

1 **Title Page**

2

3 **Classification:**

4 Social science: sustainability science

5

6 **Title:**7 **The gravity of human impacts mediates coral reef conservation gains**

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9

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78 **Key words**

79 Marine reserves, human impacts, social-ecological systems, conservation

80

81

82 **Abstract**

83 Coral reefs provide ecosystem goods and services for millions of people in the
84 tropics, but reef conditions are declining worldwide. Effective solutions to the crisis
85 facing coral reefs depends in part on understanding the context under which different
86 types of conservation benefits can be maximized. Our global analysis of nearly 1,800
87 tropical reefs reveals how the intensity of human impacts in the surrounding
88 seascape, measured as a function of human population size and accessibility to reefs
89 ('gravity'), diminishes the effectiveness of marine reserves at sustaining reef fish
90 biomass and the presence of top predators, even where compliance with reserve rules
91 is high. Critically, fish biomass in high compliance marine reserves located where
92 human impacts were intensive tended to be less than a quarter that of reserves where
93 human impacts were low. Likewise, the probability of encountering top predators on
94 reefs with high human impacts was close to zero, even in high-compliance marine
95 reserves. However, we find that the relative difference between openly fished sites
96 and reserves (what we refer to as conservation gains) are highest for fish biomass
97 (excluding predators) where human impacts are moderate and for top predators
98 where human impacts are low. Our results illustrate critical ecological tradeoffs in
99 meeting key conservation objectives: reserves placed where there are moderate to
100 high human impacts can provide substantial conservation gains for fish biomass, yet
101 they are unlikely to support key ecosystem functions like higher-order predation,
102 which is more prevalent in reserve locations with low human impacts.

103

104 **Significance Statement:**

105 Marine reserves that prohibit fishing are a critical tool for sustaining coral reef
106 ecosystems. Yet it remains unclear how human impacts in surrounding areas affect
107 the capacity of marine reserves to deliver key conservation benefits. Our global study
108 found that only marine reserves in areas of low human impact consistently sustained
109 top predators. Fish biomass inside marine reserves declined along a gradient of
110 human impacts in surrounding areas, however, reserves located where human
111 impacts are moderate had the greatest difference in fish biomass compared to openly
112 fished areas. Reserves in low human impact areas are required for sustaining
113 ecological functions like high-order predation, but reserves in high impact areas can
114 provide substantial conservation gains in fish biomass.

115

116 \body

117 **Text**

118 The world's coral reefs are rapidly degrading (1-3), which is diminishing ecological
119 functioning and potentially affecting the wellbeing of the millions of people with
120 reef-dependent livelihoods (4). Global climate change and local human impacts (such
121 as fishing) are pervasive drivers of reef degradation (1, 5). In response to this "coral
122 reef crisis", governments around the world have developed a number of reef
123 conservation initiatives (1, 6, 7). Our focus here is on the efficacy of management
124 tools that limit or prohibit fishing. Management efforts that reduce fishing mortality
125 should help to sustain reef ecosystems by increasing the abundance, mean body size,
126 and diversity of fishes that perform critical ecological functions (8-10). In practice,
127 however, outcomes from these reef management tools have been mixed (5, 11-13).

128

129 A number of studies have examined the social, institutional, and environmental
130 conditions that enable reef management to achieve key ecological outcomes, such as
131 sustaining fish biomass (5, 14, 15), coral cover (16), or the presence of top predators
132 (17). These studies often emphasize the role of: 1) types of key management
133 strategies in use such as marine reserves, where fishing is prohibited, or areas where
134 fishing gears and/or effort are restricted to reduce fishing mortality (8, 18); 2) levels
135 of compliance with management (12, 19, 20); 3) the design characteristics of these
136 management initiatives, for example the size and age of reserves, and whether they
137 are placed in remote versus populated areas (11, 21); and 4) the role of social drivers
138 such as markets, socioeconomic development, and human demography that shape
139 people's relationship with nature (14, 22).

140

141 In addition to examining when key ecological conditions are sustained, it is also
142 crucial to understand the context under which conservation gains can be maximized
143 (23, 24). By conservation gains, we are referring to the difference in a conservation
144 outcome (e.g. the amount of fish biomass) when some form of management (i.e. a
145 marine reserve or fishery restriction) is implemented relative to unmanaged areas.
146 These conservation gains can be beneficial for both people and ecosystems. For
147 example, increased fish biomass inside marine reserves is not only related to a range
148 of ecosystem states and processes (18), but can also result in spillover of adults and
149 larvae to surrounding areas, which can benefit fishers (25-27). The potential to

150 achieve conservation gains may depend on the intensity of human impacts in the
151 surrounding seascape (23, 24), yet, these effects have never been quantified.

152

153 Here, we use data from 1798 tropical coral reef sites in 44 nations, states, or
154 territories (hereafter ‘nation/states’) in every major coral reef region of the world to
155 quantify how expected conservation gains in two key ecological outcomes are
156 mediated by the intensity of human impact, namely: i) targeted reef fish biomass (i.e.
157 species generally caught in fisheries); and ii) the presence of top predators (Methods,
158 SI Appendix; Table S1). To quantify human impact at each site, we draw from a long
159 history of social science theory and practice to develop a metric referred to as
160 ‘gravity’ (Box 1). The concept of gravity (also called interactance) has been used in
161 economics and geography to measure economic interactions, migration patterns, and
162 trade flows since the late 1800s (28-30). We adapt this approach to examine potential
163 interactions with reefs as a function of how large and far away the surrounding
164 human population is (Box 1). At each site, we also determined the status of reef
165 management, grouped into either: i) openly fished, where sites are largely
166 unmanaged and national or local regulations tend to be poorly complied with; ii)
167 restricted fishing, where there are actively enforced restrictions on the types of gears
168 that can be used (e.g. bans on spear guns) or on access (e.g. marine tenure systems
169 that restrict fishing by ‘outsiders’); or iii) high-compliance marine reserves, where
170 fishing is effectively prohibited (Methods). We hypothesized that our ecological
171 indicators would decline with increasing gravity in fished areas, but that marine
172 reserves areas would be less sensitive to gravity. To test our hypotheses, we used
173 general and generalized linear mixed effects models to predict target fish biomass
174 and the presence of top predators, respectively, at each site based on gravity and
175 management status, while accounting for other key environmental and social
176 conditions thought to influence our ecological outcomes (14 ; Methods). Based on
177 our models, we calculated expected conservation gains along a gravity gradient as the
178 difference between managed sites and openly fished sites.

179

180 **Box 1**

181 Drawing on an analogy from Newton’s Law of Gravitation, the gravity concept
182 predicts that interactions between two places (e.g. cities) are positively related to

183 their mass (i.e. population) and inversely related to the distance between them (31).
184 The gravity concept is often considered one of the most successful and long-enduring
185 empirical models in economics and geography (31), but has rarely been directly
186 applied in a natural resource management setting and holds much promise in
187 informing reef conservation and management. Application of the gravity concept in a
188 reef governance context posits that human interactions with a reef are a function of
189 the population of a place divided by the squared time it takes to travel to the reefs
190 (we used travel time instead of linear distance to account for the differences incurred
191 by travelling over different surfaces such as water, roads, tracks; Box 1 Fig.; SI
192 Appendix; Table S2; 14, 32). Here, we build upon previous work (14) by developing
193 a new indicator that examines the cumulative human gravity of all populated places
194 within a 500-km radius of a given reef, which aims to capture both market and
195 subsistence pressures on reef fish biomass. We tested the predictive power of a series
196 of gravity metrics with varying radiuses (50km, 250km, 500km) and exponents of
197 travel time (travel time, travel time², travel time³; Methods, SI Appendix; Table S3).
198 A key limitation of our global gravity metric is that we are unable to capture local
199 variations in efficiencies that may affect fishing mortality per capita, such as fishing
200 fleet technology or infrastructure (e.g. road) quality.

201
202 Our analysis reveals that human gravity was the strongest predictor of fish biomass
203 (Fig. 1, S1). Fish biomass consistently declined along a human gravity gradient, a
204 trend particularly evident at the nation/state scale (Fig1B-D). However, this
205 relationship can vary by management type (Fig. 1, SI Appendix; Fig. S1).
206 Specifically, we found that biomass in reserves demonstrated a flatter (but still
207 negative) relationship with gravity (Fig. 1B) compared to openly fished and restricted
208 areas (Fig. 1C, D). Interestingly, this differential slope between reserves and fished
209 areas (Fig. 1H) was due to a strong interaction between gravity and reserve age such
210 that older reserves contributed more to biomass in high gravity situations than in low
211 gravity ones (SI Appendix; Fig. S1). This is likely due to fish stocks at high gravity
212 sites being heavily depleted and requiring decades to recover, whereas low gravity
213 sites would likely require less time to reach unfished biomass levels (8). Thus, given
214 average reserve age in our sample (15.5 years), biomass in reserves did not decline as
215 rapidly with gravity compared to fished and restricted areas (Fig. 1H). In the highest

216 gravity locations, modelled fish biomass in marine reserves was approximately five
217 times higher than in fished areas (270kg/ha compared to 56 kg/ha) (Fig.1H). At the
218 reef site scale, there was considerable variability in reef fish biomass, particularly at
219 low gravity (Fig. 1E-G). For example, at the lowest gravity locations, biomass levels
220 in reserves spanned more than 3 orders of magnitude (Fig. 1E). Importantly, there
221 was never extremely high biomass encountered in high gravity locations. Our
222 estimate of target fish biomass included top-predators. As a supplemental analysis,
223 we also examined target fish biomass with the biomass of top predators excluded,
224 which displays a similar trend, but with lower fish biomass in reserves at low gravity
225 compared to when top predators are included (SI Appendix; Fig S2).

226

227 A key finding from our study is that top predators were encountered on only 28% of
228 our reef sites, but as gravity increases, the probability of encountering top predator on
229 tropical coral reefs dropped to almost zero (<0.005), regardless of management (Fig
230 2). The probability of encountering top predators was strongly related to gravity and
231 the type of management in place, as well as sampling methodology and area surveyed
232 (Fig. 2, SI Appendix; Fig. S1). At low gravity, the probability of encountering a top
233 predator was highest in marine reserves (0.59) and lowest in fished areas (0.14),
234 when controlling for sampling and other environmental and social drivers (Fig 2, SI
235 Appendix; Fig. S1).

236

237 Our study demonstrates the degree to which fish communities inside marine reserves
238 can be affected by human impacts in the broader seascape (Fig. 1,2). Critically, high-
239 compliance marine reserves in the lowest gravity locations tended to support more
240 than four times more fish biomass than the highest gravity reserves (1150 versus 270
241 kg/ha, respectively; Fig. 1H). Likewise, the modelled probability of encountering a
242 top predator decreased by more than one hundred-fold from 0.58 in low gravity
243 reserves to 0.0046 in the highest gravity reserves (Fig 2H). Our study design meant
244 that it was not possible to uncover the mechanisms responsible for this decline of
245 ecological conditions indicators within marine reserves along a gravity gradient, but
246 this pattern of depletion is likely related to: 1) human impacts in the surrounding
247 seascape (fishing, pollution, etc.) affecting ecological processes (recruitment, feeding
248 behavior, etc.) within reserves (33, 34); 2) almost every marine reserve is likely to
249 have some degree of poaching, even where compliance is considered high (20, 35)

250 and the cumulative impacts from occasional poaching events is probably higher in
251 high gravity situations; 3) the life history of top predators, such as old age of
252 reproduction and small clutch size which makes them particularly susceptible to even
253 mild levels of exploitation (36); and/or 4) high gravity marine reserves in our sample
254 possibly being too young, or too small to provide substantial conservation gains (11,
255 37). We conducted a supplementary analysis to further examine this latter potential
256 explanation. Due to collinearity, we could not directly account for reserve size in our
257 model, but conducted a supplemental analysis where we separated reserves into small
258 ($\leq 28\text{km}^2$) and large (Methods, Fig. S3). We found that the biomass and probability of
259 encountering top predators was higher in large compared to small reserves, but
260 surprisingly, we found a flatter slope for small compared to large reserves (SI
261 Appendix; Fig. S3). However, there were no large high compliance reserves in high
262 gravity areas in our sample, likely due to the social and political difficulties in
263 establishing large reserves near people (38). Since there is little overlap between
264 large and small reserves along the gravity gradient in our sample, we are unable to
265 distinguish the effects of reserve size from those of gravity, but this is an important
266 area for future research. Additionally, we modelled how the relationship between
267 gravity and our ecological outcomes changed with reserve age, comparing outcomes
268 using the average reserve age (15.5 years) to those from reserves nearly twice as old
269 (29 years, which was the third quartile of our global distribution in reserve age).
270 Older reserves were predicted to sustain an additional 180 kg/ha (+66%) of fish
271 biomass at the highest levels of gravity compared to average age reserves. However,
272 the effects of reserve age on the probability of encountering a top predator was less
273 marked: the modelled probability of encountering a top predator in older reserves (29
274 years) was only 0.01, compared to <0.005 for average age (~15 years) reserves,
275 suggesting that small reserves common in high gravity situations can support high
276 levels of biomass, but are unlikely to sustain top predators, even when they are
277 mature.

278

279 Although absolute fish biomass under all management categories declined with
280 increasing gravity (Fig. 1B,C), the maximum expected conservation gains (i.e. the
281 difference between openly fished and managed) differed by management type along
282 the gravity gradient (Fig. 3A). Interestingly, the conservation gains for restricted
283 fishing is highest in low gravity situations, but rapidly declines as human impacts

284 increase (Fig. 3A, 39). For marine reserves, biomass conservation gains demonstrated
285 a hump-shaped pattern that peaked at very low gravity when predators were included
286 in the biomass estimates (solid blue line; Fig 3A). When top predators were excluded
287 from biomass estimates, conservation gains peaked at intermediate gravity levels, and
288 were higher in high gravity compared to low gravity (dotted blue line; Fig. 3A). Our
289 results highlight how the expected differences between openly fished and marine
290 reserves change along a gravity gradient, given a range of other social and
291 environmental conditions that are controlled for within our model (SI Appendix; Fig.
292 S1). Thus, differences in these trends are relative to average conditions, and
293 individual reserves may demonstrate larger or smaller biomass buildup over time,
294 which can vary by fish groups and/or families (e.g. 40).

295

296 In an effort to minimize costs to users, many marine reserves, particularly the large
297 ones, tend to be placed in remote locations that experience low human pressure (24,
298 41). However, critics of marine reserves in remote locations suggest that limited
299 resources could be better-spent protecting areas under higher threat that could
300 potentially yield greater conservation gains (23, 24, 42). Our results make explicit the
301 types of benefits – and the limitations- to placing reserves in high versus low human
302 impact locations. We found that for non-top predator reef fishes, substantial
303 conservation gains can occur at even the highest gravity locations but that optimal
304 gains are obtained at moderate gravity (Fig. 3A). Our results also show that low
305 gravity marine reserves (and to a lesser extent low gravity fisheries restrictions) are
306 critical to support the presence of top predators (Fig. 2). Yet, the expected
307 conservation gains for top predators declines rapidly with gravity in both marine
308 reserves and restricted areas (Fig. 3B). Our results illustrate a critical ecological
309 tradeoff inherent in the placement of marine reserves: high gravity reserves can have
310 the substantial conservation gains for fish biomass, yet they are unlikely to support
311 key ecosystem functions like predation, even with high levels of compliance. This
312 highlights the importance of having clear objectives for conservation initiatives and
313 recognizing the tradeoffs involved (43, 44).

314

315 Our analysis does not allow us to uncover the mechanisms behind why we might
316 observe the greatest differences in top predators between marine reserves and fished
317 areas in low gravity locations. A plausible explanation is that top predators such as

318 sharks are particularly vulnerable to fishing (17) and are exposed to some fishing
319 even in the most remote fished areas, driven by the extremely high price for shark
320 fins (shark fins can fetch US\$960/kg in wholesale markets (45); compared to only
321 \$43/kg for parrotfish in European supermarkets (46)). Thus, even small amounts of
322 fishing in remote openly fished areas may be depleting top predators, which creates a
323 large difference between low gravity fished areas and marine reserves. This
324 difference may diminish along the gravity because top predators tend to have large
325 home range (37), and there were only small reserves in high gravity locations (SI
326 Appendix; Fig S3), which may mean that existing high gravity reserves are not likely
327 big enough to support the large home ranges of many predators (37, 47).

328

329 Successful conservation also depends on a range of social considerations (48). For
330 example, gear restrictions often have greater support from local fishers (49) and are
331 usually implemented over greater reef areas than marine reserves. We show here that
332 there are conservation gains produced by gear restrictions, though they are low
333 relative to marine reserves (Fig. 3). Thus, in locations where a lack of support makes
334 establishing marine reserves untenable, gear restrictions may still provide
335 incremental gains towards achieving some conservation goals (8), particularly for
336 specific fish groups and/or families (39).

337

338 As a supplemental analysis, we examined the conservation gains for biomass of non-
339 target species (SI Appendix; Fig. S1D, S4). This supplemental analysis addresses
340 whether the effects of gravity on reef fish communities are from fishing or other
341 impacts, such as sedimentation or pollution. We found very different patterns for
342 non-target species compared to target species, suggesting the relationship between
343 target fish biomass and gravity (SI Appendix; Fig. S1) is primarily driven by fishing
344 pressure.

345

346 Overall, our results demonstrate that the capacity to not only sustain reef fish biomass
347 and the presence of top predators, but also the potential to achieve conservation
348 gains, may be highly dependent on the level of human impact in the surrounding
349 seascape. It is therefore essential to consider the global context of present and future
350 human gravity in coral reef governance. Consequently, we calculated gravity of
351 human impacts for every reef cell globally using a 10x10 km grid across the world's

352 coral reefs (Fig. 4). Critically, the distribution of gravity varies substantially among
353 regions, with the central and eastern Indo-Pacific demonstrating lower gravity values.
354 Even within a region, there can be substantial variability in gravity values. For
355 example, the Central Indo-Pacific has highly contrasting gravity patterns, with
356 Southeast Asian reefs (Fig. 4 panel 3) generally showing extremely high gravity
357 values while Australian and Melanesian reefs (Fig. 4 panel 4) are dominated by
358 relatively low gravity values.

359

360 The ways in which gravity will increase over time- and how the impacts of gravity on
361 reef systems can be reduced is of substantial concern for coral reef governance. The
362 potential benefits of protecting locations that are currently remote could increase over
363 time as human populations and the accessibility of reefs change (50). Demographic
364 projections of high migration and fertility rates in some countries suggest substantial
365 increases in coastal human populations in developing countries, where the majority
366 of coral reefs are located (5, 51-53). Development projects that address high rates of
367 fertility through improvements in women's education, empowerment, and the
368 expansion of family planning opportunities have successfully reduced fertility rates
369 (54, 55). Such initiatives, when partnered with resource management, have the
370 potential to be beneficial to both people and reefs. Demographic changes such as
371 increased migration in coastal areas are also expected to be coupled with coastal
372 development and road building that will increase the accessibility of reefs. For
373 example, previously uninhabited areas have become more accessible, as evidenced
374 by China's recent Belt and Roads Initiative (BRI) and island building enterprise in
375 the South China Sea (56-58). Investments in sustainable planning of coastal
376 development and road building could help to minimize unnecessary increases in reef
377 accessibility. Importantly, stemming increases in gravity is only part of the potential
378 solution space- it will also be important to dampen the mechanisms through which
379 gravity operates, such that a given level of gravity can have a lesser impact on reef
380 systems (1). People's environmental behavior is fundamentally driven by their social
381 norms, tastes, values, practices, and preferences (59), all of which can be altered by
382 policies, media, and other campaigns in ways that could change the local relationship
383 between gravity and reef degradation.

384

385 Gravity future directions

386 Our gravity index (see box 1 and methods) makes several key assumptions that could
387 potentially be refined in further applications. First, our application of gravity held
388 friction constant across each specific type of surface (i.e. all paved roads had the
389 same friction value). Future applications of more localized studies could vary travel
390 time to reflect the quality of road networks, topographic barriers to access (such as
391 cliffs), and the availability of technology. Likewise, future applications could also
392 aim to incorporate local information about fishing fleet efficiency. Secondly, our
393 adaptation of the gravity model (31) is unidirectional, assuming a constant level of
394 attraction from any reef (i.e. gravity varies based on human population size, but not
395 on the quality or quantity of fish on a specific reef). Reefs with more fish, or higher
396 fish value, could be more attractive and exert a higher pull for exploitation (60).
397 Likewise, societal values and preferences can also make certain fish more or less
398 attractive. Our adaptation of gravity was designed to examine the observed
399 conditions of reefs as a function of potential interactions with markets and local
400 settlements, so our modification of the concept for this application was appropriate.
401 However, future applications wishing to predict where reefs may be most vulnerable
402 might wish to consider incorporating fish biomass or composition (i.e. potential
403 market price of reef fish) in the gravity equation. Third, our database was not
404 designed to look at ecological changes in a single location over time. However,
405 future applications could examine whether ecological recovery in reserves (8)
406 depends on the level of gravity present. To this end, we provide a global dataset of
407 gravity for every reef pixel globally upon request (Methods).

408

409 We demonstrate that human impacts deplete reef fish stocks and how certain types of
410 management can mediate, but not eliminate these pressures. In an era of increasing
411 change, the global network of marine reserves may not safeguard reef fish
412 communities from human impacts adequately enough to ensure key ecological
413 functions such as predation are sustained. Efforts must be made to both reduce and
414 dampen key drivers of change (1, 61), while maintaining or improving the wellbeing
415 of reef dependent people. Importantly, we find evidence that both remote and human-
416 surrounded reserves can produce different types of conservation gains. Ultimately,
417 multiple forms of management are needed across the seascape to sustain coral reef
418 fishes and the people that depend on them.

419

420 **Materials and Methods**

421 Scales of data

422 Our data were organized at three spatial scales: reef site (n=1798), reef cluster (n=918),
423 and nation/state (n=44).

- 424 i) Reef site (the smallest scale, which had an average of 2.4 surveys
425 (transects) - hereafter 'reef').
- 426 ii) Reef cluster (which had an average of 2.6 +/- 2.5 reef sites). We clustered
427 reefs together that were within 4km of each other, and used the centroid to
428 estimate reef cluster-level social and environmental covariates. To define
429 reef clusters, we first estimated the linear distance between all reef sites,
430 then used a hierarchical analysis with the complete-linkage clustering
431 technique based on the maximum distance between reefs. We set the cut-
432 off at 4 km to select mutually exclusive sites where reefs cannot be more
433 distant than 4 km. The choice of 4 km was informed by a 3-year study of
434 the spatial movement patterns of artisanal coral reef fishers, corresponding
435 to the highest density of fishing activities on reefs based on GPS-derived
436 effort density maps of artisanal coral reef fishing activities (62). This
437 clustering analysis was carried out using the R functions 'hclust' and
438 'cutree'.
- 439 iii) Nation/state (nation, state, or territory, which had an average of 50 +/- 79
440 reef clusters). A larger scale in our analysis was 'nation/state', which are
441 jurisdictions that generally correspond to individual nations (but could also
442 include states, territories, overseas regions), within which sites were nested
443 for analysis.

444

445 **Targeted Fish Biomass:** Reef fish biomass estimates were based on visual counts in
446 5532 surveys collected from 2,233 reef sites. All surveys used standard belt-transects,
447 distance sampling, or point-counts, and were conducted between 2004 and 2013.
448 Where data from multiple years were available from a single reef site, we included
449 only data from the year closest to 2010. Within each survey area, reef-associated
450 fishes were identified to species level, their abundance counted, and total length (TL)
451 estimated, with the exception of one data provider who measured biomass at the
452 family level. To make estimates of targeted biomass from these transect-level data
453 comparable among studies, we:

- 454 i) Retained families that were consistently studied, commonly targeted, and
455 were above a minimum size cut-off. Thus, we retained counts of >10cm
456 diurnally-active, non-cryptic reef fish that are resident on the reef (14
457 families), excluding sharks and semi-pelagic species (Table S1). We
458 calculated total biomass of targeted fishes on each reef using standard
459 published species-level length-weight relationship parameters or those
460 available on FishBase (63). When length-weight relationship parameters
461 were not available for a species, we used the parameters for a closely
462 related species or genus. For comparison, we also calculated non-target
463 fish biomass (SI Appendix; Table S1).
- 464 ii) Directly accounted for depth and habitat as covariates in the model (see
465 “environmental conditions” section below);
- 466 iii) Accounted for differences among census methods by including each
467 census method (standard belt-transects, distance sampling, or point-
468 counts) as a covariate in the model.
- 469 iv) Accounted for differences in sampling area by including total sampling
470 area for each reef (m²) as a covariate in the model.

471

472 **Top Predators:** We examined the presence/absence of 8 families of fish considered
473 top predators (SI Appendix; Table S1). We considered presence/absence instead of
474 biomass because biomass was heavily zero inflated.

475

476 **Gravity:** We first developed a gravity index for each of our reef sites where we had
477 *in situ* ecological data. We gathered data on both population estimates and a
478 surrogate for distance: travel time.

479

480 *Population estimates*

481 We gathered population estimates for each 1 by 1 km cell within a 500 km
482 radius of each reef site using LandScanTM 2011 database. We chose a 500 km
483 radius from the reef as a likely maximum distance fishing activities for reef
484 fish are likely to occur.

485

486 *Travel time calculation*

487 The following procedure was repeated for each populated cell within the 500
488 km radius. Travel time was computed using a cost-distance algorithm that
489 computes the least ‘cost’ (in minutes) of travelling between two locations on a
490 regular raster grid. In our case, the two locations were the centroid of the reef
491 site and populated cell (i). The cost (i.e. time) of travelling between the two
492 locations was determined by using a raster grid of land cover and road
493 networks with the cells containing values that represent the time required to
494 travel across them (32, SI Appendix; Table S2), we termed this raster grid a
495 *friction-surface* (with the time required to travel across different types of
496 surfaces analogous to different levels of friction). To develop the friction-
497 surface, we used global datasets of road networks, land cover, and shorelines:
498 - Road network data was extracted from the Vector Map Level 0
499 (VMap0) from the National Imagery and Mapping Agency's (NIMA)
500 Digital Chart of the World (DCW®). We converted vector data from
501 VMap0 to 1km resolution raster.
502 - Land cover data were extracted from the Global Land Cover 2000
503 (64).
504 -To define the shorelines, we used the GSHHS (Global Self-
505 consistent, Hierarchical, High-resolution Shoreline) database version
506 2.2.2.

507
508 These three friction components (road networks, land cover, and shorelines)
509 were combined into a single friction surface with a Behrmann map projection
510 (an equal area projection). We calculated our cost-distance models in R using
511 the *accCost* function of the '*gdistance*' package. The function uses Dijkstra's
512 algorithm to calculate least-cost distance between two cells on the grid taking
513 into account obstacles and the local friction of the landscape (65). Travel time
514 estimates over a particular surface could be affected by the infrastructure (e.g.
515 road quality) and types of technology used (e.g. types of boats). These types
516 of data were not available at a global scale but could be important
517 modifications in more localized studies.

518
519 *Gravity computation*

520 To compute gravity, we calculated the population of cell and divided that by
521 the squared travel time between the reef site and the cell. We summed the
522 gravity values for each cell within 500 km of the reef site to get the “total
523 gravity” within 500 km. We used the squared distance (or in our case, travel
524 time), which is relatively common in geography and economics, although other
525 exponents can be used (31).

526

527 We also developed a global gravity index for each 10 x 10 km grid of reef in
528 the world (Box 1), which we provide as an open access dataset. The procedure
529 to calculate gravity was similar to above with the only difference being in the
530 precision of the location- the former was a single data point (reef site), while
531 the latter was a grid cell (reef cell). For the purpose of the analysis, gravity was
532 log-transformed and standardised.

533

534 We also explored various exponents (1, 2 and 3) and buffer sizes (50, 250 and
535 500 km) to build 9 gravity metrics. The metric providing the best model, so
536 with the lowest AIC, was that with a squared exponent for travel time and a
537 500-km buffer (SI Appendix; Table S4).

538

539 **Management:** For each observation, we determined the prevailing type of
540 management, including: i) marine reserve- whether the site fell within the borders of
541 a no-take marine reserve. We asked data providers to further classify whether the
542 reserve had high or low levels of compliance. For this analysis, we removed sites that
543 were categorised as low compliance reserves (n=233); ii) restricted fishing- whether
544 there were active restrictions on gears (e.g. bans on the use of nets, spearguns, or
545 traps) or fishing effort (which could have included areas inside marine protected
546 areas that were not necessarily no take); or iii) openly fished - regularly fished
547 without effective restrictions (SI Appendix; Table S5). To determine these
548 classifications, we used the expert opinion of the data providers, and triangulated this
549 with a global database of marine reserve boundaries (66). We also calculated size
550 (median= 113.6km², mean = 217516 km², SD= 304417) and age (median= 9, mean =
551 15.5 years, SD= 14.5) of the no-take portion of each reserve. Reserve size was
552 strongly related to our metric of gravity and could not be directly included in the
553 analysis. We conducted a supplemental analysis where we separated reserves into

554 small ($\leq 28 \text{ km}^2$) and large ($> 65 \text{ km}^2$) based on a natural break in the data to illustrate:
555 1) how biomass and the presence of top predators might differ between small and
556 large reserves; and 2) how large reserves are absent in our sample in high gravity.

557

558 Other Social Drivers

559 To account for the influence of other social drivers that are thought to be related to
560 the condition of reef fish biomass, we also included the following covariates in our
561 model:

562

563 *1. Local Population Growth:* We created a 100 km buffer around each site and used
564 this to calculate human population within the buffer in 2000 and 2010 based on the
565 Socioeconomic Data and Application Centre (SEDAC) gridded population of the
566 world database. Population growth was the proportional difference between the
567 population in 2000 and 2010. We chose a 100 km buffer as a reasonable range at
568 which many key human impacts from population (e.g., land-use and nutrients) might
569 affect reefs (67).

570

571 *2. Human Development Index (HDI):* HDI is a summary measure of human
572 development encompassing: a long and healthy life, being knowledgeable, and
573 having a decent standard of living. In cases where HDI values were not available
574 specific to the State (e.g. Florida and Hawaii), we used the national (e.g. USA) HDI
575 value.

576

577 *3. Population Size:* For each nation/state, we determined the size of the human
578 population. Data were derived mainly from national census reports the CIA fact book
579 ([https://www.cia.gov/library/publications/the-world-](https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html)
580 [factbook/rankorder/2119rank.html](https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html)), and Wikipedia (<https://en.wikipedia.org>). For the
581 purpose of the analysis, population size was log-transformed.

582

583 Environmental Drivers

584 *1. Depth:* The depth of reef surveys was grouped into the following categories: <4m,
585 4-10m, >10m to account for broad differences in reef fish community structure
586 attributable to a number of inter-linked depth-related factors. Categories were

587 necessary to standardise methods used by data providers and were determined by pre-
588 existing categories used by several data providers.

589

590 *2. Habitat:* We included the following habitat categories: i) Slope: The reef slope
591 habitat is typically on the ocean side of a reef, where the reef slopes down into deeper
592 water; ii) Crest: The reef crest habitat is the section that joins a reef slope to the reef
593 flat. The zone is typified by high wave energy (i.e. where the waves break). It is also
594 typified by a change in the angle of the reef from an inclined slope to a horizontal
595 reef flat; iii) Flat: The reef flat habitat is typically horizontal and extends back from
596 the reef crest for 10's to 100's of meters; iv) Lagoon / back reef: Lagoonal reef
597 habitats are where the continuous reef flat breaks up into more patchy reef
598 environments sheltered from wave energy. These habitats can be behind barrier /
599 fringing reefs or within atolls. Back reef habitats are similar broken habitats where
600 the wave energy does not typically reach the reefs and thus forms a less continuous
601 'lagoon style' reef habitat. Due to minimal representation among our sample, we
602 excluded other less prevalent habitat types, such as channels and banks. To verify the
603 sites' habitat information, we used the Millennium Coral Reef Mapping Project
604 (MCRMP) hierarchical data (68), Google Earth, and site depth information.

605

606 *3. Productivity:* We examined ocean productivity for each of our sites in mg C / m² /
607 day (<http://www.science.oregonstate.edu/ocean.productivity/>). Using the monthly
608 data for years 2005 to 2010 (in hdf format), we imported and converted those data
609 into ArcGIS. We then calculated yearly average and finally an average for all these
610 years. We used a 100 km buffer around each of our sites and examined the average
611 productivity within that radius. Note that ocean productivity estimates are less
612 accurate for nearshore environments, but we used the best available data. For the
613 purpose of the analysis, productivity was log-transformed.

614

615 *4. Climate stress:* We included an index of climate stress for corals, developed by
616 Maina et al. (69), which incorporated 11 different environmental conditions, such as
617 the mean and variability of sea surface temperature.

618

619 **Analyses**

620 We first looked for collinearity among our covariates using bivariate correlations and
621 variance inflation factor estimates. This led to the exclusion of several covariates (not
622 described above): i) *Biogeographic Realm* (Tropical Atlantic, western Indo-Pacific,
623 Central Indo-Pacific, or eastern Indo-Pacific); ii) *Gross Domestic Product*
624 (purchasing power parity); iii) *Rule of Law* (World Bank governance index); iv)
625 *Control of Corruption* (World Bank governance index); v) Voice and Accountability
626 (World Bank governance index); vi) Reef Fish Landings; vii) Tourism arrivals
627 relative to local population; viii) *Sedimentation*; and ix) *Marine Reserve Size*. Other
628 covariates had correlation coefficients 0.7 or less and Variance Inflation Factor
629 scores less than 5 (indicating multicollinearity was not a serious concern). Care must
630 be taken in causal attribution of covariates that were significant in our model, but
631 demonstrated collinearity with candidate covariates that were removed during the
632 aforementioned process. Importantly, the covariate of interest in this study, gravity,
633 was not strongly collinear with candidate covariates except reserve size ($r=-0.8$,
634 $t=3.6$, $df=104$, $p=0.0004$).

635

636 To quantify the relationships between gravity and target fish biomass, we developed
637 a general linear mixed model in R, using a log-normal distribution for biomass. To
638 quantify the relationships between gravity and presence/absence of top predators, we
639 developed a generalized linear mixed model with a Binomial family and a logit link
640 function. For both models, we set reef cluster nested within nation/state as a random
641 effect to account for the hierarchical nature of the data (i.e. reef sites nested in reef
642 clusters, reef clusters nested in nations/states). We included an interaction between
643 gravity and reserve age, as well as all the other social and environmental drivers and
644 the sampling method and total sampling area as covariates. We also tested
645 interactions between gravity and management and used AIC to select the most
646 parsimonious model. For fish biomass, the interaction between gravity and reserve
647 age had AIC values >2 lower than the interaction between gravity and management
648 (and a combination of both interactions). For the top predator models, both
649 interactions were within 2 AIC values, so we chose the interaction with reserve age
650 for consistency. All continuous covariates were standardised for the analysis, and
651 reserve age was then normalised such that non-reserves were 0 and the oldest
652 reserves were 1. In summary, our models thus predicted target fish biomass or
653 probability of top predators being observed at the reef site scale with an interaction

654 between gravity and reserve age, while accounting within the random factors for two
655 bigger scales at which the data were collected (reef cluster, and nation/state- see
656 supplementary material), and key social and environmental characteristics expected
657 to influence the biomass of reef fish (14). In addition to coefficient plots (SI
658 Appendix; Fig. S1), we conducted a supplemental analysis of relative variable
659 importance (SI Appendix; Table S4).

660

661 We ran the residuals from the models against size of the no-take areas of the marine
662 reserves and no patterns were evident, suggesting it would explain no additional
663 variance in the model. Trend lines and partial plots (averaged by site and nation/state)
664 are presented in the manuscript figures (Fig. 1B-H, 2H). We plotted the partial effect
665 of the relationship between gravity and protection on targeted fish biomass and
666 presence of top predators (Figs. 1B-G, 2B-G) by setting all other continuous
667 covariates to 0 (because they were all standardized and all categorical covariates to
668 their most common category (i.e. 4-10m for depth, slope for habitat, standard belt
669 transect for census method). For age of reserves, we set this to 0 for fished and
670 restricted areas, and to the average age of reserves (15.5 years) for reserves.

671

672 To examine the expected conservation gains of different management strategies, we
673 calculated: 1) the difference between the response of openly fished areas (our
674 counterfactual) and high-compliance marine reserves to gravity; and 2) the difference
675 between the response of openly fished areas and fisheries restricted areas to gravity.
676 For ease of interpretation, we plotted conservation gains in kg/ha (as opposed to
677 $\log[\text{kg/ha}]$, Fig. 3A). A log-normal (linear) model was used to develop the slopes of
678 the biomass (a) fished, (b) marine reserve, and (c) fisheries restricted areas, which
679 results in the differences between (a) and (b) and between (a) and (c) being non-
680 linear on an arithmetic scale (Fig 3A).

681

682 We plotted the diagnostic plots of the general linear mixed model to check that the
683 model assumptions were not violated. To check the fit of the generalized linear
684 mixed model, we used the confusion matrix (tabular representation of actual versus
685 predicted values) to calculate the accuracy of the model which came to 79.2%.

686 To examine homoscedasticity, we checked residuals against fitted values. We
687 checked our models against a null model, which contained the model structure (i.e.

688 random effects), but no covariates. We used the null model as a baseline against
689 which we could ensure that our full model performed better than a model with no
690 covariate information. In all cases our models outperformed our null models by more
691 than 2 AIC values, indicating a more parsimonious model.

692

693 All analyses were undertaken using R (3.43) statistical package.

694

695 **Data access**

696 A gridded global gravity data layer is freely available by request from the lead
697 author. The ecological data used in this manuscript are owned by individual data
698 providers. Although much of these data (e.g. NOAA CRED data and Reef Life
699 Surveys) are already open-access, some of these data are governed by intellectual
700 property arrangements and cannot be made open-access. Because the data are
701 individually owned, we have agreed upon and developed a structure and process for
702 those wishing access to the data. Our process is one of engagement and collaboration
703 with the data providers. Anyone interested can send a short (1/2-1 page) proposal for
704 use of the database that details the problem statement, research gap, research
705 question(s), and proposed analyses to the PI and database administrator
706 Joshua.cinner@jcu.edu.au , who will send the proposal to the data providers.

707 Individual data providers can agree to make their data available or not. They can also
708 decide whether they would like to be considered as a potential co-author if their data
709 is used. The administrator will then send only the data which the providers have
710 agreed to make available.

711

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713

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720 and D.M.; J.E.C. led the manuscript. All other authors contributed data and made
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722

723 **References**

724

- 725 1. Hughes TP, *et al.* (2017) Coral Reefs in the Anthropocene. *Nature*.
- 726 2. Pandolfi JM, *et al.* (2003) Global trajectories of the long-term decline of coral
727 reef ecosystems. *Science* 301(5635):955-958.
- 728 3. Hughes TP, *et al.* (2003) Climate change, human impacts, and the resilience of
729 coral reefs. *Science* 301(5635):929-933.
- 730 4. Teh LSL, Teh LCL, & Sumaila UR (2013) A global estimate of the number of
731 coral reef fishers. *Plos One* 8(6):e65397.
- 732 5. Mora C, *et al.* (2011) Global human footprint on the linkage between
733 biodiversity and ecosystem functioning in reef fishes. *Plos Biol*
734 9(4):e1000606.
- 735 6. Mora C, Chittaro PM, Sale PF, Kritzer JP, & Ludsin SA (2003) Patterns and
736 processes in reef fish diversity. *Nature* 421(6926):933-936.
- 737 7. Bellwood DR, Hughes TP, Folke C, & Nystrom M (2004) Confronting the
738 coral reef crisis. *Nature* 429(6994):827-833.
- 739 8. MacNeil MA, *et al.* (2015) Recovery potential of the world's coral reef fishes.
740 *Nature* 520(7547):341-344.
- 741 9. Hopf JK, Jones GP, Williamson DH, & Connolly SR (2016) Synergistic
742 effects of marine reserves and harvest controls on the abundance and catch
743 dynamics of a coral reef fishery. *Curr Biol* 26(12):1543-1548.
- 744 10. Krueck NC, *et al.* (2017) Marine reserve targets to sustain and rebuild
745 unregulated fisheries. *Plos Biol* 15(1):e2000537.
- 746 11. Edgar GJ, *et al.* (2014) Global conservation outcomes depend on marine
747 protected areas with five key features. *Nature* 506(7487):216-220.
- 748 12. McClanahan TR, Marnane MJ, Cinner JE, & Kiene WE (2006) A comparison
749 of marine protected areas and alternative approaches to coral-reef
750 management. *Curr Biol* 16(14):1408-1413.
- 751 13. Gill DA, *et al.* (2017) Capacity shortfalls hinder the performance of marine
752 protected areas globally. *Nature* 543(7647):665-669.
- 753 14. Cinner JE, *et al.* (2016) Bright spots among the world's coral reefs. *Nature*
754 535(7612):416-419.

- 755 15. Williams ID, *et al.* (2015) Human, oceanographic and habitat drivers of
756 Central and Western Pacific coral reef fish assemblages. *Plos One*
757 10(5):e0129407.
- 758 16. Bozec YM, O'Farrell S, Bruggemann JH, Luckhurst BE, & Mumby PJ (2016)
759 Tradeoffs between fisheries harvest and the resilience of coral reefs. *P Natl*
760 *Acad Sci USA* 113(16):4536-4541.
- 761 17. Dulvy NK, Freckleton RP, & Polunin NVC (2004) Coral reef cascades and the
762 indirect effects of predator removal by exploitation. *Ecol Lett* 7(5):410-416.
- 763 18. McClanahan TR, *et al.* (2011) Critical thresholds and tangible targets for
764 ecosystem-based management of coral reef fisheries. *P Natl Acad Sci USA*
765 108(41):17230-17233.
- 766 19. Pollnac R, *et al.* (2010) Marine reserves as linked social-ecological systems. *P*
767 *Natl Acad Sci USA* 107(43):18262-18265.
- 768 20. Bergseth BJ, Russ GR, & Cinner JE (2015) Measuring and monitoring
769 compliance in no-take marine reserves. *Fish and Fisheries* 16(2):240-258.
- 770 21. Graham NAJ & McClanahan TR (2013) The last call for marine wilderness?
771 *Bioscience* 63(5):397-402.
- 772 22. Cinner JE, *et al.* (2009) Linking social and ecological systems to sustain coral
773 reef fisheries. *Curr Biol* 19(3):206-212.
- 774 23. Pressey RL, Visconti P, & Ferraro PJ (2015) Making parks make a difference:
775 poor alignment of policy, planning and management with protected-area
776 impact, and ways forward. *Philos T R Soc B* 370(1681):20140280.
- 777 24. Devillers R, *et al.* (2015) Reinventing residual reserves in the sea: are we
778 favouring ease of establishment over need for protection? *Aquat Conserv*
779 25(4):480-504.
- 780 25. Andrello M, *et al.* (2017) Global mismatch between fishing dependency and
781 larval supply from marine reserves. *Nat Commun* 8.
- 782 26. Harrison HB, *et al.* (2012) Larval export from marine reserves and the
783 recruitment benefit for fish and fisheries. *Curr Biol* 22(11):1023-1028.
- 784 27. Januchowski-Hartley FA, Graham NAJ, Cinner JE, & Russ GR (2013)
785 Spillover of fish naivete from marine reserves. *Ecol Lett* 16(2):191-197.
- 786 28. Ravenstein EG (1889) The laws of migration. *Journal of the royal statistical*
787 *society* 52(2):241-305.

- 788 29. Dodd SC (1950) The interactance hypothesis: a gravity model fitting physical
789 masses and human groups. *American Sociological Review* 15(2):245-256.
- 790 30. Bergstrand JH (1985) The gravity equation in international trade: some
791 microeconomic foundations and empirical evidence. *The review of economics*
792 *and statistics* 67(3):474-481.
- 793 31. Anderson JE (2011) The gravity model. *Annual Review of Economics*
794 3(1):133-160.
- 795 32. Maire E, *et al.* (2016) How accessible are coral reefs to people? A global
796 assessment based on travel time. *Ecol Lett* 19(4):351-360.
- 797 33. Januchowski-Hartley FA, Graham NAJ, Cinner JE, & Russ GR (2015) Local
798 fishing influences coral reef fish behavior inside protected areas of the Indo-
799 Pacific. *Biol Conserv* 182:8-12.
- 800 34. Gil MA & Hein AM (2017) Social interactions among grazing reef fish drive
801 material flux in a coral reef ecosystem. *Proceedings of the National Academy*
802 *of Sciences* 114(18):4703-4708.
- 803 35. Bergseth BJ, Williamson DH, Russ GR, Sutton SG, & Cinner JE (2017) A
804 social-ecological approach to assessing and managing poaching by
805 recreational fishers. *Front Ecol Environ* 15(2):67-73.
- 806 36. Ward-Paige CA, *et al.* (2010) Large-Scale Absence of Sharks on Reefs in the
807 Greater-Caribbean: A Footprint of Human Pressures. *Plos One* 5(8):e11968.
- 808 37. Krueck Nils C, *et al.* (2017) Reserve Sizes Needed to Protect Coral Reef
809 Fishes. *Conservation Letters* 0(0): 1–9.
- 810 38. Christie P, *et al.* (2017) Why people matter in ocean governance:
811 Incorporating human dimensions into large-scale marine protected areas. *Mar*
812 *Policy* 84:273-284.
- 813 39. Campbell Stuart J, Edgar Graham J, Stuart-Smith Rick D, Soler G, & Bates
814 Amanda E (2017) Fishing-gear restrictions and biomass gains for coral reef
815 fishes in marine protected areas. *Conservation Biology* 32(2):401-410.
- 816 40. McClanahan TR, Graham NAJ, Calnan JM, & MacNeil MA (2007) Toward
817 pristine biomass: Reef fish recovery in coral reef marine protected areas in
818 Kenya. *Ecol Appl* 17(4):1055-1067.
- 819 41. O’Leary BC, *et al.* (2018) Addressing Criticisms of Large-Scale Marine
820 Protected Areas. *Bioscience* 68(5):359-370.

- 821 42. Ferraro PJ & Pressey RL (2015) Measuring the difference made by
822 conservation initiatives: protected areas and their environmental and social
823 impacts Introduction. *Philos T R Soc B* 370(1681):20140270.
- 824 43. Beger M, *et al.* (2015) Integrating regional conservation priorities for multiple
825 objectives into national policy. *Nat Commun* 6:8208.
- 826 44. Boon PY & Beger M (2016) The effect of contrasting threat mitigation
827 objectives on spatial conservation priorities. *Mar Policy* 68:23-29.
- 828 45. Clark P (2014) Shark fin sales in China take a dive. *Financial Times* August 6.
- 829 46. Thyresson M, Nyström M, & Crona B (2011) Trading with Resilience:
830 Parrotfish Trade and the Exploitation of Key-Ecosystem Processes in Coral
831 Reefs. *Coastal Management* 39(4):396-411.
- 832 47. Green AL, *et al.* (2014) Designing Marine Reserves for Fisheries
833 Management, Biodiversity Conservation, and Climate Change Adaptation.
834 *Coastal Management* 42(2):143-159.
- 835 48. Bennett NJ, *et al.* (2017) Conservation social science: Understanding and
836 integrating human dimensions to improve conservation. *Biol Conserv* 205:93-
837 108.
- 838 49. McClanahan TR & Abunge CA (2016) Perceptions of fishing access
839 restrictions and the disparity of benefits among stakeholder communities and
840 nations of south-eastern Africa. *Fish and Fisheries* 17(2):417-437.
- 841 50. Watson RA, *et al.* (2015) Marine foods sourced from farther as their use of
842 global ocean primary production increases. *Nat Commun* 6.
- 843 51. Gerland P, *et al.* (2014) World population stabilization unlikely this century.
844 *Science* 346(6206):234-237.
- 845 52. Mora C (2014) Revisiting the environmental and socioeconomic effects of
846 population growth: A fundamental but fading issue in modern scientific,
847 public, and political circles. *Ecol Soc* 19(1):38.
- 848 53. Mora C (2015) Perpetual struggle for conservation in a crowded world and the
849 needed paradigm shift for easing ultimate burdens. *Ecology of Fishes on Coral*
850 *Reefs*, ed Mora C (Cambridge University Press, Cambridge), pp 289-296.
- 851 54. Cottingham J, Germain A, & Hunt P (2012) Use of human rights to meet the
852 unmet need for family planning. *Lancet* 380(9837):172-180.
- 853 55. Sen A (2013) The Ends and Means of Sustainability. *J Hum Dev Capabil*
854 14(1):6-20.

- 855 56. Mora C, Caldwell IR, Birkeland C, & McManus JW (2016) Dredging in the
856 Spratly Islands: Gaining land but losing reefs. *Plos Biol* 14(6):e1002497.
- 857 57. Laurance WF & Arrea IB (2017) Roads to riches or ruin? *Science*
858 358(6362):442.
- 859 58. Alamgir M, *et al.* (2017) Economic, Socio-Political and Environmental Risks
860 of Road Development in the Tropics. *Curr Biol* 27(20):R1130-R1140.
- 861 59. Hicks CC, Crowder LB, Graham NAJ, Kittinger JN, & Le Cornu E (2016)
862 Social drivers forewarn of marine regime shifts. *Front Ecol Environ*
863 14(5):253-261.
- 864 60. Berkes F, *et al.* (2006) Ecology - Globalization, roving bandits, and marine
865 resources. *Science* 311(5767):1557-1558.
- 866 61. Cinner JE & Kittinger JN (2015) 22 Linkages between social systems and
867 coral reefs. *Ecology of Fishes on Coral Reefs*, ed Mora C (Cambridge
868 University Press, Cambridge), pp 215-220.
- 869 62. Daw T, *et al.* (2011) The spatial behaviour of artisanal fishers: Implications
870 for fisheries management and development (Fishers in Space). (WIOMSA).
- 871 63. Froese R & Pauly D (2012) FishBase. (World Wide Web electronic
872 publication.).
- 873 64. Bartholomé E, *et al.* (2002) *GLC 2000: Global Land Cover mapping for the*
874 *year 2000: Project status November 2002* (Institute for Environment and
875 Sustainability).
- 876 65. Nelson A (2008) Travel Time to Major Cities: A Global Map of Accessibility.
877 in *Global Environment Monitoring Unit-Joint Research Centre of the*
878 *European Commission* (Ispra, Italy).
- 879 66. IUCN & UNEP-WCMC (2016) The World Database on Protected Areas
880 (WDPA). ed UNEP-WCMC (Available at: www.protectedplanet.net.,
881 Cambridge, UK).
- 882 67. MacNeil MA & Connolly SR (2015) Multi-scale patterns and processes in reef
883 fish abundance. *Ecology of Fishes on Coral Reefs*, ed Mora C), pp 116-126.
- 884 68. Andréfouët S, *et al.* (2006) Global assessment of modern coral reef extent and
885 diversity for regional science and management applications: a view from
886 space. *10th International Coral Reef Symposium*, eds Suzuki Y, Nakamori T,
887 Hidaka M, Kayanne H, Casareto BE, Nadaoka K, Yamano H, Tsuchiya M, &
888 Yamazato K (Japanese Coral Reef Society, Okinawa, Japan), pp 1732-1745.

- 889 69. Maina J, McClanahan TR, Venus V, Ateweberhan M, & Madin J (2011)
890 Global Gradients of Coral Exposure to Environmental Stresses and
891 Implications for Local Management. *Plos One* 6(8):e23064.
892 70. Spalding MD, *et al.* (2007) Marine ecoregions of the world: A
893 bioregionalization of coastal and shelf areas. *Bioscience* 57(7):573-583.

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898 **Figure Legends**

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900 **Figure 1. Model-predicted relationships between human gravity and reef fish**
901 **biomass under different types of fisheries management. A) Map of our study**
902 **sites with color indicating the amount of fish biomass at each site. Partial plots**
903 **of the relationship between biomass and gravity under different types of**
904 **management at the nation/state (B-D), and reef site (F-H) scale; openly fished**
905 **(red), restricted (green), and high-compliance marine reserves (blue). Shaded**
906 **areas represent 95% confidence intervals. Bubble size in panels B-D reflect the**
907 **number of reef sites in each nation/state, scaled for each management type (such**
908 **that the largest bubble in each panel represent the highest number of sites per**
909 **nation/state for that type of management; Table S5). G) Model-predicted**
910 **relationships of how reef fish biomass declines as gravity increases by**
911 **management type.**

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913 **Figure 2. Model-predicted relationships between human gravity and the**
914 **probability of encountering top predators under different types of fisheries**
915 **management. A) Map of our study sites indicating the presence of top predators.**
916 **The presence of top predators along a gravity gradient under different types of**
917 **management at the nation/state (C-E) and site (F-H) scale; openly fished (red),**
918 **restricted (green), and high-compliance marine reserves (blue). Bubble size in**
919 **panels F-G reflect the number of reef sites in each nation/state, scaled for each**
920 **management type (such that the largest bubble in each panel represent the**
921 **highest number of sites per nation/state for that type of management; Table S5).**
922 **H) Model-predicted relationships of how the probability of encountering**

923 predators declines as gravity increases. Shaded areas represent 95% confidence
924 intervals.

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927 **Figure 3. The conservation gains (i.e. the difference between openly fished sites**
928 **and managed areas) for high-compliance marine reserves (blue line) and**
929 **restricted fishing (green line) for (A) target fish biomass (solid lines include**
930 **biomass of top predators, dotted lines exclude top predator biomass as per Fig.**
931 **S2), and (B) the probability of encountering top predators change along a**
932 **gradient of gravity.**

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935 **Figure 4. Distribution of gravity on the world's coral reefs. A) Map of gravity**
936 **calculated for every coral reef in the world ranging from blue (low gravity) to**
937 **red (high gravity). The four coral reef realms (70) are delineated. Insets**
938 **highlight gravity for key coral reef regions of the world: 1) Red Sea; 2) Western**
939 **Indian Ocean; 3) Southeast Asia; 4) Great Barrier Reef of Australia and the**
940 **South Pacific; 5) Caribbean. For visual effect, gravity values in inset maps are**
941 **also given vertical relief, with higher relief indicating higher gravity values. B)**
942 **Distribution of gravity values per coral reef realm.**

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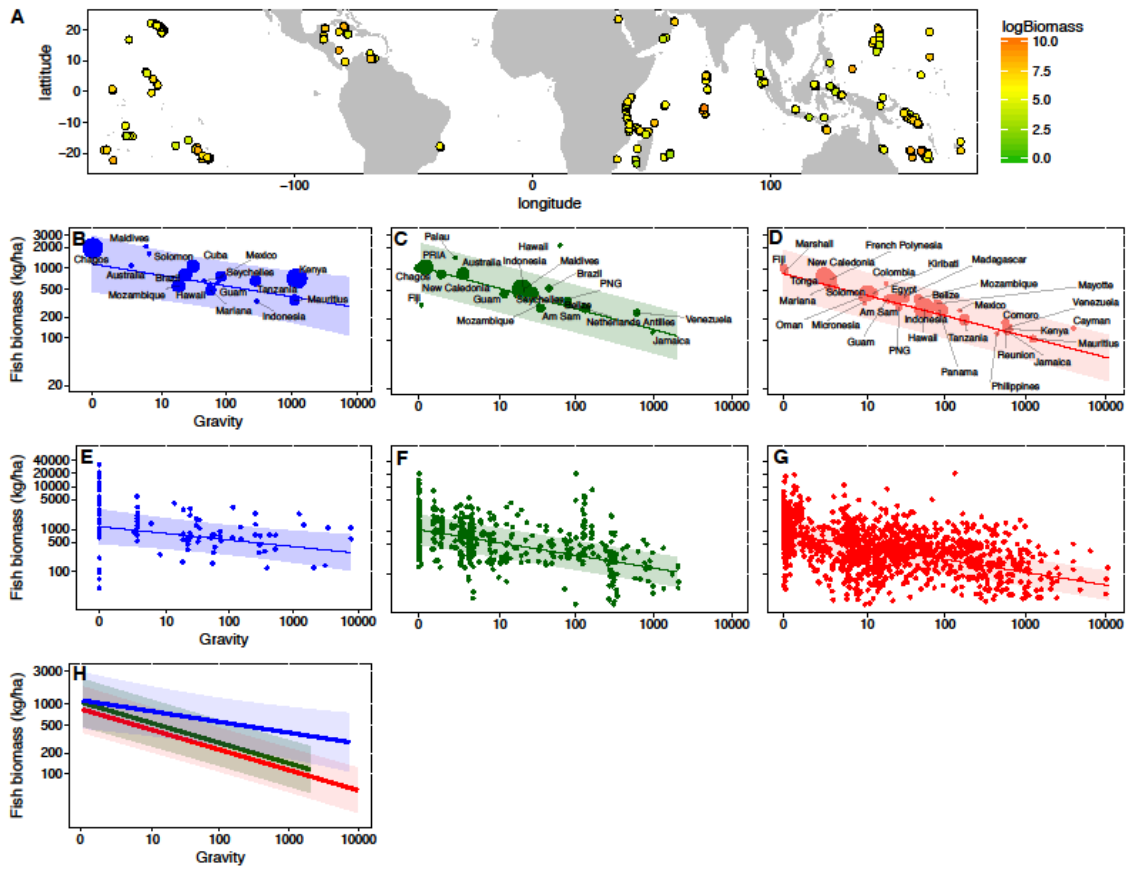
944 **Figure 5. Box 1 Figure. Operationalizing Gravity. A) Applied to coral reefs, our**
945 **heuristic of the gravity concept captures interactions between people and coral**
946 **reef fish as a function of the population of a place divided by the squared time it**
947 **takes to travel to the reefs (i.e. travel time). B) Gravity isoclines along gradients**
948 **of population size and travel time illustrate how gravity values could be similar**
949 **for places that have large populations but are far from the reefs (e.g.**
950 **population_x = 15,000 people, travel time_x = 7hours, gravity_x = 306) as to those**
951 **with small populations that are close to the reef (e.g. population_y = 300 people,**
952 **travel time_y = 1 hour, gravity_y = 300).**

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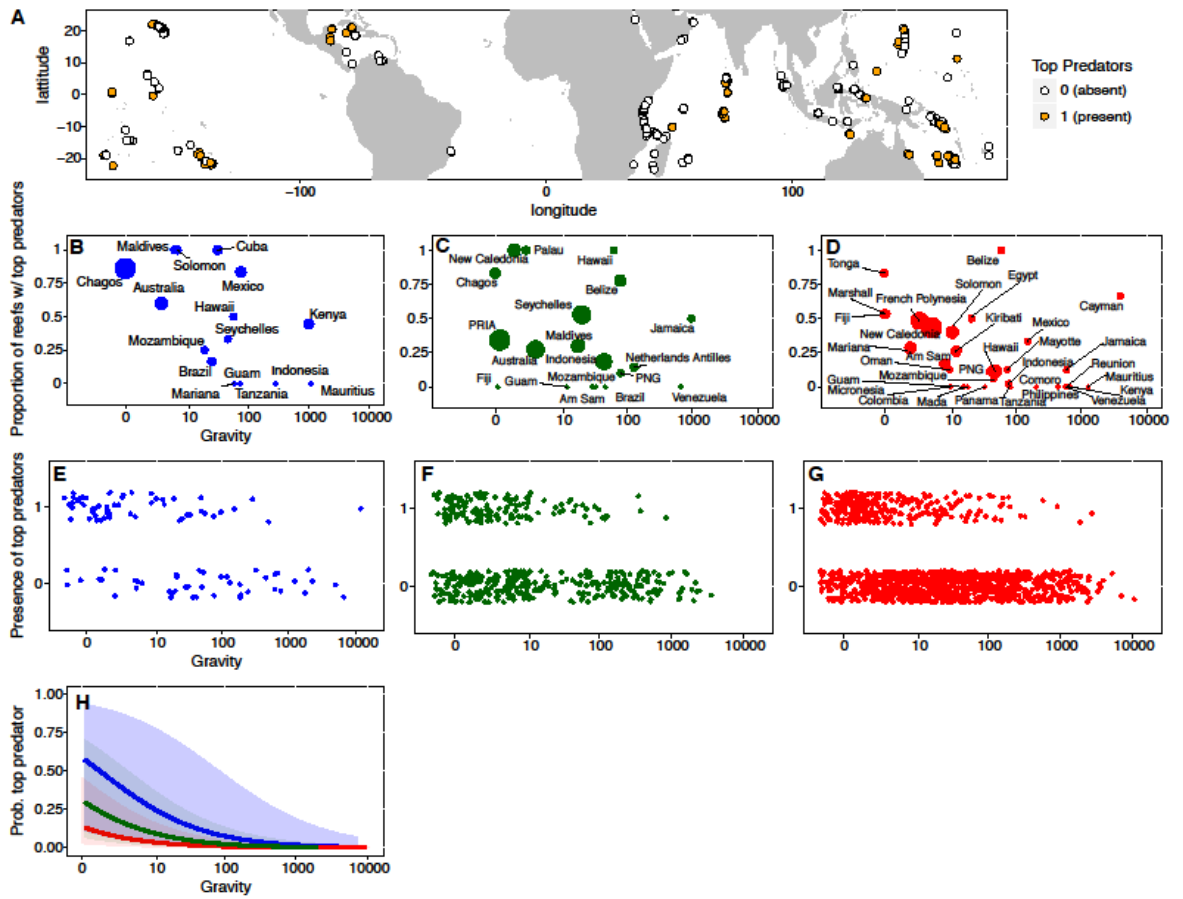
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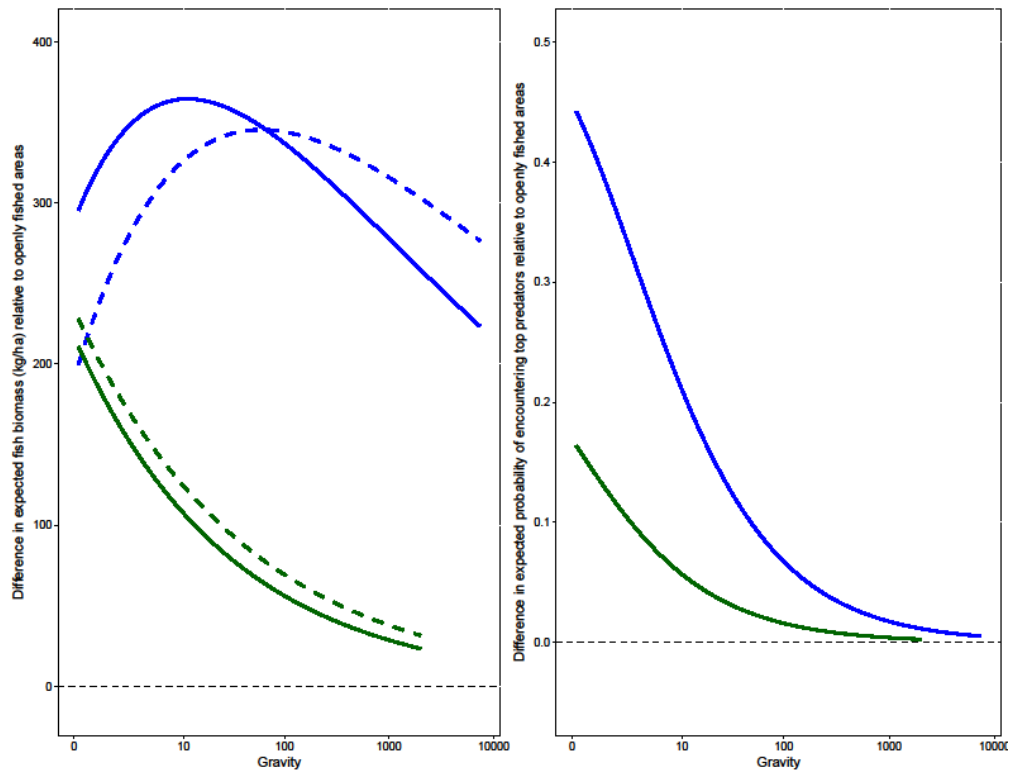
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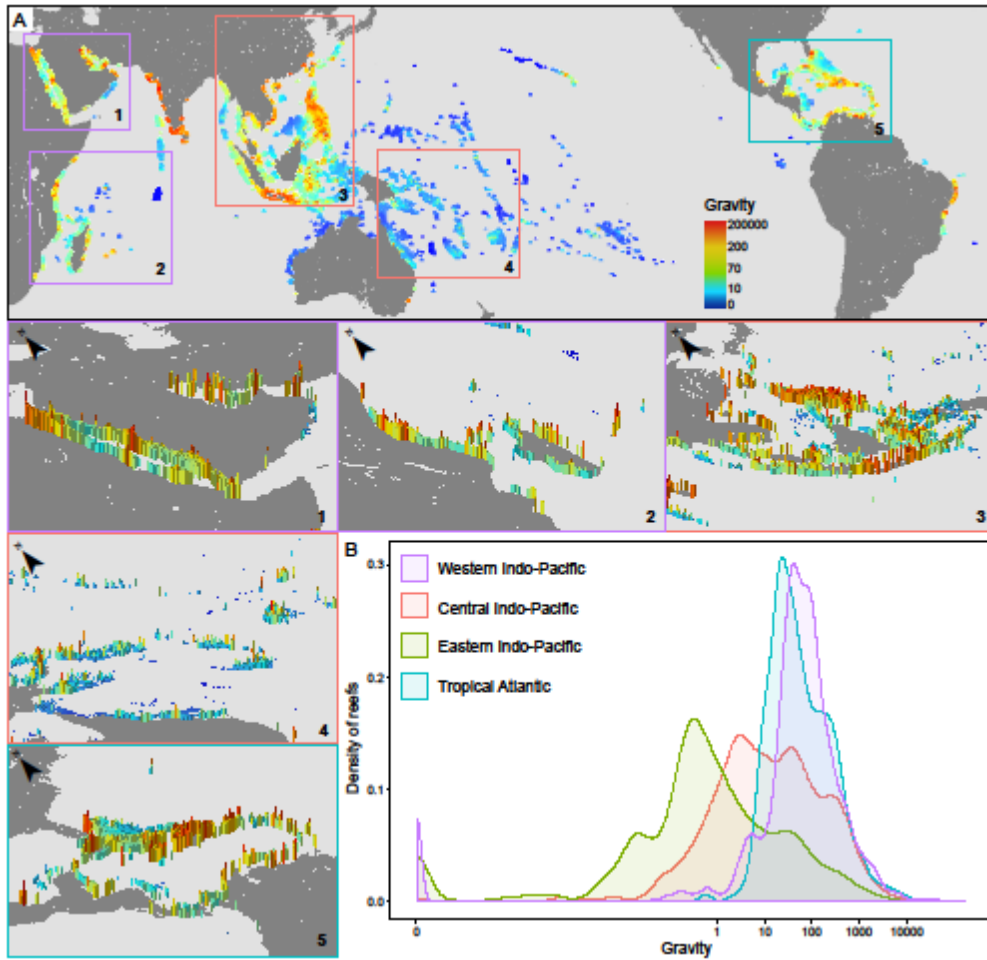
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