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

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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^{1,2}. Despite their biological and
48 socioeconomic importance, many coral reefs are being severely degraded³⁻⁵. 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)⁶⁻¹⁰.

52

53 To date, the coral reef literature has been dominated by a neo-Malthusian
54 perspective on human-environment interactions, which considers human population (size,
55 growth rate, structure) as the primary driver of degradation on coral reefs^{4,11-15}. This
56 human-environment perspective dates back to the works of Reverend Thomas Malthus,
57 who posited that human population would outpace agricultural production because the
58 former increased exponentially, while the latter increased only linearly. In the late 1960s,
59 concerns about population pressure resurfaced in an environmental context^{16,17}, often
60 referred to as neo-Malthusianism¹⁸. Modifications of this theory examine how population
61 combines with affluence and technology to generate human impacts on the environment
62 (the IPAT model)¹⁹ and Ester Boserup's more nuanced theory of how population growth
63 can spur technological innovation²⁰. Although the importance of human population in
64 shaping human-environment interactions is supported by theoretical and empirical work
65 from a broad range of systems^{13,21-24}, human population is only one of many potential
66 drivers of change. There are also impacts from less visible social and economic processes
67 that operate at larger spatial and temporal scales^{23,25,26}. These are investigated in a range of
68 alternative social theories regarding how humans impact the environment, including
69 Agricultural Location Theory²⁷, the Environmental Kuznets Curve²⁸, and New Institutional
70 Common Property Economics²⁹, each of which emphasizes different drivers of change and
71 associated policy levers.

71

72 The role of market proximity in shaping how terrestrial resources are used is
73 captured by a body of work typically referred to as Agricultural Location Theory^{26,30}.
Originating with von Thünen's 1826 Isolated State³¹, 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^{26,32}.
76 This concept is central to much contemporary work in agricultural economics, land-use
77 change, and economic geography^{23,26}, though its adaptation to marine contexts has
78 traditionally been limited to maritime transportation³⁰ and more recent applications in
79 predicting the condition of coral reef fish biomass³³⁻³⁶, diversity³⁷, and coral cover¹⁰. 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 market³⁸) and a modification which incorporates the population size of the market
83 (referred to as ‘gravity’^{33,39}). 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 conditions²⁸. 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 efficiency⁴⁰. 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-regulated⁴¹. 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^{22,40}. 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 sites⁴¹.

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 institutions⁴². 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^{43–45}.

111 There are important policy implications associated with embracing, or alternatively
112 ignoring, specific human-environment theoretical perspectives⁴⁶. 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^{22,40,46}, 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 processes⁴⁷. 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 together⁴⁷. 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^{48,49}. 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^{33,39} (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 local³⁴,
161 national^{50,51}, regional⁴¹, to global^{27,52}. 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^{41,43,51,52}); 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^{21,23,25}, agriculture^{20,31}, and conservation⁵³. 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)^{20,23,54}. 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^{27,34,51}. 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^{11–13,55}, particularly through overfishing^{4,56}. 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 high¹⁵. 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^{4,57-60}. 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 ignored⁶. 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 use⁶¹.

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 protection⁶².

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 them⁶³. 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^{42,44}.

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 biomass⁴¹. 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^{64,65}. It is often expected that this happens with some resources at a
307 national scale⁶⁶, 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’^{67,68}. 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^{67,68}. 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^{69,70}. Explanations for variability in these
322 trends can be found in the treadmill of production⁴⁰ and ecological modernization⁷¹
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 productivity⁷²) 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 dependent⁷³: 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 Geels⁴⁶ 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 space⁷⁴.

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 reefs⁷⁵. 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 reserves⁷⁶. 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 overexploitation⁷⁷. Recent research in behavioral
381 sciences, however, shows that the impacts of market relationships on behavior are more
382 complex^{71,78}. 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 duties⁷⁹; 2) people's reluctance to inflict harm on others (referred
385 to as third party externalities)⁸⁰; and 3) people's preferences for equality⁸¹. 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 modelling⁷⁷, experimental games⁸², and examining temporal trends⁸³.

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^{46,84}) or of interplay between nations (e.g.
395 world-systems theory)⁸⁵. 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 uncovering⁴⁴. 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 governance⁴², a key focus of many New Institutional studies⁸⁶, were not
400 available. Likewise, information about staff capacity and resources within marine reserves
401 has been shown to be related to ecological outcomes⁸⁷, 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^{8,72,88},
404 but were unable to be incorporated in our models. Finally, our study used a snapshot spatial
405 approach. MacNeil⁴⁷ 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 thesis⁷⁰.

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^{21,22,25}. 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^{78,89,90}. 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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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

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 predators³³, the amount of fish biomass, trait diversity, and
518 parrotfish scraping potential⁴⁹ (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^{33,49,52}. The data used in
522 this present paper comprise the sites in ^{33,49,52} 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. ³³. 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 FishBase⁹¹. When length–weight relationship
539 parameters were not available for a species, we used the parameters for a closely related
540 species, genus or family³³. We included 22 fish families that were standard across the
541 different data providers⁴⁹.

542 **Trait diversity**

543 We used the methods from Cinner et al. ⁴⁹ 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 $FD_{q=1}$ index⁹² 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 dimension⁹³. Size-specific feeding rates 570 were derived from best-fit regressions of bite rate (bites 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 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^{94,95}. Size-specific bite dimensions (mm^2) were obtained from the literature
577^{93,96-98}.

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^{99,100} [following the procedure described by
594 Gove et al.⁴², 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^{59,101,102},
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)¹⁰³,
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^{56,104}
605 clipped to only include catches from reefs divided by the area of reef¹⁰⁵, national population
606 size, national human development index¹⁰⁶, 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 settlement⁵². Market gravity was calculated as
613 the population size of the nearest market divided by the squared travel time³⁸ between the
614 city and the reef⁵². 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 reef⁵². 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 metric¹⁰⁶) and with biogeographic region, which we did not
620 include.

621

622 *Analyses:* In contrast to previous work (e.g.,³³), 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 deviations¹⁰⁷) 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-validation¹⁰⁸ (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 selection¹⁰⁹). 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:

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

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

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

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

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

$$675 \quad \mu_a = \beta_{0jka} + \beta_1 x_{deep,a} + \beta_2 x_{shallow,a} + \beta_3 x_{crest,a} + \beta_4 x_{lagoon/backreef,a} + \beta_5 x_{flat,a} + \\ 676 \quad \beta_6 x_{point\ count,a} + \beta_8 x_{samplingarea,a} + \beta_9 x_{size,a} + \beta_{10} x_{age,a} + \beta_{11} x_{atoll,a} + \\ 677 \quad \beta_{12} x_{prod,a} + \beta_{13} x_{SSTanom,a} + \beta_{14} x_{popgrowth,a} + \beta_{15} x_{marketpop,a} + \\ 678 \quad \beta_{16} x_{settlementpop,a} + \beta_{17} x_{landings,a} + \beta_{18} x_{population,a} + \beta_{19} x_{hdi,a} + \beta_{20} x_{hdi^2,a} + \\ 679 \quad \beta_{22} x_{markettt,a} + \beta_{23} x_{settlementttt,a} \quad (6)$$

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

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

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

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

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

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; δ 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 RStan¹¹⁰. 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 plots¹¹¹. 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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712

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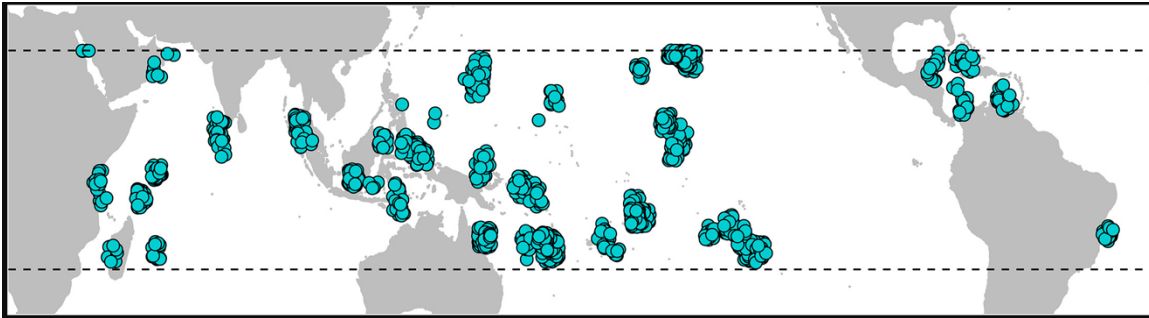
1003 **Table 1. Main rationale and hypotheses explaining the expected relationships**
 1004 **between the four reef fish metrics used in our study and fishing pressure**
 1005 Indicators are ranked from most to least sensitive to fishing pressure.
 1006

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 ^{48,49} . 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 ⁵⁰⁻⁵³ and very large well-enforced protected areas ⁵⁴ . 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 ⁵⁵ . 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 ³³ , and there is empirical evidence that management can allow the recovery of large species ⁵⁷ .	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 ^{58,59} . Yet, trait diversity moderately benefits from marine reserves, particularly close to humans ^{60,61}	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 ⁶² . Parrotfish scraping is expected to decline with fishing intensity ⁶³ and respond positively to management ⁶⁴ , yet, some parrotfish populations may provide weak signals of ecosystem exploitation or restoration ⁶⁵ .	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.

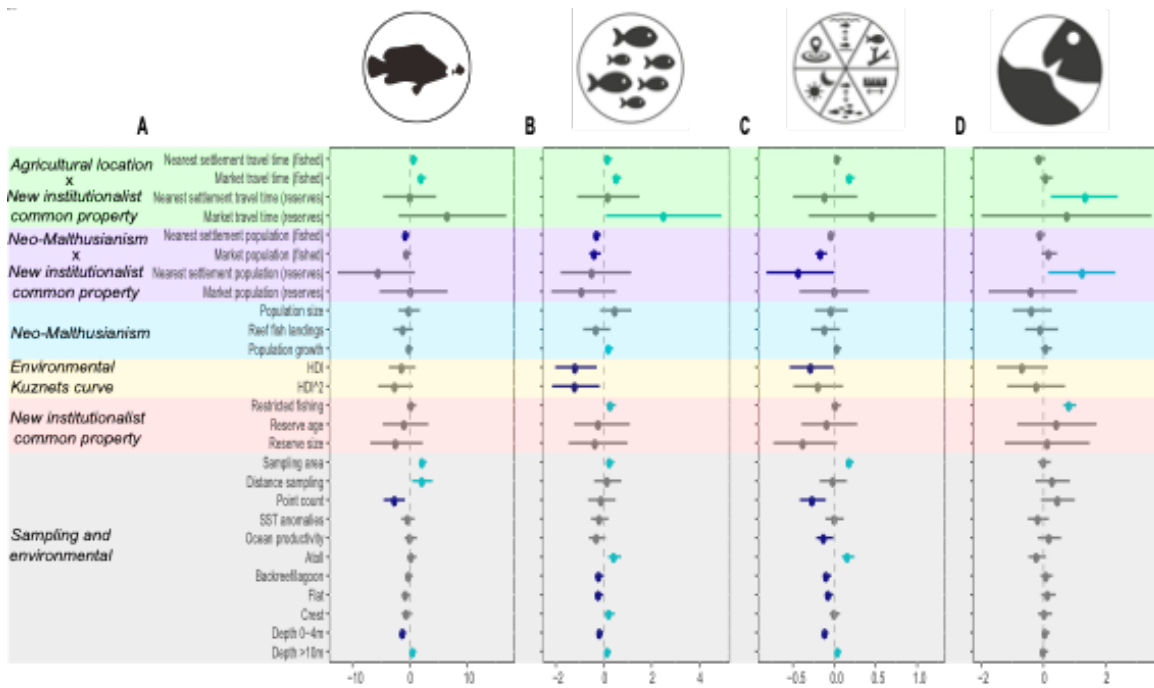


1011

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.

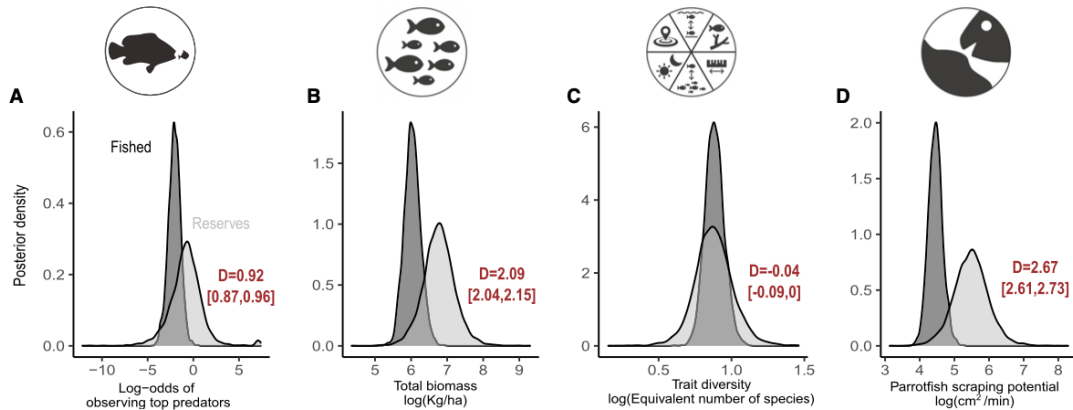
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1025 **Figure 3. Distribution of modeled intercepts between openly fished sites (darkgray)**
1026 **and reserves (lightgray) at average socioecological conditions for four ecological**
1027 **response variables**

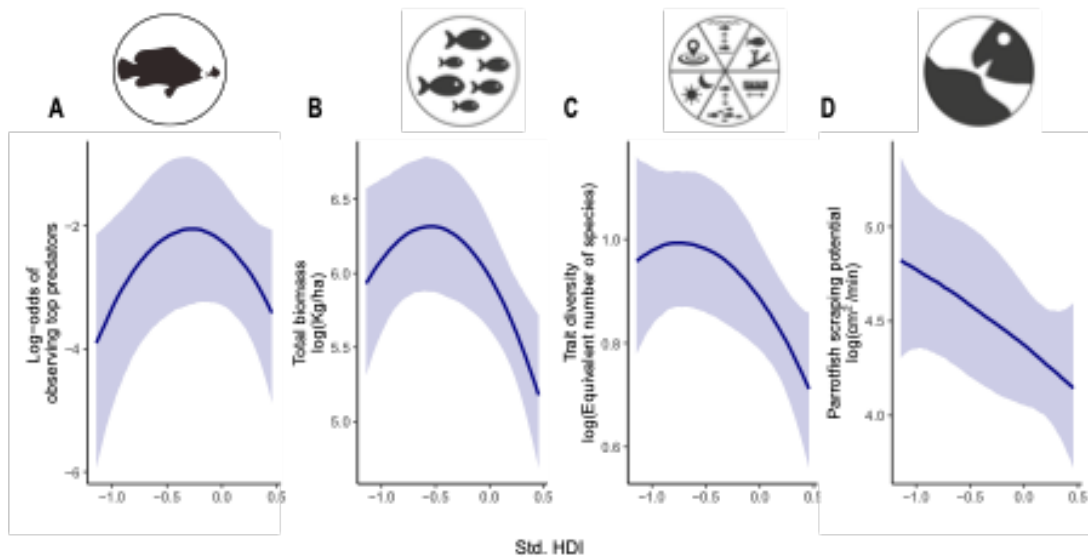
1028 (A) The probability of observing top predators, (B) the amount of fish biomass, (C) fish
1029 trait diversity, and (D) parrotfish scraping potential. Cohen's D statistic with 95%
1030 confidence intervals (within brackets) is displayed.



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