CORAL REEFS

Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world

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The worldwide decline of coral reefs necessitates targeting management solutions that can sustain reefs and the livelihoods of the people who depend on them. However, little is known about the context in which different reef management tools can help to achieve multiple social and ecological goals. Because of nonlinearities in the likelihood of achieving combined fisheries, ecological function, and biodiversity goals along a gradient of human pressure, relatively small changes in the context in which management is implemented could have substantial impacts on whether these goals are likely to be met. Critically, management can provide substantial conservation benefits to most reefs for fisheries and ecological function, but not biodiversity goals, given their degraded state and the levels of human pressure they face.

At the forefront of ongoing efforts to sustain coral reef ecosystems in the current period of intense social and environmental change is an increasing need to simultaneously manage for multiple goals, including fisheries, ecosystem functioning, and biodiversity (*1*, *2*). However, critical gaps remain in our capacity to effectively implement this type of ecosystem-based management approach in which multiple goals are pursued simultaneously (*3*). In particular, little is known about the context under which key goals can be simultaneously met and the degree to which local management efforts can help to meet them.

Here, we compiled data from ~1800 tropical reef sites across 41 countries, states, and territories to examine the conditions under which reefs simultaneously support three ecological metrics reflecting key fisheries, ecological function, and biodiversity goals (*4*) (Fig. 1 and tables S1 and S2). These are, respectively: (i) potential stocks available for multispecies coral reef fisheries, calculated as the biomass of fishes >20 cm in total length (*4*) (Fig. 1 and table S2); (ii) scraping potential, reflecting a specialized ecological function performed by parrotfish that is critical for the removal of algal biomass and the provision of bare substrate for coral settlement (*4*, *5*) (table S2); and (iii) the diversity of species traits (i.e., home range, body size, diet, diurnal activity, schooling behavior, and position in the water column), which can underpin aspects of biodiversity such as community assembly processes, ecosystem productivity, and stability (*6*). We measured trait diversity using a generalization of the Shannon entropy index accounting for both the dissimilarity of trait values present in a reef fish community and the spread of biomass across these trait values (*4*, *7*) (table S2). Our analysis shows that the three metrics are not strongly related to each other ($r < 0.54$; fig. S1).

To elucidate the capacity of reefs to simultaneously support multiple goals, we first developed reference conditions for each metric to serve as benchmarks. Reference conditions (also called reference points) are a key concept in fisheries and conservation (*8*, *9*) but are nascent in coral reef science (*10*). As key reference conditions, we used the top 10% value for each metric (corrected for sampling) but also included additional reference conditions (i.e., the top 5 and 20%) in the supplementary materials (*4*). We then set aspirational targets of 25, 50, and 75% of reference conditions. When looking at these aspirational targets across multiple goals, we found that only 5% of reef sites simultaneously had fish biomass, parrotfish scraping, and trait diversity at 75% of reference conditions (Fig. 1D). These sites, although reasonably rare, were geographically spread through the Indian, Pacific, and Atlantic Ocean basins (Fig. 1D). We found that 12.5% of sites simultaneously met the 50% target, and 29.3% of sites met the 25% target (Fig. 1D)

To examine the context under which key goals can be met, we first developed a series of Bayesian hierarchical models that quantify how the three ecological metrics are related to key socioeconomic drivers of resource exploitation while controlling for environmental conditions and sampling techniques (*4*, *11*, *12*) (fig. S2 and table S3). We then used the posterior distributions from these models to calculate how the probability of simultaneously meeting multiple goals changes along a gradient of human pressure while holding other covariates constant (*4*) (Fig. 2 and figs. S3 and S4). We measured human pressure as the size of human populations in the surrounding seascape divided by the accessibility (in minutes of travel time squared) of our reef sites to them, an adaptation of the economic gravity model used to measure the "gravitational pull" of interactions such as trade and migration (*4*, *13*). Human pressure displayed the most consistent negative relationships to our response variables (fig. S2). The distribution of human pressure and other key socioeconomic and environmental covariates among our surveyed reefs closely matched that of reefs globally (fig. S5). The probability of openly fished reef sites simultaneously having all three metrics declined with our measure of human pressure and the ambitiousness of the conservation target (Fig. 2A). In other words, on openly fished reefs, it is extremely unlikely that all three goals will be simultaneously met where human pressure is intense but this likelihood increases where human pressure is low, particularly for the 25 and 50% targets. There was considerable variability in how the probability of meeting individual goals changed along a gradient of human pressure (Fig. 2, B to D).

A critical gap remains in understanding the context in which different local management tools can help to simultaneously achieve key goals (*14*, *15*). To address this, we first examined the probability of reef sites in both fully protected Marine Protected Areas (MPAs) (where fishing is prohibited) and restricted fishing areas (where there are limitations on the fishing gear used and who can access the fishing grounds) in achieving key targets for the individual and combined ecological metrics (Fig. 2, E to L). We then calculated the conservation gains from using these different forms of management along a gradient of human pressure (*15*) (Fig. 2, M to X). By "conservation

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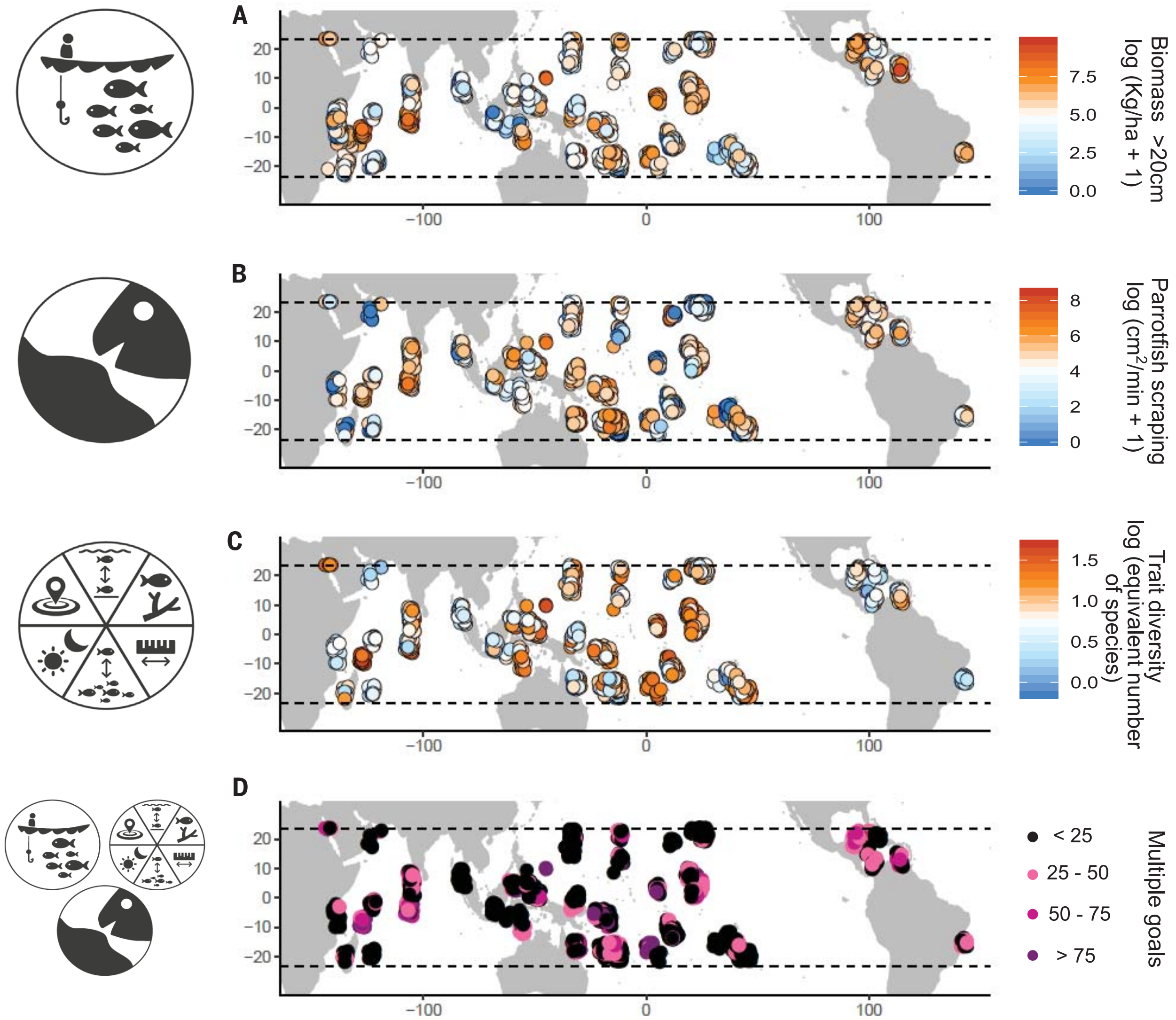

Fig. 1. Meeting multiple goals on coral reefs. Shown is the distribution of (**A**) the biomass of reef fish >20 cm (*n* =1798), (**B**) the parrotfish scraping potential (*n* = 1662), and (**C**) the trait diversity (*n* = 1662), all in natural log and corrected for sampling (*4*). Differences in the number of sites are because one data provider collected data at the family level, which could not be used in calculating parrotfish scraping potential or trait diversity. Parrotfishes were not detected at 31% of our reef sites (fig. S1). (**D**) Sites that simultaneously have fish biomass, parrotfish scraping potential, and trait diversity at >75% (purple), 50 to 75% (dark pink), 25 to 50% (light pink), and <25% (black) of reference conditions (*4*). Points are jittered to allow for visualization of overlapping reef sites.

gains," we refer to the difference in probability of achieving a specific target (e.g., 25% of reference condition biomass) when fully protected MPAs or fishery restrictions are implemented relative to openly fished areas. This concept addresses the idea that contexts with maximal conservation gains highlight the best opportunities for management to have the biggest impact; conversely, implementing management in contexts with minimal conservation gains (either because goals are already being met or because they are unlikely to be met regardless of management) provides few returns for limited conservation resources (*16*).

Critically, we found that both fully protected MPAs and restricted fishing areas have the potential to provide conservation gains but the context under which these gains can be maximized is highly variable depending on both the goal and target (Fig. 2, M to X). For simultaneously meeting fisheries, function, and biodiversity, maximal conservation gains are from fully protected MPAs in the lowest human pressure locations for the most ambitious target (75% of reference conditions) but as targets become less ambitious, conservation gains peak where human pressure is more intermediate (Fig. 2M). For all three targets, there are minimal conservation gains in locations where human pressure is most intense, which means that in this context, management is unlikely to help meet these goals. For each independent goal, the context under which conservation gains can be maximized varies considerably (Fig. 2). Trait diversity is the least responsive to management, with conservation gains never reaching above 0.4.

We then simulated how the number of our openly fished sites achieving key conservation targets would change if a fully protected MPA (Fig. 3) or fisheries restrictions (Fig S6) were implemented, given the other conditions at our reef sites. Our analysis reveals both key opportunities and constraints in the capacity for local management to simultaneously meet multiple goals. For >50% of our fished sites, the implementation of a fully protected MPA is predicted to help achieve multiple goals (Fig. 3A). Conversely, <1% of the sites starting below 25% of reference conditions are predicted to achieve the 75% of reference conditions target,

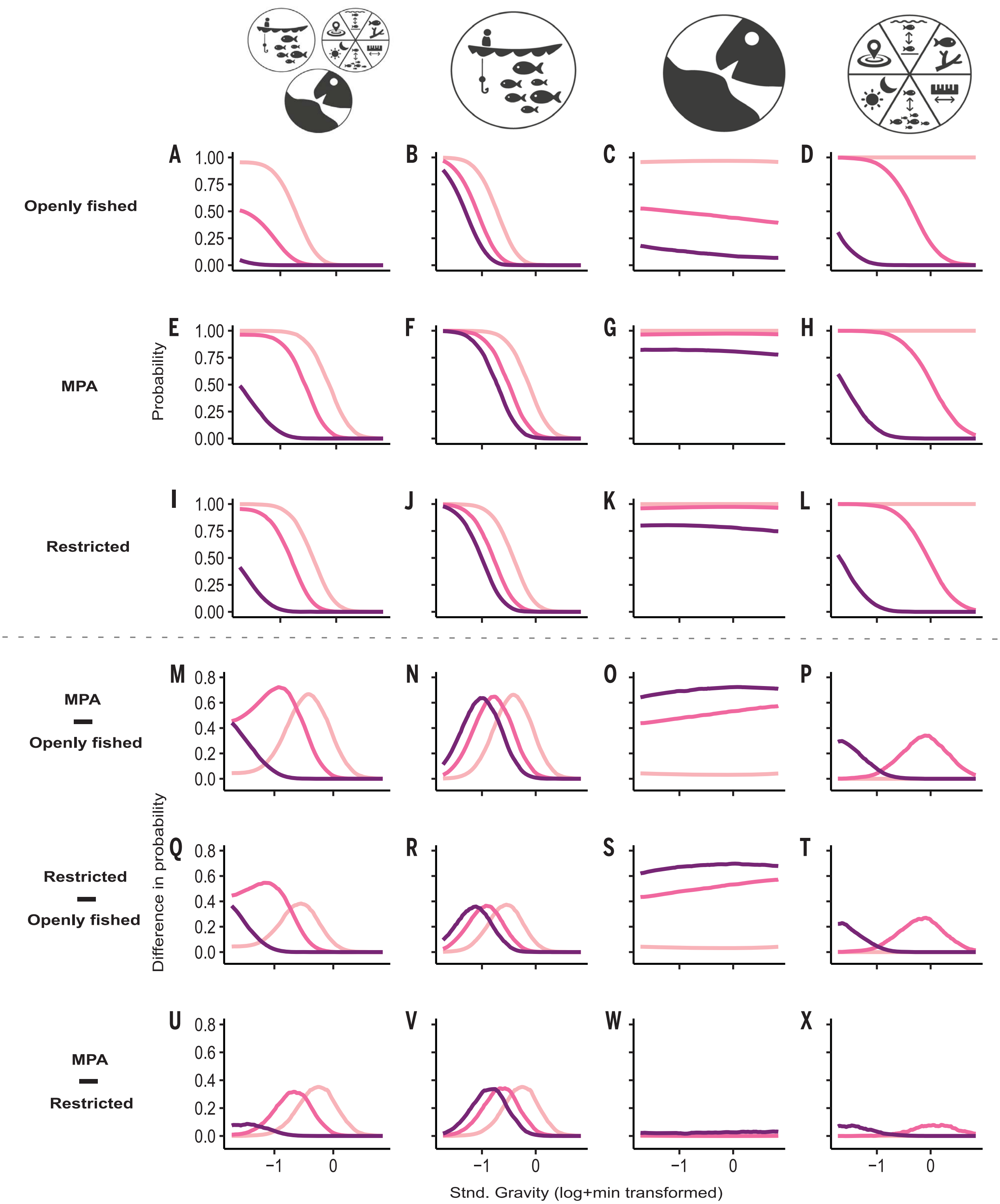

Fig. 2. Estimated probability of reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively). Shown are the combination of fish biomass (>20 cm), parrotfish scraping potential, and trait diversity (**A**) and each metric (**B** to **D**, respectively) for openly fished sites along a gradient of human pressure (gravity). Separate estimates are provided for reef sites in fully protected MPAs, where fishing is prohibited (**E** to **H**), and with restricted fishing (**I** to **L**). To highlight how the potential benefits of management change along a gradient of human pressure (gravity), we extracted the difference in the probability of achieving each target between MPAs and openly fished sites (**M** to **P**), restricted and openly fished areas (**Q** to **T**), and MPAs and restricted areas (**U** to **X**). We plotted the partial effect of the relationship between gravity and each target by setting all other continuous covariates to 0 (because they were all standardized) and all categorical covariates to their most common category (i.e., 4 to 10 m for depth, slope for habitat, standard belt transect for census method). Gravity (*x* axis) is standardized, with an average of 0.

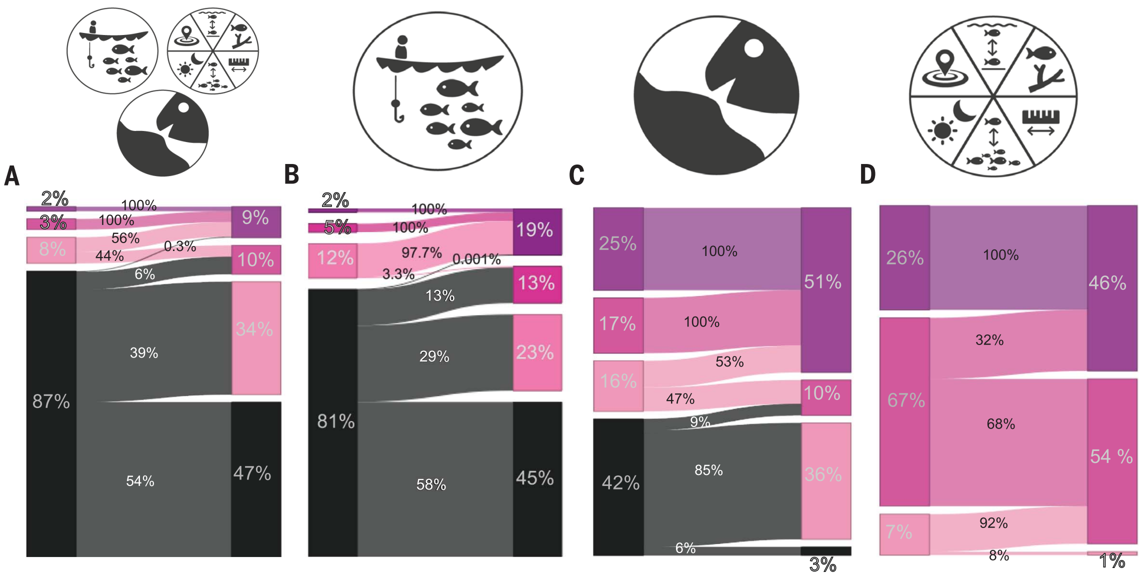

Fig. 3. Conservation target outcomes from simulating the implementation of fully protected MPAs in openly fished sites. Alluvial plots show the change in the number of sites expected to achieve key conservation targets if MPAs were implemented in our openly fished sites for (**A**) simultaneously meeting fish biomass, parrotfish scraping potential, and trait diversity and (**B** to **D**) each goal, respectively. The left side of each plot shows the current conditions and the right side shows the expected conditions if MPAs were implemented. Black, <25%; light pink, 25 to 50%; dark pink, 50 to 75%; and purple, >75% of reference conditions.

highlighting how the broader seascape context may stunt MPA potential in degraded reefs (*15*). Indeed, more than half of the 87.4% of openly fished reefs starting at <25% of reference conditions are predicted to remain in that same category (Fig. 3A). Additionally, our analysis showed that even where fishable biomass is very low, scraping potential and trait diversity are often >25% of reference conditions (Fig. 3, B to D), a finding supported by previous research showing that herbivores and a diversity of traits can still persist on degraded reefs (*17*).

In situations in which fishing prohibitions are in direct conflict with achieving certain fisheries goals, other forms of management may be necessary (*18*). We found that fisheries restrictions provide a similar, but typically lower magnitude, pattern of conservation gains than fully protected MPAs, particularly for achieving the combined goal and fisheries goal (Fig. 2, Q to X, and fig S6). For parrotfish scraping potential, fishing restrictions provide the same conservation gains as MPAs, providing multiple ways to achieve that specific goal (Fig. 2W).

Our findings provide guidance on what can be realistically achieved with various forms of local management regarding key fisheries, ecological function, and biodiversity goals on coral reefs. We highlight key pros and cons of placing management in different areas by demonstrating how potential conservation gains not only vary by goal, but are also strongly dependent on both the ambitiousness of the target and the context (Fig. 2 and figs. S3 and S4). In particular, the potential for local management to help in meeting goals is strongly related to the amount of human pressure in the surrounding seascape (Fig. 2 and S2). A key finding is that conservation gains tend to change nonlinearly with human pressure, which means that relatively small changes in the context in which management is implemented could have big impacts on whether key goals are likely to be met (Fig. 2, M to X). This not only has important implications for the placement of new MPAs, but is also relevant to how future socioeconomic changes such as infrastructure development and population growth may affect the efficacy of reef conservation. However, the impacts of these changes could potentially be buffered by making management more effective, for example, by leveraging insights about using social norms and cognitive biases to improve compliance (*19*, *20*) and learning lessons about key practices and processes from locations that have defied expectations of global reef degradation (*12*, *21*). Our global analysis makes clear the limitations of local management, especially in promoting certain aspects of biodiversity such as trait diversity. Although international action on climate change will be crucial for ensuring a future for coral-dominated reefs (*1*, *2*), effective management will also be crucial for sustaining reefs and the millions of livelihoods that depend on them.

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ACKNOWLEDGMENTS

We thank S. Pardede and Blue Ventures for data contributions. **Funding:** J.E.C. is supported by the Australian Research Council (CE140100020, FT160100047), the Pew Charitable Trust, and the CGIAR Research Program on Fish Agri-Food Systems (FISH) led by WorldFish. N.A.J.G. is supported through a Royal Society University Research Fellowship (UF140691). This research was partly funded through the 2017-2018 Belmont Forum and BiodivERsA REEF-FUTURES project under the BiodivScen ERA-Net COFUND program and with the funding organizations ANR, DFG, NSF, and NSERC. This study has been partly funded by the PRISTINE and APEX Total Foundation, Government of New Caledonia projects, and associated French Oceanographic Cruises (https://doi.org/10.17600/14004500, https://doi.org/10.17600/14003600, https://doi.org/10.17600/13100060, and https://doi.org/10.17600/13100070). **Author contributions:** J.E.C. conceived of the study with support from D.M., C.M., E.M., N.A.J.G., T.R.M., J.N.K., C.C.H., M.L.B., M.A.M., and C.C.H.; J.Z.-M., G.G.G., J.E.C., D.M., and E.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. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Data are permanently archived on the James Cook University Tropical Data Hub (*22*) and the code is archived at Zenodo (*23*).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/368/6488/307/suppl/DC1
Materials and Methods
Tables S1 to S7
Figs. S1 to S4
References (*24*–*59*)

13 May 2019; accepted 18 March 2020
10.1126/science.aax9412

Science

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Science **368** (6488), 307-311.
DOI: 10.1126/science.aax9412

A complex landscape for reef management

Coral reefs are among the most biodiverse systems in the ocean, and they provide both food and ecological services. They are also highly threatened by climate change and human pressure. Cinner *et al.* looked at how best to maximize three key components of reef use and health: fish biomass, parrotfish grazing, and fish trait diversity. They found that when human pressure is low, all three traits can be maximized at high conservation levels. However, as human use and pressure increase, it becomes increasingly difficult to promote biodiversity conservation. At some levels of human impact, even the highest amount of protection is not able to maximize biodiversity conservation.

Science, this issue p. 307

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