sup>28</sup>. This is based on the assumption that higher levels of  
88 economic development are associated with a transition to service industries, heightened  
89 environmental awareness, improved regulation, technological advancement and increased  
90 resource use efficiency<sup>40</sup>. For example, the relationships between development and  
91 degradation captured by the environmental Kuznets curve can occur through mechanisms  
92 such as spatial displacement, whereby wealthier places can displace their environmental  
93 footprint, often to areas that are poorer and less well-regulated<sup>41</sup>. Key indicators used in  
94 studies of the environmental Kuznets curve often include national-scale measures of  
95 economic output, such as Gross Domestic Product<sup>22,40</sup>. In the coral reef literature, an  
96 environmental Kuznets curve like relationship was found between a local-scale metric of  
97 socioeconomic development and reef fish biomass, such that as reefs near communities  
98 with either very low or high levels of development tended to have about four times the reef  
99 fish biomass of reefs near the intermediate development sites<sup>41</sup>.

100         New Institutional Common Property Economics (hereafter New Institutional)  
101 investigates how the rules in use (i.e. laws and norms) affect people’s relationships with  
102 each other and the environment. This branch of comparative institutional analyses can  
103 focus on modes of governance, property rights, institutional design, and enforcement

104 mechanisms. For example, Nobel Laureate Elinor Ostrom’s book “Governing the  
105 Commons: the evolution of institutions for collective action” examined the institutional  
106 design associated with long-enduring common property institutions<sup>42</sup>. Adaptations of the  
107 New Institutional perspective to the coral reef literature have, for example, examined how  
108 both the rules in use (e.g. the degree of protection) and the processes through which those  
109 rules were developed and implemented (i.e. collaborative vs top-down management) can  
110 affect both social and ecological outcomes<sup>43–45</sup>.

111         There are important policy implications associated with embracing, or alternatively  
112 ignoring, specific human-environment theoretical perspectives<sup>46</sup>. Over-emphasizing one  
113 specific theoretical perspective of human environment-interactions, for example, may  
114 hinder opportunities for positive changes or alternative management options. Yet, there are  
115 few comparative studies that empirically explore the evidence for or against key human-  
116 environment theories<sup>22,40,46</sup>, particularly on coral reefs. Doing so requires a large dataset of  
117 not only ecological conditions, but also a set of socioeconomic drivers specific to each  
118 human-environment theory.

119         Here, we use a global dataset to statistically evaluate how key indicators from  
120 several prominent human-environment theoretical perspectives explain coral reef states  
121 and processes<sup>47</sup>. More precisely, we develop a series of alternative models to quantify how  
122 key socioeconomic indicators associated with prominent human-environment theories  
123 (Tables S1-2) are related to four key metrics of ecosystem states and processes (the  
124 presence of top predator, the amount of fish biomass, fish trait diversity, and parrotfish  
125 scraping potential ; Table 1, Figure S1) across >1500 reefs in 35 countries, states, and  
126 territories, after controlling for environmental (ocean productivity, atoll, sea surface  
127 temperature anomalies) and sampling conditions (depth, habitat surveyed, sampling area,  
128 and technique) (STAR Methods, Figure 1).

129  
130

131         To explore evidence for neo-Malthusian perspectives on coral reefs, we examined  
132 the national population size, national reef fish landings, the local population growth rate,  
133 the population size of the nearest settlement, and the population size of the nearest market  
134 (Table S1). To explore evidence for the environmental Kuznets curve in relation to coral

135 reefs we examine how reef conditions are related to the quadratic function of a national  
136 scale indicator of socioeconomic development (human development index) that  
137 incorporates national income, life expectancy, and schooling (Table S1). To explore the  
138 evidence for New Institutional perspectives on coral reefs, we examine how reef conditions  
139 are related to the rules in use, as well as the age and size of any no-fishing marine reserves  
140 (Table S1). To explore evidence for Agricultural Location Theory, we examined metrics  
141 of travel time to both the nearest market and the nearest human settlement (Table S1, STAR  
142 methods). In our case, a market was defined as a port, provincial capital, or major city. We  
143 built different candidate models for each ecosystem metric, allowing us to test alternative  
144 human-environment theories independently and together<sup>47</sup>. First, we tested each human-  
145 environment theory independently, while controlling for environmental conditions.  
146 Second, we tested a model embracing all four human-environment theories. Third, we  
147 tested select interactions between human-environment theories to examine how the  
148 effectiveness of management may vary depending on the context<sup>48,49</sup>. These included  
149 interactions between New Institutional and two neo-Malthusian indicators (population of  
150 the nearest settlement and population of the nearest market) to examine whether  
151 management has different effects depending on the surrounding population; interactions  
152 between New Institutional and Agricultural Location Theory indicators to examine  
153 whether management has different effects depending their proximity to markets or human  
154 settlements; and interactions between New Institutional and Environmental Kuznets Curve  
155 indicators to examine whether management has different effects depending on the wealth  
156 (STAR Methods). Fourth, we integrated Agricultural Location Theory and neo-  
157 Malthusianism in the form of a combined 'gravity' metric<sup>33,39</sup> (STAR Methods) and  
158 examine interactions with our New Institutional indicator on the type of management.

159         This research is part of an emerging body of empirical work by our team that  
160 explores human-environment linkages on coral reefs at a range of scales, from local<sup>34</sup>,  
161 national<sup>50,51</sup>, regional<sup>41</sup>, to global<sup>27,52</sup>. The novel contributions of this paper are that we: 1)  
162 explicitly connect a range of socioeconomic drivers to their theoretical underpinnings,  
163 enabling support for differing human-environment theories to be investigated; 2) explore  
164 four distinct reef fish metrics (e.g. much of our previous work has focused primarily on  
165 biomass<sup>41,43,51,52</sup>); 3) utilize a joint modelling approach which allows us to better integrate

166 information about marine reserves in our model (i.e. to explicitly consider reserve size and  
167 age; Methods); 4) test different candidate models for each response variable, which allowed  
168 us to examine the statistical support for different theoretical perspectives.

169

## 170 **Results and Discussion**

171

### 172 **Agricultural location theory and coral reefs**

173 We found strong support for our adaptation of agricultural location theory as a key  
174 predictor of coral reef states and processes (Fig 1, Tables S2-3). Specifically, the  
175 Agricultural Location model was the best performing individual theory (i.e. it had the  
176 lowest summed leave one out information criteria) and was the best individual theory to  
177 explain top predators, biomass, and trait diversity, which provide early signals of  
178 degradation (Table S3). The New Institutional model was preferred individual theory for  
179 parrotfish grazing (Table S3). However, our analysis revealed that the best overall model  
180 not only included the other human-environment theories, but also linked Agricultural  
181 Location, New Institutional, and neo-Malthusian perspectives in the form interactions  
182 between travel time and management, and between population and management (Table  
183 S2). The best overall model showed that in fished areas travel time to market displayed a  
184 consistent positive relationship across most of our reef fish metrics (Figure 2). Specifically,  
185 in fished areas, the probability of encountering a top predator, the amount of biomass, and  
186 trait diversity increased as markets were farther away (Figure 2). Although the effect size  
187 was smaller, a similar relationship was also apparent between travel time to the nearest  
188 settlement and our two most sensitive ecological indicators: top predators and biomass.  
189 Additionally, a key finding from our study is that no fishing reserves had more fish biomass  
190 when they were farther from markets.

191

192

193 Market proximity has played a central role in shaping theories about terrestrial land  
194 use change<sup>21,23,25</sup>, agriculture<sup>20,31</sup>, and conservation<sup>53</sup>. For example, land use change  
195 theories cover issues such as how market accessibility (through road networks and market  
196 connectivity) influences land use through expansion (e.g., how unconverted ‘wildland’ or

197 ‘native’ cover is converted into agriculture), intensification (e.g., how technologies such as  
198 irrigation can increase yields, often with positive ecological outcomes), spillovers (e.g.,  
199 how some land uses might get displaced into other areas), and transitions (non-linear  
200 changes to alternative system states)<sup>20,23,54</sup>. Yet to date, there has been little integration of  
201 these theoretical insights about the potential importance of markets in shaping natural  
202 resource use and governance from agricultural economics and land use change science into  
203 studies of the marine environment<sup>27,34,51</sup>. This suggests that there is the potential to better  
204 understand both the mechanisms driving resource use and uncover underutilized policy  
205 levers by more rigorously applying insights from fields such as land use change to the  
206 marine environment. However, such applications must pay attention to how seascapes  
207 differ from landscapes, to avoid poor planning decisions and conservation outcomes by  
208 blindly applying terrestrial concepts to marine contexts. Seascapes, particularly those with  
209 small-scale wild capture fisheries rather than aquaculture, are fundamentally different from  
210 terrestrial systems in four key ways that affect resource use and ecosystem recovery  
211 potential (and hence the applicability of terrestrial concepts). First, fishing does not  
212 necessarily result in conversion of natural habitat in the same way that agricultural  
213 expansion often does. Second, intensification in a wild capture fishery generally means  
214 killing more fish since there are fewer options for investing in increased productivity in  
215 ways that can benefit nature. Third, key characteristics such as fish being highly mobile  
216 yet difficult to directly observe can lead to fisheries having lagged social-ecological  
217 feedback mechanisms compared to land systems. Fourth, seascapes are rarely privately  
218 owned or sold, which means different institutions and market forces are at play. An  
219 important future direction will be better understanding the degree to which these  
220 differences mean specific agricultural location theories and concepts may not be applicable  
221 in reef systems, and whether bespoke ‘fisheries location theories’ need to be developed to  
222 better inform this potential solution space for marine conservation.

223

### 224 **Neo-Malthusian perspectives on coral reefs**

225 For many decades, human-environment research on coral reefs was dominated by  
226 a neo-Malthusian perspective, which tends to view human population as *the* primary driver  
227 of change<sup>11–13,55</sup>, particularly through overfishing<sup>4,56</sup>. We found moderate support for the



228 neo-Malthusian perspective of human-environment interactions on coral reefs (Figure 2,  
229 Tables S2-3). Specifically, the neo-Malthusian model was the second ranked individual  
230 theory (based on summed leave one out information criteria; Tables S2-3), and the best  
231 overall model included an interaction between neo-Malthusian and New Institutional  
232 indicators (as well as an interaction between Agricultural Location and New Institutional  
233 indicators). Specifically, we found that in fished locations, the probability of encountering  
234 a top predator and biomass had a negative relationship with the population of the nearest  
235 human settlement, while biomass and trait diversity had a negative relationship with the  
236 market population size. We also found that in no fishing reserves, the population of the  
237 nearest human settlement had a negative relationship with trait diversity, but a positive  
238 relationship with parrotfish scraping potential. This latter result is consistent with previous  
239 work showing high parrotfish grazing where human population density is high<sup>15</sup>. Other  
240 neo-Malthusian indicators displayed minimal relationships to our reef fish metrics, with  
241 population growth positively associated to fish biomass. This is noteworthy because in  
242 many empirical studies of human-reef interactions, human population is the sole social  
243 driver of change investigated<sup>4,57-60</sup>. Thus, a narrow neo-Malthusian perspective can be  
244 problematic and lead to policy blind spots if it leads to other potential drivers, and their  
245 accompanying policy levers, being ignored<sup>6</sup>. Indeed, key critiques of neo-Malthusianism  
246 note that it often fails to address issues such as socioeconomic inequalities or the  
247 institutional arrangements that can drive natural resource use<sup>61</sup>.

248

#### 249 **New Institutional perspectives on coral reefs**

250 We also found strong support for the new institutionalist perspective. We found  
251 that the institutions (i.e. rules in use) used to manage coral reefs displayed strong  
252 relationships to our reef fish metrics. Our joint modelling approach showed that the  
253 presence of top predators, reef fish biomass and parrotfish scraping potential were  
254 substantially higher in high compliance no fishing marine reserves than on openly fished  
255 reefs (Cohen's  $D=0.92, 2.09, 2.67$ , respectively), while trait diversity was similar ( $D=-$   
256  $0.04$ ) (Figure 3). It suggests that while trait diversity may provide an early signal of reef  
257 degradation (like the presence of top predators and fish biomass), it is challenging to  
258 recover/rebuild through protection<sup>62</sup>.

259 Marine reserves are one of the most common conservation tools used on coral reefs,  
260 so it is not necessarily surprising that we found improved ecosystem states and processes  
261 within them<sup>63</sup>. However, our contribution here lies in quantifying the effect size of reserves  
262 across a broad range of reef fish metrics globally, while accounting for other key  
263 socioeconomic and environmental drivers (Figure 3) and in highlighting how outcomes in  
264 reserves are dependent on the socioeconomic context, including the proximity of markets  
265 and human settlements, as well as the size of the surrounding human population (Fig 2).  
266 These results make clear both the benefits and limitations of marine reserves, and also help  
267 inform where strategically sighting them could help maximise specific ecological  
268 outcomes. Key reserve features, such as reserve age and size, were highly uncertain with  
269 our four reef fish metrics (Figure 2). This uncertainty was likely due in part to the limited  
270 number of sites within high compliance reserves (n=51). Restrictions on fishing (such as  
271 effort and size limits) were positively related to biomass and parrotfish scraping potential,  
272 but not the presence of top predators and trait diversity (Figure 2), which may have to do  
273 with fishing selectively targeting larger bodied and predatory fish. In this particular study,  
274 we did not examine the processes through which the rules were established, which can play  
275 a large role in whether specific rules are complied with<sup>42,44</sup>.

276

277

### 278 **Environmental Kuznets curve and coral reefs**

279 Our results showed an inverted environmental Kuznets curve- the opposite of what  
280 would be expected under the environmental Kuznets curve hypothesis (Figure 4).  
281 Specifically, the best overall model favored the quadratic function of the national  
282 socioeconomic development context (measured as the human development index), but with  
283 an n- rather than u-shaped relationship (i.e. effect sizes for the quadratic terms were  
284 negative; Figures 2, 4). For example, reefs in countries with intermediate levels of human  
285 development tended to have more fish biomass than locations in high or low development  
286 countries (Fig 4).

287

288

289

290 Our current results contrast with previous work in the western Indian Ocean, which  
291 showed a U-shaped environmental Kuznets curve-like relationship between local-scale  
292 development and reef fish biomass<sup>41</sup>. Differences could be explained by the indicators  
293 used, as well as the range and the scale of the analyses (global versus regional). The western  
294 Indian Ocean study used a composite metric of 16 community-scale infrastructure items  
295 (e.g. hard-topped road, electricity, schools), whereas this present study used HDI, which  
296 integrates national income, life expectancy, and schooling). It is possible that these two  
297 metrics measure very different dimensions of socioeconomic development, which have  
298 different relationships to the environment. In regards to the range of the studies, the  
299 wealthiest country in the regional study was Seychelles, which has below global average  
300 HDI values in this present study. Thus, the range of the regional study may have only  
301 investigated the initial part of the global curve (i.e. as ecosystem metrics were rising).  
302 Additionally, the Kuznets curve may be a scale-dependent phenomenon, and there were  
303 differences between studies in the scale of the development indicator used (national scale  
304 versus local scale). Indeed, one of the plausible mechanisms of the Kuznets curve is what  
305 is referred to as the scale effect, whereby wealthier people can export their environmental  
306 footprint to other areas<sup>64,65</sup>. It is often expected that this happens with some resources at a  
307 national scale<sup>66</sup>, but with reef fish, which are not a major international commodity in the  
308 same way that tuna and other pelagic fish are, an intra-national scale effect may be possible.

309 Our current national-scale results are more consistent with the Jevons paradox,  
310 which notes that technological efficiency gains may be associated with increased  
311 environmental degradation as resource consumption rises in response to declining costs  
312 exhibiting what is known as a ‘rebound effect’<sup>67,68</sup>. For example, in response to improved  
313 fuel efficiency in vehicles, people may decide to take an additional long drive on the  
314 weekend, thereby increasing their total travel distance because travel is cheaper. Although  
315 Jevons paradox would generally predict a decline in resource conditions with development,  
316 it is possible for ecosystem states and processes to improve in the short term as a  
317 consequence of increased resource use efficiency but decline over the longer term as  
318 changes in preferences, technology, and investment take effect or as rates of efficiency gain  
319 relative to demand stagnate<sup>67,68</sup>. Our results may also be reflective of a feedback loop  
320 between human wellbeing and ecosystem conditions, whereby poor reef conditions and

321 human impoverishment reinforce each other<sup>69,70</sup>. Explanations for variability in these  
322 trends can be found in the treadmill of production<sup>40</sup> and ecological modernization<sup>71</sup>  
323 literatures. In our case, that might mean that nearshore fish stocks recover as societies  
324 become wealthy enough to begin fishing offshore, but then decline as offshore stocks  
325 become more exploited and less profitable. Alternatively, HDI was correlated with other  
326 covariates that were excluded from the analyses (Gross Domestic Product, a World Bank  
327 governance metric of Voice and Accountability, biogeographic region) and it is possible  
328 that this is a result of confounding with other non-tested variables. Likewise, it is important  
329 to emphasise that our study used a snapshot in time along a gradient of development, rather  
330 than a temporal study of change over time. It is possible that unmeasured environmental  
331 processes (e.g. low fish productivity<sup>72</sup>) could be different in our study countries and be  
332 influencing these observed patterns.

333

#### 334 **Linking human-environment theories on coral reefs**

335 A key finding from our global study is that there is not one dominant theoretical perspective  
336 that fully explains human-environment interactions on reefs. Indeed, the best overall model  
337 included indicators from all four human-environment theories and interactions between  
338 New Institutional, and neo-Malthusian and Agricultural Location indicators (Figure 2,  
339 Tables S2-3). In other words, it is not only the addition of different human environment  
340 theories that is necessary to explain the states and processes on coral reef ecosystems, but  
341 also key linkages between the theories. These interactions reveal how the effects of  
342 management are context dependent<sup>73</sup>: no fishing reserves can have different outcomes  
343 depending on how far they are from markets and human settlements, as well as the  
344 surrounding population. Our findings echo those of Geels<sup>46</sup> in agricultural systems, who  
345 concluded that individually, different theoretical perspectives were overly reductionistic in  
346 explaining the transition to pig farming in Dutch agricultural systems, but that juxtaposing  
347 multiple theoretical perspectives provided a more encompassing understanding. Our  
348 findings highlight that coral reefs are complex social-ecological systems, and underline the  
349 importance of interdisciplinarity in not only uncovering the key drivers of change on coral  
350 reefs, but also in better defining the potential solution space<sup>74</sup>.

351

## 352 **Ecological states and processes**

353 The four ecological response variables we included in this study are related, but also tell  
354 us something different about reef ecology and responses to human impacts (Table 1). By  
355 assessing all four metrics, a more nuanced understanding of how reef ecology is influenced  
356 by humans emerges. The presence of top predators is the most sensitive indicator of fishing  
357 pressure, followed by the amount of fish biomass, fish trait diversity and finally parrotfish  
358 scraping potential. Indeed, parrotfish scraping potential was the least sensitive to all drivers  
359 in our model, and herbivorous fish have been shown to continue to support reef fisheries  
360 and nutrient yields on heavily disturbed reefs<sup>75</sup>. As expected marine reserves had a positive  
361 effect on most of the metrics, but was weak for trait diversity where traits may respond  
362 differentially to protection, highlighting the importance of uncovering how individual traits  
363 respond to marine reserves<sup>76</sup>. While the presence of top predators, fish biomass, and fish  
364 trait diversity peak at intermediate HDI values, parrotfish scraping potential declines  
365 gradually with increasing HDI, suggesting this important ecological function has greatest  
366 potential in lower developmental settings. Together, our results suggest that these four reef  
367 fish metrics are related to different socioeconomic drivers, sometimes in opposite  
368 directions (in marine reserves, the population of the nearest settlement is negatively related  
369 to trait diversity, but positively related to parrotfish scraping potential). The sampling and  
370 environmental conditions we controlled for (i.e. our nuisance parameters) were not the  
371 focus of this present article, but were clearly also important predictors across most of our  
372 reef fish metrics. Specifically, sampling area, sampling technique, depth, habitat type, and  
373 whether the reef was an atoll had relationships that cross-cut multiple reef fish metrics.

374

## 375 **Critiques, caveats, and future directions**

376 It is important to note that although our study found strong relationships between a  
377 number of socioeconomic indicators and four reef fish metrics, it did not unravel the causal  
378 mechanisms behind these relationships. For example, one potential mechanism to explain  
379 the impact of travel time to markets is simply that as accessibility to markets increases, so  
380 do financial incentives for fisheries overexploitation<sup>77</sup>. Recent research in behavioral  
381 sciences, however, shows that the impacts of market relationships on behavior are more  
382 complex<sup>71,78</sup>. For example, markets can crowd out (i.e. displace) pro-environmental

383 behavior not directly but through their impact on: 1) people's willingness to engage in  
384 collective action and civic duties<sup>79</sup>; 2) people's reluctance to inflict harm on others (referred  
385 to as third party externalities)<sup>80</sup>; and 3) people's preferences for equality<sup>81</sup>. There is thus a  
386 need to better understand the causal mechanisms through which markets and other  
387 socioeconomic drivers affect shallow reef ecosystems. Doing so may require causal  
388 modelling<sup>77</sup>, experimental games<sup>82</sup>, and examining temporal trends<sup>83</sup>.

389 Our study focused on a set of social theoretical perspectives that offer explanations  
390 for natural resource degradation suitable for testing with available data. Though our  
391 analysis was multi-scale (local and national), it was unable to consider and test theories at  
392 the individual and supra-national scales. Consequently, this study has not considered  
393 theoretical frameworks relevant to understanding the drivers of individual behavior (e.g.  
394 attitudes, perceptions, norms, rational choice<sup>46,84</sup>) or of interplay between nations (e.g.  
395 world-systems theory)<sup>85</sup>. Additionally, many of the indicators available at a national and  
396 even local scale are relatively crude, and miss key nuances and details that local scale  
397 studies are better suited to uncovering<sup>44</sup>. For example, the global nature of our study meant  
398 that many of the institutional design principles thought to be important for the sustainability  
399 of commons governance<sup>42</sup>, a key focus of many New Institutional studies<sup>86</sup>, were not  
400 available. Likewise, information about staff capacity and resources within marine reserves  
401 has been shown to be related to ecological outcomes<sup>87</sup>, but was simply not available in our  
402 study sites. Further, some important ecological states and processes, such as fisheries  
403 productivity and wave exposure, are likely very important drivers of reef fish biomass<sup>8,72,88</sup>,  
404 but were unable to be incorporated in our models. Finally, our study used a snapshot spatial  
405 approach. MacNeil<sup>47</sup> notes that there may be variability in the relevance of different  
406 explanatory variables over time as environmental and social conditions change. Future  
407 studies could investigate whether key theories become more or less important at explaining  
408 ecological states and processes over time using time-series data. Such an analysis could  
409 also begin uncovering dynamics such as feedback loops, which could enable inclusion of  
410 other human-environment theories such as the Marginalization-Degradation thesis<sup>70</sup>.

411 An emerging body of literature has begun linking ecology with rigorous social  
412 science theory to better understand the complex and multi-scale ways that humans interact  
413 with, and affect, the environment so that underlying socioeconomic drivers of change can

414 be identified and used as policy levers for sustainability<sup>21,22,25</sup>. Here, we tested how key  
415 socioeconomic drivers associated with four key human-environment theoretical  
416 perspectives predict the ecosystem states and processes on coral reefs across the globe. We  
417 show that a broad range of drivers are related to four key reef fish metrics, and the historical  
418 dominance of the neo-Malthusian perspective in coral reef science was not completely  
419 unfounded, but was certainly incomplete. Better understanding how other key human-  
420 environment interaction theories can also help to highlight opportunities for the  
421 development of novel policy levers. Although conservation initiatives that integrate marine  
422 reserves together with a focus on fisheries management are essential to supporting coral  
423 reefs, governance strategies that seek to reduce socioeconomic drivers or mediate their  
424 negative effects are also required. Many of the social drivers we examined are amenable to  
425 governance interventions. For example, our results emphasize that conservation strategies  
426 which mediate the negative effects of markets are urgently needed<sup>78,89,90</sup>. Additionally, our  
427 study sheds light on how strategically placing reserves based on socioeconomic  
428 considerations (e.g. distance to markets, distance to human settlements, local population  
429 human size) may help to maximise specific ecological outcomes. Ultimately, good  
430 governance that promotes effective management and seeks to dampen key socioeconomic  
431 drivers of ecological change will be critical to sustaining reefs and providing people with  
432 crucial ecosystem goods and services.

433

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435

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443

444

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449 writing of the manuscript (original draft and reviewing & editing). All other authors

450 contributed to data collection and made substantive contributions to writing the original  
451 draft and reviewing & editing.

452

453 **Declaration of interest:** The authors declare no competing interests.

454

455 **Inclusion and diversity statement:** While citing references scientifically relevant for  
456 this work, we actively worked to promote gender balance in our reference list.

457

458

### 459 **Main Text Figure legends**

460

461

462 **Figure 1. Map of study sites. Points are jittered to allow better visualization of nearby**  
463 **sites. n=1571.**

464

465

466 **Figure 2. Coefficient plots of the relationships between key socioeconomic and**  
467 **environmental drivers and a) the probability of observing top predators , b) the**  
468 **amount of fish biomass, c) fish trait diversity, d) parrotfish scraping potential.**  
469 Points are the median effect sizes (i.e., slopes of the linear model). Error bars are 90%  
470 uncertainty intervals. Turquoise and blue symbols indicate that 90% of their posterior  
471 density in either a positive or negative direction, respectively. Model presented is the best  
472 overall model as determined by summed leave-one-out information criteria (Table S3),  
473 best fit models for individual response variables are presented in Figure S2.

474

475

476 **Figure 3. Distribution of modelled intercepts between openly fished sites (dark grey)**  
477 **and reserves (light grey) at average socio-ecological conditions** for a) the probability of  
478 observing top predators, b) the amount of fish biomass, c) fish trait diversity, d) parrotfish  
479 scraping potential. Cohen's D statistic with 95% confidence intervals (within brackets) are  
480 displayed.

481

482

483 **Figure 4. Marginalized relationships between standardized Human Development**  
484 **Index (HDI) and a) the probability of observing top predators , b) the amount of fish**  
485 **biomass, c) fish trait diversity, d) parrotfish scraping potential for the best-overall**  
486 **model.** Solid line is the median and polygons are 90% uncertainty intervals. These plots  
487 present the relationship between HDI and the response variable while holding all other  
488 covariates to their global average (i.e. standardized score of 0) or to the most common



489 category (i.e. slope for habitat, standard belt transect for census method, 4 to 10 m for  
490 depth).

491

## 492 **Main Text Table Legend**

493

494 **Table 1. Main rationale and hypotheses explaining the expected relationships**  
495 **between the four reef fish metrics used in our study and fishing pressure.** They are  
496 ranked from the most to the least sensitive to fishing pressure.

497

498

## 499 **STAR Methods**

500

## 501 **RESOURCE AVAILABILITY**

### 502 **Lead Contact**

503 Further information and requests should be directed and will be fulfilled by the lead  
504 contact, Josh Cinner [Joshua.cinner@jcu.edu.au](mailto:Joshua.cinner@jcu.edu.au)

505

### 506 **Materials availability:**

507 This study did not generate new unique reagents

508

509 **Data and Code Availability:** Data and code have been deposited at GitHub and are  
510 publicly available at [https://github.com/JZamborain-Mason/Cinneretal\\_hum-](https://github.com/JZamborain-Mason/Cinneretal_hum-env_theories)  
511 [env theories](https://github.com/JZamborain-Mason/Cinneretal_hum-env_theories)

512

513

## 514 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

515

516 We used four key reef fish metrics with a range of sensitivity to human threat as response  
517 variables: the presence of top predators<sup>33</sup>, the amount of fish biomass, trait diversity, and  
518 parrotfish scraping potential<sup>49</sup> (Table S2). All response variables were based on underwater  
519 visual counts of fish from reef sites (Figure 1), which were sourced from multiple data  
520 providers and compiled by the lead author (JEC) as part of a series of interdisciplinary  
521 papers exploring human-environment interactions on coral reefs<sup>33,49,52</sup>. The data used in  
522 this present paper comprise the sites in <sup>33,49,52</sup> where data for all four response variables  
523 were available (i.e. sites that were missing one or more variables were excluded). Reef  
524 surveys were conducted between 2004 and 2013, using standard belt-transects, distance

525 sampling, or point-counts. Where data from multiple years were available from a single  
526 reef site, we included only data from the year closest to 2010. Within each survey area,  
527 diurnally active, noncryptic reef fish were identified to species level, their abundance  
528 counted, and total length (TL) estimated.

529

### 530 **Top predators**

531 For the presence/absence of top predator's response variable, we used the methods from  
532 Cinner et al. <sup>33</sup>. For each site we recorded whether there was a fish from the following  
533 families greater than 50 cm in length: Carcharhinidae, Ginglymostomatidae,  
534 Heterodontidae, Sphyrnidae, and Carangidae, Lutjanidae, Serranidae and Sphyraenidae.

535

### 536 **Biomass**

537 The fish biomass metric was estimated using standard published species-level length–  
538 weight relationship parameters available on FishBase<sup>91</sup>. When length–weight relationship  
539 parameters were not available for a species, we used the parameters for a closely related  
540 species, genus or family<sup>33</sup>. We included 22 fish families that were standard across the  
541 different data providers<sup>49</sup>.

### 542 **Trait diversity**

543 We used the methods from Cinner et al. <sup>49</sup> to calculate fish trait diversity, we used six traits:  
544 (i) observed length category (10-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm, or >80 cm);  
545 (ii) mobility (i.e., sedentary, mobile within a reef, or mobile between reefs); (iii) period of  
546 activity (i.e., diurnal, both diurnal and nocturnal, or nocturnal); (iv) schooling behavior  
547 (i.e., solitary, paired, or living in small (3-20 individuals), medium (20-50 individuals), or

548 large groups (>50 groups)); (v) vertical position in the water column (i.e., benthic, benthopelagic, or pelagic); (vi) diet (i.e., herbivorous-detritivorous, macro-algal herbivorous, 549 invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrates, 550 planktivorous, piscivorous, and omnivorous). Since all traits were categorical, species with 551 identical traits were grouped into entities. We then computed the Gower distance between 552 all pairs of entities and computed trait diversity using the Chao's  $FD_{q=1}$  index<sup>92</sup> which is 553 based on the distribution of biomass among entities: 554

555

$$556 \quad FD_{q=1} = \exp \left( - \sum_{i=1}^s p_i \times \log \left( 1 - \sum_{i \neq j} \frac{1 - \min(d_{ij}, mD)}{mD} \times p_j \right) \right)$$

557

558 where  $p_i$  and  $p_j$  are the respective relative biomasses of the two entities  $i$  and  $j$  in the 559 community,  $d_{ij}$  is the Gower distance between entities  $i$  and  $j$ ,  $mD$  is the average of all 560 Gower distances between the entities present in the global pool of species. This index is 561 expressed as an equivalent numbers of species. Hence, it is minimal and equals 1 when all 562 biomass is supported by the same entity (i.e. when one species is ultra-dominant or when 563 all species have the same trait values) and it is maximal and equals the number of species 564 when all species pairs have dissimilarities higher than the average dissimilarity in the 565 species pool and equal biomasses.

566

### 567 **Parrotfish scraping potential**

568 Finally, we calculated parrotfish scraping potential (area grazed per minute) as the product 569 of parrotfish fish density, feeding rate, and bite dimension<sup>93</sup>. Size-specific feeding rates 570 were derived from best-fit regressions of bite rate (bites  $\text{min}^{-1}$ ) and total fish length (cm)

571 for each species or a closely related congener. Parrotfish bite rates and total fish length  
572 were quantified at three locations (Great Barrier Reef, Australia; Indonesia; and the Red  
573 Sea) and converted to bites  $\text{min}^{-1}$ . Individual fish were followed for a minimum of 3-  
574 minutes and 19-126 individuals (mean = 41 individuals) were observed per species. These  
575 values were supplemented with published length-feeding rate relationships for Atlantic  
576 parrotfishes<sup>94,95</sup>. Size-specific bite dimensions ( $\text{mm}^2$ ) were obtained from the literature  
577<sup>93,96-98</sup>.

578

## 579 **METHOD DETAIL**

### 580 Data

581 *Scales of data:* Our data was organized in three spatial scales nested within each other:  
582 reef sites (our lower unit of analyses;  $n=1571$ ), reef-clusters (clusters of reef sites within  
583 4km of each other;  $n=625$ ), and nations/states (jurisdictions that generally correspond to  
584 individual nations or states;  $n=35$ ).

## 585 **QUANTIFICATION AND STATISTICAL ANALYSIS**

586

587 *Predictor variables:* To explore the socioeconomic distal drivers for each response variable  
588 we adopted a Bayesian hierarchical modelling approach that, besides including the  
589 socioeconomic covariates of interest (Table S1), also included methodological and  
590 environmental covariates known to impact the response variables (i.e., nuisance  
591 parameters), and explicitly recognized the nested structure of reefs (i) within reef clusters  
592 (j) within nations/states (k) in our data.

593 Included covariates were: oceanic productivity<sup>99,100</sup> [following the procedure described by  
594 Gove et al.<sup>42</sup>, we delimited a 100km buffer around each site, removed shallow waters

595 pixels below 30m, and then calculated the average of monthly chlorophyll-a concentration  
596 using data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging  
597 Spectro-radiometer) for the years 2005-2010. Note that oceanic productivity has been  
598 found to influence coral reef fish communities in several other large-scale studies<sup>59,101,102</sup>,  
599 but will be most influential in atoll and oceanic island settings], whether or not the reef is  
600 an atoll, census method used (i.e. standard belt transect, point count, distance sampling),  
601 sampled area, habitat type sampled (i.e., flat, slope, crest, backreef), depth category of the  
602 survey (i.e., <4m, 4-10 m, >10 m), Sea Surface Temperature anomalies (SST anom)<sup>103</sup>,  
603 regional population growth (i.e., proportional difference between the population within a  
604 100km buffer in 2000 and 2010), the nations reconstructed spatial reef fish landings<sup>56,104</sup>  
605 clipped to only include catches from reefs divided by the area of reef<sup>105</sup>, national population  
606 size, national human development index<sup>106</sup>, reserve size, reserve age, whether there were  
607 any active gear or effort restrictions in place for fished reefs (e.g., ban of certain gears or  
608 size limits), the travel time (in minutes) between the reef and the nearest market (defined  
609 as a port, provincial capital, or large city), the travel time between the reef and the nearest  
610 human settlement, and the population size of both the nearest human settlement and the  
611 nearest market. We also combined the population and travel time to create a metric of  
612 'gravity' to the nearest market and nearest settlement<sup>52</sup>. Market gravity was calculated as  
613 the population size of the nearest market divided by the squared travel time<sup>38</sup> between the  
614 city and the reef<sup>52</sup>. Similarly, nearest settlement gravity was calculated as the population  
615 of the nearest human settlement to the reef divided by the squared travel time between the  
616 settlement and the reef<sup>52</sup>. Note that: (i) before including these covariates, we checked that  
617 multicollinearity was not a concern (VIF<2); and (ii) in our data, the metric of HDI is

618 correlated with other national metrics (e.g., gross domestic product or the Voice and  
619 Accountability governance metric<sup>106</sup>) and with biogeographic region, which we did not  
620 include.

621

622 *Analyses:* In contrast to previous work (e.g.,<sup>33</sup>), to account for the potential collinearity  
623 between management and reserve size and age (i.e., only reserves have age and size), we  
624 divided our model into two sub-model components: fished (a) and reserves (b) (i.e.,  $i=a+b$ ).  
625 Methodological, environmental and socio-economic effects sizes were jointly estimated  
626 from both sub-model components. However, effect sizes specific for a given sub-model  
627 component (i.e., effects of reserve age, reserve size and restrictions on fished reefs) were  
628 estimated only from their specific subset (that is, some parameter values were informed by  
629 the entire dataset but, where relevant, other parameters were informed only by one model  
630 component). Continuous covariates were standardized (subtracted their mean and divided  
631 by two standard deviations<sup>107</sup>) and categorical covariates were treated as dummy variables  
632 (1's and 0s). For each response variable we evaluated twelve alternate models through  
633 leave-out-one cross-validation<sup>108</sup> (Tables S2-3): the null model (the model excluding all  
634 covariates; model 12); individual theories separately (whilst including sampling and  
635 environmental covariates; models 1-4); full models with no interactions between the  
636 theories (model 5), and a series of full models that included select interactions between the  
637 theories, including linking Agricultural Location Theory and neo-Malthusian in the form  
638 of a combined 'gravity' metric; model 6), interactions between New Institutional and neo-  
639 Malthusian indicators to examine whether reserves have different effects depending on the  
640 surrounding nearest settlement and nearest market populations (model 7), interactions

641 between New Institutional Theory and Agricultural Location Theory indicators to examine  
642 whether management has different effects depending their proximity to settlements and  
643 markets (model 8), interactions between New Institutional and neo-Malthusian indicators,  
644 as well as New Institutional and Agricultural Location Theory indicators to examine  
645 whether management has different effects depending their surrounding populations AND  
646 proximity to markets (model 9), interaction between gravity and management, which is  
647 conceptually similar to model 9 but with population and travel time combined into a single  
648 metric (model 10), and interactions between New Institutional and Environmental Kuznets  
649 Curve indicators to examine whether management has different effects depending on the  
650 wealth (model 11) (Table S2). Note that we only considered neo-Malthusian interactions  
651 using the indicators population to the nearest market and population to the nearest  
652 settlement. During this model selection process, for each response variable, we removed  
653 observations (<5% of observations) that gave bad (i.e., >0.7) pareto-k diagnostic values  
654 (i.e., highly influential values in model selection<sup>109</sup>). Individual response variable model  
655 selection results are found in Table S3. Overall, summing all response variable's leave one  
656 out information criteria (loaic) for each candidate model, model selection results (Table  
657 S2) show that (i) models including all theories are favored over the null model or individual  
658 theories separately; and (ii) model 9 (model that included all theories together and  
659 interactions between New Institutional and Agricultural Location Theory indicators *and*  
660 interactions between New Institutional and neo-Malthusian indicators) was favored as the  
661 best-fit overall model. Thus, we use model 9 in the main text and show best-fit models for  
662 each response variable (Figure S2).

663 We used gaussian family (normal distribution) for the log transformed biomass and trait  
664 diversity metrics, a Bernoulli family for the presence/absence of top predator's response  
665 variable (with a logit function), and a hurdle-lognormal family distribution for the  
666 parrotfish scraping potential. For each response variable, our basic linear model structure  
667 for the best-ranked model was:

$$668 \quad \log(B_a) \sim N(\mu_a, \sigma_a); \log(B_b) \sim N(\mu_b, \sigma_b) \quad (1)$$

$$669 \quad \log(TD_a) \sim N(\mu_a, \sigma_a); \log(TD_b) \sim N(\mu_b, \sigma_b) \quad (2)$$

$$670 \quad PA_a \sim \text{Bernoulli\_logit}(\mu_a); PA_b \sim \text{Bernoulli\_logit}(\mu_b) \\ 671 \quad (3)$$

$$672 \quad \text{if } PS_a = 0, PS_a \sim \text{bernouilli}(\delta); \text{if } PS_b = 0, PS_b \sim \text{bernouilli}(\delta) \\ 673 \quad (4)$$

$$674 \quad \text{if } PS_a > 0, PS_a \sim \text{LN}(\mu_a, \sigma_a); \text{if } PS_b > 0, PS_b \sim \text{LN}(\mu_b, \sigma_b) \quad (5)$$

$$675 \quad \mu_a = \beta_{0jka} + \beta_1 x_{\text{deep},a} + \beta_2 x_{\text{shallow},a} + \beta_3 x_{\text{crest},a} + \beta_4 x_{\text{lagoon/backreef},a} + \beta_5 x_{\text{flat},a} + \\ 676 \quad \beta_6 x_{\text{point count},a} + \beta_8 x_{\text{sampling area},a} + \beta_9 x_{\text{size},a} + \beta_{10} x_{\text{age},a} + \beta_{11} x_{\text{atoll},a} + \\ 677 \quad \beta_{12} x_{\text{prod},a} + \beta_{13} x_{\text{SST anom},a} + \beta_{14} x_{\text{pop growth},a} + \beta_{15} x_{\text{market pop},a} + \\ 678 \quad \beta_{16} x_{\text{settlement pop},a} + \beta_{17} x_{\text{landings},a} + \beta_{18} x_{\text{population},a} + \beta_{19} x_{\text{hdi},a} + \beta_{20} x_{\text{hdi}^2,a} + \\ 679 \quad \beta_{22} x_{\text{markettt},a} + \beta_{23} x_{\text{settlementtt},a} \quad (6)$$

$$680 \quad \beta_{0jka} = N(\beta_{0ka}, \sigma_{ja}) \quad (7)$$

$$681 \quad \beta_{0ka} = N(\beta_{0a}, \sigma_{ka}) \quad (8)$$



$$\begin{aligned}
682 \quad \mu_b = & \beta_{0jkb} + \beta_1 x_{deep,b} + \beta_2 x_{shallow,b} + \beta_3 x_{crest,b} + \beta_4 x_{lagoon/backreef,b} + \beta_5 x_{flat,b} + \\
683 & \beta_6 x_{point\ count,b} + \beta_7 x_{distancesampling,b} + \beta_8 x_{samplingarea,b} + \beta_{11} x_{atoll,b} + \\
684 & \beta_{12} x_{prod,b} + \beta_{13} x_{SSTanom,b} + \beta_{14} x_{popgrowth,b} + \beta_{24} x_{marketpop,b} + \\
685 & \beta_{25} x_{settlementpop,b} + \beta_{17} x_{landings,b} + \beta_{18} x_{population,b} + \beta_{19} x_{hdi,b} + \beta_{20} x_{hdi^2,b} + \\
686 & \beta_{21} x_{restrictions,b} + \beta_{26} x_{markettt,b} + \beta_{27} x_{settlementtt,b} \\
687 & \hspace{15em} (9)
\end{aligned}$$

$$688 \quad \beta_{0jkb} = N(\beta_{0kb}, \sigma_{jb}) \quad (10)$$

$$689 \quad \beta_{0kb} = N(\beta_{0b}, \sigma_{kb}) \quad (11)$$

690 where the subscripts  $a$  and  $b$  represent the reserve and fished sites, respectively; the  
691 subscripts  $j, k$  represent the scale, reef cluster and nation/state, respectively;  $\beta_{0..}$  represents  
692 the intercepts for either log biomass, log trait diversity, log parrotfish scraping potential  
693 (when >0) or log odds of observing a top predator;  $\beta_{...}$  are the effect sizes (slopes) for the  
694 covariates  $x_{...}$ , which are jointly estimated, where relevant, between the reserve and fished  
695 sub-models for each response variable except for the highlighted interactions;  $\mu_{...}$  are the  
696 expected site-specific mean log biomass, log trait diversity, log parrotfish scraping  
697 potential (when >0) or log odds of observing a top predator;  $\delta$  is the probability of  
698 observing 0 parrotfish scraping potential; and  $\sigma_{..}$  are the standard deviations. Model  
699 parameters were given weakly informative priors.

700 Analyses were performed in *Stan* using the Hamiltonian Monte Carlo algorithm  
701 implemented in RStan<sup>110</sup>. Four chains were run for each scenario, leaving 4000 samples in  
702 the posterior distribution of each parameter. Convergence was monitored by running four  
703 chains from different starting points, examining posterior chains and distribution for

704 stability, checking that the potential scale reduction factor (also termed  $R_{\hat{}}$ ) was close  
705 to 1 and examining the effective sample sizes and rank plots<sup>111</sup>. Model fit was examined  
706 by posterior predictive checks, checking residuals against fitted values and ensuring  
707 residuals had the expected distribution (Figure S3).

708  
709  
710

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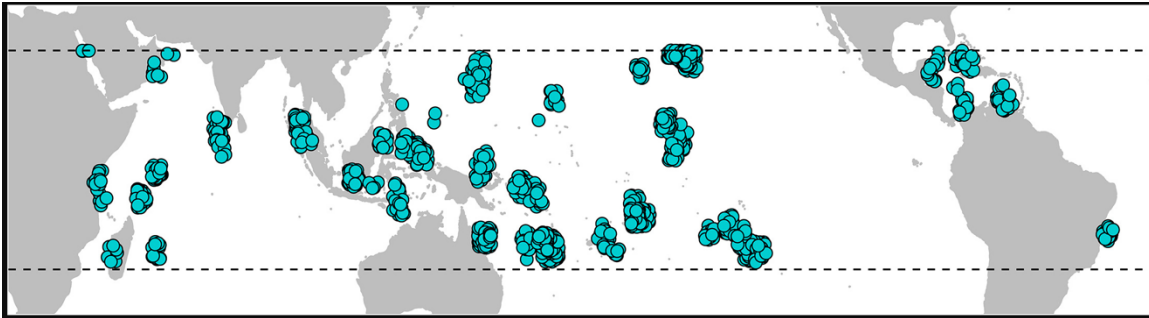
1003 **Table 1. Main rationale and hypotheses explaining the expected relationships**  
 1004 **between the four reef fish metrics used in our study and fishing pressure**  
 1005 Indicators are ranked from most to least sensitive to fishing pressure.  
 1006

Reef fish metric	Rationale and Hypotheses	Sensitivity to fishing
Presence of predator	Top predators such as sharks play unique roles in ecosystems, structuring food webs via direct and indirect effects <sup>48,49</sup> . They generally grow slow and reproduce late, making them particularly sensitive to fishing impacts and slow to recover, and often occur in only very remote locations <sup>50-53</sup> and very large well-enforced protected areas <sup>54</sup> . Depletion of top predators is strongly related to socio-economic conditions such as the size and proximity of the nearest market and human population density <sup>55</sup> . Top predators thus provide a very early signal of marine ecosystem exploitation	Very highly sensitive
Amount of biomass	Biomass captures both the size and number of fish above 10 cm in the system, which represents both food availability to people and is a proxy for a range of other ecosystem states and processes . Fish biomass is expected to decline rapidly as human impacts intensify <sup>33</sup> , and there is empirical evidence that management can allow the recovery of large species <sup>57</sup> .	Highly sensitive
Trait diversity	Trait diversity is based on the distribution of relative fish biomass across 6 trait values (diet, size, mobility, gregariousness, vertical position, period of activity). Trait diversity is low when most of fish biomass belongs to a single species or to redundant species (i.e. with same trait values) and is maximal when biomass is evenly shared by species with the most dissimilar trait values. Trait diversity is negatively affected by human activities because fisheries target some specific fish traits <sup>58,59</sup> . Yet, trait diversity moderately benefits from marine reserves, particularly close to humans <sup>60,61</sup>	Moderately sensitive
Parrotfish scraping potential	On coral reefs, parrotfish are among the most important groups of herbivorous fish. Their unique oral morphology (i.e. teeth fused to form a beak) allows them to scrape the reef substratum, removing algae and associated material thereby clearing space for the settlement of benthic organisms such as corals, and contribute to bioerosion of reef carbonates <sup>62</sup> . Parrotfish scraping is expected to decline with fishing intensity <sup>63</sup> and respond positively to management <sup>64</sup> , yet, some parrotfish populations may provide weak signals of ecosystem exploitation or restoration <sup>65</sup> .	Least sensitive

1007  
 1008

1009 **Figure 1. Map of study sites**

1010 Points are jittered to allow better visualization of nearby sites. n = 1,571.

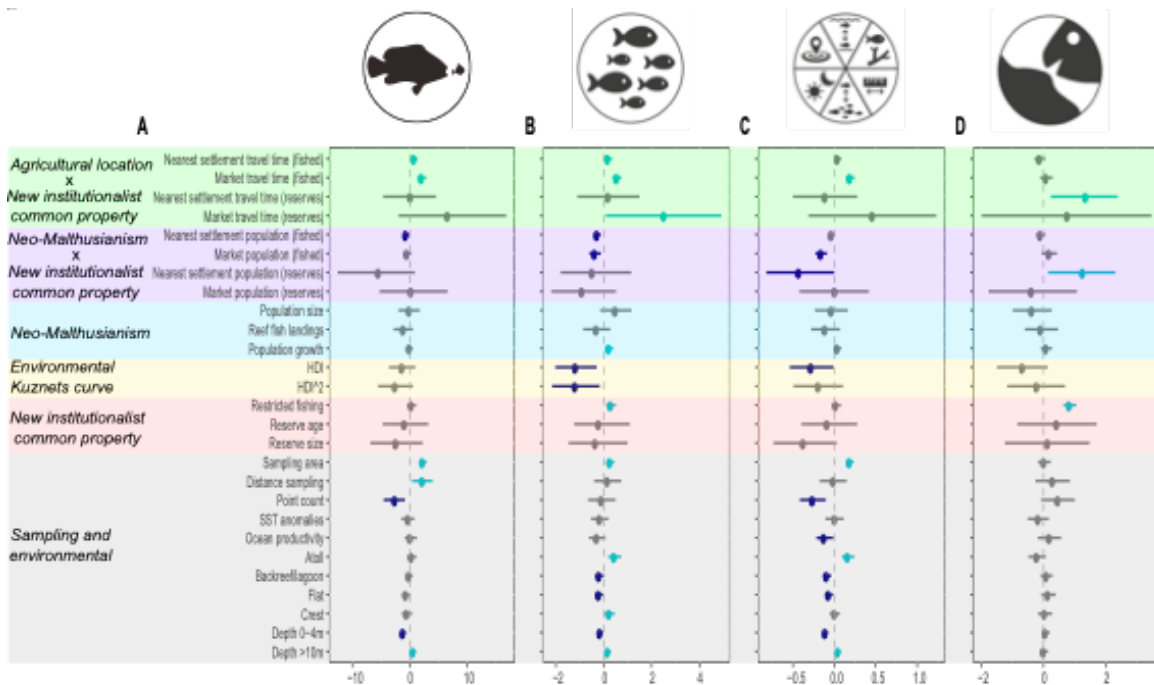


1011

1012 **Figure 2. Coefficient plots of the relationships between ecological response variables**  
 1013 **and key socioeconomic/environmental drivers**

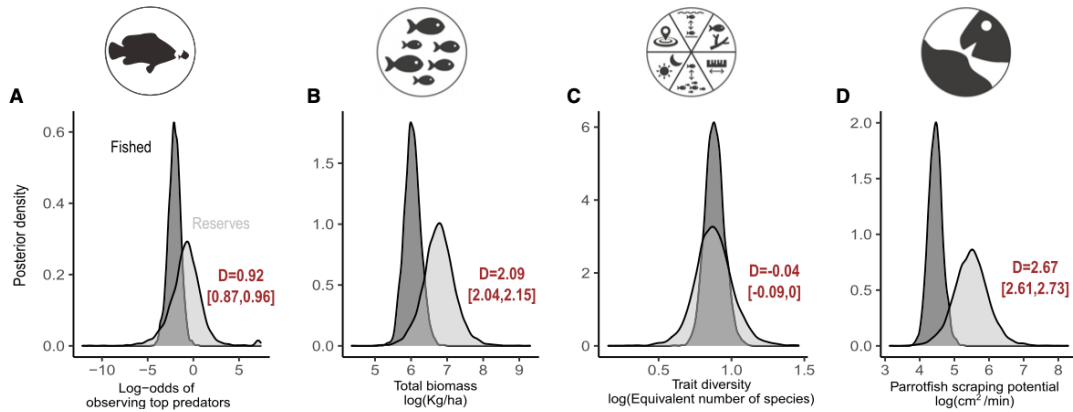
1014 (A) the probability of observing top predators, (B) the amount of fish biomass, (C) fish  
 1015 trait diversity, and (D) parrotfish scraping potential. Points are the median effect sizes  
 1016 (i.e., slopes of the linear model). Error bars are 90% uncertainty intervals. Turquoise  
 1017 symbols indicate that 90% of the posterior density is in a positive direction, while blue  
 1018 symbols indicate that 90% of the posterior distribution is in a negative direction. Model  
 1019 presented is the best overall model as determined by summed leave-one-out information  
 1020 criteria (Table S3); best fit models for individual response variables are presented in  
 1021 Figure S2.

1022



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 1024

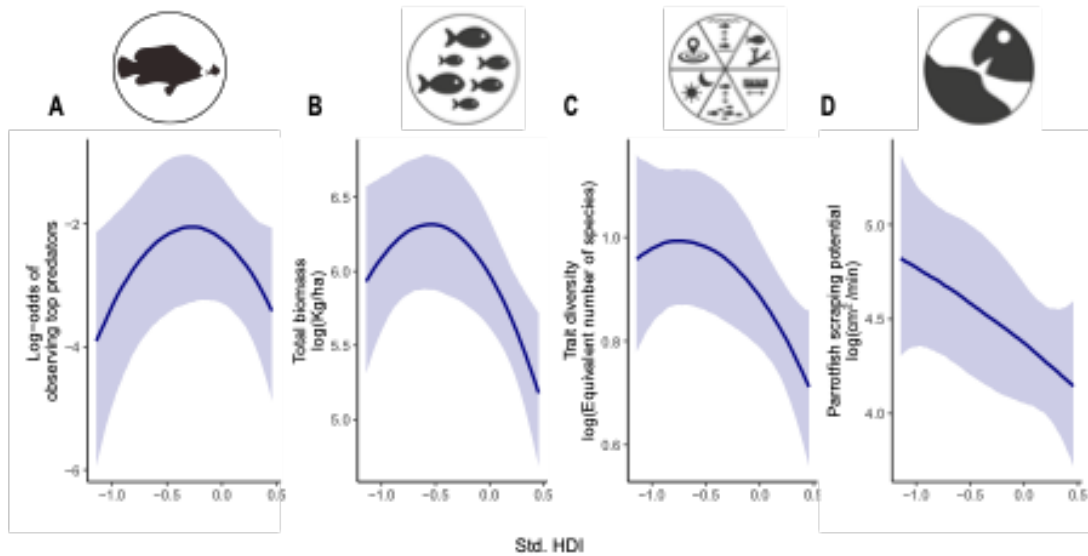
1025 **Figure 3. Distribution of modeled intercepts between openly fished sites (darkgray)**  
 1026 **and reserves (lightgray) at average socioecological conditions for four ecological**  
 1027 **response variables**  
 1028 (A) The probability of observing top predators, (B) the amount of fish biomass, (C) fish  
 1029 trait diversity, and (D) parrotfish scraping potential. Cohen's D statistic with 95%  
 1030 confidence intervals (within brackets) is displayed.



1031

1032 **Figure 4. Marginalized relationships between standardized human development**  
1033 **index (HDI) and four ecological response variables**

1034 (A) The probability of observing top predators, (B) the amount of fish biomass, (C) fish  
1035 trait diversity, and (D) parrotfish scraping potential for the best overall model. Solid line  
1036 is the median, and polygons are 90% uncertainty intervals. These plots present the  
1037 relationship between HDI and the response variable while holding all other covariates to  
1038 their global average (i.e., standardized score of 0) or to the most common category (i.e.,  
1039 slope for habitat, standard belt transect for census method, 4 to 10 m for depth).



1040