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

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Summary

Effective solutions to the ongoing "coral reef crisis" will remain limited until the underlying drivers of coral reef degradation are better understood. Here, we conduct a global-scale study of how four key metrics of ecosystem states and processes on coral reefs (top predator presence, reef fish biomass, functional diversity, and parrotfish scraping potential) are explained by 11 indicators based on key human-environment theories from the social sciences. Our global analysis of >1,500 reefs reveals three key findings that challenge existing paradigms. First, our global study shows that resource conditions tend to display a n-shaped relationship with socioeconomic development. Specifically, the probability of encountering a top predator, fish biomass, and functional diversity were highest where human development was moderate, but lower where development was either high or low. This finding contrasts with previous regional-scale research demonstrating an environmental Kuznets curve hypothesis (which predicts a U-shaped relationship between socioeconomic development and resource conditions). Second, we find that the size and proximity of the nearest markets have the strongest and most consistent relationships with these ecosystem metrics. This finding is in keeping with a body of terrestrial research on how market accessibility shapes agricultural practices, but the integration of these concepts in marine systems is nascent. Third, human population displayed a consistent but weak relationship to our reef fish metrics, providing only moderate support for the dominant neo-Malthusian perspective that human population is the main driving force behind reef degradation. Our results highlight that much of the research to date trying to explain the condition of reef fisheries based primarily on human population size has been incomplete.

Keywords: social-ecological system, coral reef, fisheries, sustainability

Introduction

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

To date, the coral reef literature has been dominated by a neo-Malthusian perspective on human-environment interactions, which considers human population (size, growth rate, structure) as the primary driver of degradation on coral reefs[4,11–15]. This human-environment perspective dates back to the works of Reverend Thomas Malthus, who posited that human population would outpace agricultural production because the former increased exponentially, while the latter increased only linearly. Modifications of this theory examine how population combines with affluence and technology to generate human impacts on the environment (the IPAT model)[16] and Ester Boserup's more nuanced theory of how population growth can spur technological innovation[17]. Although the importance of human population in shaping human-environment interactions is supported by theoretical and empirical work from a broad range of systems[13,18–21], human population is only one of many potential drivers of change. There are also impacts from less visible social and economic processes that operate at larger spatial and temporal scales[20,22,23]. These are investigated in a range of alternative social theories regarding how humans impact the environment, including Agricultural Location Theory[24], the Environmental Kuznets Curve[25], and New Institutional Economics[26], each of which emphasizes a unique set of drivers of change and associated policy levers.

The role of market proximity in shaping how terrestrial resources are used is captured by a body of work typically referred to as Agricultural Location Theory[23,27]. Originating with von Thünen's 1826 Isolated State[28], the concept is based on a central place hierarchy, which emphasizes how location affects resource use through the combined influence of environmental factors and transport costs on production and profitability[23,29]. This concept is central to much contemporary work in agricultural economics, land-use change, and economic geography[20,23], though its adaptation to marine contexts has traditionally been limited to maritime transportation[27] and more recent applications in predicting the condition of coral reef fish biomass[30–33], diversity[34], and coral cover[10]. Key indicators used in adaptations of Agricultural Location Theory in a reef context include proximity to markets (often measured as the time it takes to travel between a reef and the nearest market[35]) and a modification which incorporates the population size of the market (referred to as 'gravity'[30,36]). This modification essentially integrates agricultural location and neo-Malthusian perspectives.

The environmental Kuznets curve hypothesis suggests that economic growth drives environmental degradation until it reaches a tipping point at which further growth drives better environmental conditions[25]. This is based on the assumption that higher levels of economic development are associated with a transition to service industries, heightened environmental awareness, improved regulation, technological advancement and increased resource use efficiency[37]. For example, the relationships between development and degradation captured by the environmental Kuznets curve can occur through mechanisms such as spatial displacement, whereby wealthier places can displace their environmental footprint, often to areas that are poorer and less well-regulated[38]. Key indicators used in studies of the environmental Kuznets curve often include national-scale measures of economic output, such as Gross Domestic Product[19,37]. In the coral reef literature, an environmental Kuznets curve like relationship was found between a local-scale metric of socioeconomic development and reef fish biomass, such that as reefs near communities with either very low or high levels of development tended to have about four times the reef fish biomass of reefs near the intermediate development sites[38].

New Institutional Common Property Economics investigates how the rules in use (i.e. laws and norms) affect people's relationships with each other and the environment. This branch of comparative institutional analyses can focus on modes of governance, property rights, institutional design, and enforcement mechanisms. For example, Nobel Laureate Elinor Ostrom's book "Governing the Commons: the evolution of institutions for collective action" examined the institutional design associated with long-enduring common property institutions[39]. Adaptations of the new institutional perspective to the coral reef literature have, for example, examined how both the rules in use (e.g. the degree of protection) and the processes through which those rules were developed and implemented (i.e. collaborative vs top-down management) can affect both social and ecological outcomes[40–42].

There are important policy implications associated with embracing, or alternatively ignoring, specific human-environment theoretical perspectives[43]. Over-emphasizing one specific theoretical perspective of human environment-interactions, for example, may hinder opportunities for positive changes or alternative management options. Yet, there are few comparative studies that empirically explore the evidence for or against key human-environment theories[19,37,43], particularly on coral reefs. Doing so requires a large dataset of not only ecological conditions, but also a set of socioeconomic drivers specific to each human-environment theory.

Here, we use a global dataset to statistically evaluate how key indicators from alternative human-environment theoretical perspectives explain coral reef states and processes[44]. More precisely, we develop a series of alternative models to quantify how key socioeconomic drivers of change, associated with prominent human-environment theories (Tables S1-2), are related to four key metrics of ecosystem states and processes (the presence of top predator, the amount of fish biomass, fish functional diversity and parrotfish scraping potential ; Table 1) across >1500 reefs in 35 countries, states, and territories, after controlling for environmental (ocean productivity, atoll, sea surface temperature anomalies) and sampling conditions (depth, habitat surveyed, sampling area, and technique) (STAR Methods, Fig. 1).

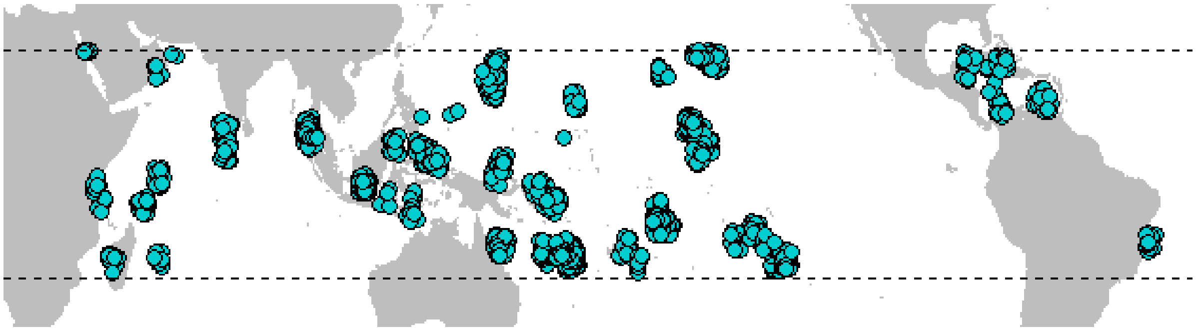


Figure 1. Map of study sites. Points are jittered to allow better visualization of nearby sites. n=1571.

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

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[45,46]. 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[47–50] and very large well-enforced protected areas[51]. 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[52]. 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 [30], and there is empirical evidence that management can allow the recovery of large species [54].	Highly sensitive
Functional diversity	Functional diversity (FD) is based on the distribution of relative fish biomass across 6 trait values (diet, size, mobility, gregariousness, vertical position, period of activity). FD 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. FD is negatively affected by human activities because fisheries target some specific fish traits[55,56]. Yet, FD moderately benefits from marine reserves, particularly close to humans [57,58]	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 REF?. Parrotfish scraping is expected to decline as human impacts intensify [59] and respond positively to management [60]. Yet, some parrotfish populations may provide weak signals of ecosystem exploitation or restoration[61].	Moderately sensitive

To explore evidence for neo-Malthusian perspectives on coral reefs, we examined the national population size, national reef fish landings, the local population growth rate, the population size of the nearest settlement, and the population size of the nearest market (Table S1). To explore evidence for the environmental Kuznets curve in relation to coral reefs we examine how reef conditions are related to the quadratic function of a national scale indicator of socioeconomic development (human development index) that incorporates national income, life expectancy, and schooling (Table S1). To explore the influence of institutional arrangements on coral reefs, we examine how reef conditions are related to the rules in use, as well as the age and size of any no-fishing marine protected areas (Table S1). To explore evidence for agricultural location theory, we examined metrics of travel time to both the nearest market and the nearest human settlement (Table S1, STAR methods). In our case, a market was defined as a port, provincial capital, or major city. We built different candidate models for each ecosystem metric, allowing us to test alternative human-environment theories independently and together[44]. First, we tested each human-environment theory independently, while controlling for environmental conditions. Second, we tested a model embracing all four human-environment theories. Third, we tested select interactions between human-environment theories, including between Agricultural Location Theory and neo-Malthusianism in the form of a combined ‘gravity' metric; interactions between New Institutionalist Economics and neo-Malthusianism to examine whether reserves have different effects depending on the surrounding population; interactions between New Institutionalist Economics and Agricultural Location Theory to examine whether management has different effects depending their proximity to markets, interactions between neo-Malthusianism, Agricultural Location Theory, and New Institutionalist Economics to examine whether management has different effects depending their surrounding populations AND proximity to markets;, interactions between New Institutionalist Economics and Environmental Kuznets Curve to examine whether management has different effects depending on the wealth.

This research is part of an emerging body of empirical work by our team that explores human-environment linkages on coral reefs at a range of scales, from local[31], national[62,63], regional[38], to global[24,64]. The novel contributions of this paper are that we: 1) explicitly connect a range of socioeconomic drivers to their theoretical underpinnings, enabling support for differing human-environment theories to be investigated; 2) explore four distinct reef fish metrics (e.g. much of our previous work has focused primarily on biomass[38,40,63,64]); 3) utilize a joint modelling approach which allows us to better integrate information about marine reserves in our model (i.e. to explicitly consider reserve size and age; Methods); 4) test different candidate models for each response variable, which allowed us to examine the support for different hypotheses (such as whether our response variables displayed a U-shaped relationship with socioeconomic development).

Results and Discussion

Agricultural location theory and coral reefs

We found strong support for our adaptation of agricultural location theory as a key predictor of coral reef states and processes (Fig 1, Tables S2-3). Specifically, the agricultural location model was the best individual theory to explain 3 out of 4 of our reef fish metrics (top predators, biomass, and trait diversity, which provide early signals of degradation), while the new institutionalist model was preferred for parrotfish grazing (Table S3). However, the best overall model not only included the other human-environment theories, but also linked agricultural location and neo-Malthusian perspectives in the form of a combined gravity metric (Table S2). The best overall model showed that both market gravity and nearest settlement gravity displayed a consistent negative relationship across most of our reef fish metrics (Fig. 2). Specifically, the probability of encountering a top predator, the amount of biomass, and functional diversity declined with increasing market and nearest settlement gravity, though the effect size of market gravity was larger (Fig. 2).

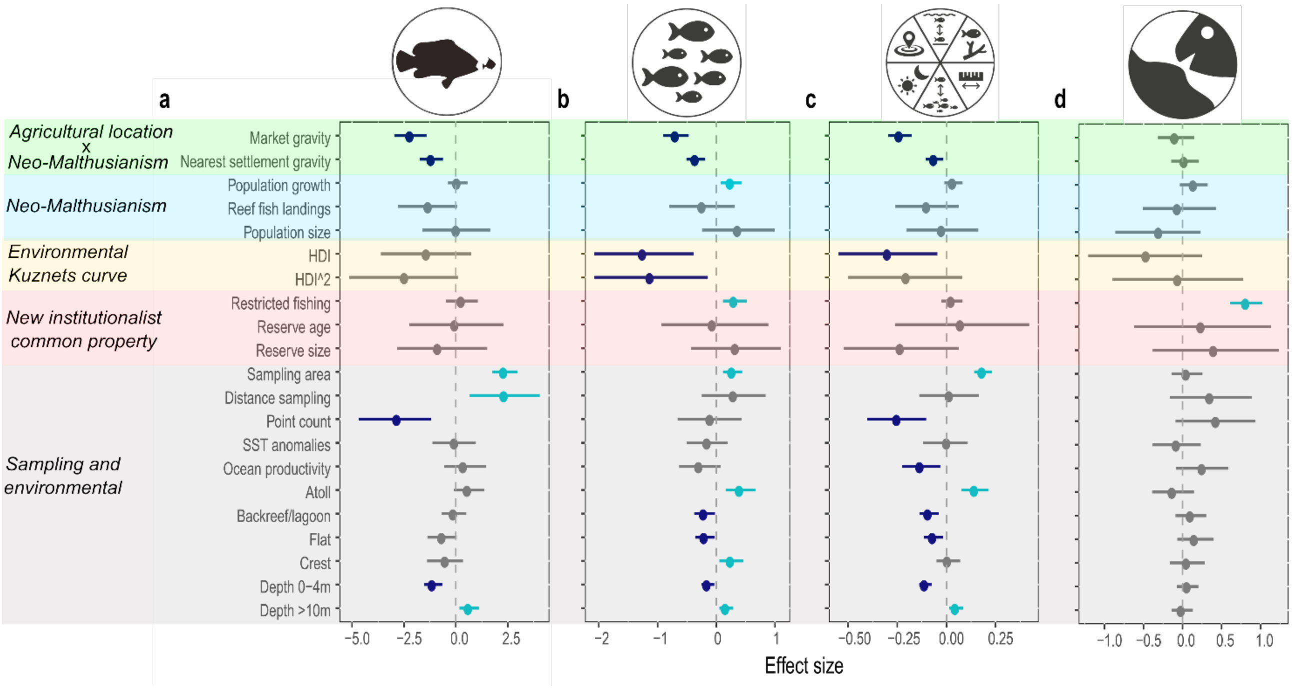


Figure 2. Coefficient plots of the relationships between key socioeconomic and environmental drivers and a) the probability of observing top predators , b) the amount of fish biomass, c) fish functional diversity, d) parrotfish scraping potential. Points are the median effect sizes (i.e., slopes of the linear model). Error bars are 90% uncertainty intervals. Turquoise and blue symbols indicate that 90% of their posterior density in either a positive or negative direction, respectively. Model presented is the best overall model as determined by summed leave-one-out information criteria (Table S3), best fit models for each individual response variables are presented in Fig. S1.

Market proximity has played a central role in shaping theories about terrestrial land use change[18,20,22], agriculture[17,28], and conservation[65]. For example, land use change theories cover issues such as how market accessibility (through road networks and market connectivity) influences land use through expansion (e.g., how unconverted ‘wildland’ or ‘native’ cover is converted into agriculture), intensification (e.g., how technologies such as irrigation can increase yields, often with positive ecological outcomes), spillovers (e.g., how some land uses might get displaced into other areas), and transitions (non-linear changes to alternative system states)[17,20,66]. Yet to date, there has been little integration of these theoretical insights about the potential importance of markets in shaping natural resource use and governance from agricultural economics and land use change science into studies of the marine environment [24,31,63]. This suggests that there is the potential to better understand both the mechanisms driving resource use and uncover underutilized policy levers by more rigorously applying insights from fields such as land use change to the marine environment. However, such applications must pay attention to how seascapes differ from landscapes, to avoid poor planning decisions and conservation outcomes by blindly applying terrestrial concepts to marine contexts. Seascapes, particularly those with small-scale wild capture fisheries rather than aquaculture, are fundamentally different from terrestrial systems in four key ways that affect resource use and ecosystem recovery potential (and hence the applicability of terrestrial concepts). First, fishing does not necessarily result in conversion of natural habitat in the same way that agricultural expansion often does. Second, intensification in a wild capture fishery generally means killing more fish since there are fewer options for investing in increased productivity in ways that can benefit nature. Third, key characteristics such as fish being highly mobile yet difficult to directly observe can lead to fisheries having lagged social-ecological feedback mechanisms compared to land systems. Fourth, seascapes are rarely privately owned or sold, which means different institutions and market forces are at play. An important future direction will be better understanding the degree to which these differences mean specific agricultural location theories and concepts may not be applicable in reef systems, and whether bespoke 'fisheries location theories' need to be developed to better inform this potential solution space for marine conservation.

New Institutionalist economics and coral reefs

We also found strong support for the new institutionalist perspective. We found that the institutions (i.e. rules in use) used to manage coral reefs displayed strong relationships to our reef fish metrics. Our joint modelling approach showed that the presence of top predators, reef fish biomass and parrotfish scraping potential were substantially higher in high compliance no fishing marine reserves than on openly fished reefs (Cohen's D=2.04, 2.91, 2.36, respectively), while functional diversity was only slightly higher (D=0.11) (Fig. 3). It suggests that functional diversity provides an early signal of reef degradation, like the presence of top predators and fish biomass, but takes longer or is challenging to recover/rebuild after protection[58].

Marine reserves are one of the most common conservation tools used on coral reefs, so it is not necessarily surprising that we found improved ecosystem states and processes within them[67]. However, our contribution here lies in quantifying the effect size of reserves across a broad range of reef fish metrics globally, while accounting for other key socioeconomic and environmental drivers (Fig. 3). Key reserve features, such as reserve age and size, were highly uncertain with our four reef fish metrics (Fig. 2). This uncertainty was likely due in part to the limited number of sites within high compliance reserves (n=51). Restrictions on fishing (such as effort and size limits) were positively related to all metrics, but with uncertainty intervals overlapping 0 for the presence of top predators and functional diversity (Fig. 2) since many species with specific traits (large home range) may remain absent from protected areas depending on the regional context[30,56]. In this particular study, we did not examine the processes through which the rules were established, which can play a large role in whether specific rules are complied with[39,41].

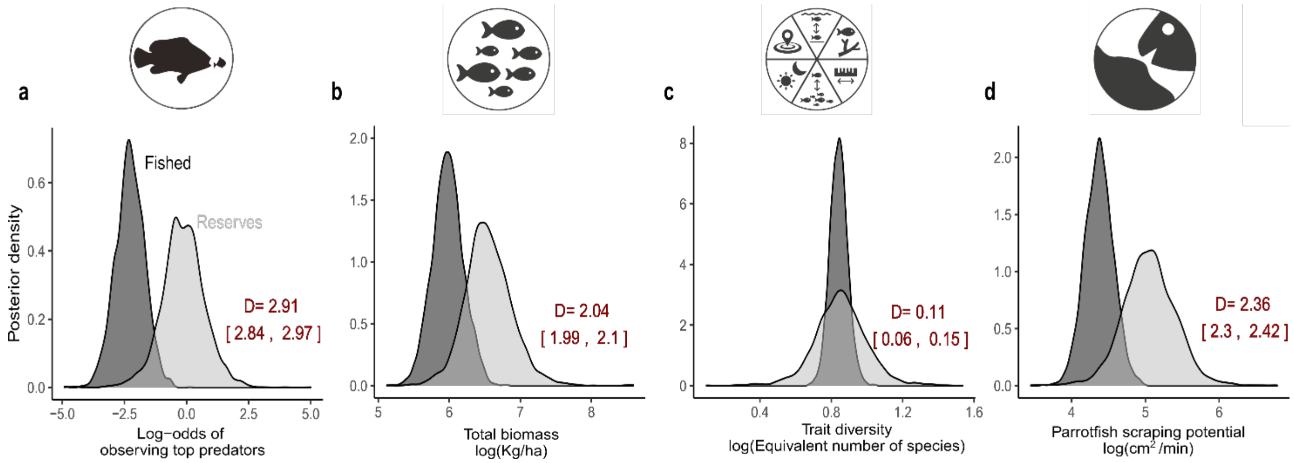


Figure 3. Distribution of modelled intercepts between openly fished sites (dark grey) and reserves (light grey) at average socio-ecological conditions for a) the probability of observing top predators , b) the amount of fish biomass, c) fish functional diversity, d) parrotfish scraping potential. Cohen's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

Environmental Kuznets curve and coral reefs

Our results showed an inverted environmental Kuznets curve- the opposite of what would be expected under the environmental Kuznets curve hypothesis (Fig. 4). Specifically, the best overall model favored the quadratic function of the national socioeconomic development context (measured as the human development index), but with an n- rather than u-shaped relationship (i.e. effect sizes for the quadratic terms were negative; Figs. 2, 4). For example, reefs in countries with intermediate levels of human development tended to have more fish biomass than locations in high or low development countries (Fig 4). While the best overall model included a quadratic with HDI, this quadratic relationship was not selected for parrotfish scraping potential individually (Table S3).

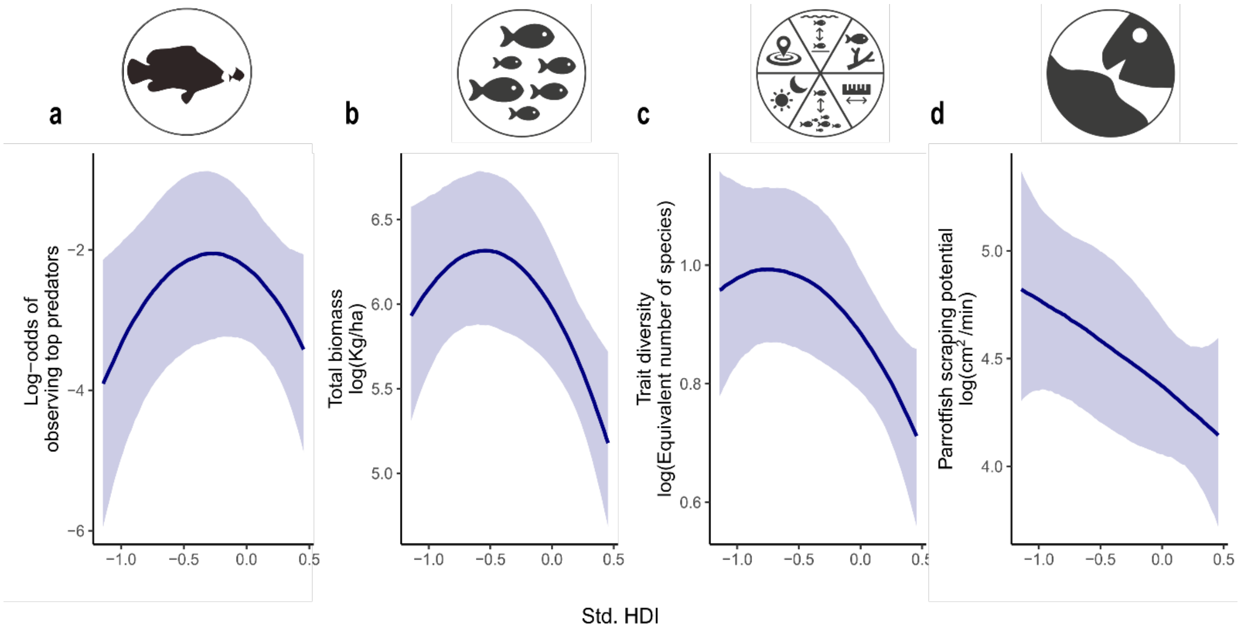


Figure 4. Marginalized relationships between standardized Human Development Index (HDI) and a) the probability of observing top predators , b) the amount of fish biomass, c) fish functional diversity, d) parrotfish scraping potential for the best-overall model. Solid line is the median and polygons are 90% uncertainty intervals. These plots present the relationship between HDI and the response variable while holding all other covariates to their global average (i.e. standardized score of 0) or to the most common category (i.e. slope for habitat, standard belt transect for census method, 4 to 10 m for depth).

Our current results contrast with previous work in the western Indian Ocean, which showed a U-shaped environmental Kuznets curve-like relationship between local-scale development and reef fish biomass[38]. Differences could be explained by the both the range and the scale of the analyses (global versus regional). The wealthiest country in the regional study was Seychelles, which has below global average HDI values in this present study. Thus, the range of the regional study may have only investigated the initial part of the global curve (i.e. as ecosystem metrics were rising). Additionally, the Kuznets curve may be a scale-dependent phenomenon, and there were differences between studies in the scale of the development indicator used (national scale versus local scale). Indeed, one of the plausible mechanisms of the Kuznets curve is what is referred to as the scale effect, whereby wealthier people can export their environmental footprint to other areas[68,69]. It is often expected that this happens with some resources at a national scale[70], but with reef fish, which are not a major international commodity in the same way that tuna and other pelagic fish are, an intra-national scale effect may be possible.

Our current national-scale results are more consistent with the Jevons paradox, which notes that technological efficiency gains may be associated with increased environmental degradation as resource consumption rises in response to declining costs exhibiting what is known as a 'rebound effect'[71,72]. For example, in response to improved fuel efficiency in vehicles, people may decide to take an additional long drive on the weekend, thereby increasing their total travel distance because travel is cheaper. Although Jevons paradox would generally predict a decline in resource conditions with development, it is possible for ecosystem states and processes to improve in the short term as a consequence of increased resource use efficiency but decline over the longer term as changes in preferences, technology, and investment take effect or as rates of efficiency gain relative to demand stagnate[71,72]. Our results may also be reflective of a feedback loop between human wellbeing and ecosystem conditions, whereby poor reef conditions and human impoverishment reinforce each other[73,74]. Explanations for variability in these trends can be found in the treadmill of production[37] and ecological modernization[73] literatures. In our case, that might mean that nearshore fish stocks recover as societies become wealthy enough to begin fishing offshore, but then decline as offshore stocks become more exploited and less profitable.

Neo-Malthusian perspectives on coral reefs

For many decades, human-environment research on coral reefs was dominated by a neo-Malthusian perspective, which tends to view human population as *the* primary driver of change[11–13,74], particularly through overfishing[4,75]. We found moderate support for the neo-Malthusian perspective of human-environment interactions on coral reefs (Fig. 2, Tables S2-3). Specifically, the Malthusian model was the second ranked individual theory for three of our reef fish metrics (Tables S2-3), and the best overall model included an integration of Malthusian and Agricultural Location perspectives into a metric of 'gravity'. However, other neo-Malthusian indicators displayed minimal relationships to our reef fish metrics, with population growth positively associated to fish biomass. This is noteworthy because in many empirical studies of human-reef interactions, human population is the sole social driver of change investigated[4,59,76–78]. Thus, a narrow neo-Malthusian perspective can be problematic and lead to policy blind spots if it leads to other potential drivers, and their accompanying policy levers, being ignored[6]. Indeed, key critiques of neo-Malthusianism note that it often fails to address issues such as socioeconomic inequalities or the institutional and legal arrangements that can drive natural resource use[79].

Linking human-environment theories on coral reefs

A key finding from our global study is that there is not one dominant theoretical perspective that fully explains human-environment interactions on reefs. Indeed, the best overall model included indicators from all four human-environment theories and a linkage between neo-Malthusian and Agricultural Location perspectives in the form of a combined gravity metric (Fig. 2, Tables S2-3). In other words, it is not only the addition of different human environment theories that is necessary to explain the states and processes on coral reef ecosystems, but also key linkages between the theories. Our findings echo those of Geels[43], who concluded that individually, different theoretical perspectives were overly reductionistic in explaining the transition to pig farming in Dutch agricultural systems, but that juxtaposing multiple theoretical perspectives provided a more encompassing understanding. Our findings highlight that coral reefs are complex social-ecological systems, and underline the importance of interdisciplinarity in not only uncovering the key drivers of change on coral reefs, but also in better defining the potential solution space[80].

Ecological states and processes

The four ecological response variables we included in this study are related, but also tell us something different about reef ecology and responses to human impacts (Table 1). By assessing all four metrics, a more nuanced understanding of how reef ecology is influenced by humans emerges. The presence of top predators is the most sensitive indictor of fishing pressure, followed by the amount of fish biomass, fish functional diversity and finally parrotfish scraping potential. Indeed, parrotfish scraping potential was the least sensitive to all drivers in our model, and herbivorous fish have been shown to continue to support reef fisheries and nutrient yields on heavily disturbed reefs. As expected marine reserves had a positive effect on most of the metrics, but was weak for functional diversity where traits may respond differentially to protection, highlighting the importance of uncovering how individual traits respond to marine reserves. While the presence of top predators, fish biomass, and fish functional diversity peak at intermediate HDI values, parrotfish scraping potential declines gradually with increasing HDI, suggesting this important ecological function has greatest potential in lower developmental settings. The sampling and environmental conditions we controlled for (i.e. our nuisance parameters) were not the focus of this present article, but were clearly also important predictors across most of our reef fish metrics. Specifically, sampling area, sampling technique, depth, habitat type, and atoll had relationships that cross-cut multiple reef fish metrics.

Critiques, caveats, and future directions

It is important to note that although our study found strong relationships between a number of socioeconomic indicators and four reef fish metrics, it did not unravel the causal mechanisms behind these relationships. For example, one potential mechanism to explain the impact of market-gravity is simply that as accessibility to markets increases, so do financial incentives for fisheries overexploitation[81]. Recent research in behavioral sciences, however, shows that the impacts of market relationships on behavior are more complex [73,82]. For example, markets can crowd out (i.e. displace) pro-environmental behavior not directly but through their impact on: 1) people's willingness to engage in collective action and civic duties[83]; 2) people's reluctance to inflict harm on others (referred to as third party externalities)[84]; and 3) people's preferences for equality[85]. There is thus a need to better understand the causal mechanisms through which markets and other socioeconomic drivers affect shallow reef ecosystems. Doing so may require causal modelling[81], experimental games[86], and examining temporal trends[87].

Our study focused on a set of social theoretical perspectives that offer explanations for natural resource degradation suitable for testing with available data. Though our analysis was multi-scale (local and national), it was unable to consider and test theories at the individual and supra-national scales. Consequently, this study has not considered theoretical frameworks relevant to understanding the drivers of individual behavior (e.g. attitudes, perceptions, norms, rational choice[43,88]) or of interplay between nations (e.g. world-systems theory)[89]. Additionally, many of the indicators available at a national and even local scale are relatively crude, and miss key nuances and details that local scale studies are better suited to uncovering[41]. For example, the global nature of our study meant that many of the institutional design principles thought to be important for the sustainability of commons governance[39], a key focus of many new institutionalist economics studies[90], were not available. Likewise, information about staff capacity and resources within marine reserves has been shown to be related to ecological outcomes[91], but was simply not available in our study sites. Finally, our study used a snapshot spatial approach. MacNeil[44] notes that there may be variability in the relevance of different explanatory variables over time as environmental and social conditions change. Future studies could investigate whether key theories become more or less important at explaining ecological states and processes over time using time-series data. Such an analysis could also begin uncovering dynamics such as feedback loops, which could enable inclusion of other human-environment theories such as the Marginalization-Degradation thesis[92].

An emerging body of literature has begun linking ecology with rigorous social science theory to better understand the complex and multi-scale ways that humans interact with, and affect, the environment so that underlying socioeconomic drivers of change can be identified and used as policy levers for sustainability[18,19,22]. Here, we tested how key socioeconomic drivers associated with four key human-environment theoretical perspectives predict the ecosystem states and processes on coral reefs across the globe. We show that a broad range of drivers are related to four key reef fish metrics, and the historical dominance of the neo-Malthusian perspective in coral reef science was not completely unfounded, but was certainly incomplete. Better understanding how other key human-environment interaction theories can also help to highlight opportunities for the development of novel policy levers. Although conservation initiatives that integrate marine reserves together with a focus on fisheries management are essential to supporting coral reefs, governance strategies that seek to reduce socioeconomic drivers or mediate their negative effects are also required. Many of the social drivers we examined are amenable to governance interventions. For example, our results emphasize that conservation strategies which mediate the negative effects of markets are urgently needed[82,93,94]. Ultimately, good governance that promotes effective management and seeks to dampen key socioeconomic drivers of ecological change will be critical to sustaining reefs and providing people with crucial ecosystem goods and services.

Acknowledgments

General: Thanks to the Social-Ecological Research Frontiers ecological team (Camilo Mora, Tim R. McClanahan, Stephanie D'agata, David A. Feary, Ivor D. Williams, Michel Kulbicki, Laurent Vigliola, Laurent Wantiez, Graham J. Edgar, Rick D. Stuart-Smith, Stuart A. Sandin, Alison L. Green, Maria Beger, Alan M. Friedlander, Shaun K. Wilson, Eran Brokovich, Andrew J. Brooks, Juan J. Cruz-Motta, David J. Booth, Pascale Chabanet, Mark Tupper, Marah J. Hardt, S. Pardede) for making data available for this analysis.

Funding: J.E.C. was supported by the Australian Research Council (CE140100020, FT160100047) and the CGIAR Research Program on Fish Agri-Food Systems (FISH) led by WorldFish.

Author Contributions: J.E.C. conceived of the study. J.Z.M developed and implemented the analyses; J.E.C. led the writing of the manuscript. All other authors contributed to data collection and made substantive contributions to the text.

Declaration of interest: The authors declare no competing interests.

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

STAR Methods

RESOURCE AVAILABILITY

Lead Contact

Further information and requests should be directed and will be fulfilled by the lead contact, Josh Cinner Joshua.cinner@jcu.edu.au

Data and Code Availability: Data and code have been deposited at GitHub and are publicly available at https://github.com/JZamborain-Mason/Cinneretal_hum-env_theories

METHOD DETAIL

Data

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Response variables: We used four key reef fish metrics with a range of sensitivity to human threat as response variables: the presence of top predators[30], the amount of fish biomass, functional trait diversity, and parrotfish scraping potential[57] (Table S2). All response variables were based on underwater visual counts of fish from reef sites (Fig. 1). Reef surveys were conducted between 2004 and 2013, using standard belt-transects, distance sampling, or point-counts. Where data from multiple years were available from a single reef site, we included only data from the year closest to 2010. Within each survey area, diurnally active, noncryptic reef fish were identified to species level, their abundance counted, and total length (TL) estimated.

Top predators

For the presence/absence of top predator's response variable, we used the methods from Cinner et al. [30]. For each site we recorded whether there was a fish from the following families greater than 50 cm in length: Carcharhinidae, Ginglymostomatidae, Heterodontidae, Sphyrnidae, and Carangidae, Lutjanidae, Serranidae and Sphyraenidae.

Biomass

The fish biomass metric was estimated using standard published species-level length–weight relationship parameters available on FishBase[95]. When length–weight relationship parameters were not available for a species, we used the parameters for a closely related species, genus or family [30].

Functional diversity

To calculate fish functional diversity, we used six traits: (i) observed length category (10-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm, or >80 cm); (ii) mobility (i.e., sedentary, mobile within a reef, or mobile between reefs); (iii) period of activity (i.e., diurnal, both diurnal and nocturnal, or nocturnal); (iv) schooling behavior (i.e., solitary, paired, or living in small (3-20 individuals), medium (20-50 individuals), or large groups (>50 groups)); (v) vertical position in the water column (i.e., benthic, bentho-pelagic, or pelagic); (vi) diet (i.e., herbivorous-detritivorous, macro-algal herbivorous, invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrates, planktivorous, piscivorous, and omnivorous). Since all traits were categorical, species with identical traits were grouped into functional entities. We then computed the Gower distance between all pairs of entities and computed functional diversity using the Chao's FDq=1 index[96] which is based on the distribution of biomass among functional entities:

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

where p_i and p_j are the respective relative biomasses of the two entities i and j in the community, d_{ij} is the Gower distance between entities i and j, mD is the average of all Gower distances between the entities present in the global pool of species. This index is expressed as an equivalent numbers of species (7). Hence, it is minimal and equals 1 when all biomass is supported by the same entity (i.e. when one species is ultra-dominant or when all species have the same trait values) and it is maximal and equals the number of species when all species pairs have dissimilarities higher than the average dissimilarity in the species pool and equal biomasses.

Parrotfish scraping potential

Finally, we calculated parrotfish scraping potential (area grazed per minute) as the product of parrotfish fish density, feeding rate, and bite dimension[97]. Size-specific feeding rates were derived from best-fit regressions of bite rate (bites min^{-1}) and total fish length (cm) for each species or a closely related congener. Parrotfish bite rates and total fish length were quantified at three locations (Great Barrier Reef, Australia; Indonesia; and the Red Sea) and converted to bites min^{-1}. Individual fish were followed for a minimum of 3-minutes and 19-126 individuals (mean = 41 individuals) were observed per species. These values were supplemented with published length-feeding rate relationships for Atlantic parrotfishes [98,99]. Size-specific bite dimensions (mm^2) were obtained from the literature [97,100–102].

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

Included covariates were oceanic productivity [103,104] (following the procedure described by Gove et al.[39] , we delimited a 100km buffer around each site, removed shallow waters pixels below 30m, and then calculated the average of monthly chlorophyll-a concentration using data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging Spectro-radiometer) for the years 2005-2010. Note that oceanic productivity has been found to influence coral reef fish communities in several other large-scale studies, but will be most influential in atoll and oceanic island settings), whether or not the reef is an atoll, census method used (i.e. standard belt transect, point count, distance sampling), sampled area, habitat type sampled (i.e., flat, slope, crest, backreef), depth category of the survey (i.e., <4m, 4-10 m, >10 m), Sea Surface Temperature anomalies (SST anom)[105], regional population growth (i.e., proportional difference between the population within a 100km buffer in 2000 and 2010), the nations reconstructed spatial reef fish landings[75,106] clipped to only include catches from reefs divided by the area of reef[107], national population size, national human development index[108], reserve size, reserve age, whether there were any active gear of effort restrictions in place for fished reefs (e.g., ban of certain gears or size limits) and market and nearest settlement gravities[64]. Market gravity was calculated as the population size of the nearest market (defined as a port, provincial capital, or large city) divided by the squared travel time[35] between the city and the reef [64]. Similarly, nearest settlement gravity was calculated as the population of the nearest human settlement to the reef divided by the squared travel time between the settlement and the reef [64] . The two gravity metrics were also broken up into their constituent metrics to better represent individual theories: travel time to the nearest market and the nearest settlement (i.e., agricultural location theory), and population size of the nearest market and the nearest settlement (i.e., Neo-Malthusianism) [30]. Note that: (i) before including these covariates, we checked that multicollinearity was not a concern (VIF<2); and (ii) in our data, the metric of HDI is correlated with other national metrics (e.g., gross domestic product or the Voice and Accountability governance metric[108]), which we did not include.

In contrast to previous work (e.g.,[30]), to account for the potential collinearity between management and reserve size and age (i.e., only reserves have age and size), we divided our model into two sub-model components: fished (a) and reserves (b) (i.e., i=a+b). Methodological, environmental and socio-economic effects sizes were jointly estimated from both sub-model components. However, effect sizes specific for a given sub-model component (i.e., effects of reserve age, reserve size and restrictions on fished reefs) were estimated only from their specific subset (that is, some parameter values were informed by the entire dataset but, where relevant, other parameters were informed only by one model component). Continuous covariates were standardized (subtracted their mean and divided by two standard deviations[109]) and categorical covariates were treated as dummy variables (1's and 0s). For each response variable we evaluated fourteen alternate models through leave-out-one cross-validation[110] (Tables S2-3): the null model (the model excluding all covariates; model 14); individual theories separately (whilst including sampling and environmental covariates; models 1-4); full models with no interactions between the theories (models 5 and 6, which differed only in that model 6 only included a linear function of HDI), and a series of full models that included select interactions between the theories, including between Agricultural Location Theory and neo-Malthusian in the form of a combined 'gravity' metric; models 7 and 8), interactions between Common Property Theory and neo-Malthusian to examine whether reserves have different effects depending on the surrounding population (model 9), interactions between Common Property Theory and Agricultural Location Theory to examine whether management has different effects depending their proximity to markets (model 10), interactions between neo-Malthusian, Agricultural Location Theory, and common property to examine whether management has different effects depending their surrounding populations AND proximity to markets (model 11-12), interactions between Common Property Theory and Environmental Kuznets Curve to examine whether management has different effects depending on the wealth (model 13) (Table S2). Note that during this model selection process, for each response variable, we removed observations (<5% of observations) that gave bad (i.e., >0.7) pareto-k diagnostic values (i.e., highly influential values in model selection[111]). Individual response variable model selection results are found in Table S3. Overall, summing all response variable’s leave one out information criteria (looic) for each candidate model, model selection results (Table S2) show that (i) models including covariates are always favored over the null model or individual theories separately; and (ii) model 7 (the HDI squared models with gravity) was favored as the best-fit overall model. Thus, we use model 7 in the main text and show best-fit models for each response variable (Fig. S1).

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

$$\log(B_a) \sim N(\mu_a, \sigma_a); \log(B_b) \sim N(\mu_b, \sigma_b) \tag{1}$$

$$\log(TD_a) \sim N(\mu_a, \sigma_a); \log(TD_b) \sim N(\mu_b, \sigma_b) \tag{2}$$

$$PA_a \sim Bernoulli\_logit(\mu_a); PA_b \sim Bernoulli\_logit(\mu_b) \tag{3}$$

$$if PS_a = 0,\ PS_a \sim bernouilli(\delta); if PS_b = 0,\ PS_b \sim bernouilli(\delta) \tag{4}$$

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

$$\mu_a = \beta_{0jka} + \beta_1 x_{deep,a} + \beta_2 x_{shallow,a} + \beta_3 x_{crest,a} + \beta_4 x_{lagoon/backreef,a} + \beta_5 x_{flat,a} + \beta_6 x_{point\ count,a} + \beta_8 x_{samplingarea,a} + \beta_9 x_{size,a} + \beta_{10} x_{age,a} + \beta_{11} x_{atoll,a} + \beta_{12} x_{prod,a} + \beta_{13} x_{SSTanom,a} + \beta_{14} x_{popgrowth,a} + \beta_{15} x_{marketgrav,a} + \beta_{16} x_{settlementgrav,a} + \beta_{17} x_{landings,a} + \beta_{18} x_{population,a} + \beta_{19} x_{hdi,a} + \beta_{20} x_{hdi^2,a} \tag{6}$$

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

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

$$\mu_b = \beta_{0jkb} + \beta_1 x_{deep,b} + \beta_2 x_{shallow,b} + \beta_3 x_{crest,b} + \beta_4 x_{lagoon/backreef,b} + \beta_5 x_{flat,b} + \beta_6 x_{point\ count,b} + \beta_7 x_{distancesampling,b} + \beta_8 x_{samplingarea,b} + \beta_{11} x_{atoll,b} + \beta_{12} x_{prod,b} + \beta_{13} x_{SSTanom,b} + \beta_{14} x_{popgrowth,b} + \beta_{15} x_{marketgrav,b} + \beta_{16} x_{settlementgrav,b} + \beta_{17} x_{landings,b} + \beta_{18} x_{population,b} + \beta_{19} x_{hdi,b} + \beta_{20} x_{hdi^2,b} + \beta_{21} x_{restrictions,b} \tag{9}$$

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

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

where the subscripts *a* and *b* represent the reserve and fished sites, respectively; the subscripts *j, k* represent the scale, reef cluster and nation/state, respectively; $\beta_{0..}$ represents the intercepts for either log biomass, log functional diversity, log parrotfish scraping potential (when>0) or log odds of observing a top predator; β… are the effect sizes (slopes) for the covariates *x*…, which are jointly estimated, where relevant, between the reserve and fished sub-models for each response variable; μ … are the expected site-specific mean log biomass, log functional diversity, log parrotfish scraping potential (when>0) or log odds of observing a top predator; δ is the probability of observing 0 parrotfish scraping potential; and $\sigma_{..}$ are the standard deviations. Model parameters were given weakly informative priors.

Analyses were performed in *Stan* using the Hamiltonian Monte Carlo algorithm implemented in RStan[112]. Four chains were run for each scenario, leaving 4000 samples in the posterior distribution of each parameter. Convergence was monitored by running four chains from different starting points, examining posterior chains and distribution for stability, checking that the potential scale reduction factor (also termed R_hat) was close to 1 and examining the effective sample sizes and rank plots . Model fit was examined by posterior predictive checks, checking residuals against fitted values and ensuring residuals had the expected distribution (Fig. S2).

References

1. Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E., and Caley, M.J. (2015). Species richness on coral reefs and the pursuit of convergent global estimates. Current Biology *25*, 500–505.

2. Woodhead, A.J., Hicks, C.C., Norström, A.V., Williams, G.J., and Graham, N.A. (2019). Coral reef ecosystem services in the Anthropocene. Functional Ecology *33*, 1023–1034.

3. Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., and Bridge, T.C. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science *359*, 80–83.

4. Newton, K., Côté, I.M., Pilling, G.M., Jennings, S., and Dulvy, N.K. (2007). Current and future sustainability of island coral reef fisheries. Current Biology *17*, 655–658.

5. Eddy, T.D., Lam, V.W., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Bruno, J.F., Ota, Y., and Cheung, W.W. (2021). Global decline in capacity of coral reefs to provide ecosystem services. One Earth *4*, 1278–1285.

6. Norström, A.V., Nyström, M., Jouffray, J., Folke, C., Graham, N.A., Moberg, F., Olsson, P., and Williams, G.J. (2016). Guiding coral reef futures in the Anthropocene. Frontiers in Ecology and the Environment *14*, 490–498.

7. Williams, G.J., Graham, N.A., Jouffray, J., Norström, A.V., Nyström, M., Gove, J.M., Heenan, A., and Wedding, L.M. (2019). Coral reef ecology in the Anthropocene. Functional Ecology *33*, 1014–1022.

8. Jouffray, J.-B., Wedding, L.M., Norström, A.V., Donovan, M.K., Williams, G.J., Crowder, L.B., Erickson, A.L., Friedlander, A.M., Graham, N.A., and Gove, J.M. (2019). Parsing human and biophysical drivers of coral reef regimes. Proceedings of the Royal Society B *286*, 20182544.

9. Donovan, M.K., Burkepile, D.E., Kratochwill, C., Shlesinger, T., Sully, S., Oliver, T.A., Hodgson, G., Freiwald, J., and van Woesik, R. (2021). Local conditions magnify coral loss after marine heatwaves. Science *372*, 977–980.

10. Darling, E.S., McClanahan, T.R., Maina, J., Gurney, G.G., Graham, N.A., Januchowski-Hartley, F., Cinner, J.E., Mora, C., Hicks, C.C., and Maire, E. (2019). Social–environmental

drivers inform strategic management of coral reefs in the Anthropocene. Nature ecology & evolution *3*, 1341–1350.

11. Pauly, D. (1990). On malthusian overfishing. Naga, the ICLARM quarterly *13*, 3–4.

12. McClanahan, T.R., Hicks, C.C., and Darling, E.S. (2008). Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecological applications *18*, 1516–1529.

13. Finkbeiner, E.M., Bennett, N.J., Frawley, T.H., Mason, J.G., Briscoe, D.K., Brooks, C.M., Ng, C.A., Ourens, R., Seto, K., and Switzer Swanson, S. (2017). Reconstructing overfishing: moving beyond Malthus for effective and equitable solutions. Fish and Fisheries *18*, 1180–1191.

14. Foale, S., Cohen, P., Januchowski-Hartley, S., Wenger, A., and Macintyre, M. (2011). Tenure and taboos: origins and implications for fisheries in the Pacific. Fish and fisheries *12*, 357–369.

15. Bellwood, D.R., Hoey, A.S., and Hughes, T.P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proceedings of the Royal Society B: Biological Sciences *279*, 1621–1629.

16. York, R., Rosa, E.A., and Dietz, T. (2003). STIRPAT, IPAT and ImPACT: analytic tools for unpacking the driving forces of environmental impacts. Ecological economics *46*, 351–365.

17. Boserup, E. (2011). The conditions of agricultural growth: The economics of agrarian change under population pressure (Transaction Publishers).

18. Geist, H.J., and Lambin, E.F. (2002). Proximate Causes and Underlying Driving Forces of Tropical Deforestation. BioScience *52*, 143–150.

19. York, R., Rosa, E.A., and Dietz, T. (2003). Footprints on the earth: The environmental consequences of modernity. American sociological review, 279–300.

20. Meyfroidt, P., Chowdhury, R.R., de Bremond, A., Ellis, E.C., Erb, K.-H., Filatova, T., Garrett, R., Grove, J.M., Heinimann, A., and Kuemmerle, T. (2018). Middle-range theories of land system change. Global Environmental Change *53*, 52–67.

21. Prates, L., and Perez, S.I. (2021). Late Pleistocene South American megafaunal extinctions associated with rise of Fishtail points and human population. Nature communications *12*, 1–11.

22. Lambin, E.F., Turner, B.L., Geist, H.J., Agbola, S.B., Angelsen, A., Bruce, J.W., Coomes, O.T., Dirzo, R., Fischer, G., and Folke, C. (2001). The causes of land-use and land-cover change: moving beyond the myths. Global environmental change *11*, 261–269.

23. VanWey, L.K., Ostrom, E., and Meretsky, V. (2005). Theories underlying the study of human-environment interactions. Seeing the forest and the trees: Human-environment interactions in forest ecosystems, 23–56.

24. Cinner, J.E., Graham, N.A., Huchery, C., and MacNeil, M.A. (2013). Global effects of local human population density and distance to markets on the condition of coral reef fisheries. Conservation Biology *27*, 453–458.

25. Stern, D.I. (2004). The rise and fall of the environmental Kuznets curve. World development *32*, 1419–1439.

26. Stevenson, T.C., and Tissot, B.N. (2014). Current trends in the analysis of co-management arrangements in coral reef ecosystems: a social–ecological systems perspective. Current Opinion in Environmental Sustainability *7*, 134–139.

27. Kellerman, A. (1989). Agricultural location theory, 2: Relaxation of assumptions and applications. Environment and Planning A *21*, 1427–1446.

28. Von Thunen, JH (1966). Isolated State (Oxford; London).

29. O'Kelly, M., and Bryan, D. (1996). Agricultural location theory: von Thunen's contribution to economic geography. Progress in Human geography *20*, 457–475.

30. Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., Barnes, M.L., Kittinger, J.N., and Hicks, C.C. (2018). Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences *115*, E6116–E6125.

31. Maire, E., D'agata, S., Aliaume, C., Mouillot, D., Darling, E.S., Ramahery, V., Ranaivoson, R., Randriamanantsoa, B., Tianarisoa, T.F., and Santisy, A. (2020). Disentangling the complex roles of markets on coral reefs in northwest Madagascar. Ecology and Society *25*.

32. McClanahan, T.R. (2020). Wilderness and conservation policies needed to avoid a coral reef fisheries crisis. Marine Policy *119*, 104022.

33. Campbell, S.J., Edgar, G.J., Stuart-Smith, R.D., Soler, G., and Bates, A.E. (2018). Fishing-gear restrictions and biomass gains for coral reef fishes in marine protected areas. Conservation Biology *32*, 401–410.

34. McDevitt-Irwin, J.M., Kappel, C., Harborne, A.R., Mumby, P.J., Brumbaugh, D.R., and Micheli, F. (2021). Coupled beta diversity patterns among coral reef benthic taxa. Oecologia *195*, 225–234.

35. Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., and Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. Ecology letters *19*, 351–360.

36. Anderson, J.E. (2011). The gravity model. Annu. Rev. Econ. *3*, 133–160.

37. Clausen, R., and York, R. (2008). Global biodiversity decline of marine and freshwater fish: a cross-national analysis of economic, demographic, and ecological influences. Social Science Research *37*, 1310–1320.

38. Cinner, J.E., McClanahan, T.R., Daw, T.M., Graham, N.A., Maina, J., Wilson, S.K., and Hughes, T.P. (2009). Linking social and ecological systems to sustain coral reef fisheries. Current Biology *19*, 206–212.

39. Ostrom, E. (1990). Governing the commons: The evolution of institutions for collective action (Cambridge university press).

40. Cinner, J.E., McClanahan, T.R., MacNeil, M.A., Graham, N.A., Daw, T.M., Mukminin, A., Feary, D.A., Rabearisoa, A.L., Wamukota, A., and Jiddawi, N. (2012). Comanagement of coral reef social-ecological systems. Proceedings of the National Academy of Sciences *109*, 5219–5222.

41. Cinner, J., Lau, J., Bauman, A., Feary, D., Januchowski-Hartley, F., Rojas, C., Barnes, M., Bergseth, B., Shum, E., and Lahari, R. (2019). Sixteen years of social and ecological dynamics reveal challenges and opportunities for adaptive management in sustaining the commons. Proceedings of the National Academy of Sciences *116*, 26474–26483.

42. McClanahan, T.R., Marnane, M.J., Cinner, J.E., and Kiene, W.E. (2006). A comparison of marine protected areas and alternative approaches to coral-reef management. Current biology *16*, 1408–1413.

43. Geels, F.W. (2009). Foundational ontologies and multi-paradigm analysis, applied to the socio-technical transition from mixed farming to intensive pig husbandry (1930–1980). Technology Analysis & Strategic Management *21*, 805–832.

44. Macneil, M.A. (2008). Making empirical progress in observational ecology. Environmental Conservation *35*, 193–196.

45. Heithaus, M.R., Frid, A., Wirsing, A.J., and Worm, B. (2008). Predicting ecological consequences of marine top predator declines. Trends in ecology & evolution *23*, 202–210.

46. Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., and Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science *315*, 1846–1850.

47. Ferretti, F., Curnick, D., Liu, K., Romanov, E.V., and Block, B.A. (2018). Shark baselines and the conservation role of remote coral reef ecosystems. Science Advances *4*, eaaq0333.

48. Goetze, J.S., Langlois, T.J., McCarter, J., Simpfendorfer, C.A., Hughes, A., Leve, J.T., and Jupiter, S.D. (2018). Drivers of reef shark abundance and biomass in the Solomon Islands. PloS one *13*, e0200960.

49. Letessier, T.B., Mouillot, D., Bouchet, P.J., Vigliola, L., Fernandes, M.C., Thompson, C., Boussarie, G., Turner, J., Juhel, J.-B., and Maire, E. (2019). Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. PLoS Biology *17*, e3000366.

50. Fenner, D. (2014). Fishing down the largest coral reef fish species. Marine pollution bulletin *84*, 9–16.

51. Dwyer, R.G., Krueck, N.C., Udyawer, V., Heupel, M.R., Chapman, D., Pratt Jr, H.L., Garla, R., and Simpfendorfer, C.A. (2020). Individual and population benefits of marine reserves for reef sharks. Current Biology *30*, 480–489.

52. MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., and Bond, M.E. (2020). Global status and conservation potential of reef sharks. Nature *583*, 801–806.

53. McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H., and Wilson, S.K. (2011). Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences *108*, 17230–17233.

54. Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S.J., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. Nature *506*, 216–220.

55. Mbaru, E.K., Graham, N.A., McClanahan, T.R., and Cinner, J.E. (2020). Functional traits illuminate the selective impacts of different fishing gears on coral reefs. Journal of Applied Ecology *57*, 241–252.

56. D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D.R., Cinner, J.E., Cowman, P.F., Kronen, M., Pinca, S., and Vigliola, L. (2014). Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. Current Biology *24*, 555–560.

57. Cinner, J.E., Zamborain-Mason, J., Gurney, G.G., Graham, N.A.J., MacNeil, M.A., Hoey, A.S., Mora, C., Villéger, S., Maire, E., McClanahan, T.R., et al. (2020). Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. Science *368*, 307–311.

58. D'agata, S., Vigliola, L., Graham, N.A., Wantiez, L., Parravicini, V., Villéger, S., Mou-Tham, G., Frolla, P., Friedlander, A.M., and Kulbicki, M. (2016). Unexpected high vulnerability of functions in wilderness areas: evidence from coral reef fishes. Proceedings of the Royal Society B: Biological Sciences *283*, 20160128.

59. Bellwood, D.R., Hoey, A.S., and Hughes, T.P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proceedings of the Royal Society B: Biological Sciences *279*, 1621–1629.

60. Mumby, P.J., Steneck, R.S., Roff, G., and Paul, V.J. (2021). Marine reserves, fisheries ban, and 20 years of positive change in a coral reef ecosystem. Conservation Biology.

61. Campbell, S.J., Darling, E.S., Pardede, S., Ahmadia, G., Mangubhai, S., and Maire, E. (2020). Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. Conservation Letters *13*, e12698.

62. Cinner, Je., and McClanahan, T. (2006). Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea. Environmental Conservation *33*, 73–80.

63. Brewer, T., Cinner, J., Green, A., and Pressey, R. (2013). Effects of human population density and proximity to markets on coral reef fishes vulnerable to extinction by fishing. Conservation Biology *27*, 443–452.

64. Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A., McClanahan, T.R., Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., and Mora, C. (2016). Bright spots among the world's coral reefs. Nature *535*, 416–419.

65. Laurance, W.F., Clements, G.R., Sloan, S., O'connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., and Balmford, A. (2014). A global strategy for road building. Nature *513*, 229–232.

66. Chayanov, A.V. (1986). AV Chayanov on the theory of peasant economy (Univ of Wisconsin Press).

67. Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., and Warner, R.R. (2009). Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series *384*, 33–46.

68. Folke, C., Kautsky, N., Berg, H., Jansson, Å., and Troell, M. (1998). The ecological footprint concept for sustainable seafood production: a review. Ecological Applications *8*, S63–S71.

69. Arrow, K., Bolin, B., Costanza, R., Dasgupta, P., Folke, C., Holling, C.S., Jansson, B.-O., Levin, S., Mäler, K.-G., and Perrings, C. (1995). Economic growth, carrying capacity, and the environment. Ecological economics *15*, 91–95.

70. Cumming, G.S., and von Cramon-Taubadel, S. (2018). Linking economic growth pathways and environmental sustainability by understanding development as alternate social–ecological regimes. Proceedings of the National Academy of Sciences *115*, 9533–9538.

71. York, R., and McGee, J.A. (2016). Understanding the Jevons paradox. Environmental Sociology *2*, 77–87.

72. Dinda, S. (2004). Environmental Kuznets curve hypothesis: a survey. Ecological economics *49*, 431–455.

73. Loring, P.A., Hinzman, M.S., and Neufeld, H. (2016). Can people be sentinels of sustainability? Identifying the linkages among ecosystem health and human well-being. Facets *1*, 148–162.

74. Robbins, P. (2019). Political ecology: A critical introduction (John Wiley & Sons).

75. Mol, A.P., and Spaargaren, G. (2000). Ecological modernisation theory in debate: A review. Environmental politics *9*, 17–49.

76. Steneck, R.S. (2009). Marine conservation: moving beyond Malthus. Current Biology *19*, R117–R119.

77. Pauly, D., and Zeller, D. (2015). Sea Around Us concepts, design and data. Vancouver, BC.

78. Williams, I., Walsh, W., Schroeder, R., Friedlander, A., Richards, B., and Stamoulis, K. (2008). Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. Environmental Conservation, 261–272.

79. Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O., and Brainard, R.E. (2015). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. PLoS One *10*, e0120516.

80. Allgeier, J.E., Valdivia, A., Cox, C., and Layman, C.A. (2016). Fishing down nutrients on coral reefs. Nature communications *7*, 1–5.

81. Ojeda, D., Sasser, J.S., and Lunstrum, E. (2020). Malthus's specter and the anthropocene. Gender, Place & Culture *27*, 316–332.

82. Haasnoot, M., Biesbroek, R., Lawrence, J., Muccione, V., Lempert, R., and Glavovic, B. (2020). Defining the solution space to accelerate climate change adaptation. Regional Environmental Change *20*, 1–5.

83. Lindsay, A.R., Sanchirico, J.N., Gilliland, T.E., Ambo-Rappe, R., Taylor, J.E., Krueck, N.C., and Mumby, P.J. (2020). Evaluating sustainable development policies in rural coastal economies. Proceedings of the National Academy of Sciences *117*, 33170–33176.

84. Cinner, J.E., Barnes, M.L., Gurney, G.G., Lockie, S., and Rojas, C. (2020). Markets and the crowding out of conservation-relevant behavior. Conservation Biology.

85. Gneezy, U., and Rustichini, A. (2000). Pay enough or don't pay at all. The Quarterly journal of economics *115*, 791–810.

86. Falk, A., and Szech, N. (2013). Morals and markets. science *340*, 707–711.

87. Bowles, S. (1998). Endogenous preferences: The cultural consequences of markets and other economic institutions. Journal of economic literature *36*, 75–111.

88. Rojas, C., and Cinner, J. (2020). Do market and trust contexts spillover into public goods contributions? Evidence from experimental games in Papua New Guinea. Ecological Economics *174*, 106661.

89. Wauchope, H.S., Amano, T., Geldmann, J., Johnston, A., Simmons, B.I., Sutherland, W.J., and Jones, J.P. (2020). Evaluating impact using time-series data. Trends in Ecology & Evolution.

90. Ajzen, I. (1991). The theory of planned behavior. Organizational behavior and human decision processes *50*, 179–211.

91. Chirot, D., and Hall, T.D. (1982). World-system theory. Annual Review of sociology *8*, 81–106.

92. Cox, M., Arnold, G., and Tomás, S.V. (2010). A review of design principles for community-based natural resource management. Ecology and Society *15*.

93. Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., and Geldmann, J. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. Nature *543*, 665–669.

94. Cramer, K.L., and Kittinger, J.N. (2021). Reef conservation off the hook: Can market interventions make coral reef fisheries more sustainable? Frontiers in Marine Science, 830.

95. Sandel, M.J. (2012). What money can’t buy: the moral limits of markets (Macmillan).

96. Froese, R., and Pauly, D. (2010). FishBase.

97. Chao, A., Chiu, C., Villéger, S., Sun, I., Thorn, S., Lin, Y., Chiang, J., and Sherwin, W.B. (2019). An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis) similarity measures. Ecological monographs *89*, e01343.

98. Hoey, A.S., and Bellwood, D.R. (2009). Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. Ecosystems *12*, 1316–1328.

99. Francini-Filho, R.B., Ferreira, C.M., Coni, E.O.C., De Moura, R.L., and Kaufman, L. (2010). Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. Marine Biological Association of the United Kingdom. Journal of the Marine Biological Association of the United Kingdom *90*, 481.

100. Bruggemann, J.H., Van Oppen, M.J., and Breeman, A.M. (1994). Foraging by the stoplight parrotfish Sparisoma viride. I. Food selection in different, socially determined habitats. Marine Ecology-Progress Series *106*, 41–41.

101. Bonaldo, R.M., and Bellwood, D.R. (2008). Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Marine Ecology Progress Series *360*, 237–244.

102. Ong, L., and Holland, K.N. (2010). Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size differences and fishery implications. Marine Biology *157*, 1313–1323.

103. Bruggemann, J.H., Van Kessel, A.M., Van Rooij, J.M., and Breeman, A.M. (1996). Bioerosion and sediment ingestion by the caribbean parrotfish Scarus vetula and Sparisoma viride: Implications of fish size, feeding mode and habitat use. Marine Ecology Progress Series *134*, 59–71.

104. Chassot, E., Bonhommeau, S., Dulvy, N.K., Mélin, F., Watson, R., Gascuel, D., and Le Pape, O. (2010). Global marine primary production constrains fisheries catches. Ecology letters *13*, 495–505.

105. Behrenfeld, M.J., and Falkowski, P.G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and oceanography *42*, 1–20.

106. Huang, B., Thorne, P., Banzon, V., Chepurin, G., Lawrimore, J., Menne, M., Smith, T., Vose, R., and Zhang, H. (2017). NOAA Extended Reconstructed Sea Surface Temperature (ERSST), Version 5.

107. Zeller, D., Palomares, M.D., Tavakolie, A., Ang, M., Belhabib, D., Cheung, W.W., Lam, V.W., Sy, E., Tsui, G., and Zylich, K. (2016). Still catching attention: Sea Around Us reconstructed global catch data, their spatial expression and public accessibility. Marine Policy *70*, 145–152.

108. UNEP-WCMC, and WRI (2010). Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project (United Nations Environmental Program World Conservation Monitoring Centre).

109. WorldBank (2015). Governance Indicators.

110. Gelman, A., and Hill, J. (2006). Data analysis using regression and multilevel/hierarchical models (Cambridge university press).

111. Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and computing *27*, 1413–1432.

112. Vehtari, A., Simpson, D., Gelman, A., Yao, Y., and Gabry, J. (2015). Pareto smoothed importance sampling. arXiv preprint arXiv:1507.02646.

113. Stan (2021). RStan: the R interface to Stan. R package version 2.17.3.

114. Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., and Bürkner, P.-C. (2020). Rank-normalization, folding, and localization: An improved $\widehat {R} $ for assessing convergence of MCMC. Bayesian Analysis.

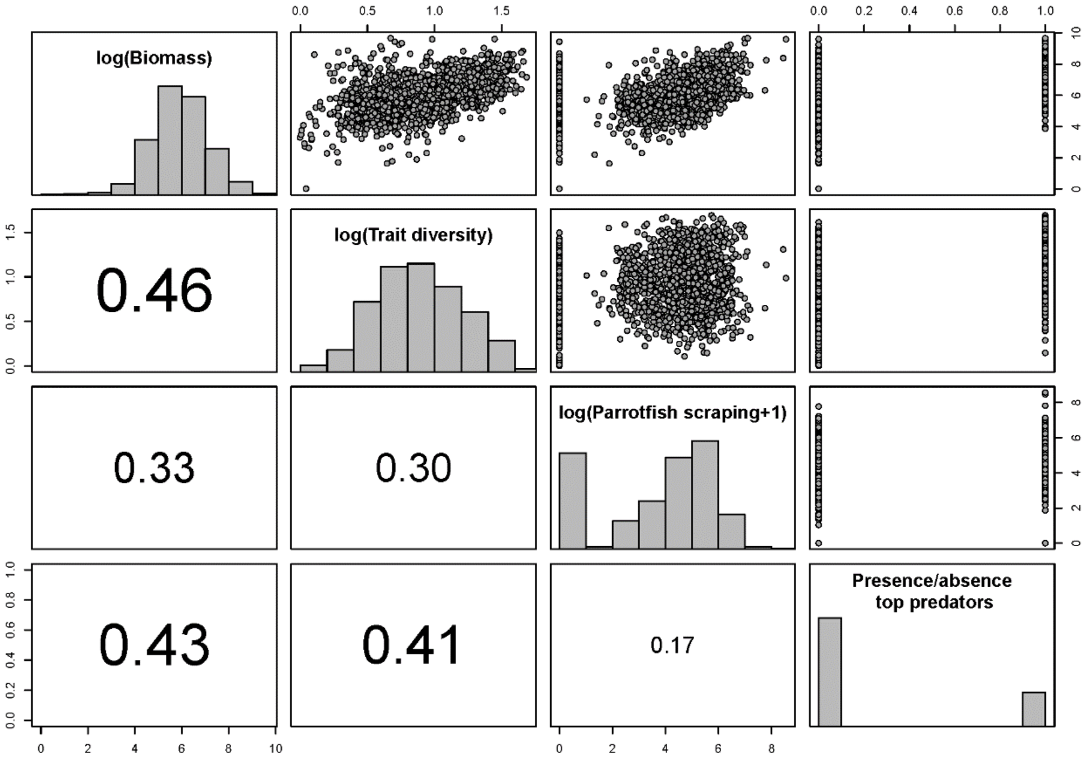
115. Network, C. for I.E.S.I. (2015). Gridded Population of the World, Version 4 (GPWv4): Population Count, Revision 11.

116. ESRI World cities.

117. Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., and Berkhout, J. (2014). Global conservation outcomes depend on marine protected areas with five key features. Nature *506*, 216–220.

118. Verburg, P.H., Ellis, E.C., and Letourneau, A. (2011). A global assessment of market accessibility and market influence for global environmental change studies. Environmental Research Letters *6*, 034019.

Supplementary Materials



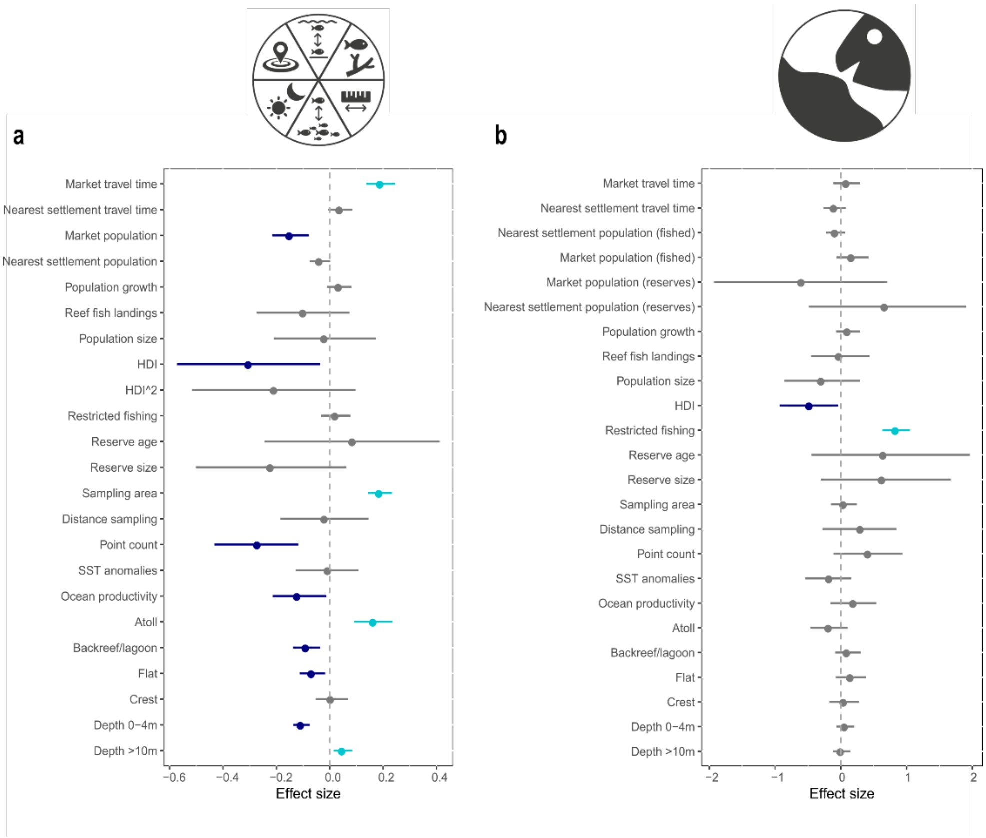


Fig. S1. Coefficient plots of best-fit individual models for functional diversity and parrotfish scraping potential. Points are the median effect sizes (i.e., slopes of the linear model). Error bars are 90% uncertainty intervals. Turquoise and blue symbols indicate that 90% of their posterior density in either a positive or negative direction, respectively. Note only functional diversity (a) and parrotfish scraping potential (b) are shown because the best-fit model for the other metrics is the overall best-fit model (Fig. 2).

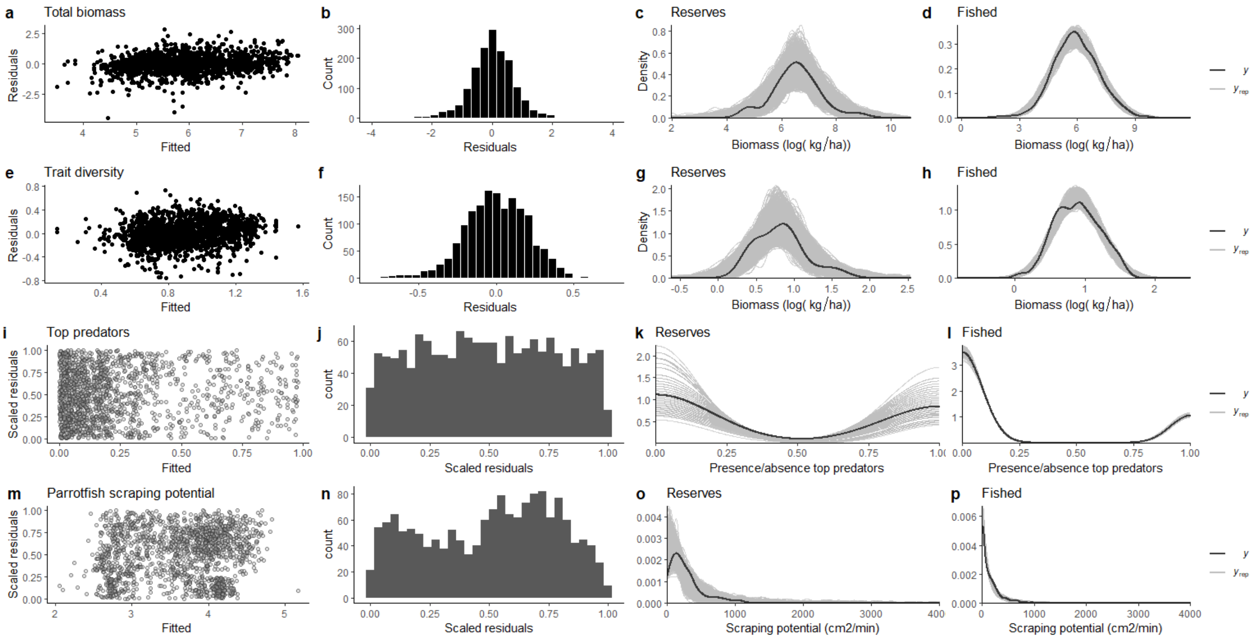


Fig. S2. Model fit statistics. Each row is a metric showing fitted vs residual values (first column), the residual distributions (second column), and densities of posterior simulations against observed metrics for the reserve (third column) and fished (fourth column) submodel components. For non-gaussian distributions (top predators and parrotfish scraping), residuals are scaled (Dharma).

Table S1. Description of socioeconomic predictor variables. Local scale means that there was a unique value for each site. National scale means there was one value per national jurisdiction.

Theoretical underpinnings	**Indicator**	**rationale**	**Measurement & scale**	**Source/ reference**
Neo-Malthusianism	Population of the nearest human settlement to the reef	Indicates the degree of subsistence pressure due to demand	Number of people; local scale	LandScan database
Neo-Malthusianism	Travel time between reef and the nearest human settlement	Indicates the degree of subsistence pressure on reefs due to proximity	Travel time (in minutes); local scale	[35]
Neo-Malthusianism	Nearest settlement gravity	Integrates both demand and proximity into a single metric	Number of people in nearest settlement/squared travel time between reef and settlement; local scale	LandScan database [64]
Neo-Malthusianism	Local population growth rate	Difference in local human population (i.e. 100km buffer around our reef clusters) between 2000-2010. Indicates demographic change pressures	People per year; local scale	Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database [17,115]
Neo-Malthusianism	Market size (population)	Indicates the degree of market pressure on reefs due to demand	Number of people; local scale	[116]
Neo-Malthusianism	National population size	National level demand and population pressure	Number of people; national scale	World Bank, census estimates, Wikipedia

Neo-Malthusianism	National reef fish landings	Gets at the total amount of fishing pressure at a national scale	Tons/year/km^2 of reef; national scale	[77,107,108]
Environmental Kuznets curve	Human Development Index (HDI)	A composite measure socioeconomic development based on life expectancy at birth, expected years of schooling, mean years of schooling, and gross national income.	We used linear and quadratic functions for HDI.; national scale	United Nations Development Program
New Institutionalist Economics	Type of management in place. Grouped into: a) marine reserve b) restricted fishing (i.e. size and effort limits) c) openly fished	The rules in use can influence the outcomes of commons governance	Nominal categories. Marine reserves were further separated into high or low compliance based on expert elicitation and low compliance reserves were discarded from the analyses; local scale	[64]
New Institutionalist Economics	Age of reserve	Indicates the length of time ecological conditions inside the reserve have had to recover	Years; local scale	[117]
New Institutionalist Economics	Size of no-take reserve	Larger reserves can support more fish	Km$^{2;}$ local scale	[117]
Agricultural location theory	Travel time between reef and nearest market (defined as	Indicates the degree of market pressure on	Travel time (in minutes); local scale	[28,35,118]

	provincial capital cities, major population centers, and ports)	reefs due to proximity		
Agricultural location theory	Market gravity	Integrates both demand and proximity into a single metric	Number of people in nearest market/squared travel time between reef and market; local scale	[36,64]

Table S2. Description of different models used, and their overall ranking based on the summed leave one out information criteria (Table S3). Note all models, except the null model, include sampling and environmental covariates. ALT= Agricultural Location Theory; NIE= New Institutionalist Economics; EKC = Environmental Kuznets Curve

Model number	Description	Overall rank (s LOOIC)
1	Only Malthusian variables included	12 (20710.3)
2	Only ALT variables included	10 (20650.6)
3	Only NIE variables included	11 (20706.2)
4	Only EKC variables included	13 (20747)
5	All Malthusian, ALT, NIE, and EKC variables included	3 (20569)
6	All Malthusian, ALT, NIE, and EKC variables included but only linear function of HDI	4 (20571.1)
7	All Malthusian, ALT, NIE, and EKC variables included, with 'interaction' between ALT and Malthusian in the form of an integrated gravity metric	**1 (20566.2)**
8	All Malthusian, ALT, NIE, and EKC variables included, with 'interaction' between ALT and Malthusian in the form of an integrated gravity metric, but only linear function of HDI	6 (20572)
9	All Malthusian, ALT, NIE, and EKC variables included, with interaction between Malthusian and CPT to test whether reserves have different effects depending on the nearby population	7 (20572.9)
10	All Malthusian, ALT, NIE, and EKC variables included, with interaction between ALT and NIEto test whether reserves have different effects depending on the nearby how far they are from markets	9 (20574.8)
11	All Malthusian, ALT, NIE, and EKC variables included, with interactions between ALT and NIEand between Malthusian and CPT	5 (20571.8)
12	All Malthusian, ALT, NIE, and EKC variables included, with interactions between Malthusian and ALT and NIEin the form of the gravity metric interacting with management	8 (20572.9)
13	All Malthusian, ALT, NIE, and EKC variables included, with interactions between NIE and HDI to test whether reserves are more effective in wealthier countries	2 (20567.5)
14	Null model	14 (23497.7)

Table S3: Model selection results from leave-out-one cross validation. Columns represent the expected log predictive density difference (elpd_diff), its standard error (se_diff), the leave out one information criteria (looic), its standard error (se_looic). Model refers to model number on table S2.

Response	Model	elpd_diff	se_diff	looic	se_looic
Top Predators	7	0.00	0.00	1211.90	46.76
Top Predators	8	-0.04	0.81	1211.98	46.66
Top Predators	5	-0.38	1.65	1212.65	47.15
Top Predators	13	-0.74	1.70	1213.38	47.15
Top Predators	11	-1.02	1.93	1213.94	47.03
Top Predators	6	-1.12	1.88	1214.14	47.00
Top Predators	2	-1.25	3.43	1214.40	46.05
Top Predators	12	-1.32	0.83	1214.54	46.66
Top Predators	9	-1.47	1.94	1214.84	47.02
Top Predators	10	-1.70	1.94	1215.29	47.01
Top Predators	1	-19.65	6.06	1251.19	47.46
Top Predators	4	-22.72	6.69	1257.34	46.91
Top Predators	3	-23.94	6.64	1259.77	46.80
Top Predators	14	-234.25	20.27	1680.39	39.34
Biomass	7	0.00	0.00	3652.43	60.98
Biomass	12	-0.80	0.76	3654.03	60.68
Biomass	13	-1.48	1.23	3655.38	60.76
Biomass	10	-1.80	1.48	3656.03	60.82
Biomass	5	-2.00	1.25	3656.43	60.79
Biomass	8	-2.23	0.77	3656.90	60.79
Biomass	9	-2.58	1.41	3657.58	60.83
Biomass	6	-2.62	1.41	3657.68	60.63
Biomass	11	-2.69	1.45	3657.81	60.73
Biomass	2	-12.84	3.45	3678.10	61.13
Biomass	1	-18.26	4.42	3688.94	61.42
Biomass	3	-21.97	4.84	3696.37	61.04
Biomass	4	-25.29	5.23	3703.01	61.45
Biomass	14	-463.46	24.72	4579.34	50.49
Trait Diversity	5	0.00	0.00	-30.40	51.53
Trait Diversity	8	-0.45	1.05	-29.50	51.51
Trait Diversity	7	-0.45	0.96	-29.49	51.51
Trait Diversity	13	-0.49	0.59	-29.41	51.43
Trait Diversity	11	-0.56	0.74	-29.29	51.44
Trait Diversity	6	-0.78	0.65	-28.85	51.51

Trait Diversity	12	-1.00	1.07	-28.41	51.50
Trait Diversity	9	-1.53	0.80	-27.35	51.64
Trait Diversity	10	-2.52	0.70	-25.36	51.55
Trait Diversity	2	-10.85	3.61	-8.70	51.52
Trait Diversity	1	-19.86	5.05	9.33	51.93
Trait Diversity	4	-25.75	6.20	21.11	51.89
Trait Diversity	3	-26.06	6.06	21.72	51.75
Trait Diversity	14	-433.62	23.90	836.85	44.48
Parrotfish scraping	9	0.00	0.00	15727.84	181.12
Parrotfish scraping	13	-0.17	0.66	15728.17	181.12
Parrotfish scraping	6	-0.17	0.62	15728.18	181.09
Parrotfish scraping	3	-0.25	2.01	15728.34	181.40
Parrotfish scraping	10	-0.52	0.80	15728.88	181.13
Parrotfish scraping	11	-0.77	0.54	15729.37	181.16
Parrotfish scraping	5	-1.22	0.63	15730.28	181.16
Parrotfish scraping	7	-1.95	1.64	15731.73	181.36
Parrotfish scraping	8	-2.38	1.62	15732.60	181.32
Parrotfish scraping	12	-2.46	1.66	15732.76	181.32
Parrotfish scraping	1	-16.50	4.97	15760.83	181.57
Parrotfish scraping	4	-18.83	5.60	15765.50	181.83
Parrotfish scraping	2	-19.50	5.50	15766.85	181.71
Parrotfish scraping	14	-336.62	21.00	16401.08	186.99