1    Title:

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

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5    **One sentence summary:** Simultaneously meeting fisheries, ecosystem
6    function, and biodiversity goals for coral reefs is possible through strategically
7    placed marine reserves and fisheries restrictions.

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10   **Authors:** Joshua E. Cinner[1,*], Jessica Zamborain-Mason[1], Georgina G. Gurney[1] ,

11   Nicholas A.J. Graham[1,2], M. Aaron MacNeil[3], Andrew S. Hoey[1], Camilo Mora[4],

12   Sébastien Villéger[5], Eva Maire[1,2,5], Tim R. McClanahan[6], Joseph M. Maina[6,7],

13   John N. Kittinger[8,9], Christina C. Hicks[1,2], Stephanie D'agata[5,6,7], Cindy Huchery[1]

14   , Michele L. Barnes[1], David A. Feary[11], Ivor D. Williams[12], Michel Kulbicki[13],

15   Laurent Vigliola[10], Laurent Wantiez [14], Graham J. Edgar[15], Rick D. Stuart-

16   Smith[15], Stuart A. Sandin[16], Alison L. Green[17], Maria Beger[18,19], Alan M.

17   Friedlander[20,21], Shaun K. Wilson[22,23], Eran Brokovich[24], Andrew J. Brooks[25],

18   Juan J. Cruz-Motta[26], David J. Booth[27], Pascale Chabanet[28], Mark Tupper[29],

19   Sebastian C.A. Ferse[30,31], U. Rashid Sumaila[32], Marah J. Hardt[33, 34], David

20   Mouillot[1,6]

21

22   **Affiliations:**

[1]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811 Australia

[2] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

[3]Department of Biology, Dalhousie University, Halifax, NS B3H 3J5 Canada

[4]Department of Geography, University of Hawai'i at Manoa, Honolulu, Hawai'i 96822 USA

[5]MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Montpellier, France.

[6]Wildlife Conservation Society, Global Marine Program, Bronx, NY 10460 USA

[7] Department of Environmental Sciences, Macquarie University, North Ryde, NSW 2109 Australia

[8]Conservation International, Center for Oceans & Betty and Gordon Moore Center for Science, Honolulu, HI 96825 USA

[9] Arizona State University, Center for Biodiversity Outcomes, Julie Ann Wrigley Global Institute of Sustainability, Tempe AZ 85281 USA

[10]Institut de Recherche pour le Développement, UMR IRD-UR-CNRS ENTROPIE, Laboratoire d'Excellence LABEX CORAIL, BP A5, 98848 Nouméa Cedex, New Caledonia

[11]MRAG Ltd, London W1J 5PN, UK

[12]Ecosystem Science Division, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI 96818 USA

[13]UMR Entropie, Labex Corail, –IRD, Université de Perpignan, 66000, Perpignan, France

[14]University of New Caledonia, BPR4 98851 Noumea cedex, New Caledonia

[15]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001 Australia

[16]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093 USA

[17]The Nature Conservancy, 48 Montague Road, South Brisbane, QLD. 4101. Australia

[18] School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, West Yorkshire LS2 9JT, United Kingdom

[19] Centre for Biodiversity and Conservation Science, University of Queensland, Brisbane, Queensland 4072, Australia

[20]National Geographic Society, Pristine Seas Program, 1145 17th Street N.W. Washington, D.C. 20036-4688, USA

[21]Fisheries Ecology Research Lab, Department of Biology, University of Hawaii, Honolulu, HI 96822, USA

[22]Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia

62 [23]Marine Science Program, Department of Biodiversity, Conservation and
63 Attractions, Kensington, Perth WA 6151 Australia
64 [24] Natural Resources Administration, Ministry of Energy, Bank Israel 7
65 Jerusalem, Israel
66 [25]Marine Science Institute, University of California, Santa Barbara, CA 93106-
67 6150, USA
68 [26]Departamento de Ciencias Marinas., Recinto Universitario de Mayaguez,
69 Universidad de Puerto Rico, 00680, Puerto Rico
70 [27]School of Life Sciences, University of Technology Sydney 2007 Australia
71 [28] UMR ENTROPIE, IRD-Université de La Réunion-CNRS, LABEX CORAIL, CS
72 41095, 97495 Sainte Clotilde, La Réunion (FR)
73 [29]ACCORD, Centre for Maritime and Ocean Studies, The University of Trinidad
74 and Tobago, 2nd Avenue North, Western Main Road, Chaguaramas, Trinidad
75 and Tobago
76 [30]Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstrasse 6, D-
77 28359 Bremen, Germany
78 [31]Department of Marine Ecology, Faculty of Biology and Chemistry (FB2),
79 University of Bremen, Bibliothekstrasse 1, D-28359 Bremen, Germany
80 [32]Fisheries Economics Research Unit, Institute for the Oceans and
81 Fisheries/Liu Institute for Global Issues, University of British Columbia, 2202
82 Main Mall, Vancouver, B.C., V6T 1Z4, Canada
83 [33]Future of Fish, Bethesda, MD, 20814, USA
84 [34]OceanInk LLC, Lafayette, CO, USA
85
86 *Correspondence to:  Joshua.cinner@jcu.edu.au
87

## Abstract:

The worldwide decline of coral reefs necessitates targeting management

solutions that can sustain not only reefs but also the livelihoods of the millions

of people who depend on them. Yet little is known about the context in which

different reef management tools can help to achieve multiple social and

ecological goals. Due to non-linearities in the likelihood of achieving combined

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94   fisheries, ecological function, and biodiversity goals along a gradient of human

95   pressure, relatively small changes in the context where management is

96   implemented could have dramatic implications on whether these goals are

97   likely to be met or not. Critically, marine reserves and fisheries restrictions

98   could provide substantial conservation benefits to the majority of reefs for

99   fisheries and ecological function, but not biodiversity goals.

100

**Main Text:**

102  At the forefront of ongoing efforts to sustain coral reef ecosystems in the

103  current period of intense social and environmental change is an increasing

104  need to simultaneously manage for multiple goals, including fisheries,

105  ecosystem functioning, and biodiversity (*1–3*). Yet, critical gaps remain in our

106  capacity to effectively implement this type of ecosystem-based management

107  approach, where multiple goals are simultaneously pursued (*4*). In particular,

108  little is known about: (i) the context under which key goals can be

109  simultaneously met, and (ii) the degree to which local management efforts can

110  help to meet them.

111

112   Here, we compiled data from ~1800 tropical reef sites across 41 countries,

113   states, and territories to examine the conditions under which reefs

114   simultaneously support three ecological metrics reflecting key fisheries,

115   ecological function, and biodiversity goals (Fig. 1, Tables S1-2, Methods). These

116   are, respectively: (1) potential stocks available for multi-species coral reef

117   fisheries, calculated as the biomass of fishes >20 cm total length (Fig. 1,

118   Methods, Table S2); (2) scraping potential, reflecting a unique ecological

119   function performed by parrotfish that is critical for the removal of algal biomass

120   and the provision of bare substrate for coral settlement (*5*, *6*) (Table S2;

121   Methods); and (3) the diversity of species traits (i.e. home range, body size, diet,

122   diurnal activity, schooling behavior, position in the water column), which can

123   underpin aspects of biodiversity such as community assembly processes,

124   ecosystem productivity, and stability (*7*). We measured trait diversity using a

125   generalization of the Shannon entropy index accounting for both the

126   dissimilarity of trait values present in a reef fish community and the spread of

127   biomass across these trait values (*8*) (Methods, Table S2). Our analysis shows

128   that the three metrics are not strongly related to each other (r<0.54; Fig S1).

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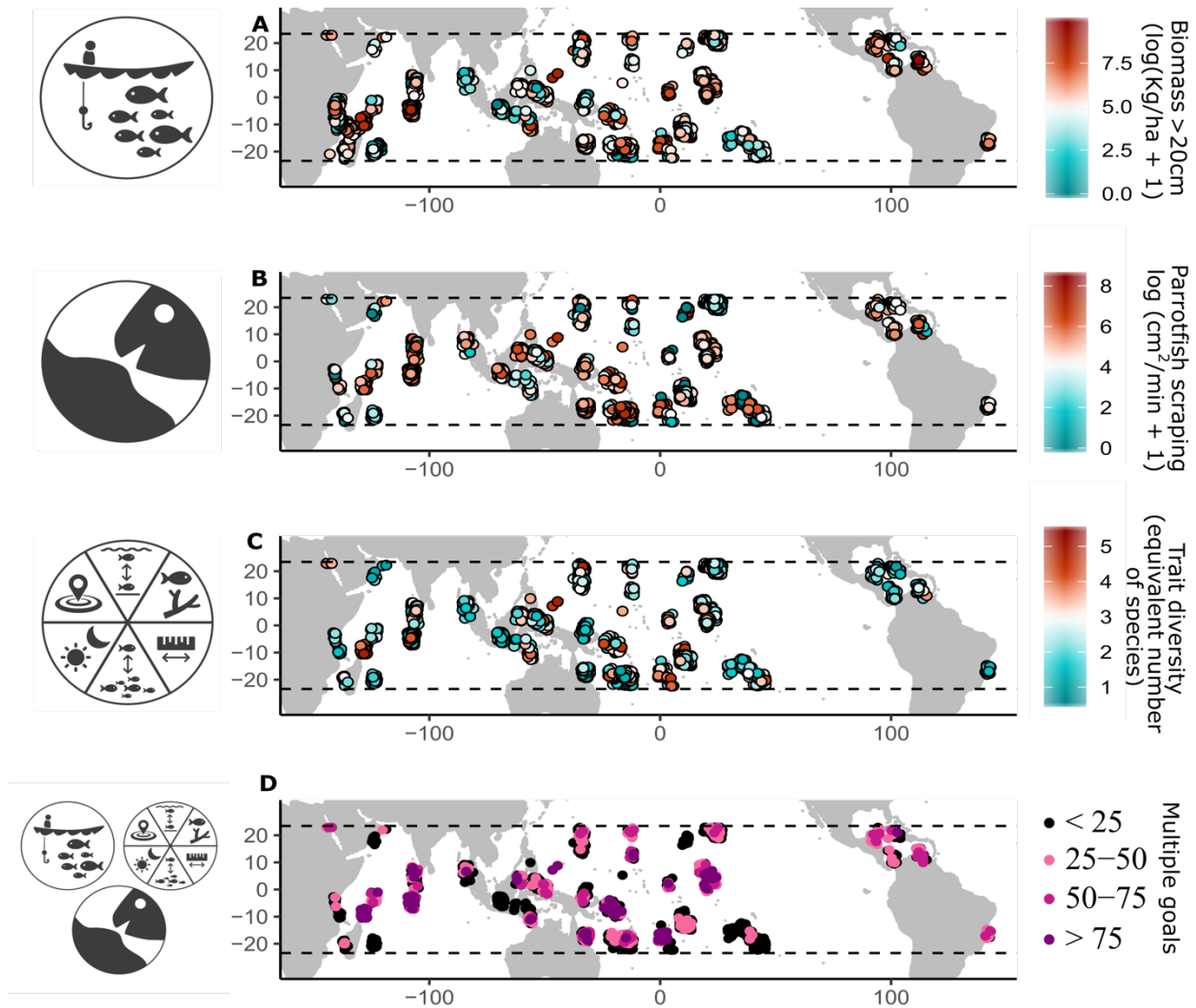
**Figure 1| Meeting multiple goals on coral reefs.** The distribution of (A) biomass of reef fish >20cm (in natural log, n=1798), (B) parrotfish scraping potential (in natural log, n=1662), and (C) trait diversity (n=1662), corrected for sampling (Methods). Differences in the number of sites are because 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), 50-75% (dark pink), 25-50% (light pink), and <25% (black) of reference conditions (Methods). Points are jittered to allow for visualization of overlapping reef sites.

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### *Simultaneously meeting multiple goals*

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144 To elucidate the capacity of reefs to simultaneously support multiple goals (i.e.

145 fisheries, ecological function, and biodiversity) we first developed a series of

146 aspirational targets (i.e. 25, 50, and 75% of reference conditions) for each

147 metric to serve as benchmarks. Reference conditions (also called reference

148 points) are a key concept in fisheries and conservation (*9*, *10*), but are nascent

149 in coral reef science (*11*, *12*). As key reference conditions, we used the top 10%

150 value for each metric (corrected for sampling), but also included additional

151 reference conditions (i.e. the top 5% and 20%) in the supplemental material

152 (Methods). We then set aspirational targets of 25, 50, and 75% of reference

153 conditions. For example, in fisheries, a key reference condition is unfished

154 biomass, while an aspirational management target is often maximum

155 sustainable yield, which is expected to be achieved at 25-50% of unfished

156 biomass in multispecies fisheries (*11*, *13*, *14*). Thus, our 25% and 50% of

157 reference conditions for potential fisheries stocks approximate the lower and

158 upper bounds of expected multispecies maximum sustainable yield; 75% of

159 reference conditions reflects a more ambitious conservation target. When

160 looking at these aspirational targets across multiple goals, we found that only

161 5% of reef sites simultaneously had fish biomass, parrotfish scraping, and trait

162 diversity at 75% of reference conditions (Fig. 1D). These sites, though

163    reasonably rare, were geographically spread through the Indian, Pacific, and

164    Atlantic ocean basins (Fig 1D). We found that 12.5% of sites simultaneously met

165    the 50% target, and 29.3% of sites met the 25% target (Fig. 1D)

166

167    **Conditions under which multiple goals can be met**

168    To examine the context under which key goals can be met, we first developed a

169    series of Bayesian hierarchical models (*15*) that quantify how the three

170    ecological metrics are related to key socioeconomic drivers of resource

171    exploitation, while controlling for environmental conditions and sampling

172    techniques (*16–18*) Fig. S2; Table S3; Methods). We then used the posterior

173    distributions from these models to calculate how the probability of

174    simultaneously meeting multiple goals changes along a gradient of human

175    pressure, while holding other covariates constant (Fig. 2, S3, S4, Methods). Our

176    measure of human pressure in the surrounding seascape was adapted from the

177    economic geography concept of gravity (*19*, *20*) and displayed the most

178    consistent negative relationships to our response variables (Fig. S2). The

179    distribution of human pressure and other key socioeconomic and

180    environmental covariates among our surveyed reefs closely matches that of

181    reefs globally (Fig. S5). The probability of openly fished reef sites

182    simultaneously having all three metrics declined with our measure of human

183 pressure and the ambitiousness of the conservation target (Fig. 2A). In other

184 words, on openly fished reefs it is extremely unlikely that all three goals will be

185 simultaneously met where human pressure is intense, but this likelihood

186 increases where human pressure is low, particularly for the 25% and 50%

187 targets.

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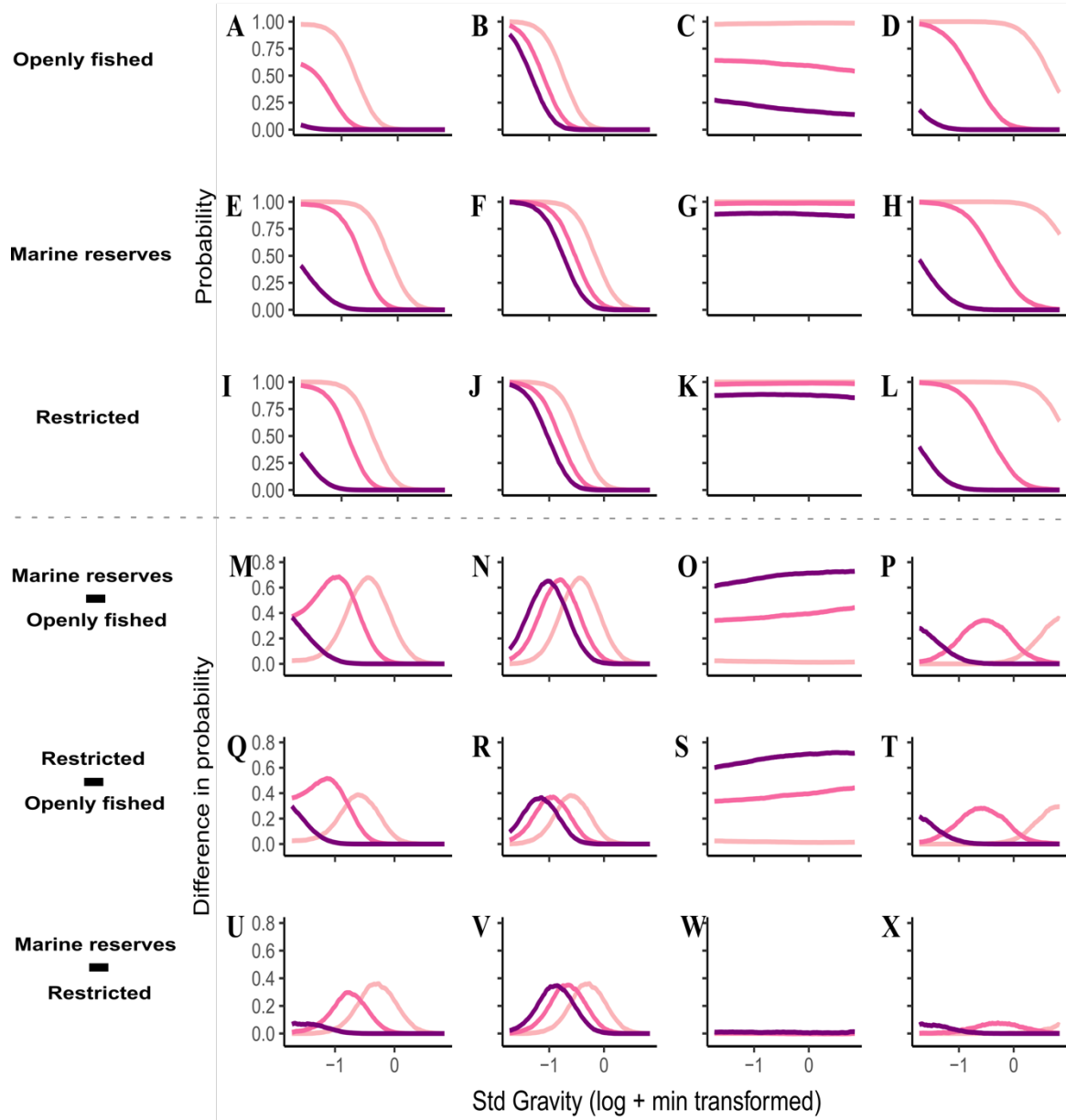
**Figure 2 | The estimated probability of openly fished reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively) for (A) a combination of fish biomass (>20cm), parrotfish scraping potential, trait diversity, and (B-D) each metric, respectively, along a gradient of human pressure (gravity).** Separate estimates are provided for reef sites in marine reserves where fishing is prohibited (E-H) and with restricted fishing (I-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 marine reserves and openly fished sites (M-P), restricted and openly fished areas (Q-T), and marine reserves and restricted areas (U-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. 4-10m for depth, slope for habitat, standard belt transect for census method). Gravity (x axis) is standardized, with an average of 0.

Importantly, there was considerable variability in how the probability of meeting individual goals changed along a gradient of human pressure (Fig. 2B-D). For example, it is extremely unlikely that openly fished reefs meet any fisheries target, except where human pressure is low. In contrast, the 25 and 50% targets may be met across a broader spectrum of human pressure for the parrotfish scraping potential and trait diversity goals (Fig. 2C,D).

***Benefits from management***

A critical gap remains in understanding the context in which different local management tools can help to simultaneously achieve key goals (*21–23*). To address this, we first examine the probability of reef sites in both marine

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218     reserves (where fishing is prohibited) and restricted fishing areas (where there

219     are limitations on fishing gears used and who can access the fishing grounds)

220     in achieving key targets for the individual and combined ecological metrics (Fig

221     2E-L). We then calculated the 'conservation gains' from employing these

222     different forms of management along a gradient of human pressure (*22*) (Fig.

223     2M-X). By conservation gain, we refer to the difference in probability of

224     achieving a specific target (e.g. 25% of reference condition biomass) when

225     marine reserves or fishery restrictions are implemented relative to openly

226     fished areas. This concept gets at the idea that contexts with maximal

227     conservation gains highlight the best opportunities for management to have the

228     biggest impact; conversely, implementing management in contexts with

229     minimal conservation gains (either because goals are already being met or

230     because they are unlikely to be met regardless of management) provides few

231     returns for limited conservation resources (*24*).

232

233     Critically, we find that both marine reserves and restricted fishing areas have

234     the potential to provide conservation gains, but the context under which these

235     gains can be maximized is highly variable depending on both the goal and target

236     (Fig. 2M-X). For simultaneously meeting all three goals, maximal conservation

237     gains are from marine reserves in the lowest human pressure locations for the

238  most ambitious target (75% of reference conditions), but as targets become

239  less ambitious, conservation gains peak where human pressure is more

240  intermediate (Fig. 2M). In other words, when the objective is simultaneously

241  meeting fisheries, function, and biodiversity goals, more ambitious targets can

242  best be met by reserves under low human pressure, but less ambitious targets

243  are best met by placing reserves in locations where human pressure is

244  intermediate. This is because the difference between marine reserves and

245  openly fished reefs is highest at intermediate human pressure for the 25 and

246  50% targets. For all three targets, there are minimal conservation gains in

247  locations where human pressure is most intense, which means that in this

248  context, management is unlikely to help meet these goals. For each independent

249  goal, the context under which conservation gains can be maximized varies

250  considerably (Fig 2). Of note is that trait diversity is the least responsive to

251  management, with conservation gains never reaching above 0.4.

252

253  We then simulated how the number of our openly fished sites achieving key

254  conservation targets would change if a marine reserve (Fig. 3) or fisheries

255  restrictions (Fig S6) were implemented, given the existing conditions at our

256  reef sites. Our analysis reveals both key opportunities and constraints in the

257  capacity for local management to simultaneously meet multiple goals. On one

hand, for more than 50% of our fished sites, the implementation of a marine

reserve is predicted to help achieve multiple goals (Fig. 3A). On the other hand,

less than 1% of the sites starting below 25% of reference conditions are

predicted to achieve the 75% of reference conditions target, highlighting how

the broader seascape context may stunt reserve potential in degraded reefs

(*22*). Indeed, more than half of the 87.4% of openly fished reefs starting below

25% of reference conditions are predicted to remain in the that same category

(Fig 3A). Additionally, our analysis shows that even where fishable biomass is

very low, scraping potential and trait diversity are often >25% of reference

conditions (Fig. 3B-D); a finding supported by previous research showing that

herbivores and a diversity of traits can still persist on degraded reefs (*25*).
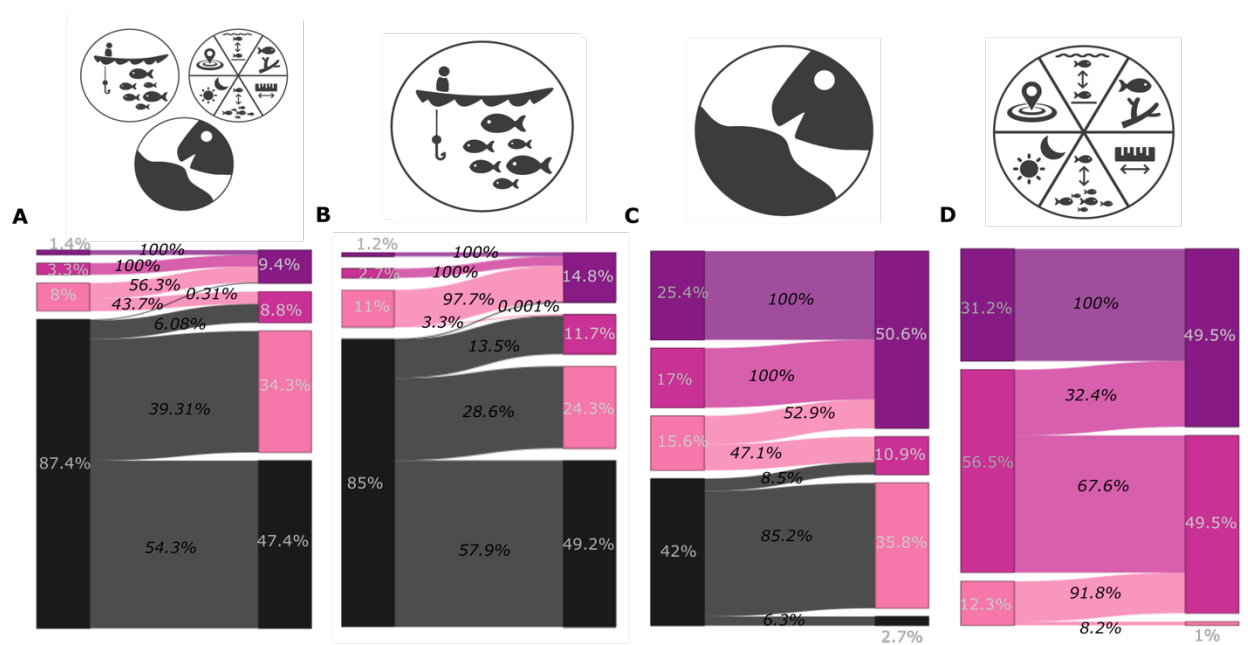
**Fig. 3. Conservation target outcomes from simulating the implementation of marine reserves in openly fished sites.** Alluvial plots show the change in the number of sites expected to achieve key conservation targets if marine reserves were implemented in our openly fished sites for (A) simultaneously meeting fish biomass, parrotfish scraping potential, and trait diversity, and (B-D) each goal, respectively.

The goal of marine reserves is to prohibit fishing, which can be in direct conflict with achieving certain fisheries goals (*26*). We found that fisheries restrictions provide a similar pattern, but typically lower magnitude, of conservation gains than marine reserves, particularly for achieving the combined goal and fisheries goal (Fig 2Q-X, Fig S6). Of note is that for parrotfish grazing potential, fishing restrictions provide the same conservation gains as marine reserves, providing multiple ways to achieve that specific goal (Fig. 2W).

Together, 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 vary not only by goal, but also are strongly dependent on both the ambitiousness of the target and the context (Fig. 2, S3, 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

294 (Fig. 2, S2). A key finding is that conservation gains tend to change non-linearly

295 with human pressure, which means that relatively small changes in the context

296 where management is implemented could have dramatic implications on

297 whether key goals are likely to be met or not (Fig. 2M-X). This not only has

298 important implications for the placement of new marine reserves, but is also

299 relevant to how future socioeconomic changes, such as infrastructure

300 development and population growth may impact the efficacy of reef

301 conservation. However, the impacts of these changes could potentially be

302 buffered by making management more effective, for example, by leveraging

303 insights about using social norms and cognitive biases to improve compliance

304 (*22*, *27*) and learning lessons about key practices and processes from locations

305 that have defied expectations of global reef degradation (*28*, *29*). Our global

306 analysis makes clear the limitations of local management, especially in

307 promoting certain aspects of biodiversity like trait diversity. While

308 international action on climate change will be crucial to ensuring a future for

309 coral-dominated reefs (*1, 2*), good governance that promotes effective

310 management will also be critical to sustaining reefs and the millions of

311 livelihoods that depend on them.

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521

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524  and implemented the analyses; J.E.C. led the manuscript. All other authors contributed to

525  data collection and made substantive contributions to the text.

526

527

528 **Competing interests:** none

529

530 **Data and materials availability:** data will be made available via a link to the James Cook

531 University Tropical Data Hub and the code used for this paper will available from GitHub

532

533 **Supplemental material**

534 **Methods**

535 **Scales of data**

536 Our data were organized at four spatial scales: survey (n=4399), reef site (n=1797), reef

537 cluster (n=734), and nation/state (n=41).

538    i)    surveys were our smallest scale of data – see details about survey methods below.

539    ii)    reef sites were aggregations of replicate surveys within a few hundred meters.

540          There were an average of 2.4 replicate surveys per reef site.

541    iii)   reef clusters- We clustered reef sites together that were within 4 km of each other,

542          and used the centroid of these reef clusters to estimate certain social and

543          environmental covariates (Table S3). To make reef clusters, we first estimated the

544          linear distance between all reef sites, then used a hierarchical analysis with the

545          complete-linkage clustering technique based on the maximum distance between

546          reef sites. We set the cut-off at 4 km to select mutually exclusive reef clusters

547          where reef sites cannot be more distant than 4 km. The choice of 4km was

548          informed by a 3-year study of the spatial movement patterns of artisanal coral

549             reef fishers, corresponding to the highest density of fishing activities on reefs

550             based on GPS-derived effort density maps of artisanal coral reef fishing activities

551             (*30*). This clustering analysis was carried out using the R functions 'hclust' and

552             'cutree', resulting in an average of 2.7 reef sites/reef cluster.

553    iv)    Nation/state (nation, state, or territory). A larger scale in our analysis was

554             'nation/state', which are jurisdictions that generally correspond to individual

555             nations (but could also include states, territories, overseas regions, or extremely

556             remote areas within a state such as the Hawaii or the British Indian Ocean

557             Territory; Table S1), within which reef clusters and reef sites were nested for

558             analysis.

559

560    **Reef fish survey methods**

561    Estimates were based on instantaneous visual counts from 4399 surveys collected from

562    1798 tropical reef sites (i.e., within 23.5 latitude degrees). All surveys used standard belt-

563    transects, distance sampling, or point-counts, and were conducted between 2004 and 2013.

564    For each site, habitat type (i.e., slope, crest, flat, lagoon/back reef), depth range (i.e., 0-4m, 4-

565    10m and >10m) and total sampling area were recorded. Where data from multiple years

566    were available for a single reef site, we included only data from the year closest to 2010.

567    Within each survey area, reef-associated fishes were identified to species level, abundance

568    counted, and total length (TL) estimated, with the exception of one data provider who

569    measured biomass at the family level.  As part of our standardization process, we:

570    i)    Retained families that were consistently studied and were above a minimum size

571          cut-off. Thus, we retained counts of >10cm non-cryptic reef fishes from families

572          that are resident on the reef (Table S4).

573    ii)   Directly accounted for depth, survey method, survey area, and habitat as

574          covariates in the model.

575

576    **Key ecological metrics**

577    We then used these surveys to calculate three key reef fish ecological metrics:

578          i) *Biomass of reef fish above 20 cm*. We calculated total biomass of fish above 20 cm

579          (TL) on each reef site (n= 1798) using standard published species-level length-weight

580          relationship parameters or those available on FishBase (*31*). When length-weight

581          relationship parameters were not available for a species, we used the parameters for

582          a closely related species or genus. Included families are specified in Table S4.

583          ii). *Parrotfish Scraping Potential*. Scraping rates (area grazed per minute) for

584          parrotfishes at each reef site (n=1662) were calculated as the product of parrotfish

585          fish density, feeding rate, and bite dimension (area) (*32*). Size-specific feeding rates

586          were derived from best-fit regressions of bite rate (bites min$^{-1}$) and fish length ([TL],

587          cm) for each species or closely related congener. Bite rates for Indo-Pacific

588          parrotfishes were quantified at three locations (Great Barrier Reef, Australia;

589          Indonesia; and the Red Sea) during which TL was estimated and the number of bites

590          on different benthic substrata (primarily epilithic algal matrix and live corals)

591          recorded and converted to bites min$^{-1}$. Individual fish were followed for a minimum

592          of 3-minutes and 19-126 individuals (mean = 41 individuals) were observed per

593    species. These values were supplemented with published length-feeding rate

594    relationships, including for Atlantic parrotfishes (reviewed in (*33*)). Size-specific bite

595    dimensions (mm$^2$) were taken from the literature (*32*, *34–36*).

596    iii). *Trait Diversity*. Trait diversity was computed for each reef site, considered as a

597    local fish community (n=1662). First, we used the trait database on tropical reef fishes

598    from Mouillot et al. (*37*) to describe species traits. The six traits considered were: (1)

599    size (observed length of each individual fish) coded using 5 ordered categories: 10-

600    15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm, >80 cm; (2) mobility coded using 3

601    ordered categories: sedentary, mobile within a reef, and mobile between reefs; (3)

602    period of activity coded using 3 ordered categories: diurnal, both diurnal and

603    nocturnal, and nocturnal; (4) schooling coded using 5 ordered categories: solitary,

604    paired, or living in small (3-20 individuals), medium (20-50 individuals), or large

605    groups (>50 groups) ; (5) vertical position in the water column coded using 3 ordered

606    categories: benthic, bentho-pelagic, and pelagic; (6) diet coded using 7 trophic

607    categories: herbivorous-detritivorous, macro-algal herbivorous, invertivorous

608    targeting sessile invertebrates, invertivorous targeting mobile invertebrates,

609    planktivorous, piscivorous, and omnivorous, (i.e. fishes that feed on both vegetal and

610    animal material). Since all traits were categorical, species with identical traits were

611    grouped into entities. We then computed the Gower distance between all pairs of

612    entities. Finally, for each fish community we computed trait-diversity using the Chao's

613    FDq=1 index (Chao et al 2019):

614

615
$$FD_{q=1} = \exp\left(-\sum_{i=1}^{S} p_i \times log\left(1 - \sum_{i \neq j} \frac{1 - \min{(d_{ij}, mD)}}{mD} \times p_j\right)\right)$$

616

617     where $p_i$ and $p_j$ are the respective relative biomasses of the two entities i and j in the

618     community, $d_{ij}$ is the Gower distance between entities i and j, mD is the average of all

619     Gower distances between the entities present in the global pool of species. This index

620     is expressed as an equivalent numbers of species (Chao et al 2019). Hence, it is

621     minimal and equals 1 when all biomass is supported by the same entity (i.e. when one

622     species is ultra-dominant or when all species have the same trait values) and it is

623     maximal and equals the number of species when all species pairs have dissimilarities

624     higher than the average dissimilarity in the global species pool and equal biomasses.

625

626     We used species-level data to calculate parrotfish scraping potential and trait diversity. Thus,

627     data from the one provider who only recorded family level data were not used in those

628     response variables.

629

630     **Social and environmental potential drivers**

631     *1. Management:* For each reef site, we determined if it was: i) unfished- whether it fell within

632     the borders of a high compliance no-take marine reserve; ii) restricted - whether there were

633     active restrictions on gears (e.g. bans on the use of nets, spearguns, or traps) or fishing effort

634     (which could have included areas under customary tenure, where 'outsiders' were

635     effectively excluded, as well as inside marine parks that were not necessarily no take); or iii)

636     openly fished - regularly fished without effective restrictions. To determine these

637 classifications, we used the expert opinion of the data providers, and triangulated this with

638 a global database of marine reserve boundaries (*38*). As a sensitivity analysis, we also

639 conducted analyses with a subset of reserves that were >2km$^2$ and that have been protected

640 for more than 4 years (see analysis section below).

641

642 *2. Local Population Growth:* We created a 100 km buffer around each reef cluster and used

643 this to calculate human population within the buffer in 2000 and 2010 based on the

644 Socioeconomic Data and Application Centre (SEDAC) gridded population of the world

645 database (*39*). Population growth was the proportional difference between the population

646 in 2000 and 2010. We chose a 100km buffer as a reasonable range at which many key human

647 impacts from population (e.g., land-use and nutrients) might affect reefs (*40*).

648

649 *3. Gravity:* We adapted the economic geography concept of *gravity* (*19*, *22*, *41*, *42*) to examine

650 the amount of human pressure within the surrounding 500km of a reef. The gravity model

651 has been used by economists and geographers since the 1880s to measure a wide range of

652 economic interactions such as trade and migration flows (*19*). To calculate gravity, we

653 gathered data on both population estimates and a surrogate for distance: travel time.

654

655     *Population estimations*

656     We gathered population estimates for every 1-by-1 km populated cell within a 500km

657     radius of each reef site using the LandScan™ 2011 database (*43*). We chose a 500km

658     radius from the nearest settlement as the maximum distance any non-market fishing

659     activities for fresh reef fish are likely to occur.

660

*Travel time calculation*

For each populated cell within 500km, we then used a cost-distance algorithm that computes the least 'cost' (in minutes) of travelling to the reef site. Cost was based on a raster grid of land cover, road networks, and shorelines data and estimated travel time over different surfaces (*44*).

*Gravity computation*

We first calculated a value for the "gravitational pull" exerted by each populated cell within 500km of a reef site, by dividing the population of that cell by the squared travel time to the reef site. We then summed the gravity values for all cells within 500km of each reef site to measure the total "gravitational pull" of human pressure that a given reef is experiencing. This application of the gravity concept infers that potential interactions increase with population size, but decay non-linearly with the effective distance. Although different exponents can be used, we used the traditional application of dividing by squared distance (in our case travel time)(*19*). This application emphasizes a non-linear decay in the propensity for interactions as distance from people to the reef increases. Our rationale for calculating gravity using squared travel time in the denominator (as opposed to just travel time) is based on the idea that our reef site is likely only one of multiple reefs that could potentially be harvested, and that the number of potential alternative reefs that could be harvested should increase with the area covered by a radius from any populated cell (i.e., based on area not linear distance). Since the decision to fish on a given reef is likely

683    dependent on how that reef compares with all other alternatives, it makes sense that

684    fishing pressure at any reef site will also decline by distance squared (i.e. comparing

685    with all other reefs within a similar distance) rather than linear distance (i.e.

686    comparing only with other reefs along the same path). To test whether this rationale

687    to use squared travel time is supported by our data, we developed gravity metrics

688    using a range of exponents (^1, ^2, ^3) and used leave-one-out cross-validation for

689    model selection to determine the best fit. For fish biomass and trait diversity, squared

690    travel time performed best, but for parrotfish grazing, travel time (i.e. exponent 1)

691    performed slightly better (though in the parrotfish grazing models, all three

692    exponents were within the standard error). Given that two out of three of our

693    response variables favored the travel time squared, this supports our decision to use

694    that for our analysis. However, due to the potential ambiguity in the parrotfish

695    grazing potential, we ran a sensitivity test, calculating how the probabilities of

696    achieving goals change along a gradient of human pressure using a gravity metric

697    calculated using the first exponent (i.e. travel time in the denominator). There were

698    no discernible differences between our results, suggesting that our decision to use

699    travel time squared as opposed to travel time in the denominator did not

700    meaningfully impact our results.

701

702    *4. Human Development Index (HDI)*: HDI is a summary measure of human development

703    encompassing: life expectancy, education, and per capita income. We obtained the HDI

704    measure from the United Nations Development Program for 2010. In cases where HDI values

705    were not available specific to the State (e.g. Hawaii), we used the national (e.g. USA) HDI

706    value, and in other cases (e.g. Marshall Islands) we had to calculate HDI from life expectancy,

707    education, and per capita income statistics.

708

709    *5. Population size.* For each nation/state, we determined the size of the human

710    Population in 2010. Data were derived mainly from the national census reports CIA fact book

711    (https://www.cia.gov/library/publications/the-world-

712    factbook/rankorder/2119rank.html),                    and                    Wikipedia

713    (https://en.wikipedia.org/wiki/Main_Page).

714

715    *6. National Reef Fish Landings:* Reconstructed reef fish catch estimates (in metric tonnes)

716    were    obtained    from    the    Sea    Around    Us    Project    (SAUP)    catch    database

717    (http://www.seaaroundus.org)(*45*). We used estimates corresponding to 2010 and only

718    included reef associated species. We calculated the catch per unit area (catch/km$^2$/y) by

719    dividing a nation/state's catch by the its estimated reef area (*46*).

720

721    *7. Oceanic productivity*: We examined oceanic net productivity for each reef following the

722    procedure described by (*47*). We delimited a 100 km buffer around each of our reef clusters,

723    we removed shallow waters pixels (those that intersected or were contained within the

724    depth    contour    of    30m    from    the    General    Bathymetric    Chart    of    the    Oceans    2014

725    (http://www.gebco.net/), a global gridded bathymetry dataset) and then calculated the

726    average of monthly chlorophyll-a concentration (proxy for phytoplankton biomass) using

727    data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging Spectro-

728    radiometer) for years 2005 to 2010.

729

8. *Climate stress.* We included an index of climate stress for corals, developed by (*48*), which
incorporated 11 different environmental conditions, including the mean and variability of
sea-surface temperature, tidal range, ultraviolet radiation, a doldrum index, and chlorophyll.

**<u>Analyses</u>**

We first looked for collinearity among our covariates using bivariate correlations and
variance inflation factor estimates. This led to the exclusion of several covariates (not
described above): i) *Gross Domestic Product* (purchasing power parity); ii) *Rule of Law*
(World Bank governance index ); iii) *Control of Corruption* (World Bank governance index
(*49*)); iv*) Sedimentation;* v) *Tourism* (tourist arrivals from the World Tourism Organization's
Compendium of Tourism Statistics relative to land area); vi) *Atoll* (i.e., a binary metric of
whether the reef site was on an atoll or not); vii) *Frequency of storms since 1980*
(http://weather.unisys.com/hurricane); viii) *Environmental performance index (EPI)*
([https://epi.envirocenter.yale.edu/](https://epi.envirocenter.yale.edu/)). ; and ix) the *GINI index* (measure of a nation/state's
inequality). Although the GINI index was not strongly correlated with other covariates, there
were numerous missing values, so that potential covariate was removed. All other covariates
had correlation coefficients lower than 0.6 and Variance Inflation Factor scores less than 2
(indicating multicollinearity was not a concern). Care must be taken in causal attribution of
covariates that were significant in our models, but demonstrated collinearity with candidate
covariates that were removed during the aforementioned process. Critically, our metric of
total gravity was colinear with atoll (i.e., most remote or low gravity reefs are atolls) but
when we restricted the analyses to only non-atolls the results did not change. Additionally,

752    correlations between mean body size of the fish assemblage (length, cm) and our response

753    variables: biomass (r=0.73), parrotfish scraping potential (r=0.2), and trait diversity (r=0.4)

754    suggest that mean body size is only predictive of biomass.

755

756    *Multilevel models*

757    To quantify the multi-scale social, environmental, and economic factors affecting the three

758    ecological metrics, we modelled each response variable separately using multilevel models

759    that explicitly recognized the three scales of spatial organization: reef site, reef cluster and

760    nation/state. Models were run using a Bayesian approach using the Hamiltonian Monte Carlo

761    algorithm implemented in Stan through the brms package (*50*) for 10000 iterations, and a

762    9000 burn in. This left 4000 samples in the posterior distribution of each parameter (four

763    chains). We did not have a priori information about parameter distributions; thus, the

764    posterior estimates were informed by the data alone (i.e. weakly informative priors).

765    Convergence was monitored by running four chains from different starting points,

766    examining posterior chains and distribution for stability, and checking that the potential

767    scale reduction factor (also termed R_hat) was close to 1. We employed a gaussian

768    distribution to analyze biomass of reef fish above 20 cm (log +1 transformed) and trait

769    diversity, and used a hurdle-lognormal to analyze parrotfish scraping potential because the

770    data for this metric contained a large number of zeros (31 %). The hurdle model is a two-

771    part model composed of (i) a binomial distribution and a logit link function to predict the

772    probability of observing the herbivory function (i.e., whether the response outcome is

773    positive or zero) and (ii) a lognormal distribution for the non-zero data.

774

775  For each model, we set reef cluster and nation/state as random effects to account for the

776  hierarchical nature of the data (i.e. reef sites nested in reef clusters, reef clusters nested in

777  nations/states). For each metric, we tested two alternate models: a null model, consisting

778  only of the hierarchical units of observation (that is, intercepts-only) and a full model that

779  included all of our covariates (potential drivers) of interest. We used the null model as a

780  baseline against which we could ensure through leave-one-out cross-validation information

781  criteria (LOOIC) (*51*) that our full model performed better than a model with no covariate

782  information. To account for any methodological effects, sampling area, census method,

783  sampled habitat and depth were also included in all the models as covariates. To control for

784  sampling effects, we marginalized response variables by subtracting the estimated sampling

785  standardized mean model effects to the observed response variables. For all the analyses,

786  continuous covariates were standardized (mean centered and divided by 2 standard

787  deviations). To examine model fit and homoscedasticity, we conducted posterior predictive

788  checks, checked residuals against fitted values and ensured residuals followed expected

789  distributions around zero (e.g., for the gaussian distribution models we checked that

790  residuals were normally distributed around zero). We also checked the residuals against all

791  covariates included in the models, and the covariates described above that were not included

792  in the models (primarily due to collinearity).  The residuals of each of the three models

793  showed no patterns with these covariates, suggesting they would not explain additional

794  information in our models. Additionally, to account for the potential effect that reserve size

795  and age could have on our response variables we ran two different analyses: (i) where we

796  included all the high compliance reserves in our data irrespective of size and age (N=106 reef

797  sites); and (ii) where we only retained reserve sites that were above a minimum threshold

798    of at least 2 km$^2$ and older than 4 years, (N=61 reef sites). These inclusion criteria were

799    informed by the literature on reserve effectiveness, which suggests that a diameter of 1-2km

800    (1-3km$^2$) is required to achieve partial protection (*52*),  but were also constrained by our

801    sample; a more conservative cutoff of say 10km$^2$ and 10 years would have left only 16 reef

802    sites.  In the main manuscript, we report (i), but highlight the differences between (i) and (ii)

803    in Fig. S7. All analyses were undertaken using R (3.02) statistic package.

804

805    **<u>Reference conditions and targets</u>**

806    We defined reference conditions for each ecological metric using the 0.9 quantile of the

807    marginalized response variables accounting for sampling, habitat sampled, and sampling

808    location (i.e., response variables minus the random effects and the model estimated effect

809    sizes of depth category, reef habitat and sampling method). Thus, reference conditions are

810    for average sampling area and "Slopes", "4-10m" and "Standard belt transects".  As expected,

811    the 90% reference point values for the fisheries target (biomass above 20 cm) was slightly

812    below the expected total biomass in remote locations (*12*).  Consequently, we then set targets

813    of 25, 50, and 75% of these reference point conditions, the lower two of which correspond

814    to typical standing biomass levels of multispecies maximum sustainable yields

815    (hypothesized to be between 25-50% of unfished biomass estimates (*11*, *14*)). Meanwhile

816    75% of reference conditions is considered a more stringent conservation target.  For

817    consistency, we used the same reference conditions  and targets (i.e. 25, 50, and 75% of

818    reference conditions) for parrotfish scraping potential and trait diversity, although

819    established ecological significance of these figures remains untested, and establishing

820    benchmarks for these is an important area of future research, as is developing region-specific

821    reference conditions. To avoid being overly prescriptive, we also ran our analyses for a range

822    of reference conditions, based on the 0.8 and 0.95 quantiles of the response variables, and

823    incorporated the results in the supplemental information (Fig. S3-S4).

824

825    To estimate the probability of passing different thresholds under a gradient of gravity (e.g.,

826    Fig. 2), for each response variable, we simulated new data from the model posteriors where

827    only gravity was modified (i.e., maintaining all the other covariates at average conditions, for

828    slopes, 4-10 m of depth and standard belt transects and not including the random effects)

829    and estimated the probability of the posterior samples being above or below the targets.  To

830    determine the probability of all three response variables passing the targets (i.e., co-

831    occurrence of metrics), we used the subset of 1662 reef sites that had all three ecological

832    metrics and multiplied the probabilities (i.e., assuming independence).

833

834    **Potential gains from management for our reef sites**

835    To estimate the number of fished sites that would pass different targets if management (i.e.,

836    high compliance marine reserves or restrictions) were implemented, we simulated new data

837    for the posterior distributions maintaining sampling consistent (i.e., sampling method and

838    sampling area) but allowing individual sites to have their own socio-ecological context (e.g.,

839    habitat,  depth, HDI, random effects). Then, we changed their protection (from openly fished

840    to high compliance marine reserves or restricted) and simulated a new set of data based on

841    that condition. This allowed us to estimate the number of our sites that could potentially pass

842    different thresholds if management was implemented given the effect of management in our

843    model and a site's own environmental and socio-economic context. We report the high

844     compliance marine results in the main manuscript and the restricted fishing in the

845     supplemental information.

846

847    **Supplemental figures**
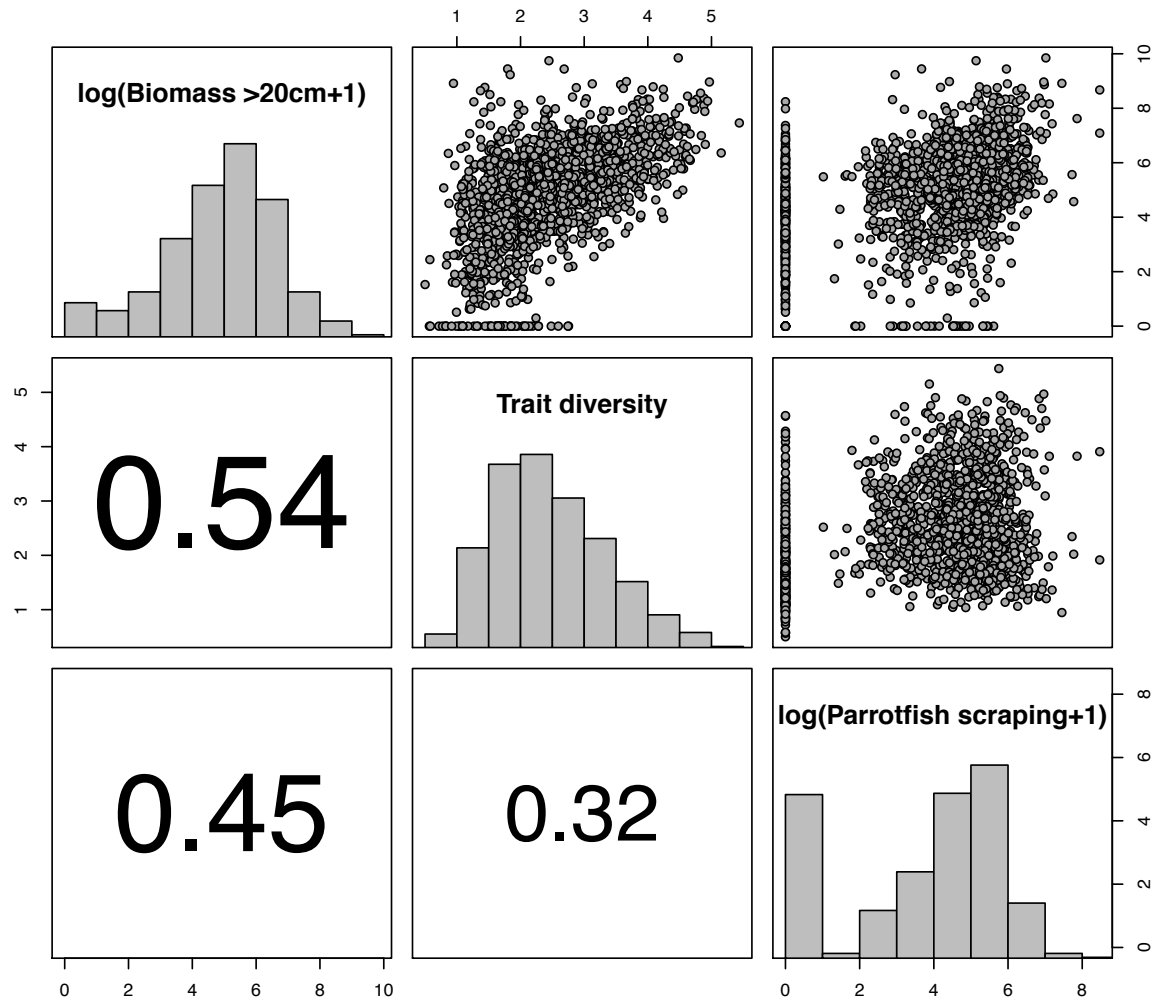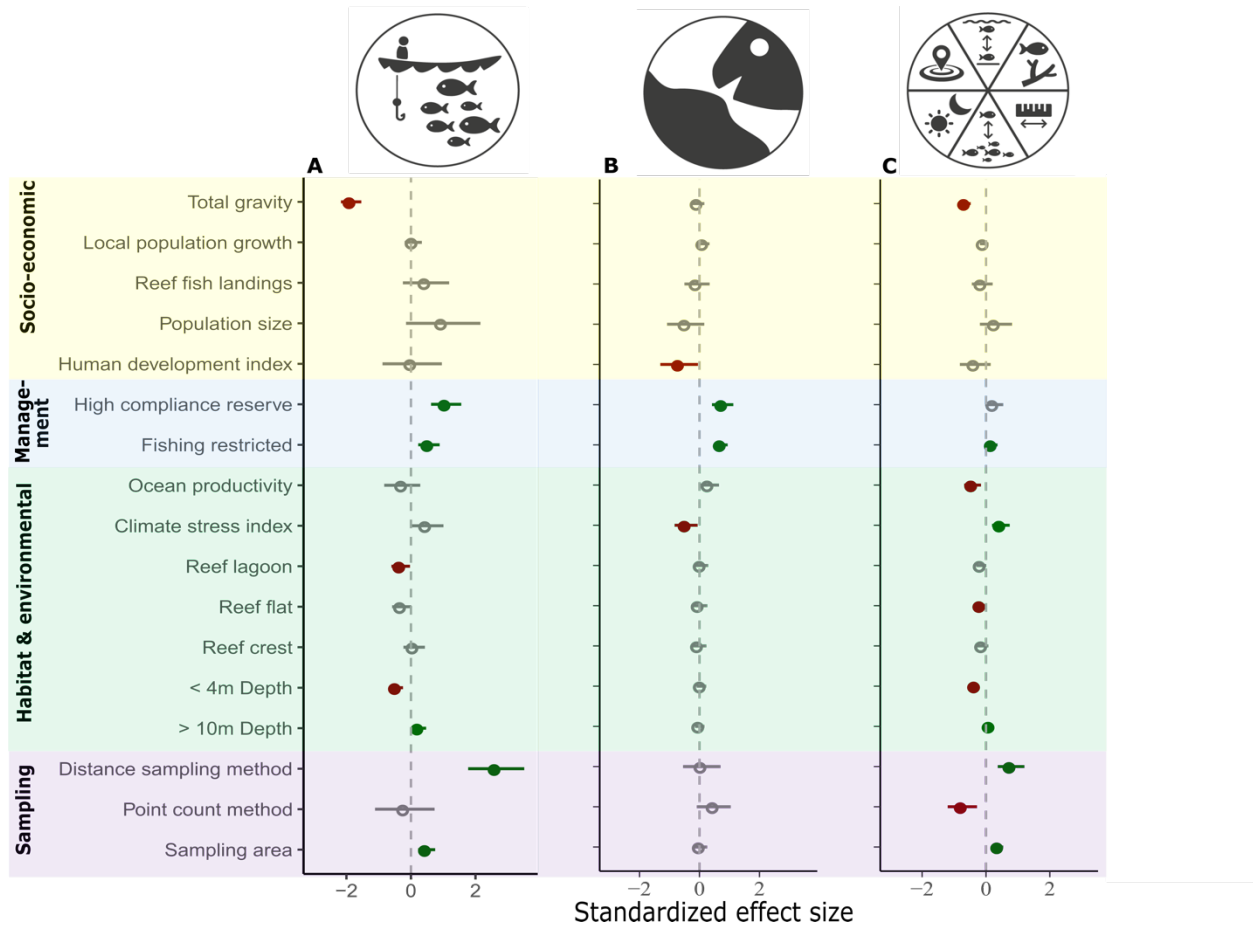


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850    **Figure S1| Correlations between the three key ecological metrics supported by fish**

851    **communities on coral reefs**

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854

**Figure S2| Effect size of eight socioeconomic drivers, management, sampling, and environmental conditions on three fish metrics. (A)** biomass of reef fish >20cm. (**B**) parrotfish scraping potential. (**C**) trait diversity. Total gravity was the most consistent socioeconomic covariate, demonstrating strong negative relationships with fish biomass and trait diversity, and a weaker negative relationship with parrotfish scraping potential (posterior slope had 65.4% of the samples negative). Continuous covariates were standardized (mean centered and divided by 2 standard deviations), while response variables were not. Thus, effect sizes are standardized within columns only. Parameter estimates are Bayesian posterior mean values and 95% uncertainty intervals (UI). Red or green dots indicate negative or positive relationships, respectively, where the 95% UI does not overlap 0. A Hurdle model was used for parrotfish scraping (b).
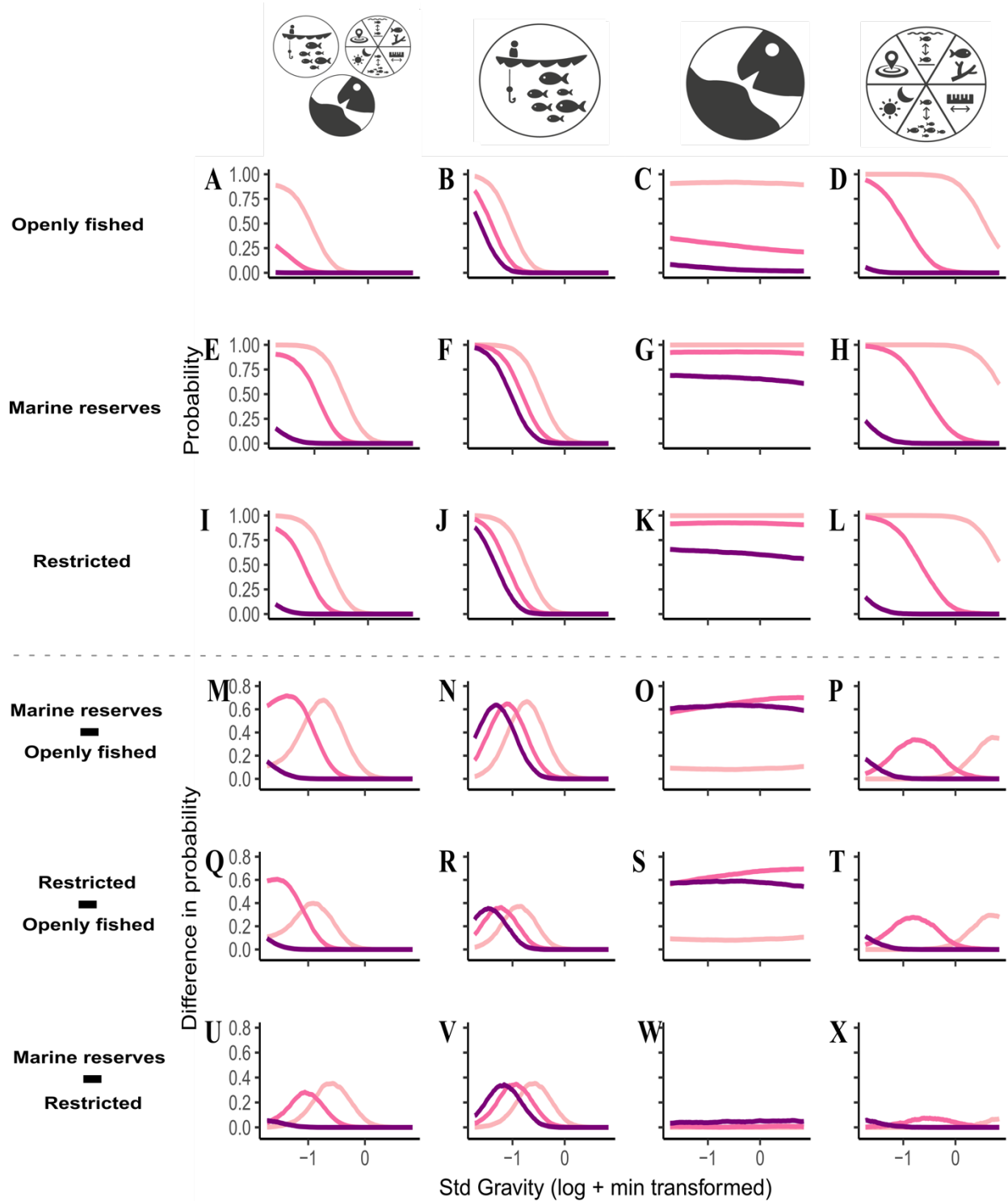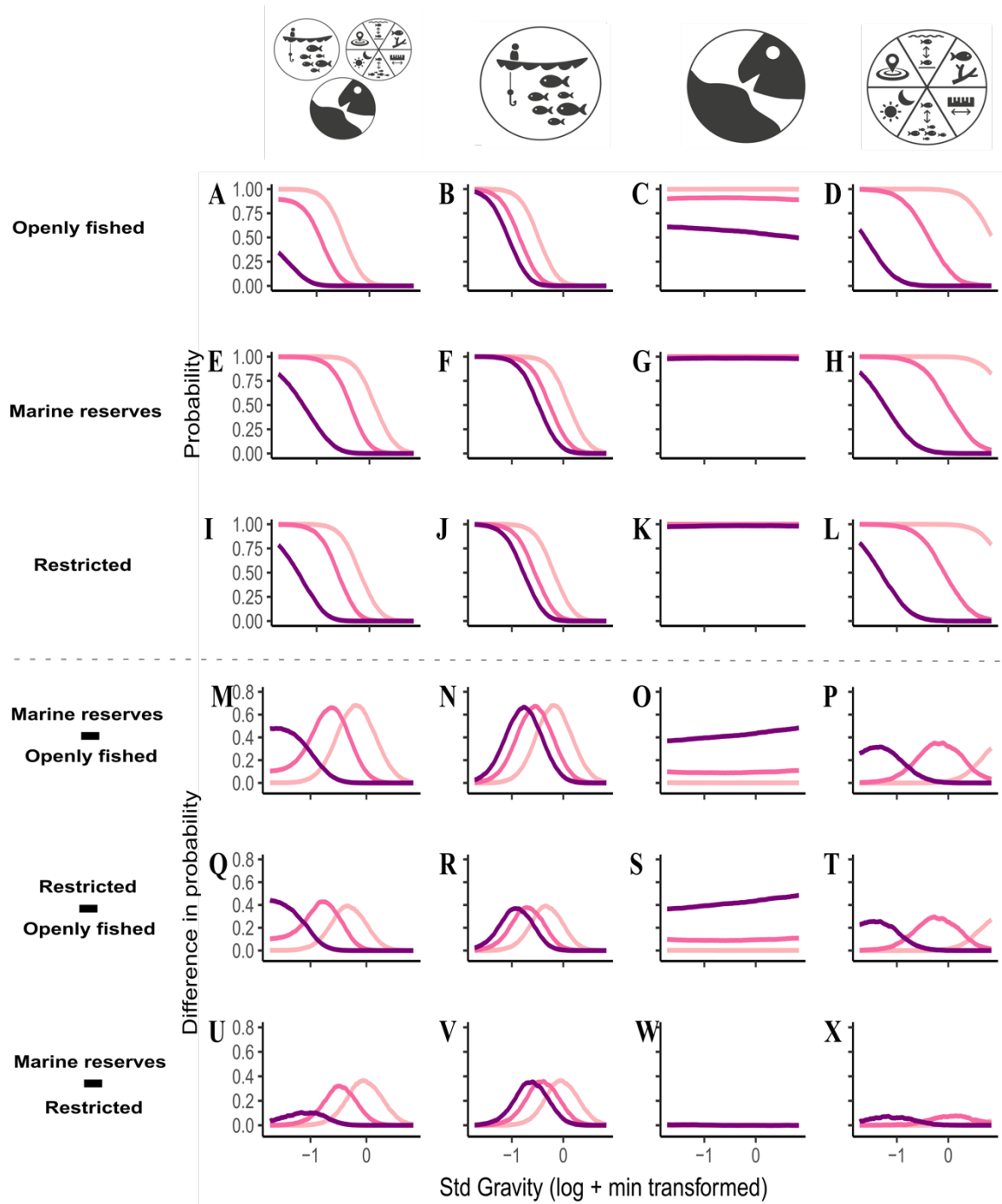
Figure S3 | The estimated probability of openly fished reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively) benchmarked from remote reefs >10 hours from the nearest settlement for (A) a combination of fish biomass (>20cm), parrotfish scraping potential, trait diversity,

880    **and (B-D) each metric, respectively, along a gradient of human pressure (gravity).**
881    Separate estimates are provided for reef sites in marine reserves (E-H) and with restricted
882    fishing (I-L). To highlight how the potential benefits of management change along a gradient
883    of human pressure (gravity), we extracted the difference in the probability of achieving each
884    target between marine reserves and openly fished sites (M-P), restricted and openly fished
885    areas (Q-T), and marine reserves and restricted areas (U-X). We plotted the partial effect of
886    the relationship between gravity and each benchmark by setting all other continuous
887    covariates to 0 (because they were all standardized) and all categorical covariates to their
888    most common category (i.e. 4-10m for depth, slope for habitat, standard belt transect for
889    census method).

890

**Figure S4 | The estimated probability of openly fished reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively) benchmarked from remote reefs >10 hours from the nearest settlement for (A) a combination of fish biomass (>20cm), parrotfish scraping potential, trait diversity, and (B-D) each metric, respectively, along a gradient of human pressure (gravity).**

896 Separate estimates are provided for reef sites in marine reserves (E-H) and with restricted
897 fishing (I-L). To highlight how the potential benefits of management change along a gradient
898 of human pressure (gravity), we extracted the difference in the probability of achieving each
899 target between marine reserves and openly fished sites (M-P), restricted and openly fished
900 areas (Q-T), and marine reserves and restricted areas (U-X). We plotted the partial effect of
901 the relationship between gravity and each benchmark by setting all other continuous
902 covariates to 0 (because they were all standardized) and all categorical covariates to their
903 most common category (i.e. 4-10m for depth, slope for habitat, standard belt transect for
904 census method).

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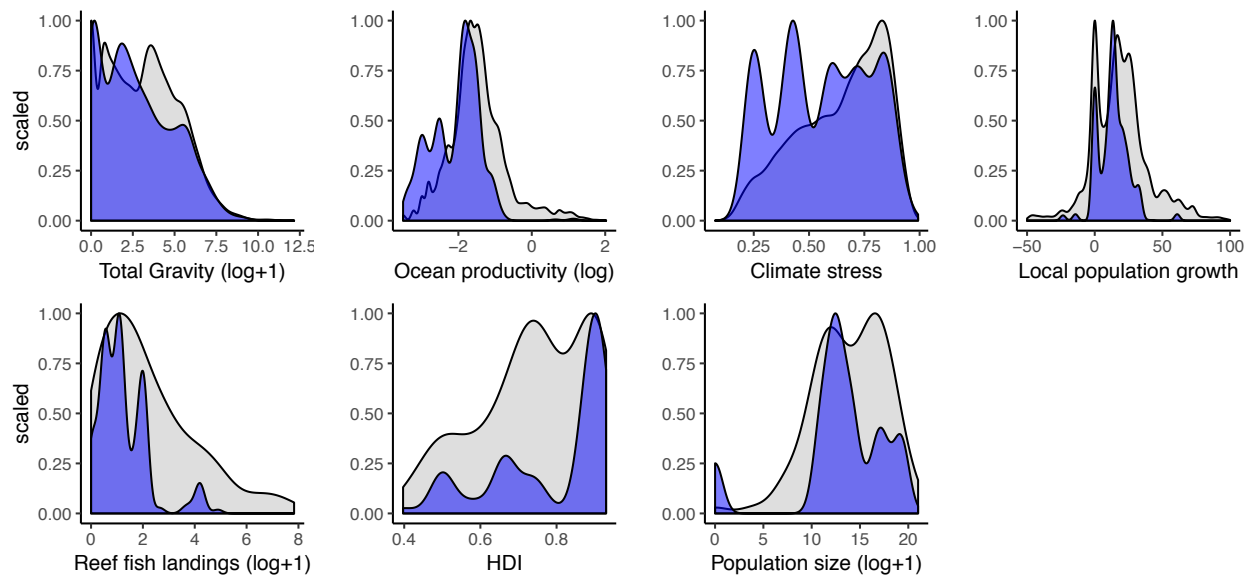
**Fig. S5. The scaled distribution of covariates for our sample of reefs (blue) and for all
tropical reefs globally (grey). Our sampled reefs display a reasonably similar
distribution and range for most covariates Note that the global gravity values were
only available rounded to the nearest integer, therefore to directly compare with our
site level values, we used a log+1 transformation, rather than log+minimum
transformation as used in the rest of the manuscript.**

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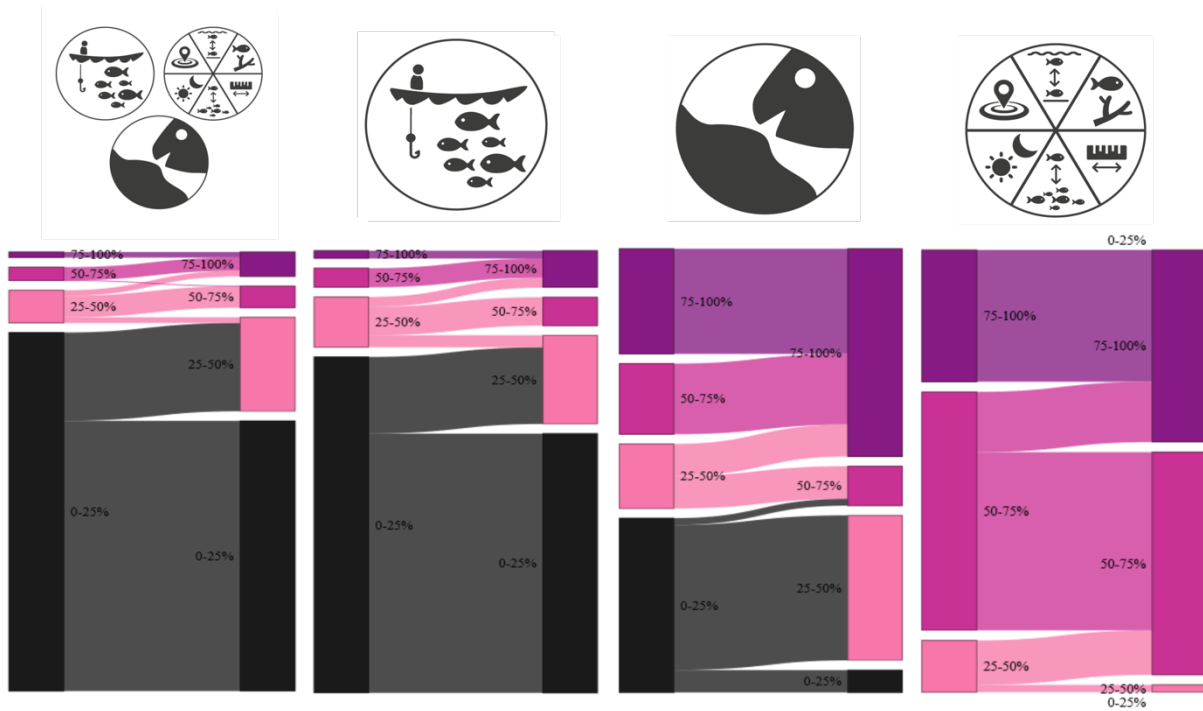
**Fig. S6. Conservation target outcomes from simulating the implementation of fishing restrictions in openly fished sites.** Alluvial plots show the change in the number of sites expected to achieve key conservation targets if fisheries restrictions were implemented in our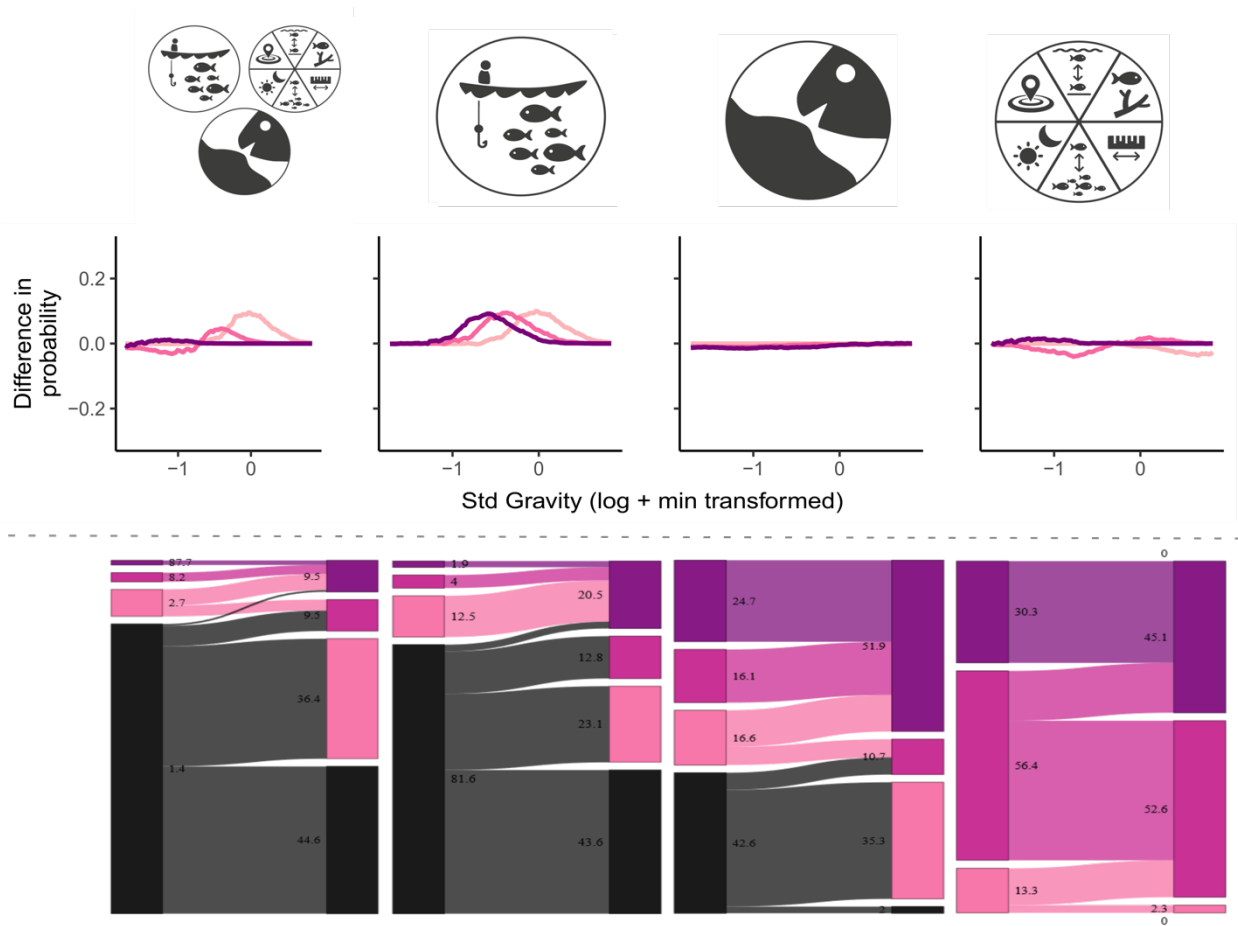 openly fished sites for (A) simultaneously meeting fish biomass, parrotfish scraping potential, and trait diversity, and (B-D) each goal, respectively.

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**Fig. S7. Difference in probability of achieving specific targets between the restricted subset of marine reserves (>2km2 and 4 years old, n=61) and all marine reserves in our sample (n=106) for** (A) simultaneously meeting fish biomass, parrotfish scraping potential, and trait diversity, and (B-D) each goal, respectively**.** Alluvial plots show the change in the number of sites expected to achieve key conservation targets if the marine reserves >2km$^2$ and 4 years old (based on our restricted subset) were implemented in our openly fished sites for (E) simultaneously meeting fish biomass, parrotfish scraping potential, and trait diversity, and (F-H) each goal, respectively.

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936 **Supplemental Tables**

937

938 **Table S1 | List of 'Nation/states' covered in study.** In most cases,

939 nation/state refers to an individual country, but can also include states (e.g.

940 Hawaii), territories (e.g. British Indian Ocean Territory), or other jurisdictions.

941

| Nation/States |
|---|
| American Samoa |
| Australia |
| Belize |
| Brazil |
| British Indian Ocean Territory |
| Cayman Islands |
| Colombia |
| Commonwealth of the Northern Mariana Islands |
| Comoro Islands |
| Cuba |
| Egypt |
| Federated States of Micronesia |
| Fiji |
| French Polynesia |
| Guam |
| Hawaii |
| Indonesia |
| Jamaica |
| Kenya |
| Kiribati |
| Madagascar |
| Maldives |
| Marshall Islands |
| Mauritius |
| Mayotte |
| Mexico |
| Mozambique |
| Netherlands Antilles |
| New Caledonia |
| Oman |

| Palau |
| Panama |
| Papua New Guinea |
| Philippines |
| PRIA |
| Reunion |
| Seychelles |
| Solomon Islands |
| Tanzania |
| Tonga |
| Venezuela |

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**Table S2| Justification of ecological metrics**

| **Biomass of fish above 20 cm** | Large fish are both key to sustain ecosystem functioning and common fishery targets. We selected a 20 cm cut-off point because it includes large fish and "plate-sized" fish, targeting not only the most valuable fish but also the fish destined to food consumption (*53*). Additionally, large fish exert top-down control on ecosystems, regulating the structure and functions of reef ecosystems (*54*). Biomass captures both the size and number of fish above 20 cm in the system, which dictates the magnitude of the function (*55*). Biomass of fish above 20 cm is expected to decline rapidly as human impacts intensify (*11*), and there is empirical evidence that management can allow the recovery of large species (*56*). |
|---|---|
| **Parrotfish scraping** | Herbivory mediates the competition between corals and algae. Bioerosion removes dead reef structures, providing suitable substrate for coral recruitment. Parrotfish are among the most important groups of herbivorous fish on coral reefs performing processes of algae removal and contributing to bioerosion, hence maintenance of good condition for reef growth. Herbivory is expected to decline as human impacts intensify (*55*) and respond positively to management (*57*). |
| **Trait diversity** | The diversity of ecological traits supported by species can represent the range of potential ecological roles present in a given community (*58*, *59*). A broader range of traits are assumed to provide a greater contribution to key ecosystem processes (e.g. biomass production, nutrient cycling) and cultural services (e.g. aesthetic value) than a smaller range of traits (*59–61*). We estimated trait diversity (TD) using the Chao's $FD_{q=1}$ index which is a generalization of the taxonomic Shannon's entropy index (Chao et al 2019). This index is high when both the dissimilarity of species' traits (e.g. diet, size) and the spread of biomass across these traits are high. We posit that TD should generally decrease as human impacts increase, because activities such as fisheries selectively target species with specific traits, which can reduce the trait space occupied and the balance of biomass among traits, and  thus TD (*62*, *63*). |

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947 **Table S3 | Summary of social and environmental covariates.** Further

948 details can be found in Methods. The smallest scale is the individual reef site.

949 Reef clusters consist of clusters of reef sites within 4km of each other.

950 Nation/states generally correspond to country, but can also include or

951 territories or states, particularly when geographically isolated (e.g. Hawaii).

952

| Covariate | Description | Scale | Key data sources |
|---|---|---|---|
| **Local population growth** | Difference in local human population (i.e. 100km buffer around our reef clusters) between 2000-2010 | Reef cluster | Socioeconomic Data and Application Centre (SEDAC) gridded population of the work database (*39*) |
| **'Gravity' of human pressure** | For each populated cell within a 500km radius of a reef site, we divided the population of that cell by the squared travel time between the reef site and the cell to get a gravity value (i.e. how much "gravitational pull" that population was exerting on the reef site). This was then summed for all cells to get the total gravity of human pressure. | Reef site | Human population size, land cover, road networks, coastlines |

| | | | |
|---|---|---|---|
| **Management status** | Whether the reef site is openly fished, restricted (e.g. effective gear bans or effort restrictions), or unfished | Reef site | Expert opinion, global map of marine protected areas. |
| **Human Development index** | A summary measure of human development encompassing: a long and healthy life, being knowledgeable and have a decent standard of living. We used linear and quadratic functions for HDI. | Nation/state | United Nations Development Programme |
| **Population Size** | Total population size of the jurisdiction | Nation/ state | World Bank, census estimates, Wikipedia |
| **Fish landings** | Landings of reef fish (tons) per Km² of reef | Nation/ state | Sea Around Us Project (Pauly and Zeller (*45*)) |
| **Climate stress** | A composite metric comprised of 11 different environmental variables that are related to coral mortality from bleaching | Reef cluster | Maina et al. (*48*) |
| **Productivity** | The monthly average (2005-2010) oceanic productivity | Reef cluster | Gove et al. 2013 (*47*), Aqua MODIS |

| | | | |
|---|---|---|---|
| **Habitat** | Whether the reef site is a slope, crest, flat, or back reef/lagoon | Reef site | Primary data |
| **Depth** | Depth of the ecological survey (<4m, 4.1-10m, >10m) | Reef site | Primary data |
| **Sampling technique** | Whether the data collector used point count, line transects, or distance sampling | Reef site | Primary data |
| **Area Sampled** | The size of the area sampled by the data provider (in m²) | Reef site | Primary data |

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**Table S4| List of fish families included in this study for both the trait diversity and the biomass above 20 cm response variables.**

| Fish family | Common family name |
|---|---|
| **Acanthuridae** | Surgeonfishes |
| **Balistidae** | Triggerfishes |
| **Carangidae** | Jacks |
| **Diodontidae** | Porcupinefishes |
| **Ephippidae** | Batfishes |
| **Haemulidae** | Sweetlips |
| **Kyphosidae** | Drummers |
| **<u>Labridae</u>** | <u>Wrasses</u> |
| **Lethrinidae** | Emperors |
| **Lutjanidae** | Snappers |
| **Monacanthidae** | Filefishes |
| **Mullidae** | Goatfishes |
| **Nemipteridae** | Coral Breams |
| **Pinguipedidae** | Sandperches |
| **Pomacanthidae** | Angelfishes |
| **Scaridae** | Wrasses and Parrotfish |
| **Serranidae** | Groupers |
| **Siganidae** | Rabbitfishes |
| **Sparidae** | Porgies |
| **Synodontidae** | Lizardfishes |
| **Tetraodontidae** | Pufferfishes |
| **Zanclidae** | Moorish Idol |

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962