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

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Abstract :

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.

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Main Text:

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*). Yet, critical gaps remain in our capacity to effectively implement this type of ecosystem-based management approach, where multiple goals are simultaneously pursued (*3*). In particular, little is known about: (i) the context under which key goals can be simultaneously met, and (ii) 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, Tables S1-2). These are, respectively: (1) potential stocks available for multi-species coral reef fisheries, calculated as the biomass of fishes >20 cm total length (*4*)(Fig. 1, Table S2); (2)

118 scraping potential, reflecting a unique ecological function performed by
119 parrotfish that is critical for the removal of algal biomass and the provision of
120 bare substrate for coral settlement (*4*, *5*) (Table S2); and (3) the diversity of
121 species traits (i.e. home range, body size, diet, diurnal activity, schooling
122 behavior, position in the water column), which can underpin aspects of
123 biodiversity such as community assembly processes, ecosystem productivity,
124 and stability (*6*). We measured trait diversity using a generalization of the
125 Shannon entropy index accounting for both the dissimilarity of trait values
126 present in a reef fish community and the spread of biomass across these trait
127 values (*4*, *7*) (Table S2). Our analysis shows that the three metrics are not
128 strongly related to each other ($r<0.54$; Fig S1).

129

130 To elucidate the capacity of reefs to simultaneously support multiple goals, we
131 first developed reference conditions for each metric to serve as benchmarks.
132 Reference conditions (also called reference points) are a key concept in
133 fisheries and conservation (*8*, *9*), but are nascent in coral reef science (*10*). As
134 key reference conditions, we used the top 10% value for each metric (corrected
135 for sampling), but also included additional reference conditions (i.e. the top 5%
136 and 20%) in the supplementary materials (*4*). We then set aspirational targets
137 of 25, 50, and 75% of reference conditions. When looking at these aspirational

138 targets across multiple goals, we found that only 5% of reef sites
139 simultaneously had fish biomass, parrotfish scraping, and trait diversity at 75%
140 of reference conditions (Fig. 1D). These sites, though reasonably rare, were
141 geographically spread through the Indian, Pacific, and Atlantic ocean basins
142 (Fig 1D). We found that 12.5% of sites simultaneously met the 50% target, and
143 29.3% of sites met the 25% target (Fig. 1D)
144
145 To examine the context under which key goals can be met, we first developed a
146 series of Bayesian hierarchical models that quantify how the three ecological
147 metrics are related to key socioeconomic drivers of resource exploitation, while
148 controlling for environmental conditions and sampling techniques (4, 11,
149 12)(Fig. S2; Table S3). We then used the posterior distributions from these
150 models to calculate how the probability of simultaneously meeting multiple
151 goals changes along a gradient of human pressure, while holding other
152 covariates constant (4) (Fig. 2, S3, S4). We measured human pressure as the
153 size of human populations in the surrounding seascape divided by the
154 accessibility (in minutes of travel time squared) of our reef sites to them - an
155 adaptation of the economic gravity model used to measure the 'gravitational
156 pull' of interactions such as trade and migration (4, 13). Human pressure
157 displayed the most consistent negative relationships to our response variables

158 (Fig. S2). The distribution of human pressure and other key socioeconomic and
159 environmental covariates among our surveyed reefs closely matches that of
160 reefs globally (Fig. S5). The probability of openly fished reef sites
161 simultaneously having all three metrics declined with our measure of human
162 pressure and the ambitiousness of the conservation target (Fig. 2A). In other
163 words, on openly fished reefs it is extremely unlikely that all three goals will be
164 simultaneously met where human pressure is intense, but this likelihood
165 increases where human pressure is low, particularly for the 25% and 50%
166 targets. There was considerable variability in how the probability of meeting
167 individual goals changed along a gradient of human pressure (Fig. 2B-D).
168
169 A critical gap remains in understanding the context in which different local
170 management tools can help to simultaneously achieve key goals (*14*, *15*). To
171 address this, we first examined the probability of reef sites in both fully
172 protected Marine Protected Areas (MPAs) (where fishing is prohibited) and
173 restricted fishing areas (where there are limitations on fishing gears used and
174 who can access the fishing grounds) in achieving key targets for the individual
175 and combined ecological metrics (Fig 2E-L). We then calculated the
176 'conservation gains' from employing these different forms of management
177 along a gradient of human pressure (*15*) (Fig. 2M-X). By conservation gain, we

178 refer to the difference in probability of achieving a specific target (e.g. 25% of
179 reference condition biomass) when fully protected MPAs or fishery restrictions
180 are implemented relative to openly fished areas. This concept gets at the idea
181 that contexts with maximal conservation gains highlight the best opportunities
182 for management to have the biggest impact; conversely, implementing
183 management in contexts with minimal conservation gains (either because goals
184 are already being met or because they are unlikely to be met regardless of
185 management) provides few returns for limited conservation resources (*16*).
186
187 Critically, we find that both fully protected MPAs and restricted fishing areas
188 have the potential to provide conservation gains, but the context under which
189 these gains can be maximized is highly variable depending on both the goal and
190 target (Fig. 2M-X). For simultaneously meeting fisheries, function, and
191 biodiversity, maximal conservation gains are from fully protected MPAs in the
192 lowest human pressure locations for the most ambitious target (75% of
193 reference conditions), but as targets become less ambitious, conservation gains
194 peak where human pressure is more intermediate (Fig. 2M). For all three
195 targets, there are minimal conservation gains in locations where human
196 pressure is most intense, which means that in this context, management is
197 unlikely to help meet these goals. For each independent goal, the context under

198 which conservation gains can be maximized varies considerably (Fig 2). Of note
199 is that trait diversity is the least responsive to management, with conservation
200 gains never reaching above 0.4.
201
202 We then simulated how the number of our openly fished sites achieving key
203 conservation targets would change if a fully protected MPA (Fig. 3) or fisheries
204 restrictions (Fig S6) were implemented, given the other conditions at our reef
205 sites. Our analysis reveals both key opportunities and constraints in the
206 capacity for local management to simultaneously meet multiple goals. On one
207 hand, for more than 50% of our fished sites, the implementation of a fully
208 protected MPA is predicted to help achieve multiple goals (Fig. 3A). On the
209 other hand, less than 1% of the sites starting below 25% of reference conditions
210 are predicted to achieve the 75% of reference conditions target, highlighting
211 how the broader seascape context may stunt MPA potential in degraded reefs
212 (*15*). Indeed, more than half of the 87.4% of openly fished reefs starting below
213 25% of reference conditions are predicted to remain in the that same category
214 (Fig 3A). Additionally, our analysis shows that even where fishable biomass is
215 very low, scraping potential and trait diversity are often >25% of reference
216 conditions (Fig. 3B-D); a finding supported by previous research showing that
217 herbivores and a diversity of traits can still persist on degraded reefs (*17*).

In situations where 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 pattern, but typically lower magnitude, of conservation gains than fully protected MPAs, particularly for achieving the combined goal and fisheries goal (Fig 2Q-X, Fig S6). Of note is that for parrotfish scraping potential, fishing restrictions provide the same conservation gains as MPAs, 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 (Fig. 2, S2). A key finding is that conservation gains tend to change non-linearly with human pressure, which means that relatively small changes in the context

where management is implemented could have big impacts on whether key goals are likely to be met (Fig. 2M-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 impact 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 like trait diversity. While international action on climate change will be crucial for ensuring a future for coral-dominated reefs (*1, 2*), effective management will also be critical to sustaining reefs and the millions of livelihoods that depend on them.

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Supplementary Materials
Materials and Methods

390 Table S1 – S7
391 Fig S1 – S4
392 References (24 – 59)
393

394 **Figure Legends**

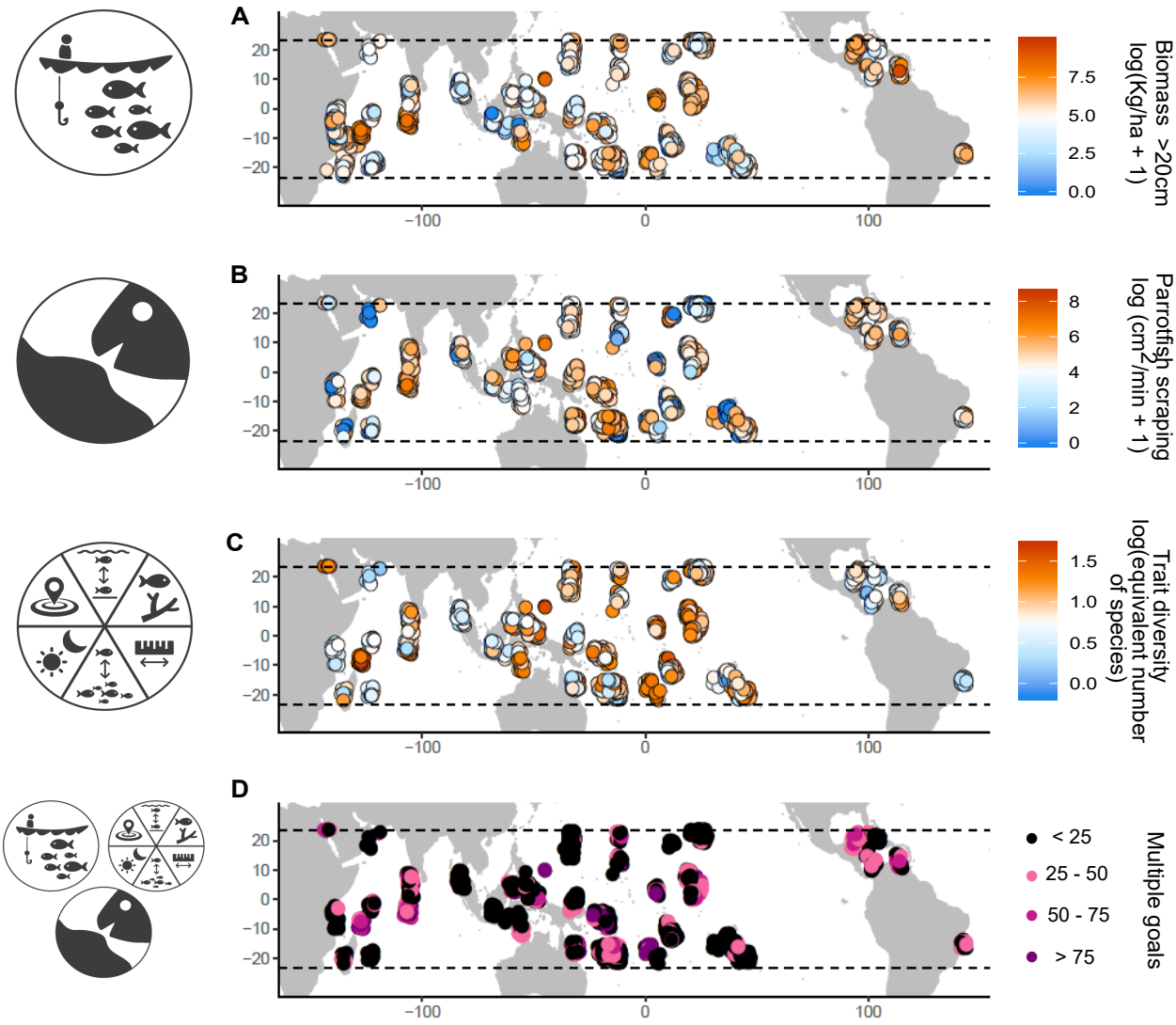
395 **Figure 1| Meeting multiple goals on coral reefs.** The distribution of (A)
396 biomass of reef fish >20cm (n=1798), (B) parrotfish scraping potential
397 (n=1662), and (C) trait diversity (n=1662), all in natural log and corrected for
398 sampling (*4*). Differences in the number of sites are because one data provider
399 collected data at the family level, which could not be used in calculating
400 parrotfish scraping potential or trait diversity. Parrotfishes were not detected
401 at 31% of our reef sites (Fig. S1). (D) Sites that simultaneously have fish
402 biomass, parrotfish scraping potential, and trait diversity at >75% (purple), 50-
403 75% (dark pink), 25-50% (light pink), and <25% (black) of reference
404 conditions (*4*). Points are jittered to allow for visualization of overlapping reef
405 sites.

406

407 **Figure 2 | The estimated probability of openly fished reef sites having 25,**
408 **50, and 75% of reference conditions (light, medium, and dark purple,**
409 **respectively).** (A) a combination of fish biomass (>20cm), parrotfish scraping
410 potential, trait diversity, and (B-D) each metric, respectively, along a gradient
411 of human pressure (gravity). Separate estimates are provided for reef sites in

412 fully protected Marine Protected Areas (MPAs) where fishing is prohibited (E-
413 H) and with restricted fishing (I-L). To highlight how the potential benefits of
414 management change along a gradient of human pressure (gravity), we
415 extracted the difference in the probability of achieving each target between
416 MPAs and openly fished sites (M-P), restricted and openly fished areas (Q-T),
417 and MPAs and restricted areas (U-X). We plotted the partial effect of the
418 relationship between gravity and each target by setting all other continuous
419 covariates to 0 (because they were all standardized) and all categorical
420 covariates to their most common category (i.e. 4-10m for depth, slope for
421 habitat, standard belt transect for census method). Gravity (x axis) is
422 standardized, with an average of 0.
423
424 **Fig. 3| Conservation target outcomes from simulating the implementation**
425 **of fully protected Marine Protected Areas (MPAs) in openly fished sites.**
426 Alluvial plots show the change in the number of sites expected to achieve key
427 conservation targets if MPAs were implemented in our openly fished sites for
428 (A) simultaneously meeting fish biomass, parrotfish scraping potential, and
429 trait diversity, and (B-D) each goal, respectively. The left hand side of each plot
430 shows the current conditions and the right hand side shows the expected

431 conditions if MPAs were implemented. Black <25%, light pink =25-50%, dark
432 pink=50-75%, and purple >75% of reference conditions.
433
434


A
B
C
D
20
10
0
−10
−20
−100
0
100
Biomass >20cm
log(Kg/ha + 1)
7.5
5.0
2.5
0.0
Parrotfish scraping
log (cm²/min + 1)
8
6
4
2
0
Trait diversity
log(equivalent number
of species)
1.5
1.0
0.5
0.0
Multiple goals
< 25
25 - 50
50 - 75
> 75



Openly fished

MPA

Restricted

Probability

A B C D

E F G H

J K L

MPA

Openly fished

Restricted

Openly fished

MPA

Restricted

Difference in probability

M N O P

Q R S T

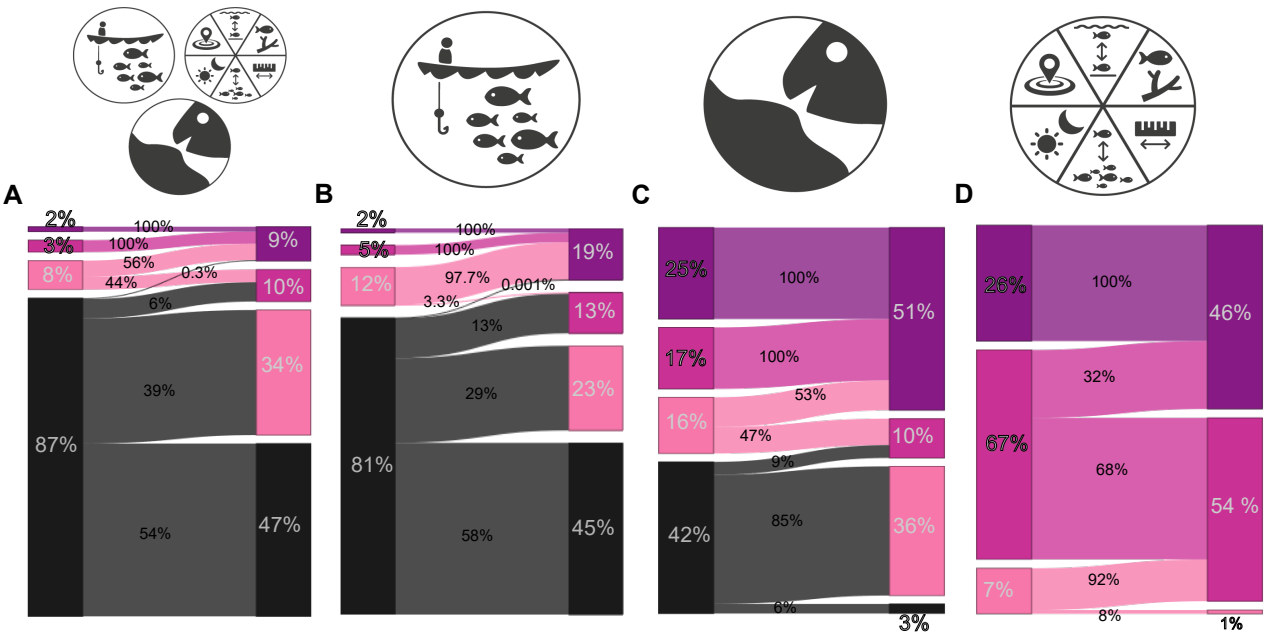
U V W X

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Science
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Supplementary Materials for

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

Joshua E. Cinner, Jessica Zamborain-Mason, Georgina G. Gurney, Nicholas A.J. Graham, M. Aaron MacNeil, Andrew S. Hoey, Camilo Mora, Sébastien Villéger, Eva Maire, Tim R. McClanahan, Joseph M. Maina, John N. Kittinger, Christina C. Hicks, Stephanie D'agata, Cindy Huchery, Michele L. Barnes, 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, Sebastian C.A. Ferse, U. Rashid Sumaila, Marah J. Hardt, David Mouillot

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Materials and Methods

Scales of data

Our data were organized at four spatial scales: survey (n=4399), reef site (n=1797), reef cluster (n=734), and nation/state (n=41).

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

ii) reef sites were aggregations of replicate surveys within a few hundred meters. There were an average of 2.4 replicate surveys per reef site.

iii) reef clusters- We clustered reef sites together that were within 4 km of each other, and used the centroid of these reef clusters to estimate certain social and environmental covariates (Table S3). To make reef clusters, we first estimated the linear distance between all reef sites, then used a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reef sites. We set the cut-off at 4 km to select mutually exclusive reef clusters where reef sites cannot be more distant than 4 km. The choice of 4km was informed by a 3-year study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities (*24*). This clustering analysis was carried out using the R functions 'hclust' and 'cutree', resulting in an average of 2.7 reef sites/reef cluster.

iv) Nation/state (nation, state, or territory). A larger scale in our analysis was 'nation/state', which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions, or extremely remote areas

within a state such as the Hawaii or the British Indian Ocean Territory; Table S1), within which reef clusters and reef sites were nested for analysis.

Reef fish survey methods

Estimates were based on instantaneous visual counts from 4399 surveys collected from 1798 tropical reef sites (i.e., within 23.5 latitude degrees). All surveys used standard belt-transects, distance sampling, or point-counts, and were conducted between 2004 and 2013. For each site, habitat type (i.e., slope, crest, flat, lagoon/back reef), depth range (i.e., 0-4m, 4-10m and >10m) and total sampling area were recorded. Where data from multiple years were available for a single reef site, we included only data from the year closest to 2010. Within each survey area, reef-associated fishes were identified to species level, abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. As part of our standardization process, we:

i) Retained families that were consistently studied and were above a minimum size cut-off. Thus, we retained counts of >10cm non-cryptic reef fishes from families that are resident on the reef (Table S4).

ii) Directly accounted for depth, survey method, survey area, and habitat as covariates in the model.

Key ecological metrics

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

i) *Biomass of reef fish above 20 cm*. We calculated total biomass of fish above 20 cm (TL) on each reef site (n= 1798) using standard published species-level length-weight relationship parameters or those available on FishBase (*25*). When length-weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus. Included families are specified in Table S4.

ii). *Parrotfish Scraping Potential*. Scraping rates (area grazed per minute) for parrotfishes at each reef site (n=1662) were calculated as the product of parrotfish fish density, feeding rate, and bite dimension (area) (*26*). Size-specific feeding rates were derived from best-fit regressions of bite rate (bites min^{-1}) and fish length ([TL], cm) for each species or closely related congener. Bite rates for Indo-Pacific parrotfishes were quantified at three locations (Great Barrier Reef, Australia; Indonesia; and the Red Sea) during which TL was estimated and the number of bites on different benthic substrata (primarily epilithic algal matrix and live corals) recorded 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, including for Atlantic parrotfishes (reviewed in (*27*)). Size-specific bite dimensions (mm^2) were taken from the literature (*26*, *28*–*30*).

iii). *Trait Diversity*. Trait diversity was computed for each reef site, considered as a local fish community (n=1662). First, we used the trait database on tropical reef fishes from Mouillot et al. (*31*) to describe species traits. The six traits considered were: (1) size (observed length of each individual fish) coded using 5 ordered categories: 10-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm, >80 cm; (2) mobility coded using 3 ordered

categories: sedentary, mobile within a reef, and mobile between reefs; (3) period of activity coded using 3 ordered categories: diurnal, both diurnal and nocturnal, and nocturnal; (4) schooling coded using 5 ordered categories: solitary, paired, or living in small (3-20 individuals), medium (20-50 individuals), or large groups (>50 groups) ; (5) vertical position in the water column coded using 3 ordered categories: benthic, bentho-pelagic, and pelagic; (6) diet coded using 7 trophic categories: herbivorous-detritivorous, macro-algal herbivorous, invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrates, planktivorous, piscivorous, and omnivorous, (i.e. fishes that feed on both vegetal and animal material). Since all traits were categorical, species with identical traits were grouped into entities. We then computed the Gower distance between all pairs of entities. Finally, for each fish community we computed trait-diversity using the Chao's FDq=1 index (7):

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

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 global species pool and equal biomasses.

We used species-level data to calculate parrotfish scraping potential and trait diversity. Thus, data from the one provider who only recorded family level data were not used in those response variables.

Social and environmental potential drivers

1. Management: For each reef site, we determined if it was: i) unfished- whether it fell within the borders of a high compliance fully protected Marine Protected Area (MPA); ii) restricted - whether there were active restrictions on gears (e.g. bans on the use of nets, spearguns, or traps) or fishing effort (which could have included areas under customary tenure, where 'outsiders' were effectively excluded, as well as inside marine parks that were not necessarily no take); or iii) openly fished - regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and triangulated this with a global database of MPA boundaries (*32*). As a sensitivity analysis, we also conducted analyses with a subset of fully protected MPAs that were >2km^2 and that have been protected for more than 4 years (see analysis section below).

2. Local Population Growth: We created a 100 km buffer around each reef cluster and used this to calculate human population within the buffer in 2000 and 2010 based on the Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database (*33*). Population

growth was the proportional difference between the population in 2000 and 2010. We chose a 100km buffer as a reasonable range at which many key human impacts from population (e.g., land-use and nutrients) might affect reefs (*34*).

3. Gravity: We adapted the economic geography concept of *gravity* (*13*, *15*, *35*, *36*) to examine the amount of human pressure within the surrounding 500km of a reef. Based on an analogy from Newtonian gravity (gravity=mass/distance^2), the gravity model (also called interactance) has been used by economists and geographers since the 1880s to measure the 'gravitational pull' of a wide range of economic interactions such as trade and migration flows (13). This application of the gravity concept infers that potential economic interactions increase with human population size (e.g. mass), but decay exponentially with the effective distance between two points. To calculate gravity, we gathered data on both population estimates and a surrogate for distance: travel time.

Population estimations

We gathered population estimates for every 1-by-1 km populated cell within a 500km radius of each reef site using the LandScan^{TM} 2011 database (*37*). We chose a 500km radius from the nearest settlement as the maximum distance any non-market fishing activities for fresh reef fish are likely to occur.

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 (*38*).

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 gravity 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)(*13*). 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 dependent on how that reef compares with all other alternatives, it makes sense that fishing pressure at any reef site will also decline by distance squared (i.e.

comparing with all other reefs within a similar distance) rather than linear distance (i.e. comparing only with other reefs along the same path). To test whether this rationale to use squared travel time is supported by our data, we developed gravity metrics using a range of exponents (^1, ^2, ^3) and used leave-one-out cross-validation for model selection to determine the best fit. Squared travel time performed best for all three response variables, which supports our decision to use that for our analysis. However, for parrotfish scraping, it travel time (i.e. exponent 1) was within the standard error. Due to the potential ambiguity in the parrotfish scraping potential, we ran a sensitivity test, calculating how the probabilities of achieving goals change along a gradient of human pressure using a gravity metric calculated using the first exponent (i.e. travel time in the denominator). There were no discernible differences between our results, suggesting that our decision to use travel time squared as opposed to travel time in the denominator did not meaningfully impact our results.

4. Human Development Index (HDI): HDI is a summary measure of human development encompassing: life expectancy, education, and per capita income. We obtained the HDI measure from the United Nations Development Program for 2010. In cases where HDI values were not available specific to the State (e.g. Hawaii), we used the national (e.g. USA) HDI value, and in other cases (e.g. Marshall Islands) we had to calculate HDI from life expectancy, education, and per capita income statistics.

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

Population in 2010. Data were derived mainly from the national census reports CIA fact book (https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html), and Wikipedia (https://en.wikipedia.org/wiki/Main_Page).

6. National Reef Fish Landings: Reconstructed reef fish catch estimates (in metric tonnes) were obtained from the Sea Around Us Project (SAUP) catch database (http://www.seaaroundus.org)(*39*). We used estimates corresponding to 2010 and only included reef associated species. We calculated the catch per unit area (catch/km^2/y) by dividing a nation/state's catch by the its estimated reef area (*40*).

7. Oceanic productivity: We examined oceanic net productivity for each reef following the procedure described by (*41*). We delimited a 100 km buffer around each of our reef clusters, we removed shallow waters pixels (those that intersected or were contained within the depth contour of 30m from the General Bathymetric Chart of the Oceans 2014 (http://www.gebco.net/), a global gridded bathymetry dataset) and then calculated the average of monthly chlorophyll-a concentration (proxy for phytoplankton biomass) using data provided at a 4km-resolution by Aqua MODIS (Moderate Resolution Imaging Spectro-radiometer) for years 2005 to 2010.

8. *Climate stress*. We included an index of climate stress for corals, developed by (*42*), which incorporated 11 different environmental conditions, including the mean and variability of sea-surface temperature, tidal range, ultraviolet radiation, a doldrum index, and chlorophyll.

Analyses

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 (*43*)); 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/). ; 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 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, correlations between mean body size of the fish assemblage (length, cm) and our response variables: biomass (r=0.73), parrotfish scraping potential (r=0.2), and trait diversity (r=0.4) suggest that mean body size is only predictive of biomass.

Multilevel models

To quantify the multi-scale social, environmental, and economic factors affecting the three ecological metrics, we modelled each response variable separately using multilevel models that explicitly recognized the three scales of spatial organization: reef site, reef cluster and nation/state. Models were run using a Bayesian approach using the Hamiltonian Monte Carlo algorithm implemented in Stan through the brms package (*44*) for 10000 iterations, and a 9000 burn in. This left 4000 samples in the posterior distribution of each parameter (four chains). We did not have a priori information about parameter distributions; thus, the posterior estimates were informed by the data alone (i.e. weakly informative priors). Convergence was monitored by running four chains from different starting points, examining posterior chains and distribution for stability, and checking that the potential scale reduction factor (also termed R_hat) was close to 1. We employed a gaussian distribution to analyze biomass of reef fish above 20 cm (log +1 transformed) and trait diversity (log transformed), and used a hurdle-lognormal to analyze parrotfish scraping potential because the data for this metric contained a large number of zeros (31 %). The hurdle model is a two-part model composed of (i) a binomial distribution and a logit link function to predict the probability of observing the herbivory function (i.e., whether the response outcome is positive or zero) and (ii) a lognormal distribution for the non-zero data.

For each model, we set reef cluster and nation/state as random effects to account for the hierarchical nature of the data (i.e. reef sites nested in reef clusters, reef clusters nested in nations/states). For each metric, we tested two alternate models: a null model, consisting only of the hierarchical units of observation (that is, intercepts-only) and a full model that included all

of our covariates (potential drivers) of interest. We used the null model as a baseline against which we could ensure through leave-one-out cross-validation information criteria (LOOIC) (*45*) that our full model performed better than a model with no covariate information. To account for any methodological effects, sampling area, census method, sampled habitat and depth were also included in all the models as covariates. To control for sampling effects, we marginalized response variables by subtracting the estimated sampling standardized mean model effects to the observed response variables. For all the analyses, continuous covariates were standardized (mean centered and divided by 2 standard deviations). To examine model fit and homoscedasticity, we conducted posterior predictive checks, checked residuals against fitted values and ensured residuals followed expected distributions around zero (e.g., for the gaussian distribution models we checked that residuals were normally distributed around zero). We also checked the residuals against all covariates included in the models, and the covariates described above that were not included in the models (primarily due to collinearity). The residuals of each of the three models showed no patterns with these covariates, suggesting they would not explain additional information in our models. Additionally, to account for the potential effect that MPA size and age could have on our response variables we ran two different analyses: (i) where we included all the high compliance MPAs in our data irrespective of size and age (N=106 reef sites); and (ii) where we only retained MPA sites that were above a minimum threshold of at least 2 km^2 and older than 4 years, (N=61 reef sites). These inclusion criteria were informed by the literature on MPA effectiveness, which suggests that a diameter of 1-2km (1-3km^2) is required to achieve partial protection (*46*), but were also constrained by our sample; a more conservative cutoff of say 10km^2 and 10 years would have left only 16 reef sites. In the main manuscript, we report (i),

but highlight the differences between (i) and (ii) in Fig. S7. All analyses were undertaken using R (3.02) statistic package.

Reference conditions and targets

We defined reference conditions for each ecological metric using the 0.9 quantile of the marginalized response variables accounting for sampling, habitat sampled, and sampling location (i.e., response variables minus the random effects and the model estimated effect sizes of depth category, reef habitat and sampling method). Thus, reference conditions are for average sampling area and "Slopes", "4-10m" and "Standard belt transects". As expected, the 90% reference point values for the fisheries target (biomass above 20 cm) was slightly below the expected total biomass in remote locations (*47*). Consequently, we then set targets of 25, 50, and 75% of these reference point conditions, the lower two of which correspond to typical standing biomass levels of multispecies maximum sustainable yields (hypothesized to be between 25-50% of unfished biomass estimates (*10*, *48*)). Meanwhile 75% of reference conditions is considered a more stringent conservation target. For consistency, we used the same reference conditions and targets (i.e. 25, 50, and 75% of reference conditions) for parrotfish scraping potential and trait diversity, although established ecological significance of these figures remains untested, and establishing benchmarks for these is an important area of future research, as is developing region-specific reference conditions. To avoid being overly prescriptive, we also ran our analyses for a range of reference conditions, based on 0.8 and 0.95 of the response variables, and incorporated the results in the supplemental information (Fig. S3-S4).

To estimate the probability of passing different thresholds under a gradient of gravity (e.g., Fig. 2), for each response variable, we simulated new data from the model posteriors where only gravity was modified (i.e., maintaining all the other covariates at average conditions, for slopes, 4-10 m of depth and standard belt transects and not including the random effects) and estimated the probability of the posterior samples being above or below the targets. To determine the probability of all three response variables passing the targets (i.e., co-occurrence of metrics), we used the subset of 1662 reef sites that had all three ecological metrics and multiplied the probabilities (i.e., assuming independence).

Potential conservation gains from management for our reef sites

To estimate the number of fished sites that would pass different targets if management (i.e., high compliance marine MPAs or restrictions) were implemented, we simulated new data for the posterior distributions maintaining sampling consistent (i.e., sampling method and sampling area) but allowing individual sites to have their own socio-ecological context (e.g., habitat, depth, HDI, random effects). Then, we changed their protection (from openly fished to high compliance MPAs or restricted) and simulated a new set of data based on that condition. This allowed us to estimate the number of our sites that could potentially pass different thresholds if management was implemented given the effect of management in our model and a site's own environmental and socio-economic context. We report the high compliance MPA results in the main manuscript and the restricted fishing in the supplemental information.

Fig. S1.

Correlations between the three key ecological metrics supported by fish communities on coral reefs.

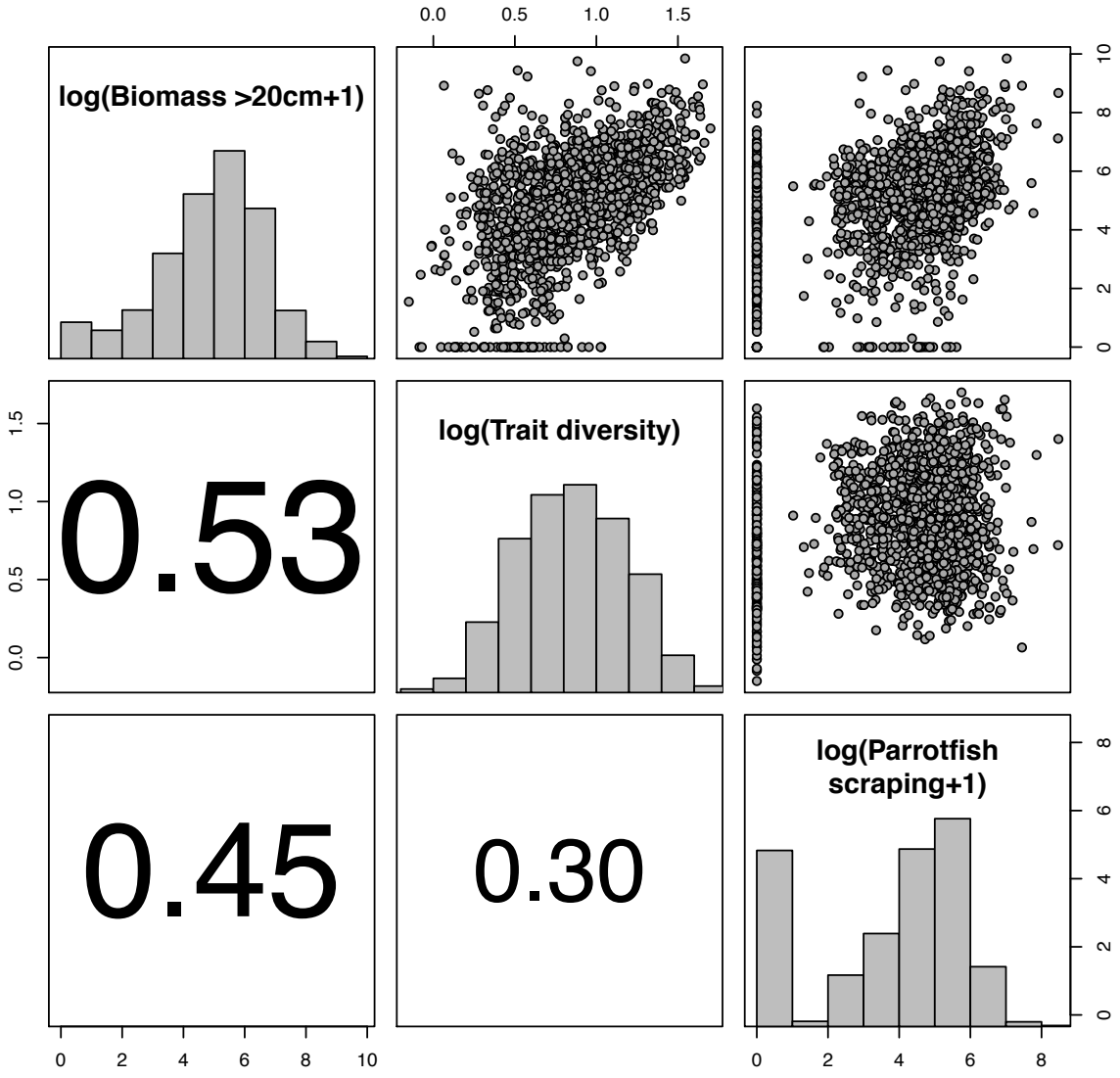


Fig. S2.

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).

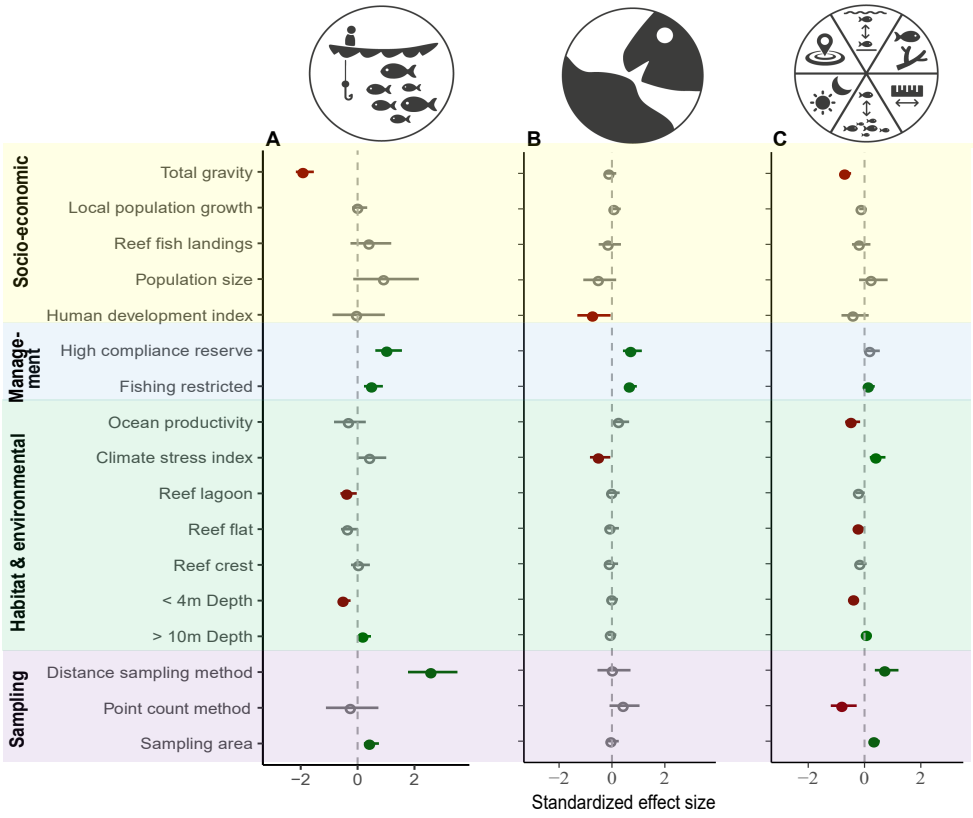


Fig. S3.

The estimated probability of openly fished reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively). (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 fully protected MPAs (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 MPAs and openly fished sites (M-P), restricted and openly fished areas (Q-T), and MPAs and restricted areas (U-X). We plotted the partial effect of the relationship between gravity and each benchmark 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).

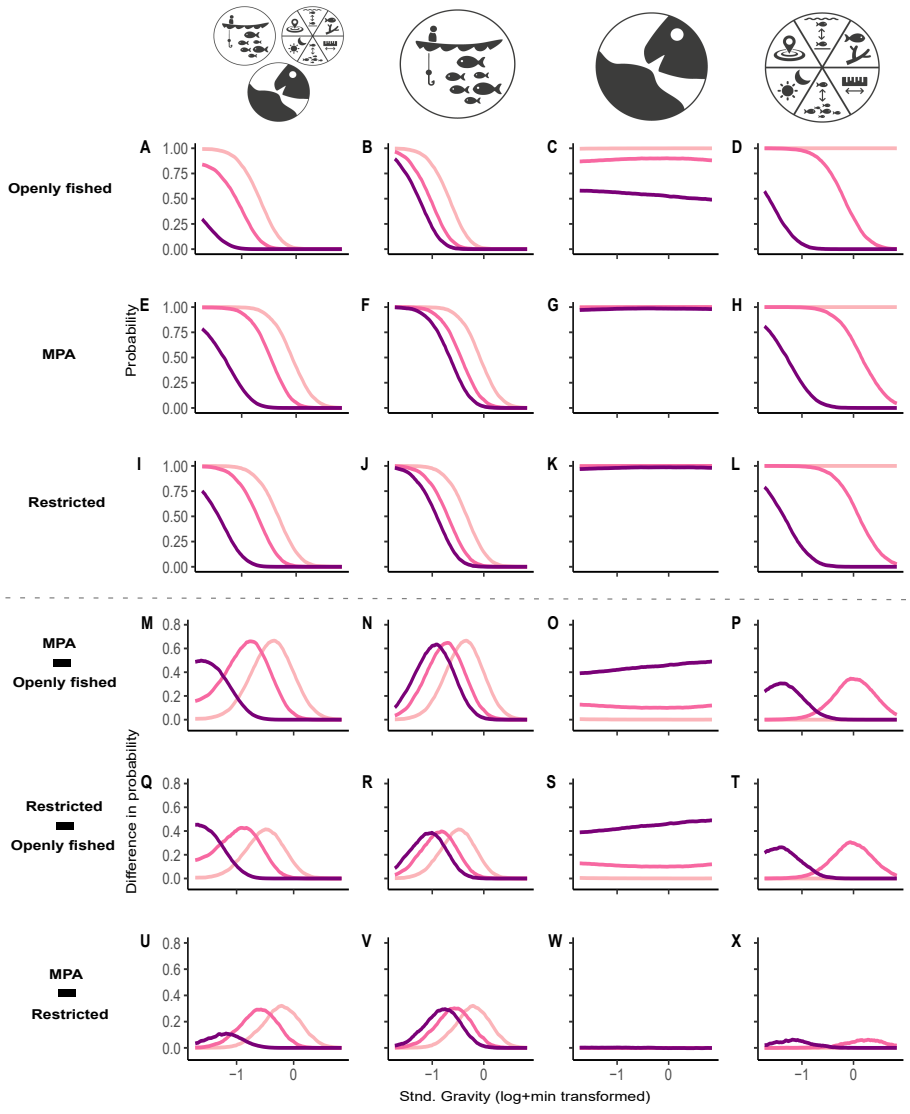


Fig. S4.

The estimated probability of openly fished reef sites having 25, 50, and 75% of reference conditions (light, medium, and dark purple, respectively). (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 MPAs (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 MPAs and openly fished sites (M-P), restricted and openly fished areas (Q-T), and MPAs and restricted areas (U-X). We plotted the partial effect of the relationship between gravity and each benchmark 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).

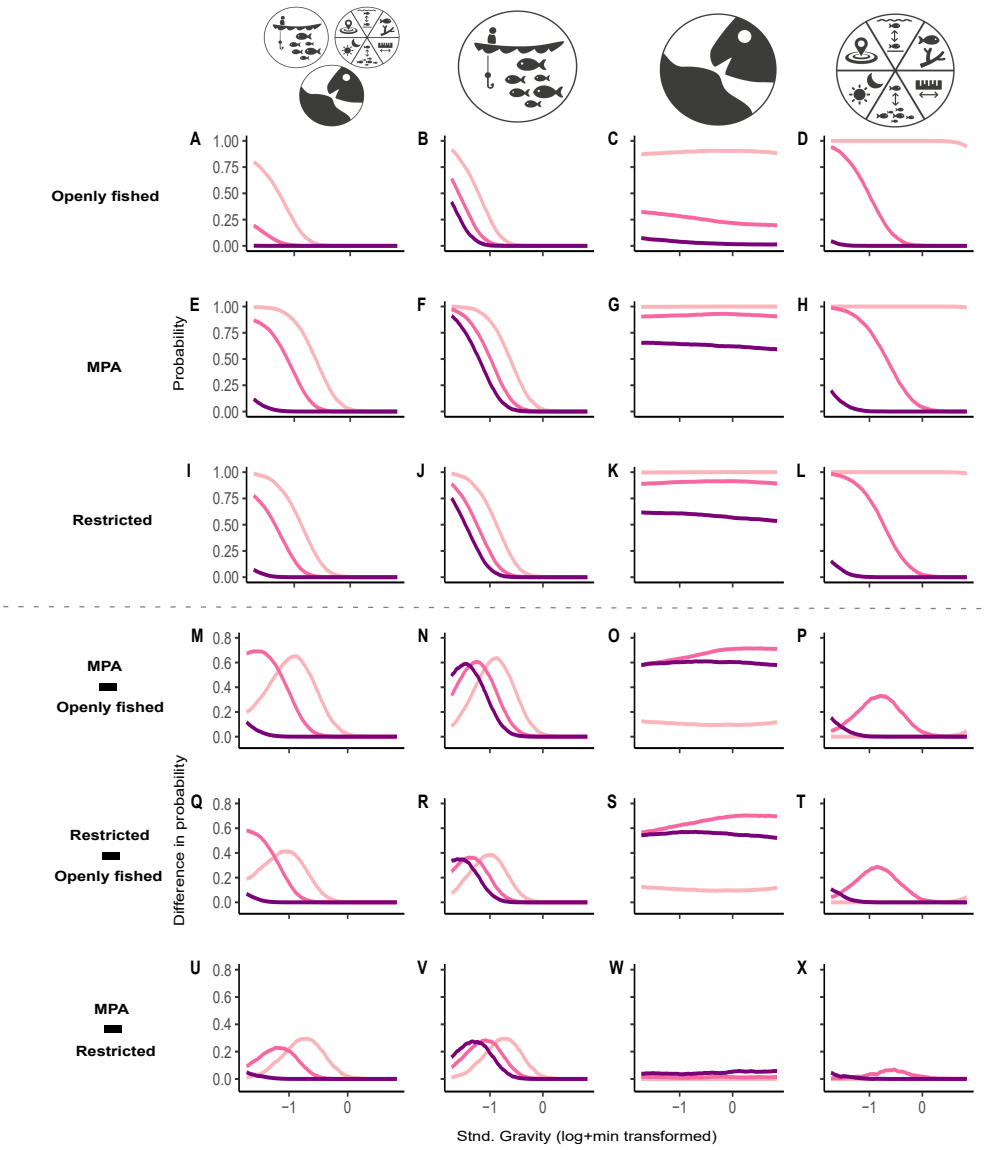


Fig. S5.

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.

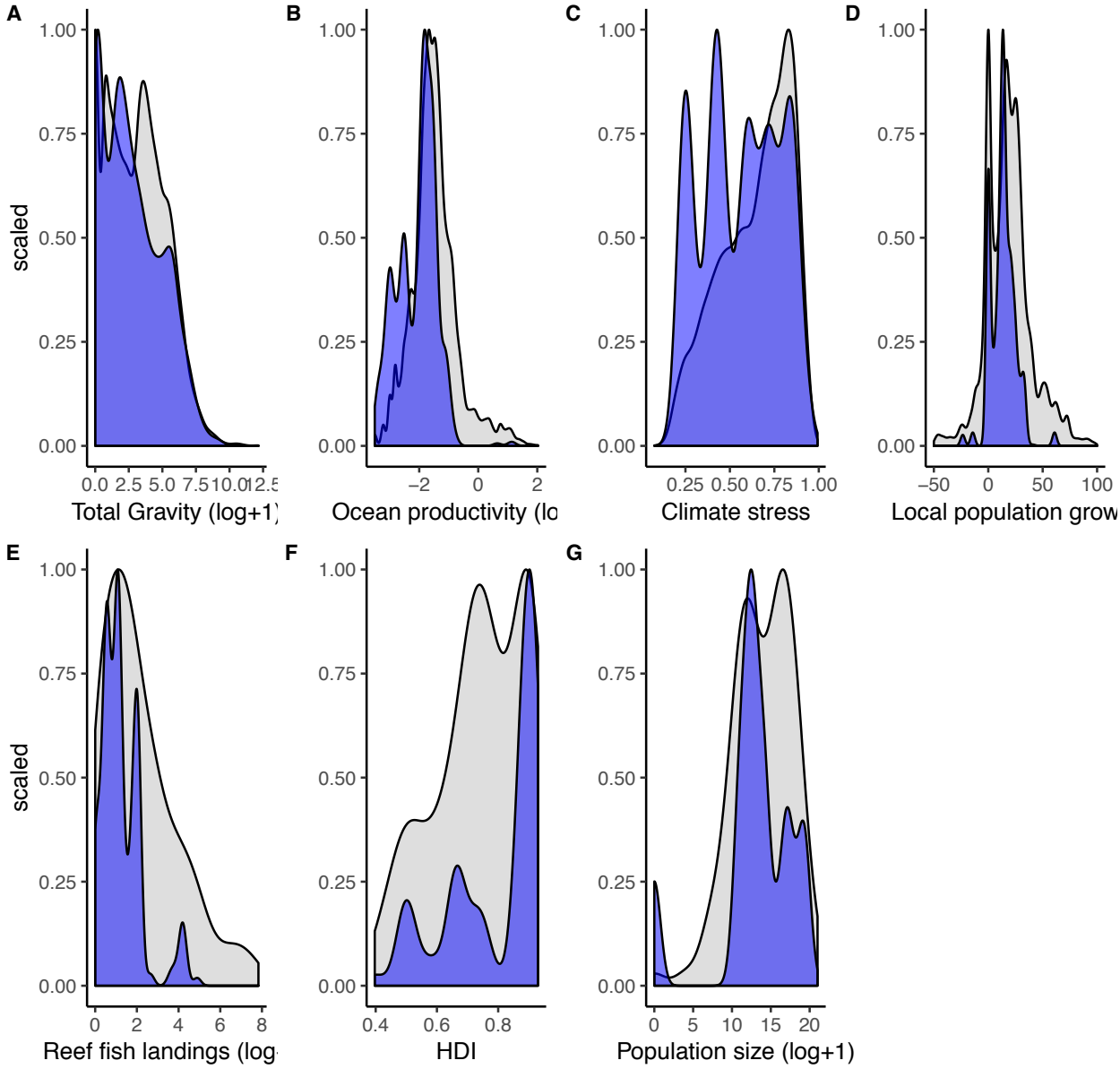


Fig. S6.

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.

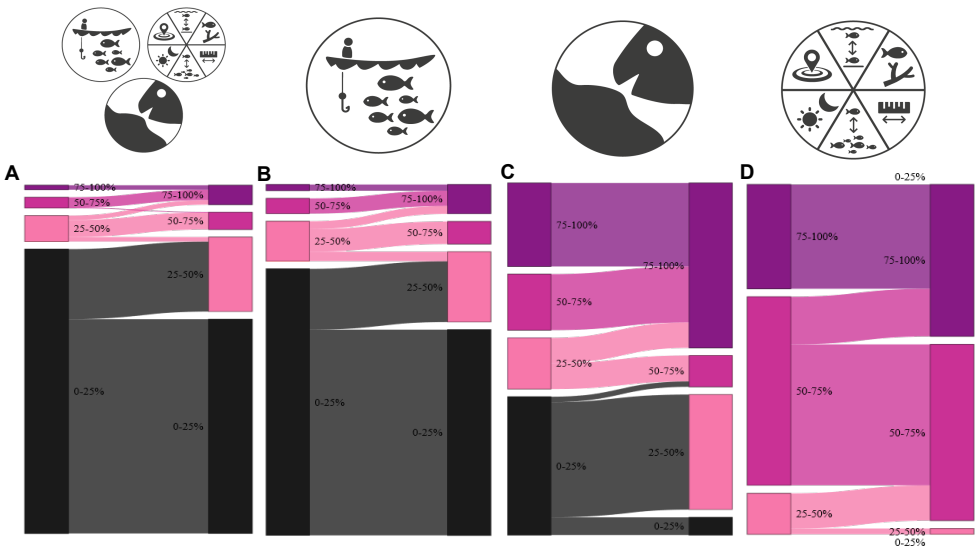


Fig. S7.

Difference in probability of achieving specific targets between the restricted subset of fully protected Marine Protected Areas (MPAs) (>2km^2 and 4 years old, n=61) and all MPAs in our sample (n=106). (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. Black <25%, light pink =25-50%, dark pink=50-75%, and purple >75% of reference conditions.

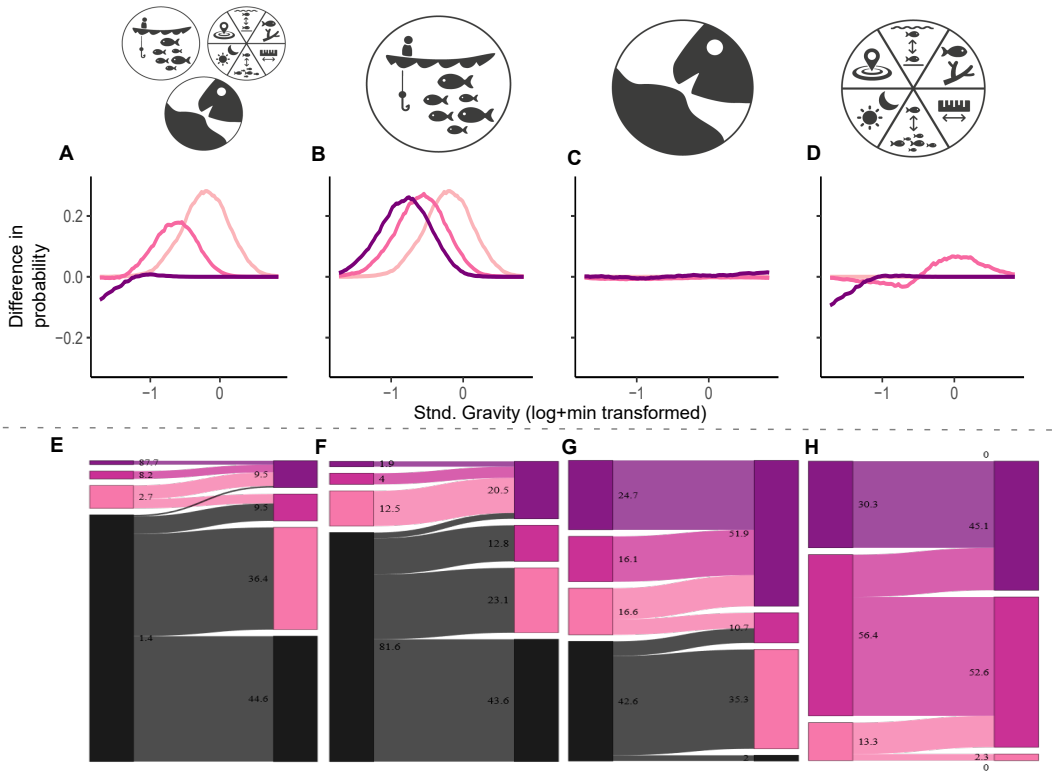


Table S1.

List of 'Nation/states' covered in study. In most cases, nation/state refers to an individual country, but can also include states (e.g. Hawaii), territories (e.g. British Indian Ocean Territory), or other jurisdictions.

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

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 (*49*). Additionally, large fish exert top-down control on ecosystems, regulating the structure and functions of reef ecosystems (*50*). Biomass captures both the size and number of fish above 20 cm in the system, which dictates the magnitude of the function (*51*). Biomass of fish above 20 cm is expected to decline rapidly as human impacts intensify (*10*), and there is empirical evidence that management can allow the recovery of large species (*52*).
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 (*49*) and respond positively to management (*53*).
Trait diversity	The diversity of ecological traits supported by species can represent the range of potential ecological roles present in a given community (*54*, *55*). 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 (*55*–*57*). We estimated trait diversity (TD) using the Chao's $FD_{q=1}$ index which is a generalization of the taxonomic Shannon's entropy index (7). 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 (*58*, *59*).

Table S3.

Summary of social and environmental covariates. Further details can be found in Methods. The smallest scale is the individual reef site. Reef clusters consist of clusters of reef sites within 4km of each other. Nation/states generally correspond to country, but can also include or territories or states, particularly when geographically isolated (e.g. Hawaii).

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 (*33*)
'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	Reef site	Human population size, land cover, road networks, coastlines

	get the total gravity of human pressure.		
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 Km^2 of reef	Nation/ state	Sea Around Us Project (*39*)
Climate stress	A composite metric comprised of 11 different environmental	Reef cluster	Maina et al. (*42*)

	variables that are related to coral mortality from bleaching		
Productivity	The monthly average (2005-2010) oceanic productivity	Reef cluster	Gove et al. 2013 (*41*), 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 m^2)	Reef site	Primary data

Table S4.

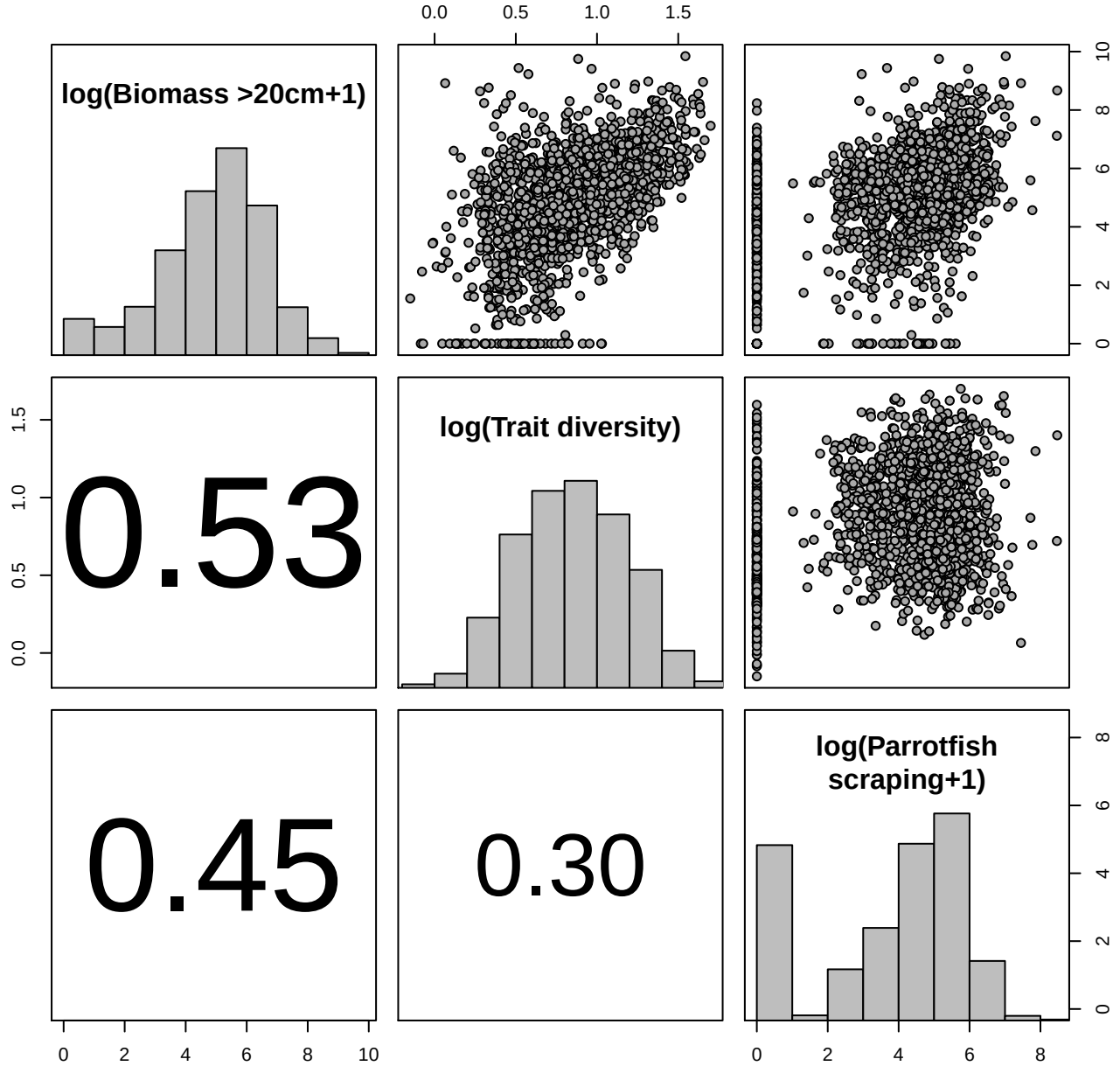
List of fish families included in this study for both the trait diversity and the biomass above 20 cm response variables.

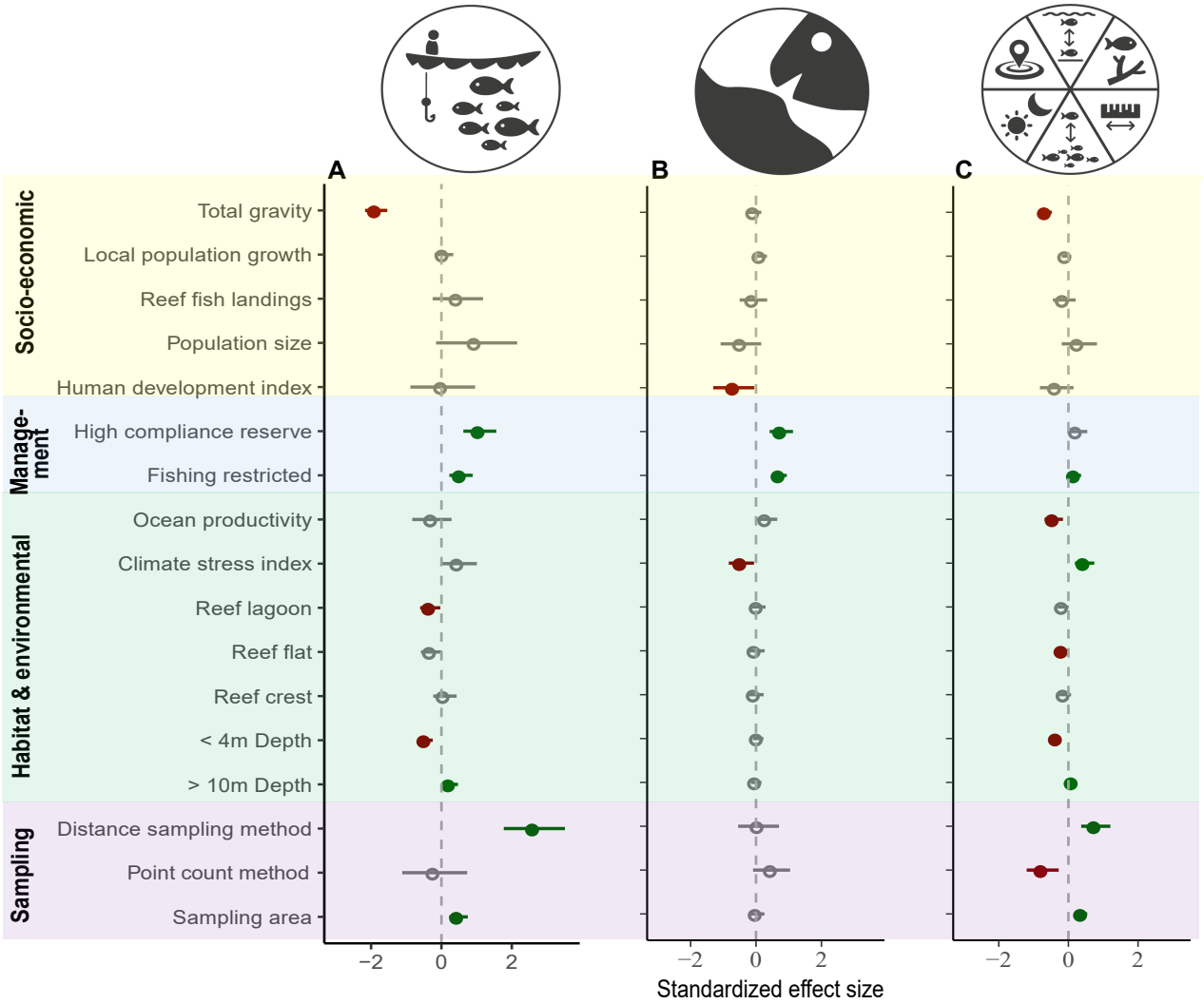
Fish family	Common family name
Acanthuridae	Surgeonfishes
Balistidae	Triggerfishes
Carangidae	Jacks
Diodontidae	Porcupinefishes
Ephippidae	Batfishes
Haemulidae	Sweetlips
Kyphosidae	Drummers
Labridae	Wrasses
Lethrinidae	Emperors
Lutjanidae	Snappers
Monacanthidae	Filefishes
Mullidae	Goatfishes
Nemipteridae	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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log(Biomass >20cm+1)
log(Trait diversity)
log(Parrotfish scraping+1)
0.53
0.45
0.30
0.0
0.5
1.0
1.5
0
2
4
6
8
10


A
B
C
Socio-economic
Total gravity
Local population growth
Reef fish landings
Population size
Human development index
Manage-ment
High compliance reserve
Fishing restricted
Habitat & environmental
Ocean productivity
Climate stress index
Reef lagoon
Reef flat
Reef crest
< 4m Depth
> 10m Depth
Sampling
Distance sampling method
Point count method
Sampling area
−2
0
2
Standardized effect size



Openly fished

MPA

Restricted

MPA
Openly fished

Restricted
Openly fished

MPA
Restricted

A B C D E F G H I J K L M N O P Q R S T U V W X

Probability

Difference in probability

1.00 0.75 0.50 0.25 0.00

0.8 0.6 0.4 0.2 0.0

−1 0

Stnd. Gravity (log+min transformed)



Openly fished

MPA

Restricted

MPA
Openly fished

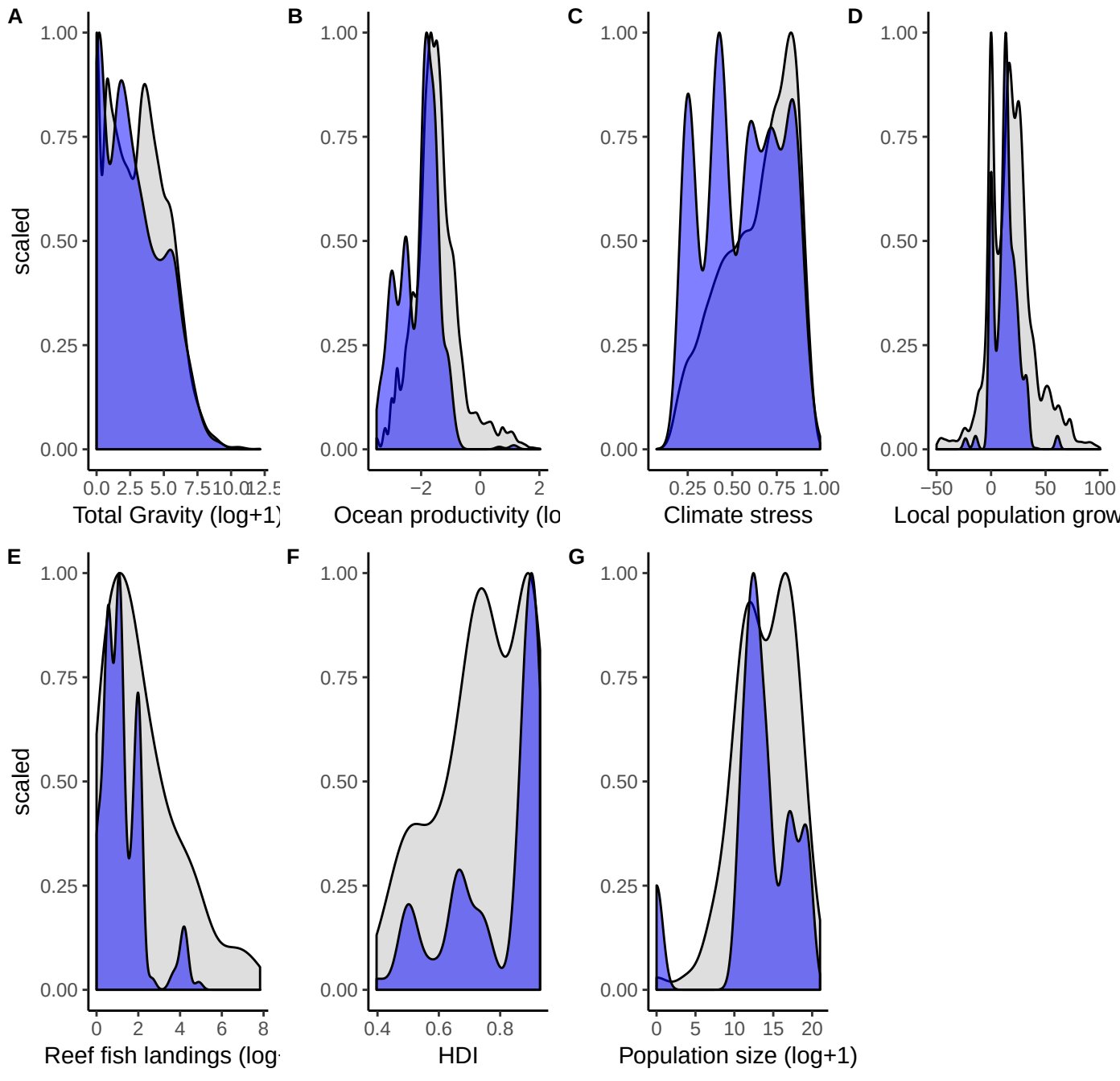
Restricted
Openly fished

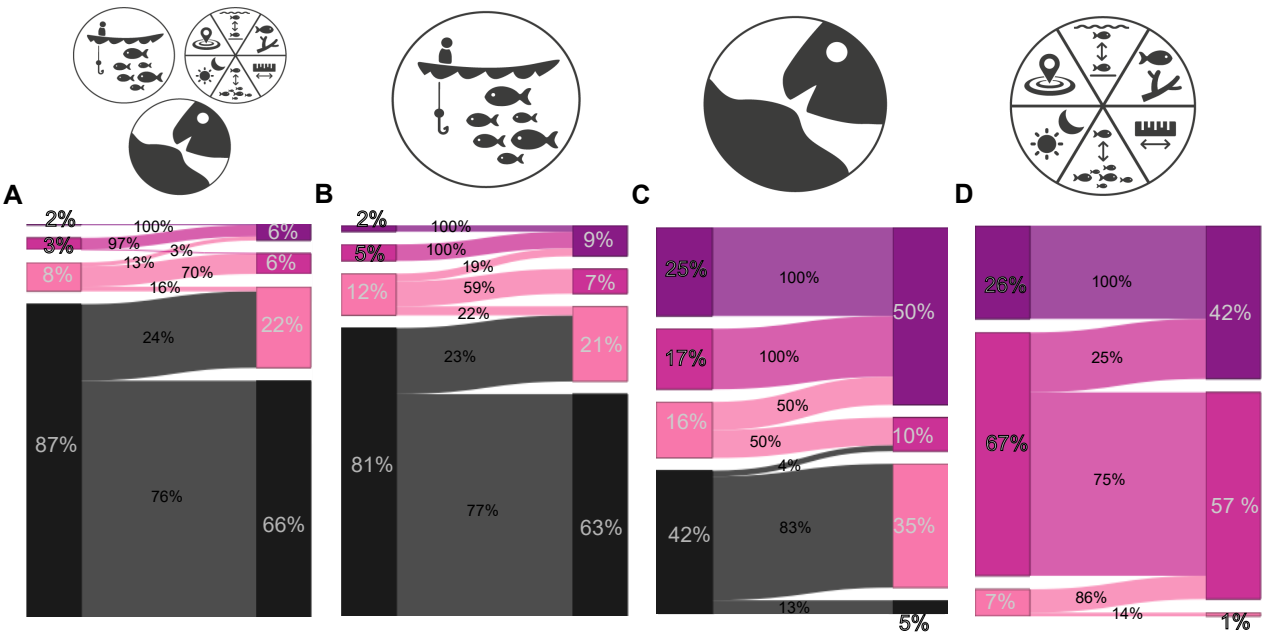
MPA
Restricted

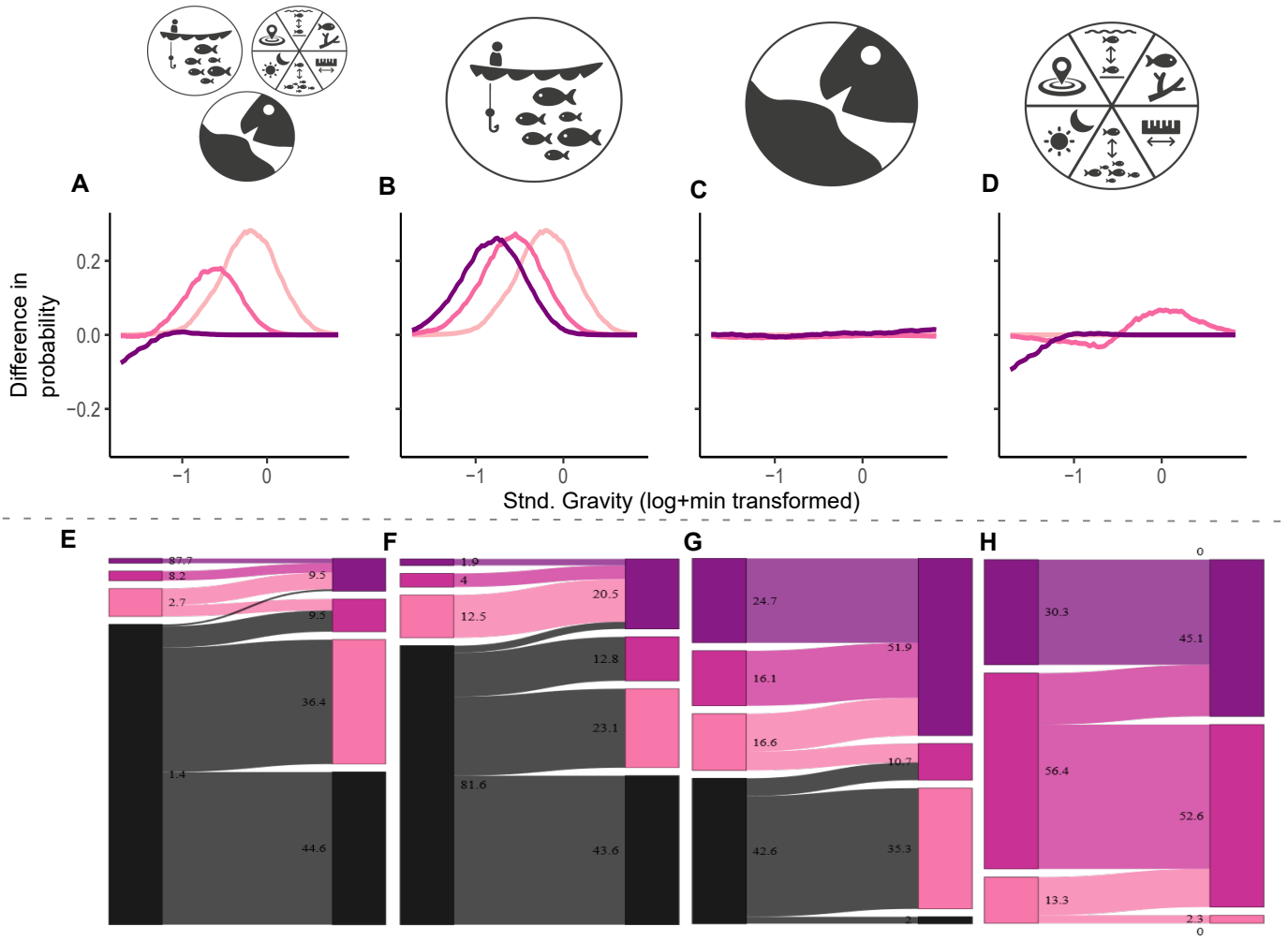
Probability

Difference in probability

Stnd. Gravity (log+min transformed)


A
B
C
D
E
F
G
scaled
scaled
1.00
0.75
0.50
0.25
0.00
0.0 2.5 5.0 7.5 10.0 12.5
Total Gravity (log+1)
−2 0 2
Ocean productivity (lo
0.25 0.50 0.75 1.00
Climate stress
−50 0 50 100
Local population grow
0 2 4 6 8
Reef fish landings (log
0.4 0.6 0.8
HDI
0 5 10 15 20
Population size (log+1)


A
2%
3%
8%
100%
97%
13%
3%
70%
16%
6%
6%
22%
24%
87%
76%
66%
B
2%
5%
12%
100%
100%
19%
59%
22%
9%
7%
21%
23%
81%
77%
63%
C
25%
17%
16%
42%
100%
100%
50%
50%
4%
83%
13%
50%
10%
35%
5%
D
26%
67%
7%
100%
25%
75%
86%
14%
42%
57 %
1%


A
B
C
D
Difference in probability
0.2
0.0
−0.2
−1
0
Stnd. Gravity (log+min transformed)
E
F
G
H
87.7
8.2
2.7
9.5
9.5
36.4
1.4
44.6
1.9
4
12.5
20.5
12.8
23.1
81.6
43.6
24.7
16.1
16.6
51.9
10.7
42.6
35.3
30.3
45.1
56.4
52.6
13.3
2.3
0