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## Bright spots among the world's coral reefs

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1 **Bright spots among the world's coral reefs**

2

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76

77 **Ongoing declines among the world's coral reefs<sup>1,2</sup> require novel approaches to**  
78 **sustain these ecosystems and the millions of people who depend on them<sup>3</sup>. A**  
79 **presently untapped approach that draws on theory and practice in human health**  
80 **and rural development<sup>4,5</sup> is systematically identifying and learning from the**  
81 **'outliers'- places where ecosystems are substantially better ('bright spots') or**  
82 **worse ('dark spots') than expected, given the environmental conditions and**  
83 **socioeconomic drivers they are exposed to. Here, we compile data from more**  
84 **than 2,500 reefs worldwide and develop a Bayesian hierarchical model to**  
85 **generate expectations of how standing stocks of reef fish biomass are related to**  
86 **18 socioeconomic drivers and environmental conditions. We then identified 15**  
87 **bright spots and 35 dark spots among our global survey of coral reefs, defined as**  
88 **sites that had biomass levels more than two standard deviations from**  
89 **expectations. Importantly, bright spots were not simply comprised of remote**  
90 **areas with low fishing pressure- they include localities where human populations**  
91 **and use of ecosystem resources is high, potentially providing novel insights into**  
92 **how communities have successfully confronted strong drivers of change.**  
93 **Alternatively, dark spots were not necessarily the sites with the lowest absolute**  
94 **biomass and even included some remote, uninhabited locations often considered**  
95 **near-pristine<sup>6</sup>. We surveyed local experts about social, institutional, and**  
96 **environmental conditions at these sites to reveal that bright spots were**  
97 **characterised by strong sociocultural institutions such as customary taboos and**  
98 **marine tenure, high levels of local engagement in management, high dependence**  
99 **on marine resources, and beneficial environmental conditions such as deep-**  
100 **water refuges. Alternatively, dark spots were characterised by intensive capture**  
101 **and storage technology and a recent history of environmental shocks. Our**

102 **results suggest that investments in strengthening fisheries governance,**  
103 **particularly aspects such as participation and property rights, could facilitate**  
104 **innovative conservation actions that help communities defy expectations of**  
105 **global reef degradation.**

106



107 *Main text*

108 Despite substantial international conservation efforts, many of the world's ecosystems  
109 continue to decline<sup>1,7</sup>. Most conservation approaches aim to identify and protect  
110 places of high ecological integrity under minimal threat<sup>8</sup>. Yet, with escalating social  
111 and environmental drivers of change, conservation actions are also needed where  
112 people and nature coexist, especially where human impacts are already severe<sup>9</sup>. Here,  
113 we highlight an approach for implementing conservation in coupled human-natural  
114 systems focused on identifying and learning from outliers - places that are performing  
115 substantially better than expected, given the socioeconomic and environmental  
116 conditions they are exposed to. By their very nature, outliers deviate from  
117 expectations, and consequently can provide novel insights on confronting complex  
118 problems where conventional solutions have failed. This type of positive deviance, or  
119 'bright spot' analysis has been used in fields such as business, health, and human  
120 development to uncover local actions and governance systems that work in the  
121 context of widespread failure<sup>10,11</sup>, and holds much promise in informing conservation.

122

123 To demonstrate this approach, we compiled data from 2,514 coral reefs in 46  
124 countries, states, and territories (hereafter 'nation/states') and developed a Bayesian  
125 hierarchical model to generate expected conditions of how standing reef fish biomass  
126 (a key indicator of resource availability and ecosystem functions<sup>12</sup>) was related to 18  
127 key environmental variables and socioeconomic drivers (Box 1; Extended Data  
128 Tables 1,2; Methods). A key and significant finding from our global analysis is that  
129 the size and accessibility of the nearest market, more so than local or national  
130 population pressure, management, environmental conditions, or national  
131 socioeconomic context, was the strongest driver of reef fish biomass globally (Box 1).

132

133 Next, we identified 15 ‘bright spots’ and 35 ‘dark spots’ among the world’s coral reefs,  
134 defined as sites with biomass levels more than two standard deviations higher or  
135 lower than expectations from our global model, respectively (Fig. 1; Methods;  
136 Extended Data Table 3). Rather than simply identifying places in the best or worst  
137 condition, our bright spots approach reveals the places that most strongly defy  
138 expectations. Using them to inform the conservation discourse will certainly  
139 challenge established ideas of where and how conservation efforts should be focused.  
140 For example, remote places far from human impacts are conventionally considered  
141 near-pristine areas of high conservation value<sup>6</sup>, yet most of the bright spots we  
142 identified occur in fished, populated areas (Extended Data Table 3), some with  
143 biomass values below the global average. Alternatively, some remote places such as  
144 parts of the NW Hawaiian Islands underperform (i.e. were identified as dark spots).

145

146 Detailed analysis of why bright spots can evade the fate of similar areas facing  
147 equivalent stresses will require a new research agenda gathering detailed site-level  
148 information on social and institutional conditions, technological innovations, external  
149 influences, and ecological processes<sup>13</sup> that are simply not available in a global-scale  
150 analysis. As a preliminary hypothesis-generating exercise to begin uncovering why  
151 bright and dark spots may diverge from expectations, we surveyed data providers and  
152 other experts about the presence or absence of 10 key social and environmental  
153 conditions at the 15 bright spots, 35 dark spots, and 14 average sites with biomass  
154 values closest to model expectations (see Methods for details). Our survey revealed  
155 that bright spots were more likely to have high levels of local engagement in the  
156 management process, high dependence on coastal resources, and the presence of

157 sociocultural governance institutions such as customary tenure or taboos (Fig. 2,  
158 Methods). For example, in one bright spot, Karkar Island, Papua New Guinea,  
159 resource use is restricted through an adaptive rotational harvest system based on  
160 ecological feedbacks, marine tenure that allows for the exclusion of fishers from  
161 outside the local village, and initiation rights that limit individuals' entry into certain  
162 fisheries<sup>14</sup>. Bright spots were also generally proximate to deep water, which may help  
163 provide a refuge from disturbance for corals and fish<sup>15</sup> (Fig. 2, Extended Data Fig. 6).  
164 Conversely, dark spots were distinguished by having fishing technologies allowing  
165 for more intensive exploitation, such as fish freezers and potentially destructive  
166 netting, as well as a recent history of environmental shocks (*e.g.* coral bleaching or  
167 cyclone; Fig. 2). The latter is particularly worrisome in the context of climate change,  
168 which is likely to lead to increased coral bleaching and more intense cyclones<sup>16</sup>.  
169  
170 Our global analyses highlight two novel opportunities to inform coral reef governance.  
171 The first is to use bright spots as agents of change to expand the conservation  
172 discourse from the current focus on protecting places under minimal threat<sup>8</sup>, toward  
173 harnessing lessons from places that have successfully confronted high pressures.  
174 Our bright spots approach can be used to inform the types of investments and  
175 governance structures that may help to create more sustainable pathways for impacted  
176 coral reefs. Specifically, our initial investigation highlights how investments that  
177 strengthen fisheries governance, particularly issues such as participation and property  
178 rights, could help communities to innovate in ways that allow them to defy  
179 expectations. Conversely, the more typical efforts to provide capture and storage  
180 infrastructure, particularly where there are environmental shocks and local-scale  
181 governance is weak, may lead to social-ecological traps<sup>17</sup> that reinforce resource

182 degradation beyond expectations. Effectively harnessing the potential to learn from  
183 both bright and dark spots will require scientists to increase research efforts in these  
184 places, NGOs to catalyze lessons from other areas, donors to start investing in novel  
185 solutions, and policy makers to ensure that governance structures foster flexible  
186 learning and experimentation. Indeed, both bright and dark spots may have much to  
187 offer in terms of how to creatively confront drivers of change, identify the paths to  
188 avoid and those offering novel management solutions, and prioritizing conservation  
189 actions. Critically, the bright spots we identified span the development spectrum from  
190 low (Solomon Islands and Papua New Guinea) to high (territories of the USA and  
191 UK; Fig. 1) income, showing that lessons about effective reef management can  
192 emerge from diverse places.

193

194 A second opportunity stems from a renewed focus on managing the socioeconomic  
195 drivers that shape reef conditions. Many social drivers are amenable to governance  
196 interventions, and our comprehensive analysis (Box 1) shows how an increased policy  
197 focus on social drivers such as markets and development could result in  
198 improvements to reef fish biomass. For example, given the important influence of  
199 markets in our analysis, reef managers, donor organisations, conservation groups, and  
200 coastal communities could improve sustainability by developing interventions that  
201 dampen the negative influence of markets on reef systems. A portfolio of market  
202 interventions, including eco-labelling and sustainable harvesting certifications,  
203 fisheries improvement projects, and value chain interventions have been developed  
204 within large-scale industrial fisheries to increase access to markets for seafood that is  
205 sourced sustainably<sup>21-23</sup>. Although there is considerable scope for adapting these  
206 interventions to artisanal coral reef fisheries in both local and regional markets,

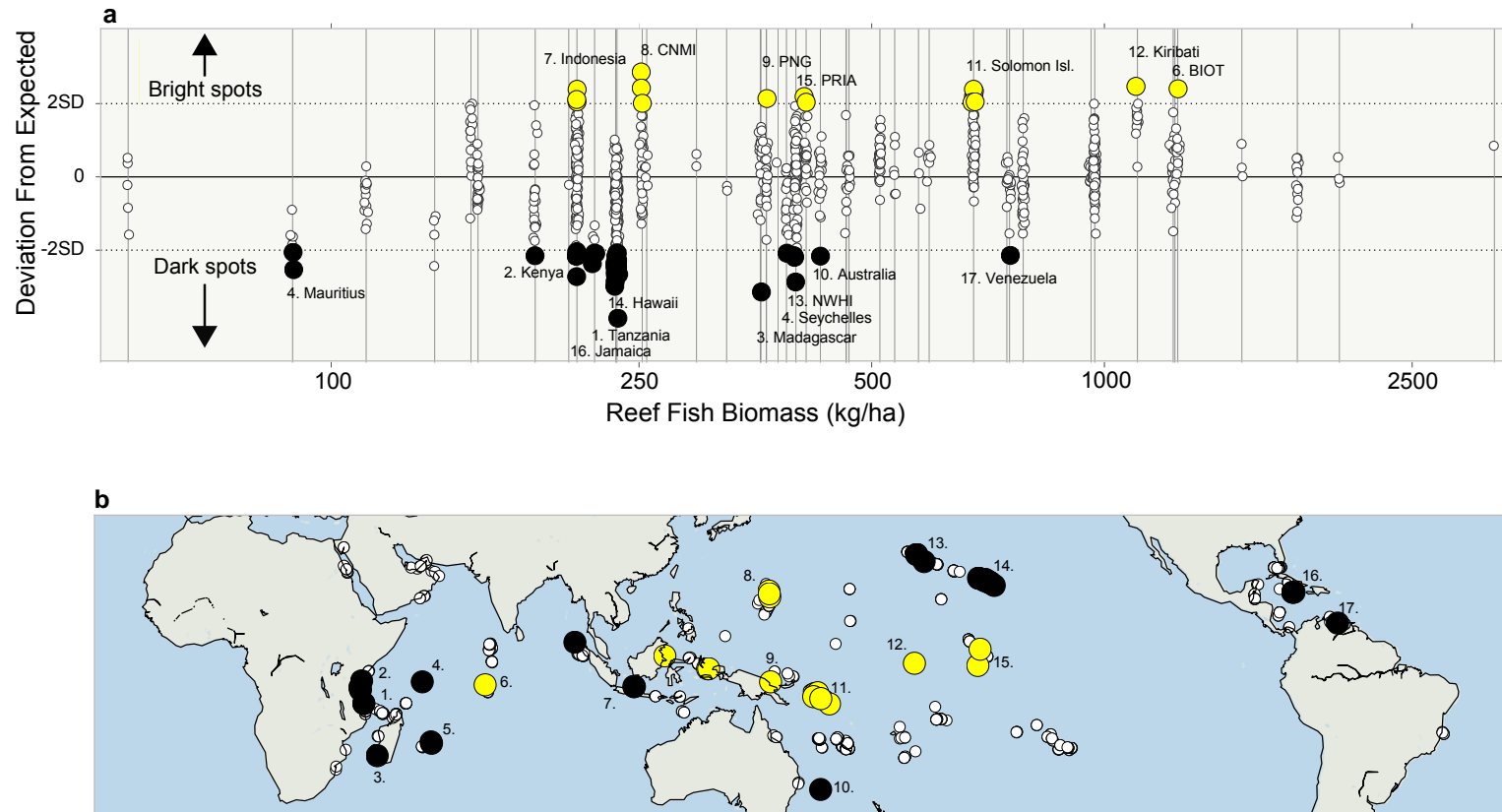
207 effectively dampening the negative influence of markets may also require developing  
208 novel interventions that address the range of ways in which markets can lead to  
209 overexploitation. Existing research suggests that markets create incentives for  
210 overexploitation not only by affecting price and price variability for reef products<sup>18</sup>, ,  
211 but also by influencing people's behavior<sup>19</sup>, including their willingness to cooperate in  
212 the collective management of natural resources<sup>20</sup>.

213

214 The long-term viability of coral reefs will ultimately depend on international action to  
215 reduce carbon emissions<sup>16</sup>. However, fisheries remain a pervasive source of reef  
216 degradation, and effective local-level fisheries governance is crucial to sustaining  
217 ecological processes that give reefs the best chance of coping with global  
218 environmental change<sup>25</sup>. Seeking out and learning from bright spots has uncovered  
219 novel solutions in fields as diverse as human health, development, and business<sup>10,11</sup>,  
220 and this approach may offer insights into confronting the complex governance  
221 problems facing coupled human-natural systems such as coral reefs.

222

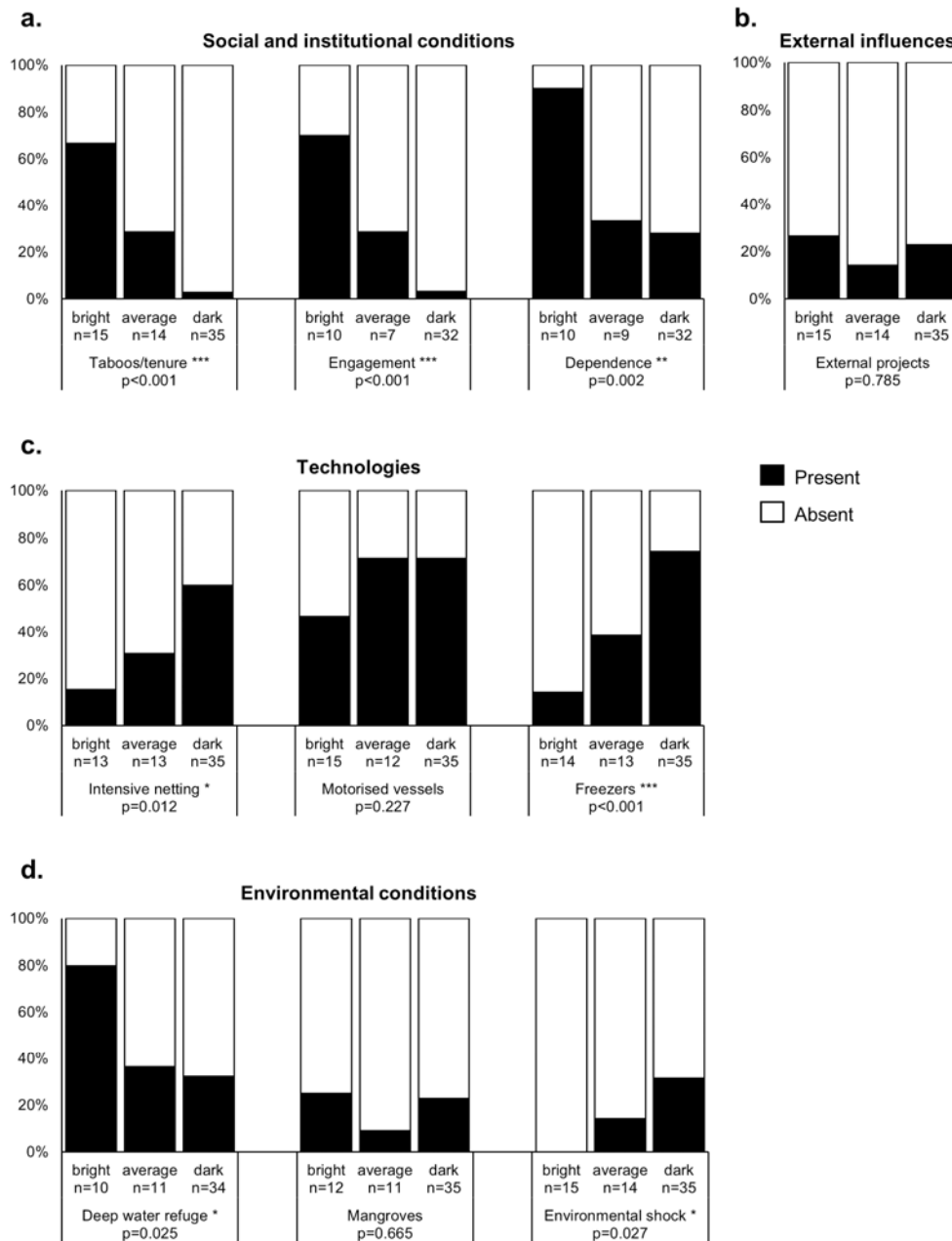
223 **Figures**



224

225 **Figure 1 | Bright and dark spots among the world's coral reefs.** (a) Each site's deviation from expected biomass (y-axis) along a gradient of  
 226 nation/state mean biomass (x-axis). Sites with biomass values >2 standard deviations above or below expected values were considered bright and  
 227 dark spots, respectively. The 15 bright and 35 dark spots are indicated with yellow and black dots respectively. Each grey vertical line represents

228 a nation/state in our analysis. Nation/states with bright or dark spots are labelled and numbered, corresponding to the numbers in panel b. There  
229 can be multiple bright or dark spots in each nation/state, thus the 50 bright and dark spots are distributed among 17 nation/states. As a  
230 conservative precaution, we did not consider a site a bright or dark spot if there were fewer than 5 sites sampled in a nation/state (Methods);  
231 consequently there is one site with biomass levels lower than 2 SD below expectations that is not labelled as a dark spot. BIOT= British Indian  
232 Ocean Territory (Chagos); PNG= Papua New Guinea; CNMI= Commonwealth of the Northern Mariana Islands; NWHI= Northwest Hawaiian  
233 Islands; PRIA= Pacific Remote Island Areas. (b) Map highlighting bright spots and dark spots with large circles, and other sites in small circles.  
234 Bright spots are mostly concentrated on islands of the Pacific and Southeast Asia, while dark spots are spread among every major tropical ocean  
235 basin.



236

237

**Figure 2 | Differences in social and environmental conditions between bright**

238

**spots, dark spots, and ‘average’ sites. \*=p<0.05, \*\*=p<0.01, \*\*\*=p<0.001. P**

239

values are determined using Fisher’s Exact test. Intensive netting includes beach seine

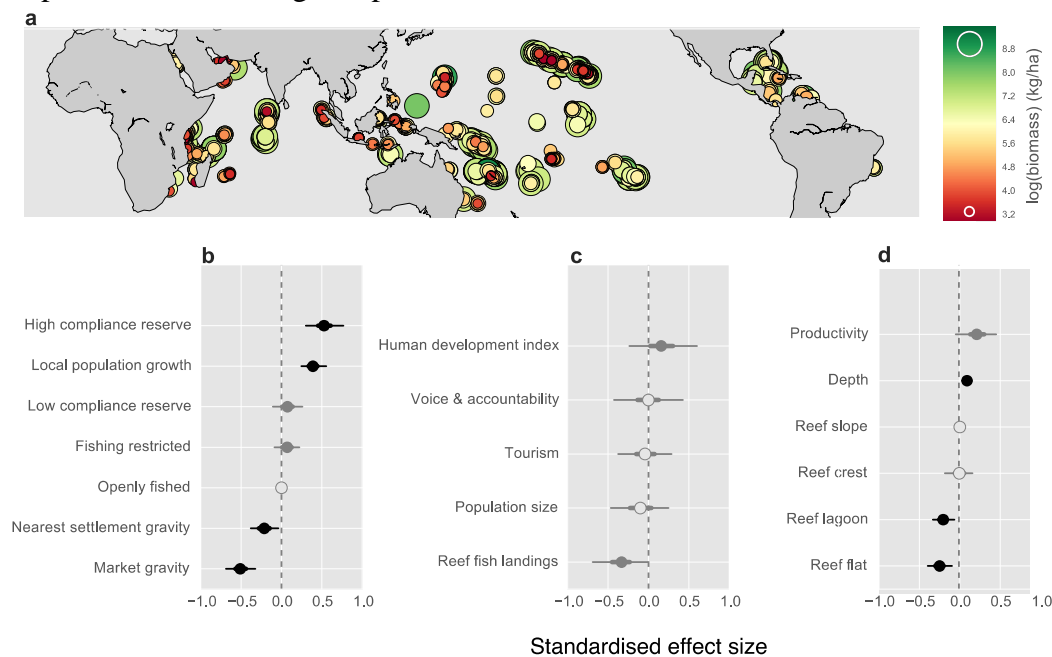
240

nets, surround gill nets, and muro-ami.



### Box 1

Drawing on a broad body of theoretical and empirical research in the social sciences<sup>24,26,27</sup> and ecology<sup>2,6,28</sup> on coupled human-natural systems, we quantified how reef fish biomass (panel a) was related to distal social drivers such as markets, affluence, governance, and population (panels b,c), while controlling for well-known environmental conditions such as depth, habitat, and productivity (panel d) (Extended Data Table 1, Methods). In contrast to many global studies of reef systems that are focused on demonstrating the severity of human impacts<sup>6</sup>, our examination seeks to uncover potential policy levers by highlighting the relative role of specific social drivers. Critically, the strongest driver of reef fish biomass (*i.e.* the largest standardized effect size) was our metric of potential interactions with urban centres, called market gravity<sup>29</sup> (Extended Data Fig. 1, 2, 3; Methods). Specifically, we found that reef fish biomass decreased as the size and accessibility of markets increased (Extended Data Fig. 2b, and Extended Data Fig. 3). Somewhat counter-intuitively, fish biomass was higher in places with high local human population growth rates, likely reflecting human migration to areas of better environmental quality<sup>30</sup> -a phenomenon that could result in increased degradation at these sites over time. We found a strong positive, but less certain relationship (*i.e.* a high standardized effect size, with >75% of the posterior distribution above zero) with the Human Development Index, meaning that reefs tended to be in better condition in wealthier nations/states (panel c). Our analysis also confirmed the role that marine reserves can play in sustaining biomass on coral reefs, but only when compliance is high (panel b), reinforcing the importance of fostering compliance for reserves to be successful.



**Global patterns and drivers of reef fish biomass. (a) Reef fish biomass [in (log)kg/ha] among 918 study sites across 46 nations/states. For illustration purposes and to avoid the overlap of sites in a global map, we display sites as points that vary in size and colour proportional to amount of fish biomass, with small, red dots indicating low fish biomass and large, green dots indicating high biomass. b-d) Standardised effect size of local scale social drivers, nation/state scale social drivers, and environmental covariates, respectively. Parameter estimates are Bayesian posterior median values, 95% uncertainty intervals (UI; thin lines), and 50% UI (thick lines). Black dots indicate that the 95% UI does not overlap 0; Grey closed circles indicates that 75% of the posterior distribution lies to one side of 0; and grey open circles indicate that the 50% UI overlaps 0.**

241 **Methods**

242

243 Scales of data

244 Our data were organized at three spatial scales: reef (n=2514), site (n=918), and  
245 nation/state (n=46).

246 i) reef (the smallest scale, which had an average of 2.4 surveys/transects -  
247 hereafter 'reef').

248 ii) site (a cluster of reefs). We clustered reefs together that were within 4km  
249 of each other, and used the centroid of these clusters (hereafter 'sites') to  
250 estimate site-level social and site-level environmental covariates  
251 (Extended Data Table 1). To make these clusters, we first estimated the  
252 linear distance between all reefs, then used a hierarchical analysis with the  
253 complete-linkage clustering technique based on the maximum distance  
254 between reefs. We set the cut-off at 4km to select mutually exclusive sites  
255 where reefs cannot be more distant than 4km. The choice of 4km was  
256 informed by a 3-year study of the spatial movement patterns of artisanal  
257 coral reef fishers, corresponding to the highest density of fishing activities  
258 on reefs based on GPS-derived effort density maps of artisanal coral reef  
259 fishing activities<sup>31</sup>. This clustering analysis was carried out using the R  
260 functions 'hclust' and 'cutree', resulting in an average of 2.7 reefs/site.

261 iii) Nation/state (nation, state, or territory). A larger scale in our analysis was  
262 'nation/state', which are jurisdictions that generally correspond to  
263 individual nations (but could also include states, territories, overseas  
264 regions, or extremely remote areas within a state such as the northwest

265 Hawaiian Islands; Extended Data Table 2), within which sites and reefs  
266 were nested for analysis.

267

### 268 Estimating Biomass

269 Reef fish biomass can reflect a broad selection of reef fish functioning and benthic  
270 conditions<sup>12,32-34</sup>, and is a key metric of resource availability for reef fisheries. Reef  
271 fish biomass estimates were based on instantaneous visual counts from 6,088 surveys  
272 collected from 2,514 reefs. All surveys used standard belt-transects, distance sampling,  
273 or point-counts, and were conducted between 2004 and 2013. Where data from  
274 multiple years were available from a single reef, we included only data from the year  
275 closest to 2010. Within each survey area, reef associated fishes were identified to  
276 species level, abundance counted, and total length (TL) estimated, with the exception  
277 of one data provider who measured biomass at the family level. To make estimates of  
278 biomass from these transect-level data comparable among studies, we:

279 i) Retained families that were consistently studied and were above a  
280 minimum size cut-off. Thus, we retained counts of >10cm diurnally-active,  
281 non-cryptic reef fish that are resident on the reef (20 families, 774 species),  
282 excluding sharks and semi-pelagic species (Extended Data Table 4). We  
283 also excluded three groups of fishes that are strongly associated with coral  
284 habitat conditions and are rarely targets for fisheries (Anthiinae,  
285 Chaetodontidae, and Cirrhitidae). We calculated total biomass of fishes on  
286 each reef using standard published species-level length-weight relationship  
287 parameters or those available on FishBase<sup>35</sup>. When length-weight  
288 relationship parameters were not available for a species, we used the  
289 parameters for a closely related species or genus.

- 290 ii) Directly accounted for depth and habitat as covariates in the model (see  
291 “environmental conditions” section below);
- 292 iii) Accounted for any potential bias among data providers (capturing  
293 information on both inter-observer differences, and census methods) by  
294 including each data provider as a random effect in our model.

295

296 Biomass means, medians, and standard deviations were calculated at the reef-scale.

297 All reported log values are the natural log.

298

### 299 Social Drivers

300 *1. Local Population Growth:* We created a 100km buffer around each site and used  
301 this to calculate human population within the buffer in 2000 and 2010 based on the  
302 Socioeconomic Data and Application Centre (SEDAC) gridded population of the  
303 world database<sup>36</sup>. Population growth was the proportional difference between the  
304 population in 2000 and 2010. We chose a 100km buffer as a reasonable range at  
305 which many key human impacts from population (e.g., land-use and nutrients) might  
306 affect reefs<sup>37</sup>.

307

308 *2. Management:* For each site, we determined if it was: i) unfished- whether it fell  
309 within the borders of a no-take marine reserve. We asked data providers to further  
310 classify whether the reserve had high or low levels of compliance; ii) restricted -  
311 whether there were active restrictions on gears (e.g. bans on the use of nets, spearguns,  
312 or traps) or fishing effort (which could have included areas inside marine parks that  
313 were not necessarily no take); or iii) fished - regularly fished without effective

314 restrictions. To determine these classifications, we used the expert opinion of the data  
315 providers, and triangulated this with a global database of marine reserve boundaries<sup>38</sup>.

316

317 3. *Gravity*: We adapted the economic geography concept of *gravity*, also called  
318 interactance<sup>39</sup>, to examine potential interactions between reefs and: i) major urban  
319 centres/markets (defined as provincial capital cities, major population centres,  
320 landmark cities, national capitals, and ports); and ii) the nearest human settlements  
321 (Extended Data Fig. 1). This application of the gravity concept infers that potential  
322 interactions increase with population size, but decay exponentially with the effective  
323 distance between two points. Thus, we gathered data on both population estimates and  
324 a surrogate for distance: travel time.

325

#### 326 *Population estimations*

327 We gathered population estimates for: 1) the nearest major markets (which  
328 includes national capitals, provincial capitals, major population centres, ports,  
329 and landmark cities) using the World Cities base map from ESRI<sup>TM</sup>; and 2) the  
330 nearest human settlement within a 500km radius using LandScan<sup>TM</sup> 2011  
331 database. The different datasets were required because the latter is available in  
332 raster format while the former is available as point data. We chose a 500km  
333 radius from the nearest settlement as the maximum distance any non-market  
334 fishing activities for fresh reef fish are likely to occur.

335

#### 336 *Travel time calculation*

337 Travel time was computed using a cost-distance algorithm that computes the  
338 least 'cost' (in minutes) of travelling between two locations on a regular raster

339 grid. In our case, the two locations were either: 1) the centroid of the site (i.e.  
340 reef cluster) and the nearest settlement, or 2) the centroid of the site and the  
341 major market. The cost (i.e. time) of travelling between the two locations was  
342 determined by using a raster grid of land cover and road networks with the  
343 cells containing values that represent the time required to travel across them<sup>40</sup>  
344 (Extended Data Table 5), we termed this raster grid a *friction-surface* (with the  
345 time required to travel across different types of surfaces analogous to different  
346 levels of friction). To develop the friction-surface, we used global datasets of  
347 road networks, land cover, and shorelines:

- 348 - Road network data was extracted from the Vector Map Level 0  
349 (VMap0) from the National Imagery and Mapping Agency's (NIMA)  
350 Digital Chart of the World (DCW®). We converted vector data from  
351 VMap0 to 1km resolution raster.
- 352 - Land cover data were extracted from the Global Land Cover 2000<sup>41</sup>.
- 353 -To define the shorelines, we used the GSHHS (Global Self-consistent,  
354 Hierarchical, High-resolution Shoreline) database version 2.2.2.

355

356 These three friction components (road networks, land cover, and water bodies)  
357 were combined into a single friction surface with a Behrmann map projection.  
358 We calculated our cost-distance models in R<sup>42</sup> using the *accCost* function of  
359 the '*gdistance*' package. The function uses Dijkstra's algorithm to calculate  
360 least-cost distance between two cells on the grid and the associated distance  
361 taking into account obstacles and the local friction of the landscape<sup>43</sup>. Travel  
362 time estimates over a particular surface could be affected by the infrastructure  
363 (e.g. road quality) and types of technology used (e.g. types of boats). These

364 types of data were not available at a global scale but could be important  
365 modifications in more localised studies.

366

367 *Gravity computation*

368 i) To compute the gravity to the nearest market, we calculated the population  
369 of the nearest major market and divided that by the squared travel time  
370 between the market and the site. Although other exponents can be used<sup>44</sup>, we  
371 used the squared distance (or in our case, travel time), which is relatively  
372 common in geography and economics. This decay function could be  
373 influenced by local considerations, such as infrastructure quality (e.g. roads),  
374 the types of transport technology (i.e. vessels being used), and fuel prices,  
375 which were not available in a comparable format for this global analysis, but  
376 could be important considerations in more localised adaptations of this study.

377 ii) To determine the gravity of the nearest settlement, we located the nearest  
378 populated pixel within 500kms, determined the population of that pixel, and  
379 divided that by the squared travel time between that cell and the reef site.

380 As is standard practice in many agricultural economics studies<sup>45</sup>, an assumption in  
381 our study is that the nearest major capital or landmark city represents a market.

382 Ideally we would have used a global database of all local and regional markets for  
383 coral reef fish, but this type of database is not available at a global scale. As a  
384 sensitivity analysis to help justify our assumption that capital and landmark cities  
385 were a reasonable proxy for reef fish markets, we tested a series of candidate  
386 models that predicted biomass based on: 1) cumulative gravity of all cities within  
387 500km; 2) gravity of the nearest city; 3) travel time to the nearest city; 4)  
388 population of the nearest city; 5) gravity to the nearest human population above 40

389 people/km<sup>2</sup> (assumed to be a small peri-urban area and potential local market); 6)  
390 the travel time between the reef and a small peri-urban area; 7) the population size  
391 of the small peri-urban population; 8) gravity to the nearest human population  
392 above 75 people/km<sup>2</sup> (assumed to be a large peri-urban area and potential market);  
393 9) the travel time between the reef and this large peri-urban population; 10) the  
394 population size of this large peri-urban population; and 11) the total population  
395 size within a 500km radius. Model selection revealed that the best two models  
396 were gravity of the nearest city and gravity of all cities within 500km (with a 3  
397 AIC value difference between them; Extended Data Table 6). Importantly, when  
398 looking at the individual components of gravity models, the travel time  
399 components all had a much lower AIC value than the population components,  
400 which is broadly consistent with previous systematic review studies<sup>46</sup>. Similarly,  
401 travel time to the nearest city had a lower AIC score than any aspect of either the  
402 peri-urban or urban measures. This suggests our use of capital and landmark cities  
403 is likely to better capture exploitation drivers from markets rather than simple  
404 population pressures. This may be because market dynamics are difficult to  
405 capture by population threshold estimates; for example some small provincial  
406 capitals where fish markets are located have very low population densities, while  
407 some larger population centres may not have a market. Downscaled regional or  
408 local analyses could attempt to use more detailed knowledge about fish markets,  
409 but we used the best proxy available at a global scale.

410

411 *4. Human Development Index (HDI):* HDI is a summary measure of human  
412 development encompassing: a long and healthy life, being knowledgeable, and having



413 a decent standard of living. In cases where HDI values were not available specific to  
414 the State (e.g. Florida and Hawaii), we used the national (e.g. USA) HDI value.

415

416 *5. Population Size:* For each Nation/state, we determined the size of the human  
417 population. Data were derived mainly from census reports, the CIA fact book, and  
418 Wikipedia.

419

420 *6. Tourism:* We examined tourist arrivals relative to the nation/state population size  
421 (above). Tourism arrivals were gathered primarily from the World Tourism  
422 Organization's Compendium of Tourism Statistics.

423

424 *7. National Reef Fish Landings:* Catch data were obtained from the Sea Around Us  
425 Project (SAUP) catch database ([www.searoundus.org](http://www.searoundus.org)), except for Florida, which  
426 was not reported separately in the database. We identified 200 reef fish species and  
427 taxon groups in the SAUP catch database<sup>47</sup>. Note that reef-associated pelagics such as  
428 scombrids and carangids normally form part of reef fish catches. However, we chose  
429 not to include these species because they are also targeted and caught in large  
430 amounts by large-scale, non-reef operations.

431

432 *8. Voice and Accountability:* This metric, from the World Bank survey on governance,  
433 reflects the perceptions of the extent to which a country's citizens are able to  
434 participate in selecting their government, as well as freedom of expression, freedom  
435 of association, and a free media. In cases where governance values were not available  
436 specific to the Nation/state (e.g. Florida and Hawaii), we used national (e.g. USA)  
437 values.

438

439 Environmental Drivers

440 *1. Depth:* The depth of reef surveys were grouped into the following categories: <4m,  
441 4-10m, >10m to account for broad differences in reef fish community structure  
442 attributable to a number of inter-linked depth-related factors. Categories were  
443 necessary to standardise methods used by data providers and were determined by pre-  
444 existing categories used by several data providers.

445

446 *2. Habitat:* We included the following habitat categories: i) Slope: The reef slope  
447 habitat is typically on the ocean side of a reef, where the reef slopes down into deeper  
448 water; ii) Crest: The reef crest habitat is the section that joins a reef slope to the reef  
449 flat. The zone is typified by high wave energy (i.e. where the waves break). It is also  
450 typified by a change in the angle of the reef from an inclined slope to a horizontal reef  
451 flat; iii) Flat: The reef flat habitat is typically horizontal and extends back from the  
452 reef crest for 10's to 100's of metres; iv) Lagoon / back reef: Lagoonal reef habitats  
453 are where the continuous reef flat breaks up into more patchy reef environments  
454 sheltered from wave energy. These habitats can be behind barrier / fringing reefs or  
455 within atolls. Back reef habitats are similar broken habitats where the wave energy  
456 does not typically reach the reefs and thus forms a less continuous 'lagoon style' reef  
457 habitat. Due to minimal representation among our sample, we excluded other less  
458 prevalent habitat types, such as channels and banks. To verify the sites' habitat  
459 information, we used the Millennium Coral Reef Mapping Project (MCRMP)  
460 hierarchical data<sup>48</sup>, Google Earth, and site depth information.

461

462 3. *Productivity*: We examined ocean productivity for each of our sites in mg C / m<sup>2</sup> /  
463 day (<http://www.science.oregonstate.edu/ocean.productivity/>). Using the monthly data  
464 for years 2005 to 2010 (in hdf format), we imported and converted those data into  
465 ArcGIS. We then calculated yearly average and finally an average for all these years.  
466 We used a 100km buffer around each of our sites and examined the average  
467 productivity within that radius. Note that ocean productivity estimates are less  
468 accurate for nearshore environments, but we used the best available data.

469

#### 470 Analyses

471 We first looked for collinearity among our covariates using bivariate correlations and  
472 variance inflation factor estimates (Extended Data Fig. 4, Extended Data Table 7).  
473 This led to the exclusion of several covariates (not described above): i) *Geographic*  
474 *Basin* (Tropical Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-  
475 Pacific); ii) *Gross Domestic Product* (purchasing power parity); iii) *Rule of Law*  
476 (World Bank governance index); iv) *Control of Corruption* (World Bank governance  
477 index); and v) *Sedimentation*. Additionally, we removed an index of climate stress,  
478 developed by Maina et al.<sup>49</sup>, which incorporated 11 different environmental  
479 conditions, such as the mean and variability of sea surface temperature due to  
480 repeated lack of convergence for this parameter in the model, likely indicative of  
481 unidentified multi-collinearity. All other covariates had correlation coefficients 0.7 or  
482 less and Variance Inflation Factor scores less than 5 (indicating multicollinearity was  
483 not a serious concern). Care must be taken in causal attribution of covariates that were  
484 significant in our model, but demonstrated colinearity with candidate covariates that  
485 were removed during the aforementioned process. Importantly, the covariate that

486 exhibited the largest effect size in our model, market gravity, was not strongly  
487 collinear with other candidate covariates.

488

489 To quantify the multi-scale social, environmental, and economic factors affecting reef  
490 fish biomass we adopted a Bayesian hierarchical modelling approach that explicitly  
491 recognized the three scales of spatial organization: reef ( $j$ ), site ( $k$ ), and nation/state ( $s$ ).

492

493 In adopting the Bayesian approach we developed two models for inference: a null  
494 model, consisting only of the hierarchical units of observation (i.e. intercepts-only)  
495 and a full model that included all of our covariates (drivers) of interest. Covariates  
496 were entered into the model at the relevant scale, leading to a hierarchical model  
497 whereby lower-level intercepts (averages) were placed in the context of higher-level  
498 covariates in which they were nested. We used the null model as a baseline against  
499 which we could ensure that our full model performed better than a model with no  
500 covariate information. We did not remove 'non-significant' covariates from the model  
501 because each covariate was carefully considered for inclusion and could therefore  
502 reasonably be considered as having an effect, even if small or uncertain; removing  
503 factors from the model is equivalent to fixing parameter estimates at exactly zero - a  
504 highly-subjective modelling decision after covariates have already been selected as  
505 potentially important<sup>50</sup>.

506

507 The full model assumed the observed, environmental-scale observations of fish  
508 biomass ( $y_{ijks}$ ) were modelled using a noncentral-T distribution, allowing for fatter  
509 tails than typical log-normal models of reef fish biomass<sup>32</sup>.

510

$$\log(y_{ijks}) \sim \text{Noncentral}T(\mu_{ijks}, \tau_{reef}, 3.5)$$

$$\mu_{ijks} = \beta_{0jks} + \beta_{reef} X_{reef}$$

$$\tau_{reef} \sim U(0, 100)^{-2}$$

511

512 with  $X_{reef}$  representing the matrix of observed environmental-scale covariates and  
 513  $\beta_{reef}$  the array of estimated reef-scale parameters. The  $\tau_{reef}$  (and all subsequent  $\tau$ 's)  
 514 were assumed common across observations in the final model and were minimally  
 515 informative<sup>50</sup>. Using a similar structure, the environmental-scale intercepts ( $\beta_{0jks}$ )  
 516 were structured as a function of site-scale covariates ( $X_{sit}$ ):

517

$$\beta_{0jks} \sim N(\mu_{jks}, \tau_{sit})$$

$$\mu_{jks} = \gamma_{0ks} + \gamma_{sit} X_{sit}$$

$$\tau_{sit} \sim U(0, 100)^{-2}$$

518

519 with  $\gamma_{sit}$  representing an array of site-scale parameters. Building upon the hierarchy,  
 520 the site-scale intercepts ( $\gamma_{0ks}$ ) were structured as a function of state-scale covariates  
 521 ( $X_{sta}$ ):

522

$$\gamma_{0ks} \sim N(\mu_{ks}, \tau_{sta})$$

$$\mu_{ks} = \gamma_{0s} + \gamma_{sta} X_{sta}$$

$$\tau_{sta} \sim U(0, 100)^{-2}$$

523

524 Finally, at the top scale of the analysis we allowed for a global (overall) estimate of  
 525 average log-biomass ( $\mu_0$ ):

526

$$\gamma_{0s} \sim N(\mu_0, \tau_{glo})$$

$$\mu_0 \sim N(0.0, 1000)$$

527  $\tau_{glo} \sim U(0, 100)^{-2}$ .

528

529 The relationships between fish biomass and environmental, site, and state scale  
530 drivers was carried out using the PyMC package<sup>51</sup> for the Python programming  
531 language, using a Metropolis-Hastings (MH) sampler run for  $10^6$  iterations, with a  
532 900,000 iteration burn in, leaving 10,000 samples in the posterior distribution of each  
533 parameter; these long burn-in times are often required with a complex model using  
534 the MH algorithm. Convergence was monitored by examining posterior chains and  
535 distributions for stability and by running multiple chains from different starting points  
536 and checking for convergence using Gelman-Rubin statistics<sup>52</sup> for parameters across  
537 multiple chains; all were at or close to 1, indicating good convergence of parameters  
538 across multiple chains.

539

540 *Overall model fit*

541

542 We conducted posterior predictive checks for goodness of fit (GoF) using Bayesian p-  
543 values<sup>40</sup> (BpV), whereby fit was assessed by the discrepancy between observed or  
544 simulated data and their expected values. To do this we simulated new data ( $y_i^{new}$ ) by  
545 sampling from the joint posterior of our model ( $\theta$ ) and calculated the Freeman-Tukey  
546 measure of discrepancy for the observed ( $y_i^{obs}$ ) or simulated data, given their expected  
547 values ( $\mu_i$ ):

548

549 
$$D(y|\theta) = \sum_i (\sqrt{y_i} - \sqrt{\mu_i})^2$$

550

551 yielding two arrays of median discrepancies  $D(y^{obs}/\theta)$  and  $D(y^{new}/\theta)$  that were then  
552 used to calculate a BpV for our model by recording the proportion of times  $D(y^{obs}/\theta)$   
553 was greater than  $D(y^{new}/\theta)$  (Extended Data Fig. 5). A BpV above 0.975 or under 0.025  
554 provides substantial evidence for lack of model fit. Evaluated by the Deviance  
555 Information Criterion (DIC), the full model greatly outperformed the null model  
556 ( $\Delta DIC=472$ ).

557

558 To examine homoscedasticity, we checked residuals against fitted values. We also  
559 checked the residuals against all covariates included in the model, and several  
560 covariates that were not included in the model (primarily due to collinearity),  
561 including: 1) *Atoll* - A binary metric of whether the reef was on an atoll or not; 2)  
562 *Control of Corruption*: Perceptions of the extent to which public power is exercised  
563 for private gain, including both petty and grand forms of corruption, as well as  
564 'capture' of the state by elites and private interests. Derived from the World Bank  
565 survey on governance; 3) *Geographic Basin*- whether the site was in the Tropical  
566 Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-Pacific; 4)  
567 *Connectivity* – we examined 3 measures based on the area of coral reef within a 30km,  
568 100km, and 600km radius of the site; 5) *Sedimentation*; 6) *Coral Cover* (which was  
569 only available for a subset of the sites); 7) *Climate stress*<sup>49</sup>; and 8) *Census method*.  
570 The model residuals showed no patterns with these eight additional covariates,  
571 suggesting they would not explain additional information in our model.

572

573 *Bright and dark spot estimates*

574 Because the performance of site scale locations are of substantial interest in

575 uncovering novel solutions for reef conservation, we defined bright and dark spots at  
576 the site scale. To this end, we defined bright (or dark) spots as locations where  
577 expected site-scale intercepts ( $\gamma_{0ks}$ ) differed by more than two standard deviations  
578 from their nation/state-scale expected value ( $\mu_{ks}$ ), given all the covariates present in  
579 the full hierarchical model:

$$580 \quad SS_{spot} = |(\mu_{ks} - \gamma_{0ks})| > 2[SD(\mu_{ks} - \gamma_{0ks})].$$

581 This, in effect, probabilistically identified the most deviant sites, given the model,  
582 while shrinking sites toward their group-level means, thereby allowing us to  
583 overcome potential bias due to low and varying sample sizes that can lead to extreme  
584 values from chance alone. As a conservative precaution, we did not consider a site a  
585 bright or dark spot if the group-level (i.e. nation/state) mean had fewer than 5  
586 estimates (sites).

587

#### 588 *Analysing conditions at bright spots*

589 For our preliminary investigation of why bright and dark spots may diverge from  
590 expectations, we surveyed data providers and other experts about key social,  
591 institutional, and environmental conditions at the 15 bright spots, 35 dark spots, and  
592 14 sites that performed most closely to model specifications. Specifically, we  
593 developed an online survey using Survey Monkey<sup>TM</sup> software, which we asked data  
594 providers who sampled those sites to complete with input from local experts where  
595 necessary. Data providers generally filled in the survey in consultation with  
596 nationally-based field team members who had detailed local knowledge of the  
597 socioeconomic and environmental conditions at each of the sites. Research on bright  
598 spots in agricultural development<sup>13</sup> highlights several types of social and



599 environmental conditions that may lead to bright spots, which we adapted and  
600 developed proxies for as the basis of our survey into why our bright and dark spots  
601 may diverge from expectations. These include:

- 602 i) *Social and institutional conditions.* We examined the presence of  
603 customary management institutions such as taboos and marine tenure  
604 institutions, whether there was a high level of engagement by local people  
605 in management, whether there was high levels of dependence on marine  
606 resources (whether a majority of local residents depend on reef fish as a  
607 primary source of food or income). All social and institutional conditions  
608 were recorded as presence/absence. Dependence on resources and  
609 engagement were limited to sites that had adjacent human populations. All  
610 other conditions were recorded regardless of whether there is an adjacent  
611 community;
- 612 ii) *Technological use/innovation.* We examined the presence of motorised  
613 vessels, intensive capture equipment (such as beach seine nets, surround  
614 gill nets, and muro-ami nets), and storage capacity (i.e. freezers); and
- 615 iii) *External influences* (such as donor-driven projects). We examined the  
616 presence of NGOs, fishery development projects, development initiatives  
617 (such as alternative livelihoods), and fisheries improvement projects. All  
618 external influences were recorded as present/absent then summarised into  
619 a single index of whether external projects were occurring at the site;
- 620 iv) *Environmental/ecological processes* (e.g. recruitment & connectivity). We  
621 examined whether sites were within 5km of mangroves and deep-water  
622 refuges, and whether there had been any major environmental disturbances

623                   such as coral bleaching, tsunami, and cyclones within the past 5 years. All  
624                   environmental conditions were recorded as present/absent.  
625  
626    To test for associations between these conditions and whether sites diverged more or  
627    less from expectations, we used two complementary approaches. The link between the  
628    presence/absence of the aforementioned conditions and whether a site was bright,  
629    average, or dark was assessed using a Fisher's Exact Test. Then we tested whether the  
630    mean deviation in fish biomass from expected was similar between sites with  
631    presence or absence of the mechanisms in question (i.e. the presence or absence of  
632    marine tenure/taboo) using an ANOVA assuming unequal variance. The two tests  
633    yielded similar results, but provide slightly different ways to conceptualise the issue,  
634    the former is correlative while the latter explains deviation from expectations based  
635    on conditions, so we provide both (Figure 2, Extended Data Fig. 6).  
636

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768

769



770 **End Notes**

771 Supplementary Information is linked to the online version of the paper at

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773

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780 J.E.C. conceived of the study with support from M.A.M, N.A.J.G, T.R.M, J.K, C.H,

781 D.M, C.M, E.A, and C.C.H; C.H. managed the database; M.A.M. and J.E.C.

782 developed and implemented the analyses; J.E.C. led the manuscript with M.A.M, and

783 N.A.J.G. All other authors contributed data and made substantive contributions to the

784 text.

785

786 **Author Information**

787 Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The

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791

792 **Extended Data Tables**

793

794 **Extended Data Table 1 | Summary of social and environmental covariates.**

795 Further details can be found in the Supplemental Online Methods. The smallest scale  
796 is the individual reef. Sites consist of clusters of reefs within 4km of each other.

797 Nation/states generally correspond to country, but can also include or territories or  
798 states, particularly when geographically isolated (e.g. Hawaii).

799

<b>Covariate</b>	<b>Description</b>	<b>Scale</b>	<b>Key data sources</b>
<b>Local population growth</b>	Difference in local human population (i.e. 100km buffer around our sites) between 2000-2010	Site	Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database <sup>36</sup>
<b>‘Gravity’ of major markets within 500km</b>	The population of the major market divided by the squared travel time between the reef sites and the market. This value was summed for all major markets within 500km of the site.	Site	Human population size, land cover, road networks, coastlines
<b>‘Gravity’ of the closest human settlement</b>	The population of the nearest human settlement divided by the squared travel time between the reef site and the settlement.	Site	Human population size, land cover, road networks, coastlines
<b>Protection</b>	Whether the reef is	Reef	Expert opinion, global map of

<b>status</b>	openly fished, restricted (e.g. effective gear bans or effort restrictions), or unfished		marine protected areas.
<b>Human Development index</b>	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
<b>Population Size</b>	Total population size of the jurisdiction	Nation/state	World Bank, census estimates, Wikipedia
<b>Tourism</b>	Proportion of tourist visitors to residents	Nation/state	World Tourism Organization's Compendium of Tourism Statistics, census estimates
<b>Voice and accountability</b>	Perceptions of the extent to which a country's citizens are able to participate in selecting their government.	Nation/state	World Bank
<b>Fish landings</b>	Landings of reef fish (tons) per Km <sup>2</sup>	Nation/state	Teh et al. <sup>47</sup>

	of reef		
<b>National fisheries poaching</b>	Results from survey of national fisheries managers about levels of compliance with national fisheries regulations	Nation/ state	Mora et al. <sup>53</sup>
<b>Climate stress</b>	A composite metric comprised of 11 different environmental variables that are related to coral mortality from bleaching	Site	Maina et al. <sup>49</sup>
<b>Productivity</b>	The average (2005-2010) ocean productivity in mg C / m <sup>2</sup> / day	Site	<a href="http://www.science.oregonstate.edu/ocean.productivity/">http://www.science.oregonstate.edu/ocean.productivity/</a>
<b>Habitat</b>	Whether the reef is a slop, crest, flat, or back reef/lagoon	Reef	Primary data
<b>Depth</b>	Depth of the ecological survey (<4m, 4.1-10m, >10m)	Reef	Primary data

801 **Extended Data Table 2 | List of ‘Nation/states’ covered in study and their**  
802 **respective average biomass (plus or minus standard error)** In most cases,  
803 nation/state refers to an individual country, but can also include states (e.g. Hawaii or  
804 Florida), territories (e.g. British Indian Ocean Territory), or other jurisdictions. We  
805 treated the NW Hawaiian Islands and Farquhar as separate ‘nation/states’ from  
806 Hawaii and Seychelles, respectively, because they are extremely isolated and have  
807 little or no human population. In practical terms, this meant different values for a few  
808 nation/state scale indicators that ended up having relatively small effect sizes, anyway  
809 (Fig. 1b): Population, tourism visitations, and in the case of NW Hawaiian Island, fish  
810 landings.  
811

<b>Nation/states</b>	<b>Average biomass</b>	<b>(± SE)</b>
<b>American Samoa</b>	235.93	(± 17.75)
<b>Australia</b>	735.01	(± 136.85)
<b>Belize</b>	981.16	(± 65.32)
<b>Brazil</b>	663.35	(± 115.17)
<b>British Indian Ocean Territory (Chagos)</b>	2975.58	(± 603.99)
<b>Cayman Islands</b>	464.09	(± 25.41)
<b>Colombia</b>	846.07	(± 162.49)
<b>Commonwealth of the Northern Mariana Islands</b>	505.54	(± 99.3)
<b>Comoros Islands</b>	305.62	(± 38.73)
<b>Cuba</b>	2107.37	(± 466.34)
<b>Egypt</b>	552.73	(± 70.18)
<b>Farquhar</b>	2665.48	(± 492.62)
<b>Federated States of Micronesia</b>	377.90	NA (n=1)
<b>Fiji</b>	1464.54	(± 144.39)
<b>Florida</b>	1661.35	(± 198.42)
<b>French Polynesia</b>	1077.20	(± 101.4)
<b>Guam</b>	118.98	(± 16.81)
<b>Hawaii</b>	380.45	(± 25.11)
<b>Indonesia</b>	275.76	(± 19.89)
<b>Israel</b>	445.16	(± 105.13)
<b>Jamaica</b>	275.77	(± 50.75)
<b>Kenya</b>	335.25	(± 65.81)
<b>Kiribati</b>	1219.93	(± 93.2)
<b>Madagascar</b>	409.48	(± 46.1)
<b>Maldives</b>	688.64	(± 97.07)
<b>Marshall Islands</b>	707.72	(± 174.38)
<b>Mauritius</b>	166.93	(± 73.7)
<b>Mayotte</b>	631.43	(± 68.25)
<b>Mexico</b>	1930.81	(± 737.09)

<b>Mozambique</b>	461.01	(± 60.14)
<b>Netherlands Antilles</b>	428.01	(± 53.99)
<b>New Caledonia</b>	1460.27	(± 143.18)
<b>NW Hawaiian Islands</b>	729.71	(± 46.33)
<b>Oman</b>	282.79	(± 70.22)
<b>Palau</b>	3212.26	(± 332.02)
<b>Panama</b>	373.78	(± 85.41)
<b>Papua New Guinea</b>	566.70	(± 31.76)
<b>Philippines</b>	202.62	NA (n=1)
<b>Pacific Remote Island Areas (PRIA), USA</b>	641.47	(± 79.25)
<b>Reunion</b>	172.32	(± 30.67)
<b>Seychelles</b>	446.99	(± 46.6)
<b>Solomon Islands</b>	1280.30	(± 216.74)
<b>Tanzania</b>	346.29	(± 41.51)
<b>Tonga</b>	1149.97	(± 151.27)
<b>United Arab Emirates</b>	81.35	(± 28.66)
<b>Venezuela</b>	1472.39	(± 496.95)

812

813 **Extended Data Table 3| List of Bright and Dark Spot locations, population status,**  
814 **and protection status.**

815

<b>Bright or Dark</b>	<b>Nation/State</b>	<b>Location</b>	<b>Populated</b>	<b>Protection</b>
Bright	British Indian Ocean Territory	Chagos	Unpopulated	Unfished (high compliance)
	Commonwealth of the Northern Mariana Islands	Agrihan	Unpopulated	Fished
		Guguan	Unpopulated	Fished
	Indonesia	Raja Ampat 1	Populated	Restricted
		Raja Ampat 2	Populated	Restricted
		Kalimantan	Populated	Restricted
	Kiribati	Tabueran 1	Populated	Fished
		Tabueran 2	Populated	Fished
	Papua New Guinea	Karkar	Populated	Restricted
	PRIA	Baker	Unpopulated	Restricted
		Jarvis Island	Unpopulated	Restricted
	Solomon Islands	Choiseul	Populated	Fished
		Isabel	Populated	Fished
		Makira	Populated	Fished
New Georgia		Populated	Fished	
Australia	Lord Howe	Populated	Unfished (high compliance)	
Dark	Hawaii	Hawaii	Populated	Fished
		Kauai 1	Populated	Fished
		Kauai 2	Populated	Fished
		Lanai	Populated	Fished
		Maui 1	Populated	Fished
		Maui 2	Populated	Fished
		Molokai	Populated	Fished
		Oahu 1	Populated	Fished
		Oahu 2	Populated	Fished
		Oahu 3	Populated	Fished
		Oahu 4	Populated	Fished
		Oahu 5	Populated	Fished
		Oahu 6	Populated	Fished
		Indonesia	Karimunjawa 1	Populated
Karimunjawa 2	Populated		Unfished (low compliance)	
Karimunjawa 3	Populated		Unfished (low compliance)	
Pulau Aceh	Populated		Fished	
Jamaica	Montego Bay 1	Populated	Unfished (low compliance)	
	Montego Bay 2	Populated	Fished	

	Rio Bueno	Populated	Fished
Kenya	Diani	Populated	Fished
Madagascar	Toliara	Populated	Fished
Mauritius	Anse Raie	Populated	Fished
	Grand Sable	Populated	Fished
NW Hawaii	Lisianski	Unpopulated	Unfished (high compliance)
	Pearl & Hermes 1	Unpopulated	Unfished (high compliance)
	Pearl & Hermes 2	Unpopulated	Unfished (high compliance)
Reunion	Reunion	Populated	Fished
Seychelles	Bel Ombre	Populated	Restricted
Tanzania	Bongoyo	Populated	Unfished (high compliance)
	Chapwani	Populated	Fished
	Mtwara	Populated	Fished
	Stone Town, Zanzibar	Populated	Fished
Venezuela	Chuspa	Populated	Fished

816



817 **Extended Data Table 4| List of fish families included in the study, their common**  
 818 **name, and whether they are commonly targeted in artisanal coral reef fisheries.**

819 Note: Targeting of reef fishes can vary by location due to gear, cultural preferences,  
 820 and a range of other considerations.

821

<b>Fish family</b>	<b>Common family name</b>	<b>Fishery target</b>
<b>Acanthuridae</b>	Surgeonfishes	Target
<b>Balistidae</b>	Triggerfishes	Non-target
<b>Diodontidae</b>	Porcupinefishes	Non-target
<b>Ephippidae</b>	Batfishes	Target
<b>Haemulidae</b>	Sweetlips	Target
<b>Kyphosidae</b>	Drummers	Target
<b>Labridae</b>	Wrasses and Parrotfish	Target >20cm
<b>Lethrinidae</b>	Emperors	Target
<b>Lutjanidae</b>	Snappers	Target
<b>Monacanthidae</b>	Filefishes	Non-target
<b>Mullidae</b>	Goatfishes	Target
<b>Nemipteridae</b>	Coral Breams	Target
<b>Pinguipedidae</b>	Sandperches	Non-target
<b>Pomacanthidae</b>	Angelfishes	Target >20cm
<b>Serranidae</b>	Groupers	Target
<b>Siganidae</b>	Rabbitfishes	Target
<b>Sparidae</b>	Porgies	Target
<b>Synodontidae</b>	Lizardfishes	Non-target
<b>Tetraodontidae</b>	Pufferfishes	Non-target
<b>Zanclidae</b>	Moorish Idol	Non-target

822

823 **Extended Data Table 5 | Travel time estimates by land cover type.** Adapted from  
 824 Nelson<sup>40</sup>  
 825

<b>Global Land Cover Global Class</b>	<b><i>Speed associated (km/h)</i></b>
Tree Cover, broadleaved, deciduous & evergreen, closed; regularly flooded Tree Cover, Shrub, or Herbaceous Cover (fresh, saline, & brackish water)	1
Tree Cover, broadleaved, deciduous, open ( <i>open= 15-40% tree cover</i> )	1.25
Tree Cover, needle-leaved, deciduous & evergreen, mixed leaf type; Shrub Cover, closed-open, deciduous & evergreen; Herbaceous Cover, closed-open; Cultivated and managed areas; Mosaic: Cropland / Tree Cover / Other natural vegetation, Cropland / Shrub or Grass Cover	1.6
Mosaic: Tree cover / Other natural vegetation; Tree Cover, burnt	1.25
Sparse Herbaceous or sparse Shrub Cover	2.5
Water	20
Roads	60
Track	30
Artificial surfaces and associated areas	30
Missing values	1.4

826

827 **Extended Data Table 6 | Variance Inflation Factor Scores (VIF) for continuous**  
 828 **data before and after removing variables due to colinearity. X = covariate**  
 829 removed.

830

<b>Covariate</b>	<b>starting VIF</b>	<b>ending VIF</b>
<b>Market gravity (log)</b>	1.9	1.5
<b>nearest settlement gravity</b>	1.4	1.3
<b>Population growth</b>	1.4	1.3
<b>Climate stress</b>	2.7	2.0
<b>Ocean productivity</b>	6.5	2.2
<b>Sedimentation</b>	6.0	X
<b>Tourism</b>	2.5	X
<b>Control Corruption</b>	10.5	X
<b>GDP</b>	8.2	X
<b>HDI</b>	5.5	3.3
<b>Population size</b>	1.9	1.8
<b>Reef fish landings</b>	3.1	2.2
<b>Rule of Law</b>	33.8	x
<b>Voice and Accountability</b>	3.2	3.2

831

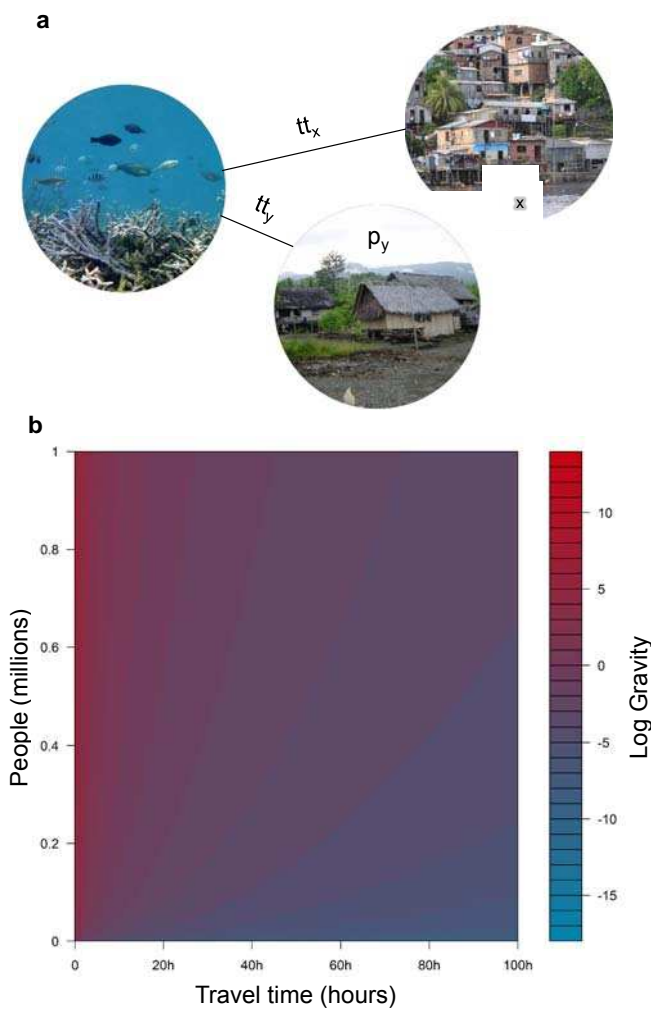
832 **Extended Data Table 7| Model selection of potential gravity indicators and**  
 833 **components.**

834

<b>Model</b>	<b>Covariates</b>	<b>AIC</b>	<b>Delta AIC</b>
<b>M2</b>	Gravity of nearest city	2666.4	0
<b>M1</b>	Gravity of all cities in 500km	2669.5	3.1
<b>M3</b>	Travel time to nearest city	2700.0	33.6
<b>M5</b>	Gravity of nearest small peri-urban area (40 people/km <sup>2</sup> )	2703.9	37.5
<b>M11</b>	Total Population in 500km radius	2712.0	45.6
<b>M9</b>	Travel time to the nearest large peri-urban area (75 people/km <sup>2</sup> )	2712.1	45.7
<b>M6</b>	Travel time to nearest small peri-urban area (40 people/km <sup>2</sup> )	2713.8	47.4
<b>M8</b>	Gravity to the nearest large peri-urban area (75 people/km <sup>2</sup> )	2722.9	56.5
<b>M7</b>	Population of nearest small peri-urban area (40 people/km <sup>2</sup> )	2792.7	126.3
<b>M4</b>	Population of the nearest city	2812.8	146.5
<b>M10</b>	Population of the nearest large peri-urban area (75 people/km <sup>2</sup> )	2822.2	155.8
<b>M0</b>	Intercept only	2827.7	161.27

835

836 **Extended Data Figure Legends**



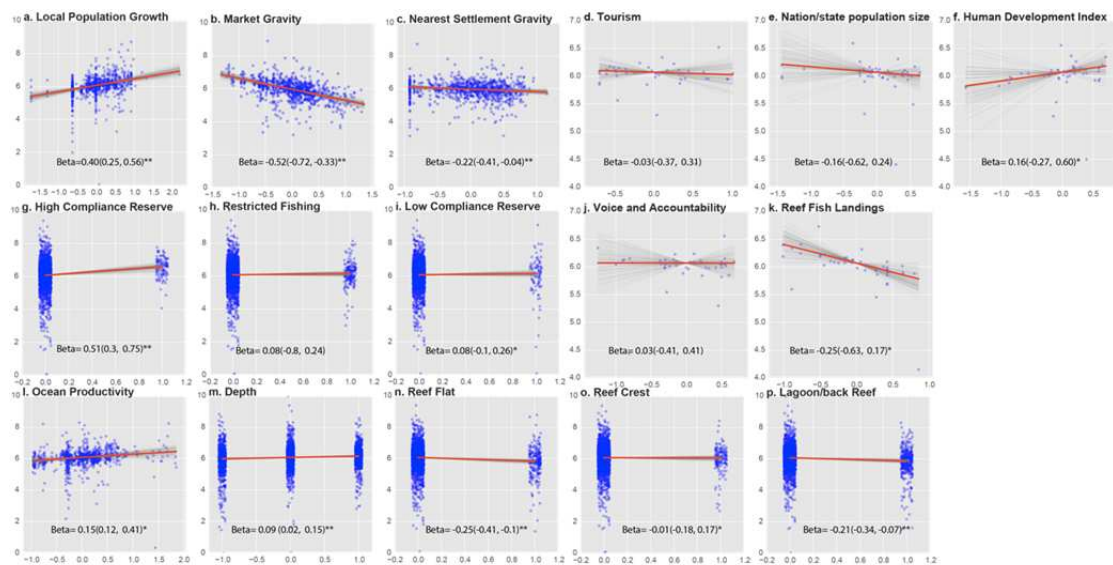
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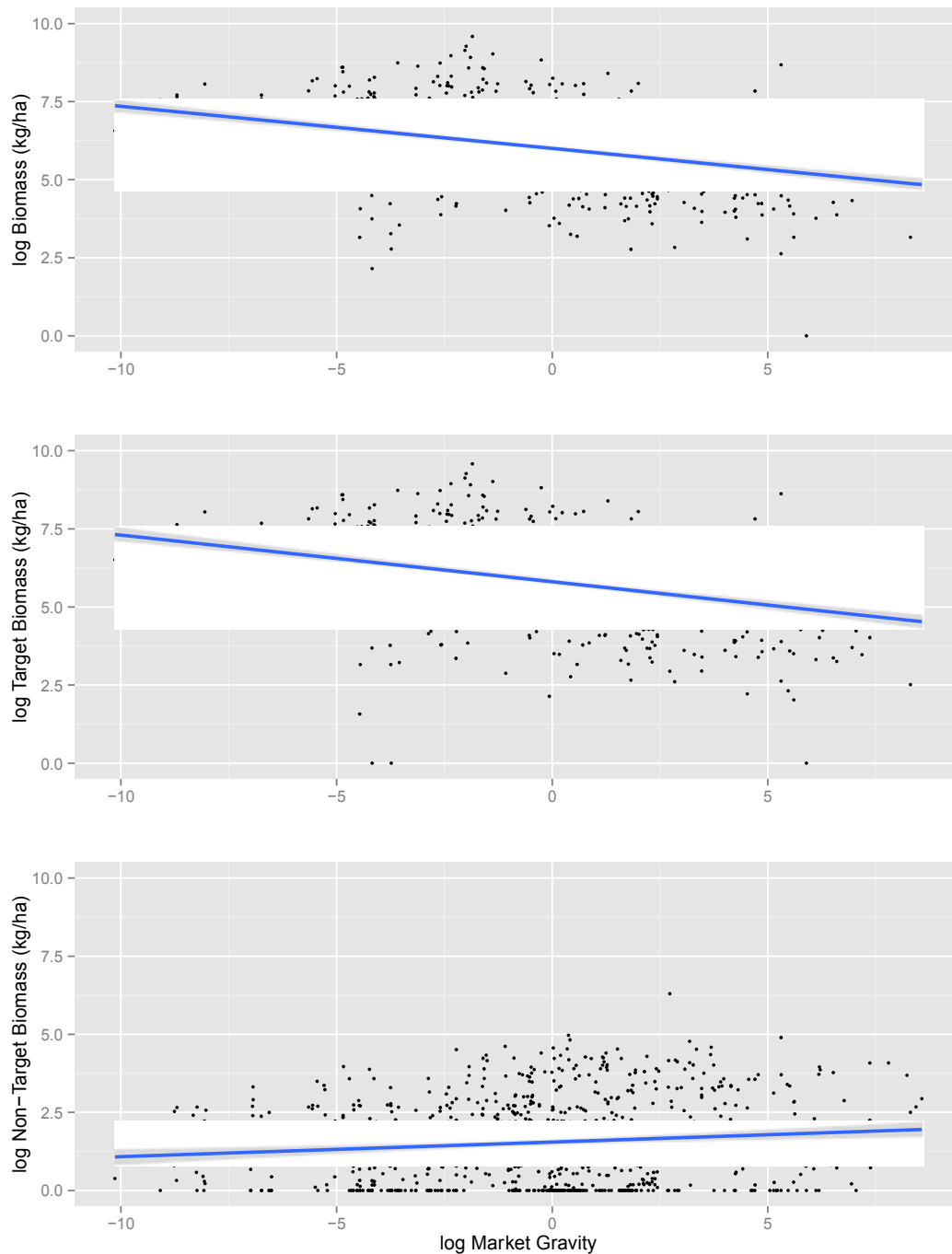
839 **Extended Data Figure 1** | a) A heuristic of the gravity concept where interactions  
 840 between people and reefs are a function of population size ( $p$ ) and the time it takes to  
 841 travel to the reef ( $tt$ ). Beginning in the 1800s, the concept of ‘gravity’ has been  
 842 applied to measure economic interactions, migration patterns, and trade flows<sup>29,54-56</sup>.  
 843 Drawing on an analogy from Newton’s Law of Gravitation, the gravity concept  
 844 predicts that interactions between two points are positively related to their mass (i.e.,  
 845 population) and inversely related to the distance between them. Here, we adapt the  
 846 gravity concept to examine interactions between people and reefs. We posit that  
 847 human interactions with a reef will be a function of the population of a place ( $p$ )  
 848 divided by the squared time it takes to travel ( $tt$ ) to the reefs (i.e. travel time). Thus,  
 849 gravity values could be similar for places that are large but far from the reefs (e.g.  $p_x$   
 850 = 30,000 people,  $tt_x = 10$ hours) as to those with small populations that are close to the  
 851 reef (e.g.  $p_y = 300$  people,  $tt_y = 1$  hour). We used travel time instead of linear distance

852 to account for the differences incurred by travelling over different surfaces (e.g. water,  
853 roads, tracks—see Methods). We developed gravity measures for the nearest human  
854 settlement and for the nearest major market (defined as provincial capitals, ports, and  
855 other large, populated places- see Methods). b) Gravity isoclines along gradients of  
856 population size and travel time.  
857

858 **Extended Data Figure 2 | Marginal relationships between reef fish biomass and**  
 859 **site-level social drivers.** a) local population growth, b) market gravity, c) nearest  
 860 settlement gravity, d) tourism, e) nation/state population size, f) Human development  
 861 Index, g) high compliance marine reserve (0 is fished baseline), h) restricted fishing  
 862 (0 is fished baseline), i) low compliance marine reserve (0 is fished baseline), j) voice  
 863 and accountability, k) reef fish landings, l) ocean productivity; m) depth (-1= 0-4m,  
 864 0= 4-10m, 1=>10m), n) reef flat (0 is reef slope baseline), o) reef crest flat (0 is reef  
 865 slope baseline), p) lagoon/back reef flat (0 is reef slope baseline). All X variables are  
 866 standardized. \*\* 95% of the posterior density is either a positive or negative direction  
 867 (Box 1); \* 75% of the posterior density is either a positive or negative direction.



868  
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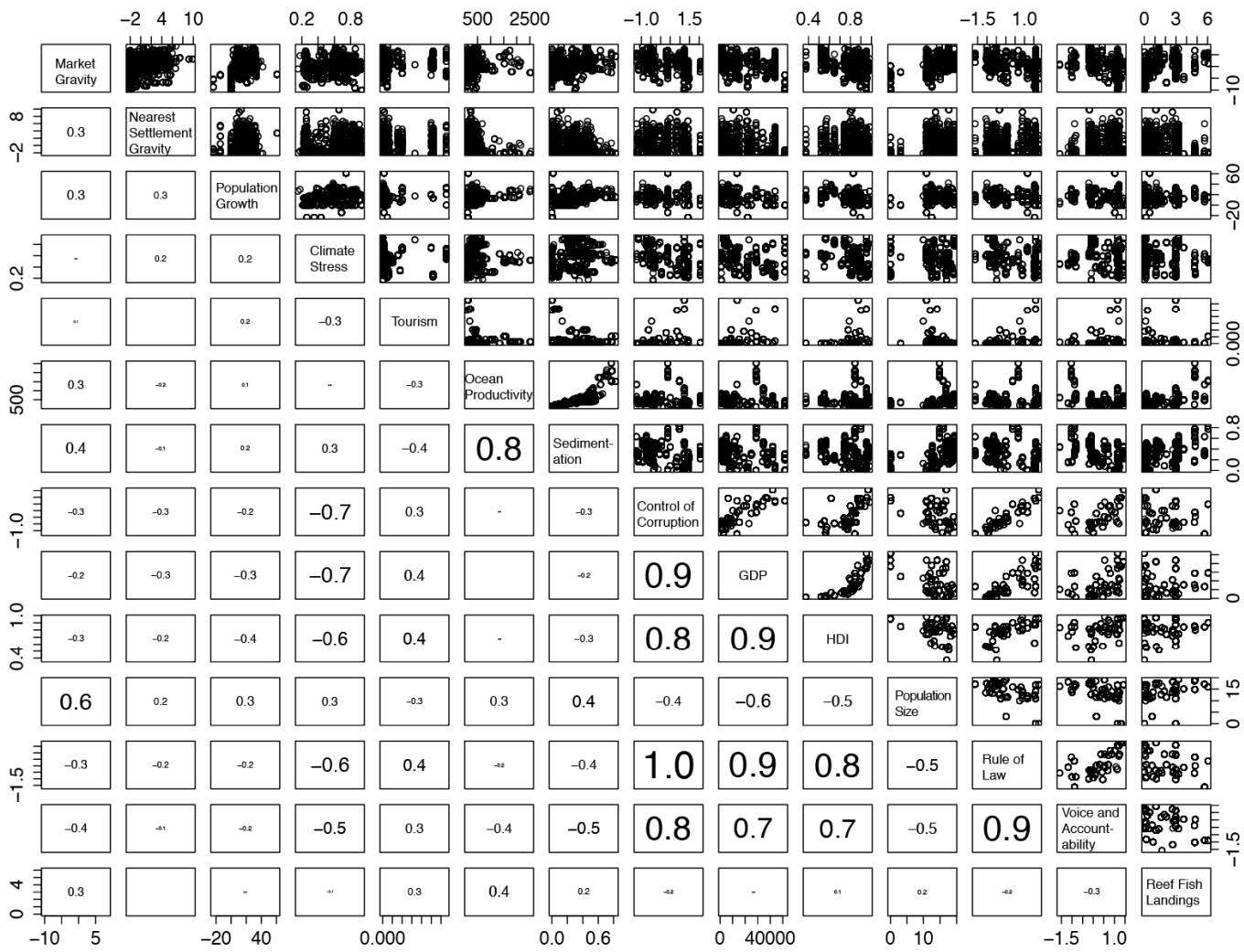


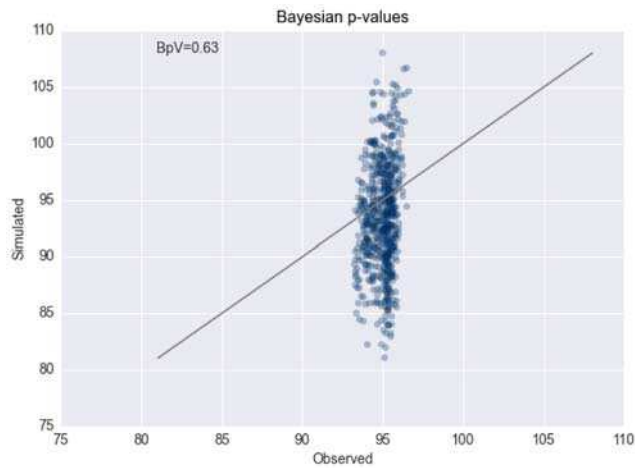
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**Extended Data Figure 3 | Market gravity and fish biomass.** Relationship between market gravity and a) reef fish biomass; b) targeted reef fish biomass (using fish families targeted by artisanal fisheries specified in Extended Data Table 2); c) non-target reef fish biomass. The strong relationship between gravity and reef fish biomass is very similar for the biomass of fishes generally targeted by artisanal fisheries, but very different for non-target fishes. This suggests that the relationship between market gravity and fish biomass is primarily driven by fishing, rather than other potential human impacts of urban areas (sedimentation, nutrients, pollution, etc.).



879 **Extended Data Figure 4| Correlation plot of candidate continuous covariates before accounting for colinearity (Extended Data Table 7).**  
880 Colinearity between continuous and categorical covariates (including biogeographic region, habitat, protection status, and depth) were analysed  
881 using boxplots.  
882

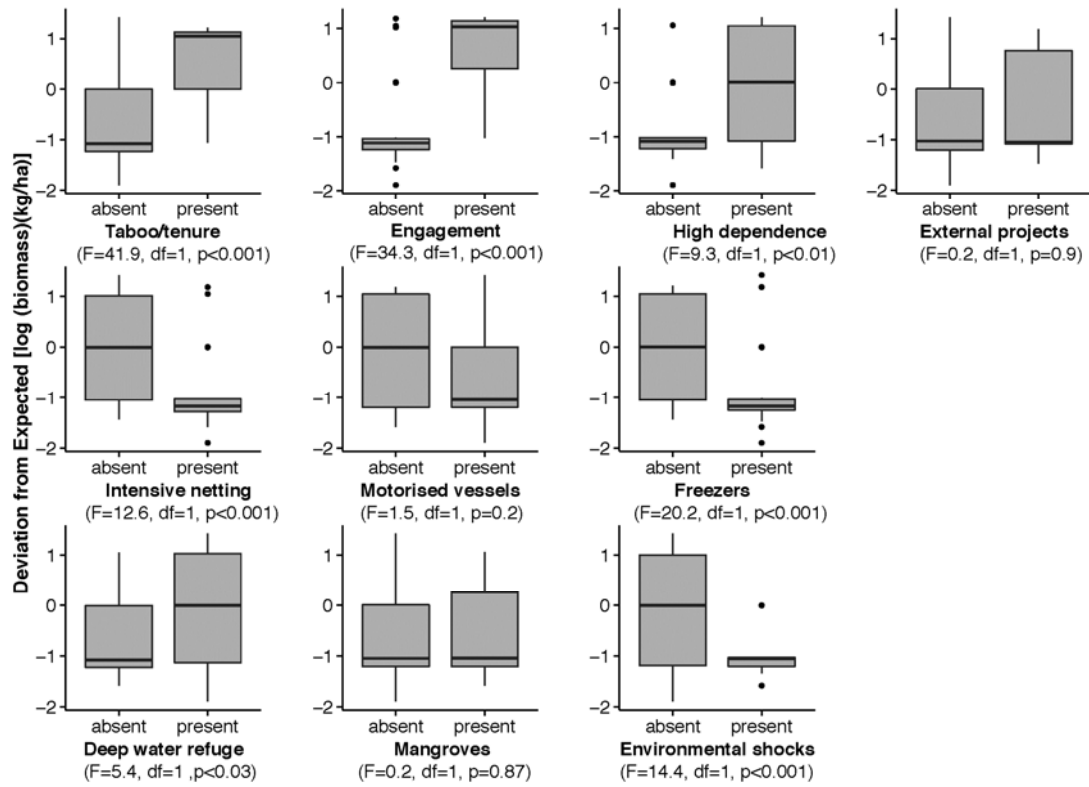




884

885 **Extended Data Figure 5 | Model fit statistics.** Bayesian p Values (BpV) for the full  
886 model indicating goodness of fit, based on posterior discrepancy. Points are Freeman-  
887 Tukey differences between observed and expected values, and simulated and expected  
888 values. Plot shows no evidence for lack of fit between the model and the data.

889



890

891 **Extended Data Figure 6| Box plot of deviation from expected as a function of the**

892 **presence or absence of key social and environmental conditions expected to**

893 **produce bright spots.**

894

895