

# Global status and conservation potential of reef sharks

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Decades of overexploitation have devastated shark populations, leaving considerable doubt as to their ecological status<sup>1,2</sup>. Yet much of what is known about sharks has been inferred from catch records in industrial fisheries, whereas far less information is available about sharks that live in coastal habitats<sup>3</sup>. Here we address this knowledge gap using data from more than 15,000 standardized baited remote underwater video stations that were deployed on 371 reefs in 58 nations to estimate the conservation status of reef sharks globally. Our results reveal the profound impact that fishing has had on reef shark populations: we observed no sharks on almost 20% of the surveyed reefs. Reef sharks were almost completely absent from reefs in several nations, and shark depletion was strongly related to socio-economic conditions such as the size and proximity of the nearest market, poor governance and the density of the human population. However, opportunities for the conservation of reef sharks remain: shark sanctuaries, closed areas, catch limits and an absence of gillnets and longlines were associated with a substantially higher relative abundance of reef sharks. These results reveal several policy pathways for the restoration and management of reef shark populations, from direct top-down management of fishing to indirect improvement of governance conditions. Reef shark populations will only have a high chance of recovery by engaging key socio-economic aspects of tropical fisheries.

Global demand for shark products, such as fins and meat, as well as high levels of bycatch, have caused widespread declines in shark populations globally<sup>1–3</sup>, with the potential to affect the function of ocean ecosystems<sup>4</sup> and jeopardize associated fishing and tourism sectors<sup>5,6</sup>. However, there are large gaps in our knowledge regarding the population status of sharks in coastal environments such as coral reefs, where the majority of threatened species occur<sup>1</sup>. Scientific surveys of reef fish typically use underwater visual census by divers, which can lead to under- or overestimates of the abundance of large roving animals such as sharks<sup>7</sup>. Although a handful of studies from remote, uninhabited or no-access reefs have recorded exceptionally high reef shark biomass<sup>8,9</sup> and evidence of declines<sup>9,10</sup>, there are large differences in environmental features<sup>11</sup> and sampling<sup>7</sup> that undermine the use of pristine remote areas as conservation baselines for inhabited coastal environments<sup>12</sup>. In practice, shark conservation targets for most reefs should reflect the levels of abundance found in the best-managed places where people are present, acknowledging the environmental and social contexts in which people use ocean resources<sup>13</sup>.

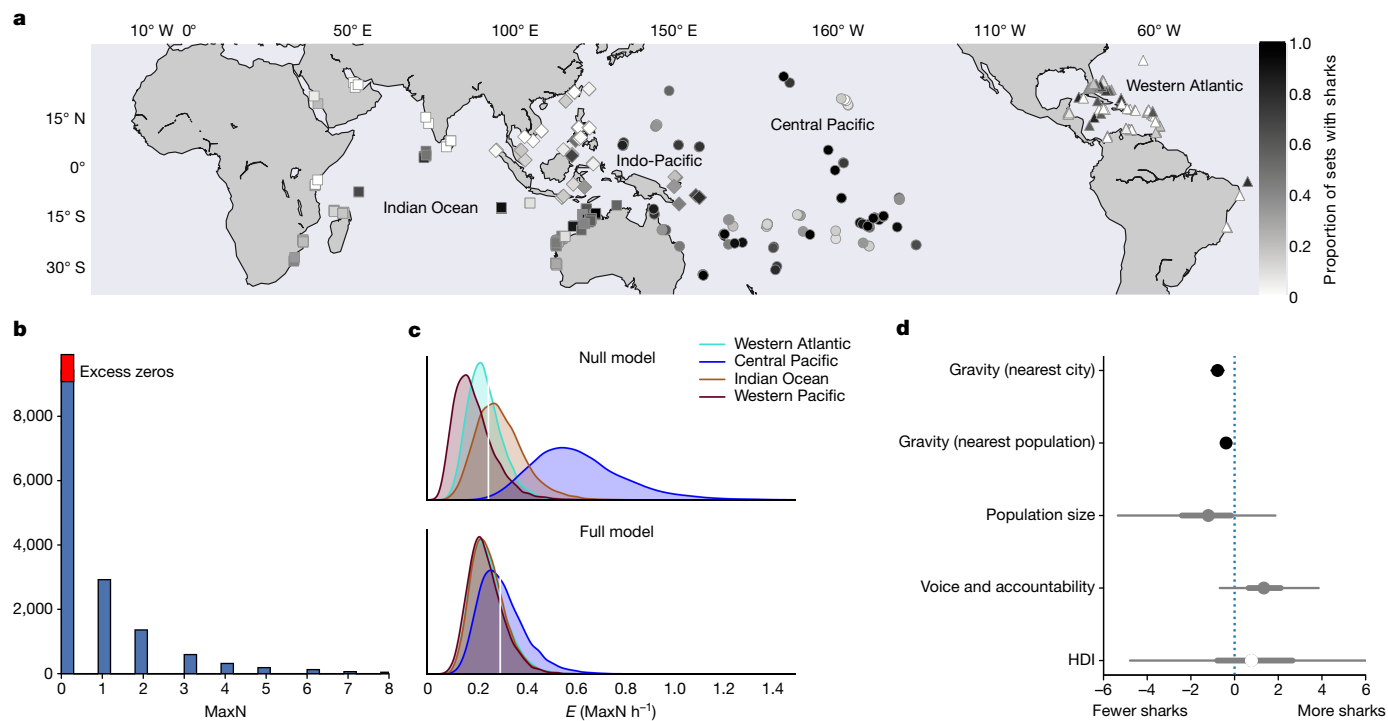
We used baited remote underwater video systems (BRUVS) in a dedicated global survey (Global FinPrint, <https://globalfinprint.org>) to quantify the status of reef sharks in 58 countries, states and territories (hereafter, nations). BRUVS footage was analysed to provide a standardized index of relative shark abundance—given as the maximum number of sharks seen in a single frame of each video set (MaxN; see Methods)—that has been shown to compare well with alternative methods of estimating the relative abundance of sharks<sup>14</sup> (Extended Data Fig. 1). Global FinPrint surveys included sightings of 59 shark species; the vast majority of sightings (93%) comprised species that complete their life cycle on coral reefs or frequently visit them (see Methods). Despite our assumption that sharks would be present on all of the world's coral reefs<sup>15</sup>, they were not observed on 19% (69 out of 371) of reefs surveyed

and 63% of the 15,165 BRUVS sets in our survey did not record the presence of a shark, indicating that there has been widespread depletion of reef sharks across much of the world's tropical oceans (Fig. 1a, b).

## Evaluating the relative abundance of reef sharks

We developed a set of Bayesian hierarchical models to quantify the relative abundance of reef sharks across a range of management regimes and to understand how the abundance of reef sharks varies globally. We used a zero-inflated modelling approach that enabled us to examine factors that influenced both the presence or absence of reef sharks (the occurrence of excess zeros) and the relative abundance of sharks among reefs, nations and regions (see Methods). Although the conditional mode of regional-level random effects for reef sharks was 40% higher in the central Pacific than other regions (Fig. 1c; null model), these differences disappeared under our full model, suggesting that the observed inter-regional disparities were largely due to reef- and national-scale effects captured by the covariates that we included (Fig. 1c; full model). In other words, although we observed strong regional differences in our data, these were largely attributable to differences in key human drivers of resource exploitation.

Our results show that declines in reef sharks from the coastal tropical oceans correlate with key socio-economic differences among reefs and nations (Fig. 1d). Our civil society metric (voice and accountability) was associated with a higher likelihood of sharks being observed. In addition, nations with larger coastal populations coincided with sharks not being observed, whereas we found little evidence for an effect of increased national wealth (through the human development index). We also found that the relative abundance of reef sharks had a negative relationship with the 'gravitational pull' of the closest human settlement and any markets within 500 km of each BRUVS set (our



**Fig. 1 | Distribution of reef sharks from Global FinPrint. a**, Observed proportion of sets containing reef sharks from BRUVS among 371 study reefs. The regions include: Indian Ocean (squares), Western Pacific (diamonds), Central Pacific (circles) and Western Atlantic (triangles). **b**, Observed distribution of MaxN from  $n = 15,165$  individual BRUVS sets, with model-estimated 'excess' zeros ( $n = 1,481$ ) indicated in red that correspond to the proportion of observed zeros that are inconsistent with the observed distribution of counts. The x-axis is truncated at 8, which includes more than 99% of observations. **c**, Conditional modes of regional-level random effects for MaxN per BRUVS set from both null (spatial hierarchy and nuisance parameters only) and full (null + additional management and socio-economic covariates included) models, illustrating the degree to which the full model accounts for inter-regional disparity. Vertical white lines are the global median expected MaxN values. Regional estimates (median and 90% uncertainty intervals)

under the null model were: Western Atlantic, 0.23 (0.14–0.37) sharks per hour; Central Pacific, 0.59 (0.36–0.97); Indian Ocean, 0.29 (0.16–0.48); Western Pacific, 0.18 (0.09–0.35). Regional estimates (median and 90% uncertainty intervals) under the full model were: Western Atlantic, 0.24 (0.15–0.39); Central Pacific, 0.29 (0.18–0.49); Indian Ocean, 0.24 (0.15–0.38); Western Pacific, 0.23 (0.14–0.38). **d**, Estimated relative effect sizes for the influence of national socio-economic conditions (including the human development index (HDI)) on the expected proportion of negative binomial variates on BRUVS sets or, for gravity metrics, on expected MaxN  $\text{h}^{-1}$ . The reported values are the highest posterior density median values (circles), with 50% (thick lines) and 90% (thin lines) uncertainty intervals. Black symbols indicate that the 90% uncertainty intervals did not overlap zero; grey symbols indicate that the 50% uncertainty intervals did not overlap zero; and white symbols indicate that the 50% uncertainty intervals did overlap zero.

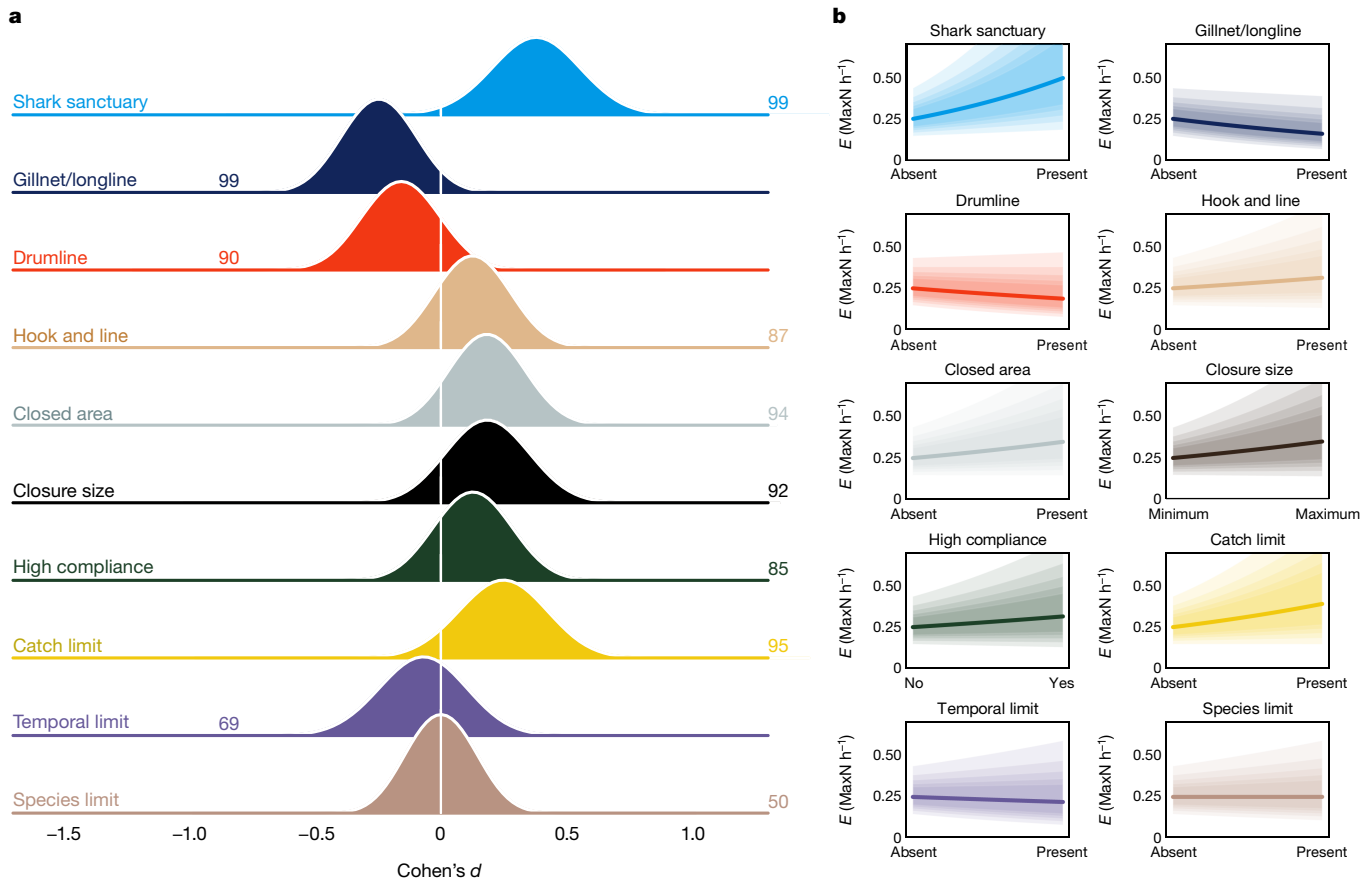
gravity metric was calculated as the size of human populations divided by their squared distance from surveyed reefs<sup>13</sup>; see Methods). Given that shark fins are effectively non-perishable and it is common for fishers to travel long distances and for fin-traders to regularly visit remote communities<sup>16</sup>, we expected some decoupling of our gravity metrics and the relative abundance of reef sharks. By contrast, our results suggest that there may be high levels of local consumption in many areas<sup>13</sup>, supporting recent findings that markets for shark meat have followed the increase in catches for the global fin trade<sup>6</sup>, making local-market interventions aimed at reducing the consumption of shark meat a potentially valuable conservation investment in some areas. Our results also suggest that long-term, socio-economic disparities have very probably led to the functional extinction of sharks from survey reefs in up to eight nations (that is, where the probability of sharks being observed was  $<0.1\%$ ; see Methods and Extended Data Fig. 2). This emphasizes that, for many places, there are no clear solutions to promoting the recovery of reef sharks without addressing the socio-economic challenges that indirectly lead to overexploitation.

## Management of reef shark abundances

The prevalence of impoverished countries, weak governance and the high economic value of wildlife products is a fundamental driver of

overexploitation in many of the world's marine and terrestrial ecosystems<sup>17</sup>. Although there are some notable successes in moving communities away from shark fishing and into tourism or other less-destructive sectors<sup>16,18</sup>, livelihood diversification requires substantial long-term investment and capacity-building efforts that are suited to local contexts<sup>19</sup>. Therefore, to understand how top-down management interventions relate to reef shark abundances, we estimated the relative effect sizes for a range of direct management actions globally (Fig. 2a). At the national level, the presence of a shark sanctuary (that is, no targeted catch or trade in shark or shark products) supported a 50% (20%–68%) (median (90% highest posterior density uncertainty intervals)) higher relative abundance than nations without sanctuary status (Fig. 2b). Legislation that establishes shark sanctuaries has generally been introduced in nations in which local communities did not heavily fish sharks for cultural or economic reasons (for example, shark ecotourism)<sup>20</sup>, which makes its potential effectiveness difficult to predict in jurisdictions in which people currently fish for sharks. Despite this, our survey shows that the nine nations with shark sanctuaries that we surveyed are globally and regionally important refuges for reef sharks.

In places in which people engage in shark fishing, we found clear benefits of top-down fisheries management and closed areas (that is, no-take reserves; Fig. 2). The use of gillnets and longlines had the strongest negative influence on the relative abundance of reef sharks, with an



**Fig. 2 | Effect sizes of the management interventions for reef sharks.** **a**, Standardized effect sizes of the presence of various management interventions on the average relative abundance of sharks (expected MaxN). Density plots show the posterior distributions of the estimated effect sizes (Cohen's *d* scores plotted on a logit scale). The values on the left and right side

of zero (vertical white line) indicate the posterior probabilities of a negative or positive effect of each type of management (as percentages), respectively. Closure size refers to the size of the closed area. **b**, Expected change in MaxN given the presence or absence of management interventions. The shading indicates the posterior uncertainty intervals from 50 to 90%.

average reduction in relative abundance of 36% (11–54%) in jurisdictions in which one or both gear types were used, reflecting their widespread efficiency in capturing sharks, often as bycatch<sup>21,22</sup>. We also found evidence that the use of catch limits (that is, restraints on the number of sharks permitted to be caught per day per vessel or fisher or season) were associated with a higher abundance of reef sharks. However, the effect of catch limits on relative abundance was inconsistent across jurisdictions (36% (0–58%)), possibly owing to the greater difficulty in enforcing catch-based, rather than gear-based, regulations<sup>23</sup>. Banning drumlines (29% (–13–52%)) or moving towards more selective hook and line fishing (25% (–8–48%)) were estimated to be less effective but may be more-acceptable management interventions in some contexts. Gear restrictions were found to be more effective than closed areas in supporting higher numbers of reef sharks (28% (0–50%); Fig. 2a, b); however, the benefits increased twofold among the largest (around 20,000 km<sup>2</sup>) closed areas (49% (11–71%)).

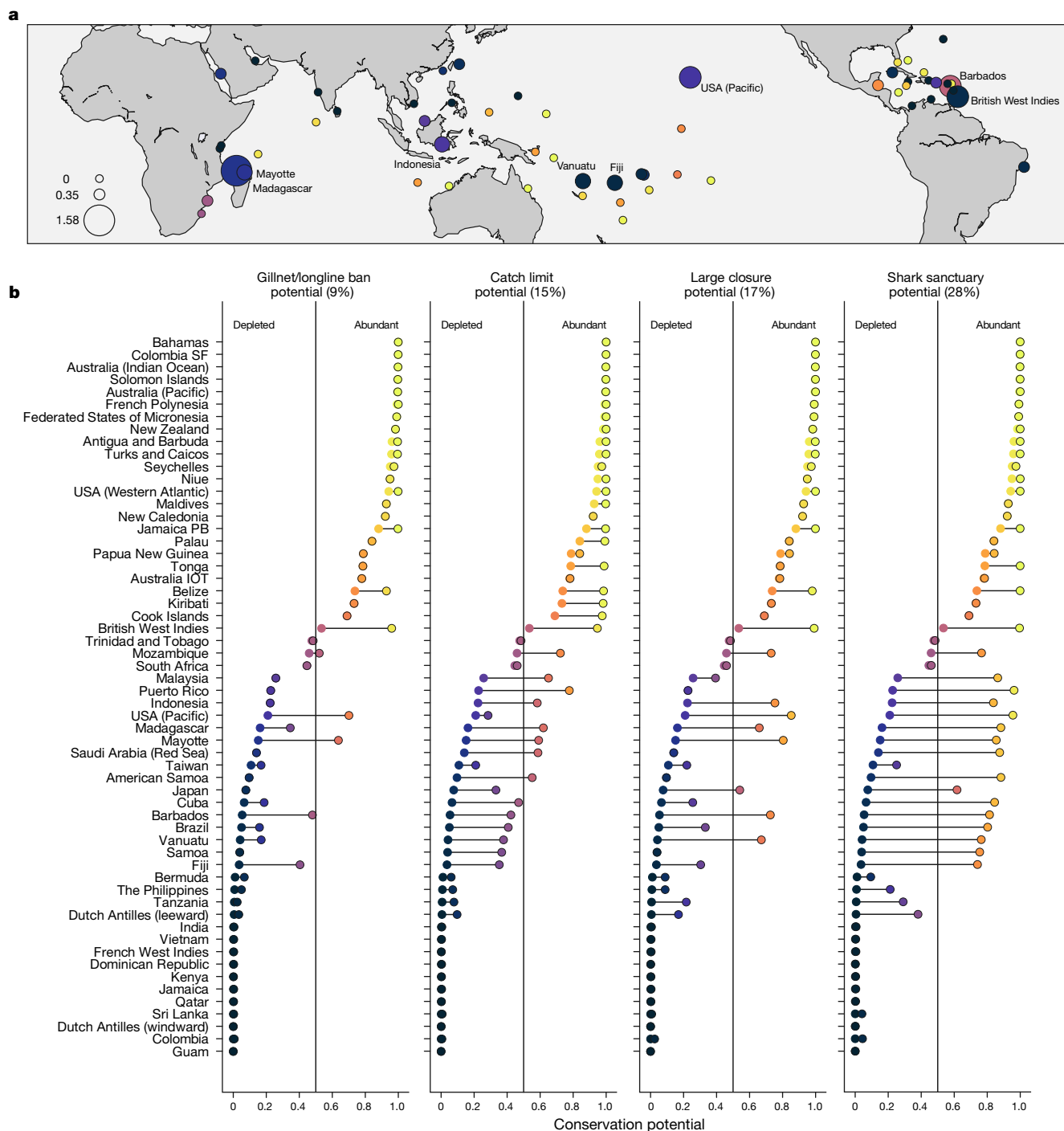
## Conservation potential

Identifying the most-appropriate direct management strategies for conservation depends heavily on the nature of local fisheries, social norms and cultures, as well as on the understanding of the relative stock status. Therefore, to evaluate the relative status of reef shark abundances among nations, we developed an abundance status score, given by the posterior probability of national expected MaxN values being greater than the regional average under our null model (see Methods). This placed each nation in its observed regional context, scoring

it relative to its neighbours and reflecting levels of recovery that do not rely on achieving global maxima.

The best-performing nations relative to regional expectations included the Bahamas, continental Australia, Solomon Islands, the Federated States of Micronesia and French Polynesia (Fig. 3). These nations had many of the key attributes that we found to be associated with increased abundances of reef sharks, including being well-governed and/or remote, and having strong, directed management of shark fisheries or shark sanctuaries (Fig. 2). By contrast, the worst-ranked nations for reef sharks included Qatar, the Dominican Republic, continental Colombia, Sri Lanka and Guam, which have suffered from varying levels of poor governance<sup>13</sup> and extreme overfishing. Overall, 59% of nations (34 out of 58) had abundance scores below 50% of their regional expectation, suggesting that loss of reef sharks is pervasive among reefs globally.

Given this level of depletion, the restoration of reef shark populations will require dedicated and effective management of some form. To evaluate the potential conservation benefits of the most-promising management interventions, we estimated the relative impact of gillnet and/or longline bans, closures, catch limits and shark sanctuaries through the expected change in national abundance scores given implementation under our model. Our results show that fisheries management actions are likely to be most effective for the conservation of reef sharks overall, with the average increase in regional score for catch limits (15%) and gillnet or longline bans (9%) exceeding the benefits of average-sized closed areas (8%) in places in which such regulations are currently absent. Although closed areas that are



**Fig. 3 | Conservation potential for reef sharks. a**, Regionally scaled abundance scores (colours, corresponding to abundance scores in **b**) and conservation potential (circle sizes) for 58 nations surveyed by Global FinPrint (nations with a conservation potential >0.9 are labelled). **b**, Net abundance scores (circles without border), relative to region-scale expected values (Fig. 1c, null model), and expected change in abundance score (black horizontal lines, net abundance score gain,  $\Delta_{\text{gain},m}$ , for management intervention,  $m$ ) given the implementation of potential management interventions (circles with black border) and estimated average effect sizes from the full model. Line lengths vary according to the shape of the estimated posterior average for each nation

and are scaled by the percentage of reefs that are currently not under each management intervention. The increases in mean percentage abundance score that are greater than zero are included in parentheses at the top of each panel. Note the capacity to increase conservation scores is limited in many of the lowest-scoring sites owing to the exceptionally low probabilities of sharks being present. In regions in which management interventions are already implemented, the conservation potential remains the same. National abbreviations are Sea Flower Biosphere Reserve (SF), Pedro Bank (PB) and Indian Ocean Territory (IOT).

large, old, isolated and well-enforced have been shown to be among the most-successful conservation measures for reef fishes<sup>24</sup>, only very large (around 20,000 km<sup>2</sup>) closures outperformed these other measures ('Large closures' in Fig. 3).

The apparent difference in the effectiveness of average-sized closed areas for sharks relative to reef fish is probably due to the smaller home range sizes of reef-associated fish, which tend to remain within the bounds of a given closed area, whereas sharks range more widely and

are therefore likely to stray outside a closed area<sup>25</sup>. In many places, fisheries management has the potential to be applied across a much larger area than fully closed areas, which are difficult to implement at very large scales as people are typically unwilling or unable to stop fishing entirely<sup>25</sup>. As a result, many closed areas are simply not designed to protect sharks<sup>26</sup>. However, if measures to stop catches and trade in sharks and shark products could be implemented at the national scale, shark sanctuaries could have the greatest potential benefit (a 25% increase, on average) for reef sharks (Fig. 3). Again, the economic feasibility and cultural acceptance of this approach is expected to be limited in most places that currently catch sharks and trade in shark products.

Given the clear conservation benefits of a range of direct top-down management actions for sharks, a key question remains as to where the greatest conservation gains could be made if regulations were well-enforced. To address this question, we calculated a total conservation potential score for each nation, given as the maximum of the sum of estimated conservation benefits from gillnet or longline bans, closed areas, and catch limits or implementation of a shark sanctuary (Supplementary Information). Nations with the highest conservation potential included Madagascar, Mayotte, Vanuatu, USA-Pacific (Hawaii), the British West Indies and Barbados (Fig. 3a), all of which lack established management schemes for sharks and have some level of degradation in the relative abundance of reef sharks. As with any fishery type, realizing the conservation potential of these nations will require strong engagement with and participation by judicial systems, fisheries managers and local fishers to ensure compliance, monitoring and enforcement of regulations.

Without an absolute estimate of the abundance of sharks, it is difficult to know how effective the estimated levels of conservation potential might be in restoring shark populations in reef ecosystems that have been degraded by overfishing. Although research has shown that fully recovered reef fish communities have biomasses between 1,000 kg ha<sup>-1</sup> (ref. <sup>27</sup>) and 1,500 kg ha<sup>-1</sup> (ref. <sup>12</sup>), we have no current estimate of the size of the forage base that is required by a recovered shark population, or how the bottom-up effects of prey biomass might influence the recovery potential of reef sharks. A key question remains as to whether management strategies that only pursue shark conservation can make substantial or limited gains, relative to those that include the restoration of the wider reef ecosystem. If the restoration of the whole ecosystem is necessary to fully restore shark populations, our results underscore the need for managers to engage with the wider social, economic and cultural drivers of marine exploitation<sup>28</sup>.

Our study makes clear that concern over the global status of reef sharks is warranted, especially in the Western Pacific, Indian Ocean and Western Atlantic regions in which multiple nations are characterized by dense coastal populations and poor governance. Furthermore, our results identify two management pathways—socio-economic policies (indirect) and direct management (top-down)—that could yield positive conservation outcomes for sharks when implemented and enforced. From national bans on the targeting and trade of sharks, to reef-level gear restrictions and closed areas, the societal contexts in which management actions are used will influence where they are likely to be accepted and achieve meaningful conservation gains. Fishery and marine area managers are faced with a daunting problem and, although there is no panacea that will succeed everywhere, these results provide insights into a portfolio of approaches that could begin to restore the populations of reef sharks throughout the world.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-020-2519-y>.

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## Methods

### Data reporting

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

### Surveys

Our study began in July 2015, but it also incorporates a minority of BRUVS that were deployed before 2015, collected according to the standard methodology described below (6% of all sets were deployed before June 2015). Sampling ended in June 2018. Each sampling site (hereafter referred to as a reef;  $n = 371$ ) consisted of a continuous reef tract of around 10 km in length. Reefs were selected for sampling based on access through a local collaborator and the operational range of the vessel used for sampling. Within nations, we generally attempted to sample at least one reef that was closed to fishing and one reef that was open to fishing and/or had restricted fishing. When larger numbers of reefs were sampled within a nation, as far as practical, sampling included reefs across a range of distances from urban centres. Each deployment of a BRUVS was considered a set (which are referred to as a 'drop').

BRUVS consisted of a video camera (primarily GoPro HERO2, GoPro HERO3, GoPro Hero4 Silver (<https://www.gopro.com>) or Sony CX7, but also Sony Legria HF10 and Sony Handycam DCR-HC52 in sets made before July 2015) fixed on a stainless steel, aluminium or rebar frame with bait mounted on a 1.5 m long pole in the field of view of the camera, with a rope and float tied to the top of the frame to facilitate deployment, relocation and retrieval<sup>14</sup>. Each BRUVS set was baited with approximately 1 kg of oily fish (for example, primarily from the families Clupeidae and Scombridae). Metal cages prevented baits from being eaten although plastic was used in some cases. Nearly all reefs were sampled with replicate BRUVS sets over a single period of fewer than 10 days (mean BRUVS per reef, 39; range, 9–71).

Nearly all (>98%) BRUVS sets were deployed during daylight hours (07:00–17:00) and the initial deployment coordinates for each day were determined using a randomly generated position within the sampling area. The first BRUVS sets were then deployed as close as possible to these coordinates and the remainder were then set at least 500 m away from previous sets<sup>14,29</sup>, at depths of 2–40 m. This spacing was designed to reduce the likelihood of individuals being recorded on multiple cameras. Bottom depth and sea surface temperature were recorded at deployment. Visibility, substrate complexity and substrate type were estimated for each deployment using a still frame from the footage after the BRUVS set settled to the bottom using Benthobox software (<https://benthobox.com/>). BRUVS sets were retrieved after at least 70 min to ensure a standard 60 min of data collection from the time of settlement. Videos were reviewed by at least two trained and independent readers at normal play speed and reviewed by a master annotator to ensure accuracy in species identification. Where images were ambiguous (4.82% of cases), the lowest taxa to which the shark could be confidently assigned (genus, family, and so on) was used. As such we assumed there was no ambiguity in assignment of species as being reef sharks (see below).

Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure (<http://www.seagis.com/>) to record species present and the number of individuals observed.

### MaxN

By convention, the quantity reported using BRUVS data is an index of relative abundance known as MaxN, which is the maximum number of individuals of each species seen on any given frame of a BRUVS video set. MaxN has become the standard metric for reporting due to concerns by researchers that they will recount the same individual should they leave the field of view and return<sup>30</sup>. Here we define MaxN as the

maximum number of individual reef sharks seen on any one frame of a single BRUVS video set.

Note that we defined reef sharks as being those species that spend the majority of their life history on or around reef habitats or species that regularly visit reefs. The most common species observed included grey reef (*Carcharhinus amblyrhynchos*), whitetip reef (*Triaenodon obesus*), blacktip reef (*Carcharhinus melanopterus*), Caribbean reef (*Carcharhinus perezi*), silvertip (*Carcharhinus albimarginatus*), Galapagos (*Carcharhinus galapagensis*), nurse (*Ginglymostoma cirratum*), tiger (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*) and lemon (*Negaprion acutidens* and *Negaprion brevirostris*) sharks. We calculated MaxN as the collective MaxN across all species of shark, calculated as the sum of the MaxN values for all reef shark species observed on a single BRUVS set.

### Potential MaxN bias

As MaxN has been criticized for hyperstability (that is, counts remaining high as true abundance decreases)<sup>31</sup>, we examined the relationship between MaxN and the mean count—the average number of sharks observed in video frames at regular intervals—which has been shown to be linearly related to absolute abundance<sup>32</sup>. For a subset of 62 reefs, spanning MaxN ranges from 0 to 24 (within the top 0.001% of observed values), we examined the relationship between MaxN and the average mean count, taken as the average number of sharks observed across 360 still images (that is, 10-s intervals over an hour). For our data, MaxN was linearly related to the mean count (Extended Data Fig. 1), suggesting that MaxN is an unbiased index of abundance within the context of our study. This result is consistent with the results of a previously published study<sup>31</sup>, in which hyperstability in MaxN values at true abundances beyond 20 individuals was found. Given that this study is quantifying relative abundance of sharks, which occur in low numbers, there is no evidence of a saturation effect in the video by which hyperstability occurs.

However, we conducted three additional analyses to support our original conclusions regarding the relationship between MaxN and the mean count. First, we calculated a mean count for an additional 20 BRUVS sites and again estimated the slope of the relationship with MaxN: we found a similar slope to our original analysis (2.30 (1.65–3.30)). Second, we conducted a bootstrap resampling procedure, sampling 5 observations 1,000 times at random without replacement from our original dataset and estimating the slope of the relationship between MaxN and mean count; again we found a similar slope to our original analysis (3.17 (1.89–6.49)). Lastly, we conducted a bootstrap-based power analysis, in which we sampled from 3 to 11 observations, 1,000 times each at random with replacement from our original dataset and calculated, at each step, the proportion of bootstrap replicates for which the 95% confidence intervals of the estimated slope did not overlap zero. Our results show that 7 samples are sufficient to have >95% probability of observing a positive slope between MaxN and mean count (Extended Data Fig. 1).

### Variable selection

Extensive work by the Social-Ecological Research Frontiers working group has explored relationships between numerous social–ecological factors and reef fish exploitation<sup>13,27,33,34</sup>. However, owing to the data limitations of surveying sharks<sup>7</sup>—which are inconsistently observed and recorded—relationships between many of the factors that affect reef fish have not been explored for sharks. Therefore, we built on this previous research, and have selected a set of variables that have been shown to affect reef fish or have other theoretical support.

As social and ecological processes operate at various spatial scales, the variables that we selected occurred at one of four scales. (1) Region, that is, Western Atlantic, Indian Ocean, Western Pacific or Central Pacific. (2) National—the major jurisdiction, encompassing country, territory or large-scale division (for example, continental Australia was

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divided into the Pacific and Indian Ocean coasts given distinctive state jurisdictions). Australia, Jamaica and Colombia were also divided into the core sampling area along the main coastline and offshore locations of each nation (Australia Indian Ocean Territories, Jamaica Pedro Bank and Colombia Seaflower Biosphere Reserve, respectively) given differences in governance, population density and remoteness of these jurisdictions. (3) Reef, each continuous association of hard corals, ranging from hundreds of metres to tens of kilometres across, separated by a deep channel, within which BRUVS were deployed<sup>35</sup>. (4) Set, each individual BRUVS deployment, consisting of a single baited drop recording a continuous hour of standardized video. All variables were checked for problematic collinearity (Pearson's correlations > 0.9)<sup>36</sup>; none were removed aside from gross domestic product (GDP)—which was collinear with HDI—and our longline/gillnet difficulties, as reported below.

**National-scale variables.** National-scale variables were primarily related to socio-cultural, economic and political conditions—within each nation—that have been associated with rates of environmental degradation<sup>13</sup>. These include the following variables. Human development index (HDI), a composite measure (0–100) of life expectancy, income and education factors developed by the UN Development Programme (<http://hdr.undp.org/en/content/human-development-index-hdi>). Voice and accountability (VOICE), a composite metric (–2.5–2.5) developed by the World Bank that represents the extent to which people in each nation are able to participate in governance, free expression, free media and free association (<https://info.worldbank.org/governance/wgi/pdf/va.pdf>). POP, the size of the coastal population within 50 km of the sampled reef (<https://sedac.ciesin.columbia.edu/data/collection/gpw-v4/sets/browse>). Shark sanctuary (BAN), a dummy variable (0 or 1) that indicates whether a nation is a designated 'shark sanctuary' that 'prohibits targeted commercial shark fishing at a minimum, and intends to make it unlawful to possess, sell or trade sharks or their parts'<sup>20</sup>. Note that Palau is widely regarded as the world's first shark sanctuary, both domestically and internationally; however, as this has only recently been passed into law; we regarded this country as a de facto shark sanctuary in our data. Coast length (CLN), length of the national marine coastline in km.

**Reef-scale variables.** Reef-scale variables were primarily associated with the shark-related management scheme in place at the sampling location. Note dummy variables below consist of 0 or 1 values to indicate presence or absence. Shark protection status (PRO), mutually exclusive dummy variables that indicate whether reefs included fishing restrictions (restricted) or were closed to fishing (closed). MPS, the size ( $\log(\text{km}^2)$ ) of the closed area (where present). HIG, dummy variable that indicates whether the closed area is high compliance, that is, that it is likely that little to no poaching occurs. GEAR, dummy variables for each shark-related fishing gear in use, including gillnets/longlines (GIL), drumlines (DRU), and hook and line (HLN) fishing. Gillnets and longlines were analysed as one variable owing to strong co-linearity in our dataset. Drumlines were defined as single baited hooks anchored to the substrate and left alone. Hook and line was defined as fishers from vessels who used baited hand lines. REM, dummy variable that indicates whether a reef is more than 200 km from human settlement<sup>13,27</sup>. Gravity (GRAV), we developed two gravity metrics: (1) the nearest population, equal to the population of the nearest human settlement divided by the squared travel time between the reef site and the settlement; and (2) the nearest market, equal to the population of the nearest market (defined as a port, provincial capital or major city) divided by the squared travel time between the reef site and the market (further details are provided in the methods in a previous study<sup>13</sup>). BAG, dummy variable that indicates whether catch limits are in place for sharks. TEM, dummy variable that indicates whether temporal limits are in place for sharks. SPP, dummy variable that indicates whether species limits are in place

for sharks. RTY, reef type; mutually exclusive dummy variable that indicates whether the surveyed reef was from a reef slope, lagoon, flat or other reef type.

**Set-scale variables.** Set-scale variables were primarily used to alleviate bias in potential BRUVS deployments within each nation. DEPTH, depth of BRUVS deployment (in m). VIS, estimated visibility in the water column (in m). HC, percentage of hard coral cover present in the field of view. RUG, 0 to 5 ranked score for structural complexity of the surrounding reef (in field of view)<sup>37</sup>. BAIT, a mutually exclusive dummy variable that indicated the fish family group used for bait; one of Clupeidae, Scombridae, Sphyrnidae, mixed or other (one-off/rare). TIME, the number of minutes away from noon at the start of the BRUVS set (min) to account for diurnal activity.

Note that all variables were standardized before analysis (mean centred, divided by  $2 \times$  the standard deviation) to make their relative effect broadly comparable.

## Bayesian hierarchical model

To quantify the relationship between candidate variables of interest and observed reef-shark MaxN, we developed a Bayesian hierarchical model that encompassed regional ( $r$ ), national ( $k$ ), reef ( $j$ ) and set ( $i$ ) spatial scales. Note that although more reefs were observed from jurisdictions such as Australia, this hierarchical model structure explicitly accounts for such imbalances. In addition, as more than 60% of BRUVS did not observe a single shark, we compared the model fit of a conventional negative binomial likelihood model for counts with that of a zero-inflated negative binomial (ZINB) model, which allows for excess zeros that exceed those expected given a negative binomial model (Extended Data Table 1). Note also that, in terms of selecting a negative binomial model, we had initially fit Poisson (which has theoretical support due to MaxN being derived from a collection of individual shark arrivals at the BRUVS station) and zero-inflated Poisson models to the data, but the presence of substantial overdispersion led to poor model fit and our adoption of the negative binomial model (which can be equivalent to the Poisson as a special case).

We developed a set of alternative model structures beyond our zero-inflated full model, for null (intercept only), partial null (hierarchical model with nuisance parameters relating to sampling) and full (hierarchical model with all covariates) model approaches, both with and without zero inflation. Using this set, we implemented a weighted-model approach to inference, using Pareto smoothed importance sampling leave-one-out (PSIP-LOO) cross-validation methods<sup>38</sup> to calculate individual model weights, which are provided by convenience functions within PyMC3 (see <https://docs.pymc.io/api/stats.html?highlight=compare#pymc3.stats.compare> for documentation). The weighted-model method proceeds by summing posterior parameter estimates from each model that have been multiplied by their PSIP-LOO model weights, thus integrating the relative support for each model in the final weighted model used for inference, conditional on the data. Note this places the national-scale variables of HDI, VOICE and POP in both the zero and count parts of the final weighted ZINB model (see parameter estimates in Extended Data Fig. 3).

Under the weighted ZINB model, we estimated that excess zeros occurred in 10% of BRUVS sets ( $n = 1,481$ ; Fig. 1b), which—by placing posterior weight (77%, using PSIP-LOO) on having key national-scale covariates in the zero component of the ZINB model—we assumed reflects long-term degradation that has led to the presence or absence of sharks among reefs. Conversely, under the ZINB count-only model (16% PSIP-LOO weight) these national-scale covariates were part of the count component, which we assume represents contemporary conditions amenable to management. Lastly, the PSIP-LOO results revealed 11 high-leverage observations for which the observation-wise Pareto  $\hat{k}$  estimate<sup>38</sup> was  $> 0.7$  (Supplementary Information), which we removed before final model comparison.



The observation model for each BRUVS set assumed that BRUVS counts occurred as a mixture of presence or absence (the 'zeros model') and counts (the 'count model'), each of which contained a hierarchical component that were jointly ZINB distributed for set ( $i$ ), reef ( $j$ ), nation ( $k$ ) and region ( $r$ ):

$$\text{MaxN}_{ijk} \sim \text{ZINB}(\phi_{ijk}, \mu_{ijk}, \alpha)$$

where  $\phi$  is the probability of an excess zero,  $\mu$  is the mean count conditional on an excess zero not occurring, and  $\alpha$  is the dispersion parameter of the negative binomial, given a  $-\Gamma(0.001, 0.001)$  prior. For the full ZINB model, the log-transformed odds of an excess zero ( $\eta_{z0kr}$ ) was modelled as a linear function of three national-level covariates, using a non-centred parameterization<sup>39</sup> to handle divergent transitions that we detected during the process of peer review (Extended Data Fig. 4):

$$\text{logit}(\phi_{ijk}) = \eta_{z0kr}$$

$$\eta_{z0kr} \sim N(\eta_{z0r} + \eta_{z1}\text{HDI}_k + \eta_{z2}\text{VOICE}_k + \eta_{z3}\text{POP}_k, \sigma_{z0\eta})$$

$$\sigma_{z0\eta} \sim \text{Exp}(1)$$

$$\eta_{z0r} = \pi_{z0} + \sigma_{z0v}\tilde{\pi}_{z0r}$$

$$\tilde{\pi}_{z0r} \sim N(0, 1)$$

$$\sigma_{z0v} \sim \text{Exp}(1)$$

$$\pi_{z0} \sim \text{Cauchy}(0, 10)$$

$$\eta_{z1}, \eta_{z2}, \eta_{z3} \sim \text{Cauchy}(0, 3).$$

For the ZINB count-only model, parameters  $\eta_{z1}$  to  $\eta_{z3}$  were passed to the count component (as additional parameters  $v_3$ ,  $v_4$  and  $v_5$  in the national-scale model below; data not shown), leaving only the intercepts in the hierarchical structure of the zeros-model. For both models, the log of the conditional mean count was modelled as a linear function of multiple covariates at the three smaller scales:

$$\log(\mu_{ijk}) = \kappa_{0jkr} + \rho_1\text{DEPTH}_i + \rho_2\text{VIS}_i + \rho_3\text{HC}_i + \rho_4\text{RUG}_i + \rho_5\text{BAIT}_i$$

$$\kappa_{0jkr} \sim N(\mu_{0jkr}, \sigma_{0jkr})$$

$$\begin{aligned} \mu_{0jkr} = & \eta_{0kr} + \kappa_1\text{RTY}_j + \kappa_2\text{CLO}_j + \kappa_3\text{MPS}_j + \kappa_4\text{HIG}_j \\ & + \kappa_5\text{GIL}_j + \kappa_6\text{DRU}_j + \kappa_7\text{HLN}_j + \kappa_8\text{REM}_j + \kappa_9\text{GRAV}_j \\ & + \kappa_{10}\text{GRAV}_{\text{NC},j} + \kappa_{11}\text{BAG}_j + \kappa_{12}\text{TEM}_j + \kappa_{13}\text{SPP}_j \end{aligned}$$

$$\eta_{0kr} \sim N(\mu_{0kr}, \sigma_{0kr})$$

$$\mu_{0kr} = v_{0r} + v_1\text{BAN}_k + v_2\text{CLN}_k$$

$$v_{0r} = \pi_0 + \sigma_{0v}\tilde{\pi}_{0r}$$

$$\tilde{\pi}_{0r} \sim N(0, 1)$$

$$\sigma_{0jkr}, \sigma_{0kr}, \sigma_{0v} \sim U(0, 100)$$

$$\pi_0 \sim N(0, 3).$$

We chose priors that allowed for a wide range of parameter values before consideration of the data, representing our relative ignorance about the necessary parameters for our model before analysis, but these were set within realistic ranges. We checked our choice of prior across realistic ranges from  $N(0, 1)$  to  $N(0, 8)$  for the count model parameters, and over Cauchy(0, 1) to Cauchy(0, 8) for the zero model parameters. Results show that our posterior parameter estimates had low sensitivity to the choices of prior across these ranges, with the greatest effects seen among larger-scale parameters including HDI, VOICE, POP and the overall MaxN rate (Extended Data Fig. 5). Although these effects were evident, they did not substantially affect the inferences made in our analysis.

We implemented all our models using the PyMC3 package<sup>40</sup> for the Python programming language, and assessed model convergence using Gelman–Rubin statistics (R-hat), in which values very near to one are deemed to have converged, and by examining posterior traces. We also assessed model fit using posterior predictive distributions, for which observed values are compared to the posterior distribution for each observation (Extended Data Fig. 6). Well-calibrated models should include the observation within higher-density regions, rather than out on the tails of the posterior distribution. The highest posterior density of the  $\alpha$  parameter of the ZINB was 6.64 (5.79–7.73). We also found important sampling effects (that is, locally varying conditions) among our nuisance parameters related to depth (0.08 (0.04–0.13)), rugosity (0.07 (0.02–0.12)), visibility (0.32 (0.27–0.39)), season (winter = –0.21 (–0.33–0.08), shoulder = –0.03 (–0.16–0.08) and bait type (Scombridae = 0.23 (0.05–0.42), mixed = –0.12 (–0.32–0.07), other = –0.27 (–0.48–0.05), Sphyracidae = 1.07 (0.65–1.47)) that constituted potential sampling bias and necessitated inclusion in our partial null model (Extended Data Fig. 3).

### No sharks observed

The zero density portion of ZINB model that we used allows for an excess of zeros (no sharks observed) at the reef and national levels such that, if no sharks were observed in the data, this can arise naturally by random chance (given by the negative binomial likelihood component, given the distribution of the counts) or due to a zero-inflation process that may be unknown. This does not mean that sharks are necessarily locally extinct from any nation that we surveyed; rather it is a statistical result that most likely means that sharks are at such low local densities that they are unlikely to be observed among the reefs that we surveyed. In general, we regard these locations as places where sharks are functionally extinct, meaning that they likely have little to no role in the function of the ecosystem, rather than locally extinct, meaning that they do not occur. In addition, readers may note that places with near-zero probability of presence (Extended Data Fig. 2) nonetheless have a positive expected MaxN, conditional on an excess zero not occurring (Extended Data Fig. 7), in places such as the Dominican Republic. This apparent paradox is often present in zero-inflated models and stems from the observed data assuming to have arisen from a mixture of two processes: one for excess zeros, and one for counts when excess zeros do not occur. The near-zero probability of presence was because no sharks were observed across 120 BRUVS sets in the Dominican Republic (0/120). Yet nearby nations, such as Puerto Rico (4/77), Cuba (30/241), and Turks and Caicos (3/37), all observed sharks to various levels. So, in the absence of any counts, the expected MaxN given presence increases towards an expected value given the Caribbean-wide average and the national-level covariates in the count portion of the model. However, for the data that we observed, the estimated values were given by the product of this large average and the near-zero estimate, meaning that the unconditional expected counts in the Dominican Republic are near to zero.

### Abundance scores

Given the complete lack of baselines for reef sharks globally, we developed a national-scale scoring system to evaluate the national

conservation status of reef sharks relative to the expected average MaxN within each region under our null ZINB model.

$$\Pr(E(\eta_{0kr}) > \nu_{0r} | \eta_{z0kr}).$$

In doing so, it is important to recognize that we explicitly ranked national performance under something akin to a bell curve, assigning ‘winners’ and ‘losers’. However, our scoring system is more nuanced than this—the abundance score for each nation is the proportion of their posterior density of the expected MaxN for that nation that was greater than their regional expected MaxN (that is, regional posterior median). If all nations within a region had the same posterior expected MaxN, then they would all have abundance scores of 0.5 (that is, their expected MaxN would be the same as their regional expected MaxN, leading to 50% of their posterior density above and below their posterior regional median). What this means in practice is that our abundance scores represent national-scale performance that is evaluated as greater or less than the average (0.5), with high (>0.9) and low (<0.1) scores indicating a relatively high and low conservation status, respectively.

The null model was used to evaluate the current status conditional only on nuisance parameters (that is, parameters that have the potential to bias sampling but are not of direct interest) to alleviate sampling bias, rather than model-adjusted status given by the national-scale intercepts under our full model, which would not include realized benefits from closed areas or losses from destructive gears. The null-model national estimates reflect the observed data while still accounting for sampling, while the full-model national estimates would reflect remaining national-scale differences given the covariates in our model. In other words, we calculated national abundance scores based on their observed (but bias-corrected) data, rather than model-derived estimates based on average conditions globally. Although national-scale estimates are our best-available data for the relative abundance of reef sharks and resultant abundance scores, the number of reefs sampled varies in proportion to the total coastline. For example, among the lowest-performing nations, the four reefs surveyed along the 1,288-km-long coast of Dominican Republic are likely more representative than the two reefs surveyed from the 7,516-km-long coast of India and we did find evidence of slightly lower MaxN values on longer coastlines (Extended Data Fig. 3). Ultimately, additional reefs from a representative sample within each nation will provide more-precise, and potentially more-accurate, estimates than those we report here.

## Benchmarking BRUVS data with other approaches

Although it is difficult to compare relative shark abundance estimates among studies that use different abundance indices (all methods are biased to an often-unknown degree), we found our results are broadly comparable to smaller-scale surveys among subsets of our survey nations. For example, recreational SCUBA diver surveys found very similar spatial patterns to what we observed with BRUVS in the greater Caribbean, reporting an absence or very few sharks observed at sites where we did not observe sharks (mainland Jamaica, Dominican Republic and French West Indies) and reporting that sharks were commonly observed in our highest abundance locations, such as the Bahamas and Florida Keys<sup>7</sup>. Furthermore, similar species richness and seasonal abundance trends have been observed for sharks surveyed with BRUVS and longlines in the Bahamas<sup>41</sup>. Lastly, recent work has shown that Bahamas and Turks and Caicos had greater shark diversities and abundances than Belize and Jamaica when compared using environmental DNA (eDNA)<sup>42</sup>.

## Conservation potential

To represent the conservation potential of management options under average conditions in our model, we first estimated the individual conservation gains expected within each nation, given their successful implementation. We estimated conservation gain as the expected

difference between the current abundance score under the null model (that is, current, sampling-corrected estimated relative abundance,  $\eta_{0kr}$ ) and the expected abundance score given implementation of each management effect ( $\kappa_m$ ), weighted by the proportion of reefs where they are not currently in place ( $P_m$ ):

$$\Delta_{\text{gain},m} = \Pr(E(\eta_{0kr} + \kappa_m P_m) > \nu_{0r} | \eta_{z0kr}) - \Pr(E(\eta_{0kr}) > \nu_{0r} | \eta_{z0kr}).$$

In essence, these scores represent the marginal gains that remain to be made given each management action ( $m$ ) and current conditions, and are the horizontal black lines shown in Fig. 3. Conservation gains were calculated by adding (or subtracting) posterior effect sizes, conditional on our model.

We calculated total conservation potential as the maximum change in abundance score from either: (1) implementing a shark sanctuary or (2) the sum of changes in the abundance score for implementing a gillnet/longline ban, catch limits and large-scale closed areas (shark bans are mutually exclusive to the other measures). Note, this summation assumes that benefits can be accrued additively, as specified by our statistical model. However, in practice, we expect local cultural features to affect conservation outcomes in ways that deviate from the globally averaged conditions presented here.

## Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

## Data availability

Data used to reproduce the analysis—except for geolocations—can be accessed at <https://github.com/mamacneil/FinPrint>.

## Code availability

Code used to reproduce the analysis can be accessed at <https://github.com/mamacneil/FinPrint>.

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**Author contributions** D. Chapman and M. Heithaus conceived the study with assistance from M. Heupel, C.A.S., M.M., E.H. and M.A.M. D. Chapman, M. Heithaus, M. Heupel, C.A.S., M.M. and E.H. directed fieldwork run by J.G., J.K., M.E.B., L.M.C.-R., C.W.S., K.I.F., J.V.-A., G.C. and C.S.S. Database management was by T. Gorham. M.A.M. and D. Chapman drafted the

manuscript, with help from M. Heithaus, M. Heupel, C.A.S., J.E.M.C., M.M., E.H., J.G., J.K., M.E.B., L.M.C.-R., C.W.S., C.S.S., M.J.R., V.U. and T. Gorham. All other authors contributed equally, made substantial contributions to data collection, provided input and approved the text in the manuscript.

**Competing interests** The authors declare no competing interests.

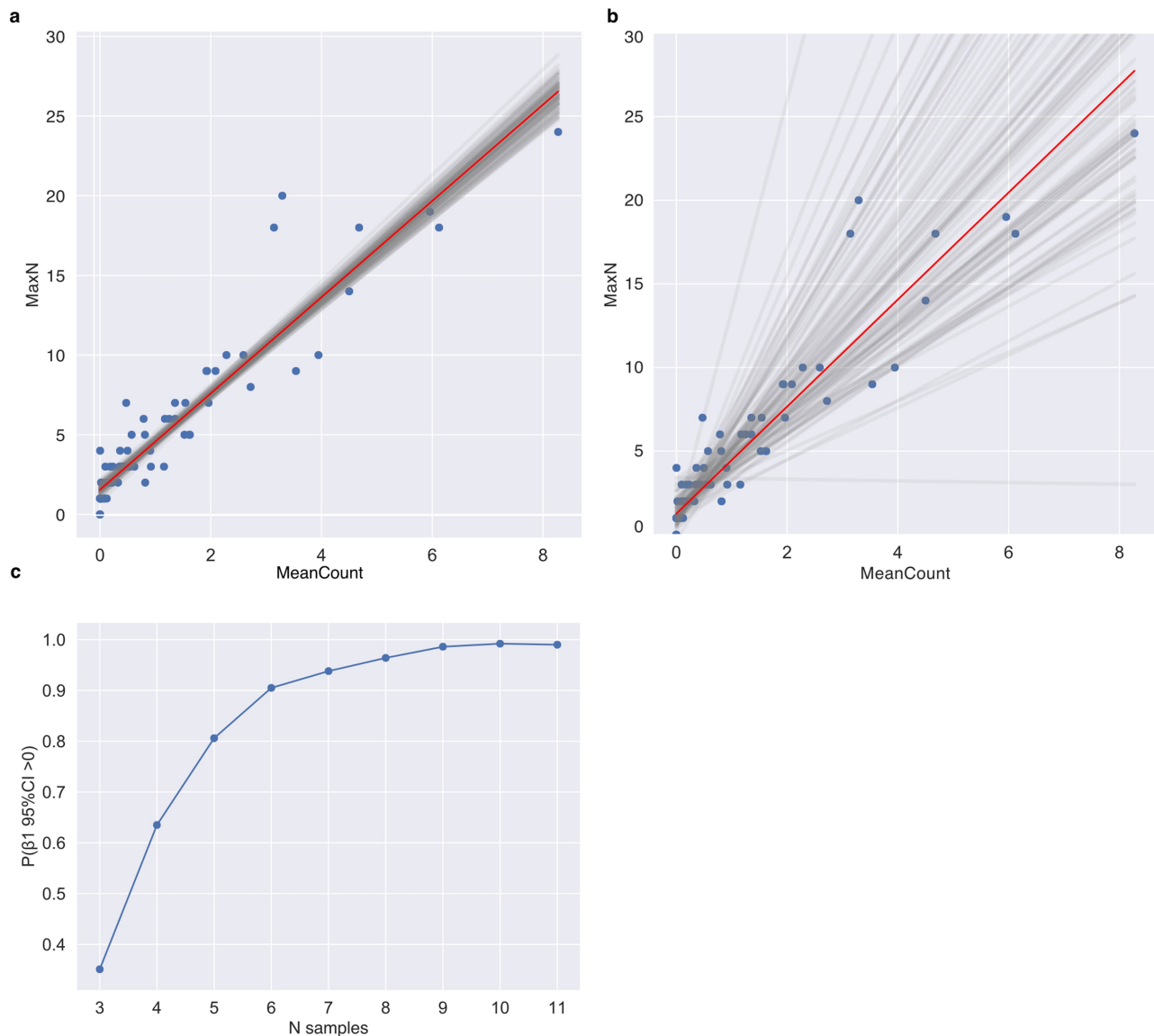
**Additional information**

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41586-020-2519-y>.

**Correspondence and requests for materials** should be addressed to M.A.M.

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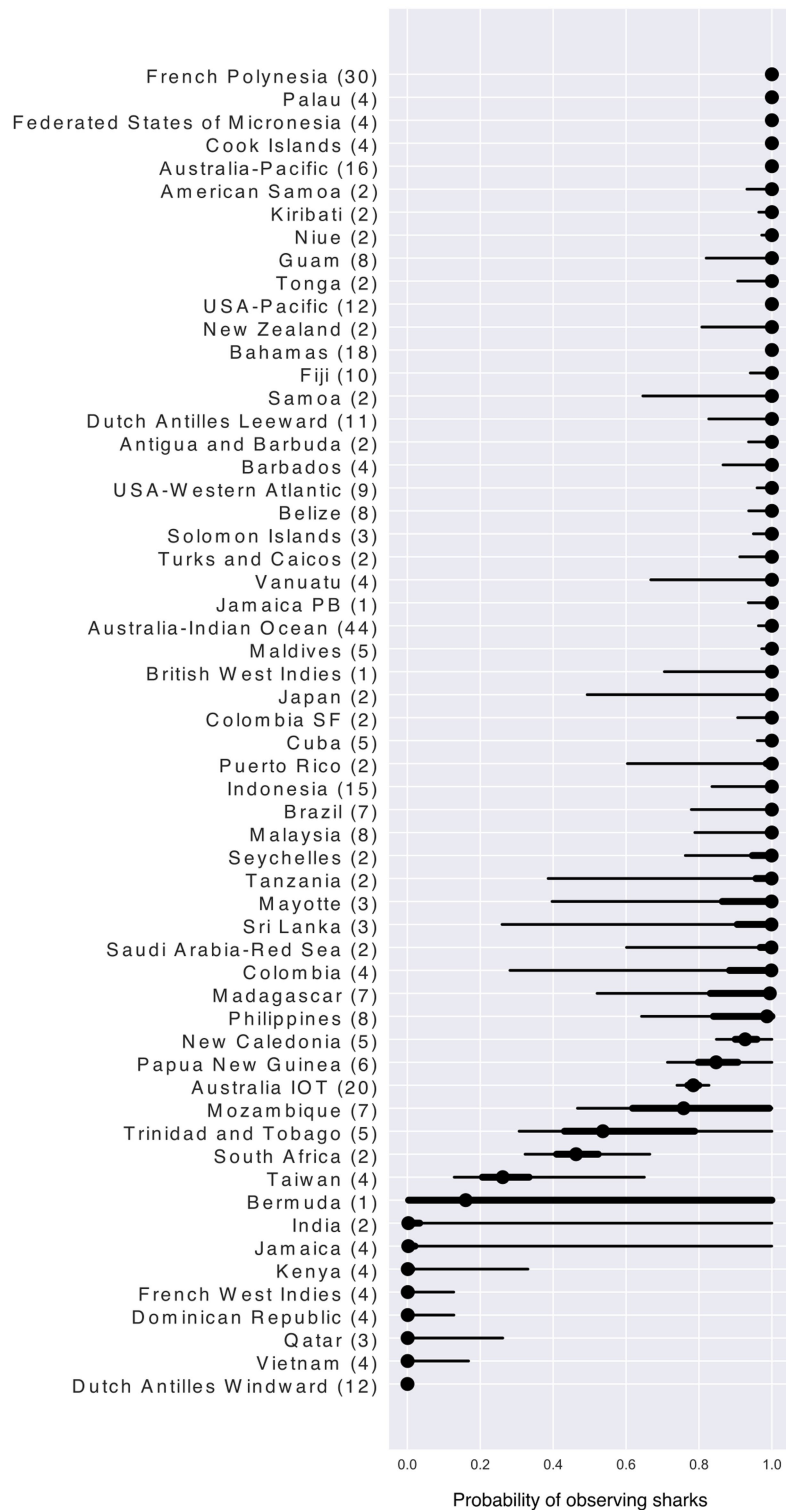


#### Extended Data Fig. 1 | Relationships between MaxN and mean count.

**a**, Relationships for 82 BRUVS sets across the range of MaxN values observed by Global FinPrint. Linear model estimates (median (95% uncertainty intervals of the highest posterior density)) are 1.56 (1.09–2.05) (intercept) and 3.03 (2.75–3.26) (slope). The red line is the highest posterior density model fit; grey lines are 100 realizations of possible model fits given random samples from the model posteriors, showing a tight relationship to the estimated red line.

**b**, Bootstrap-based linear model estimates (using 1,000 repetitions) from samples of 5 BRUVS sets (with replacement) from the sample of 82 BRUVS sets

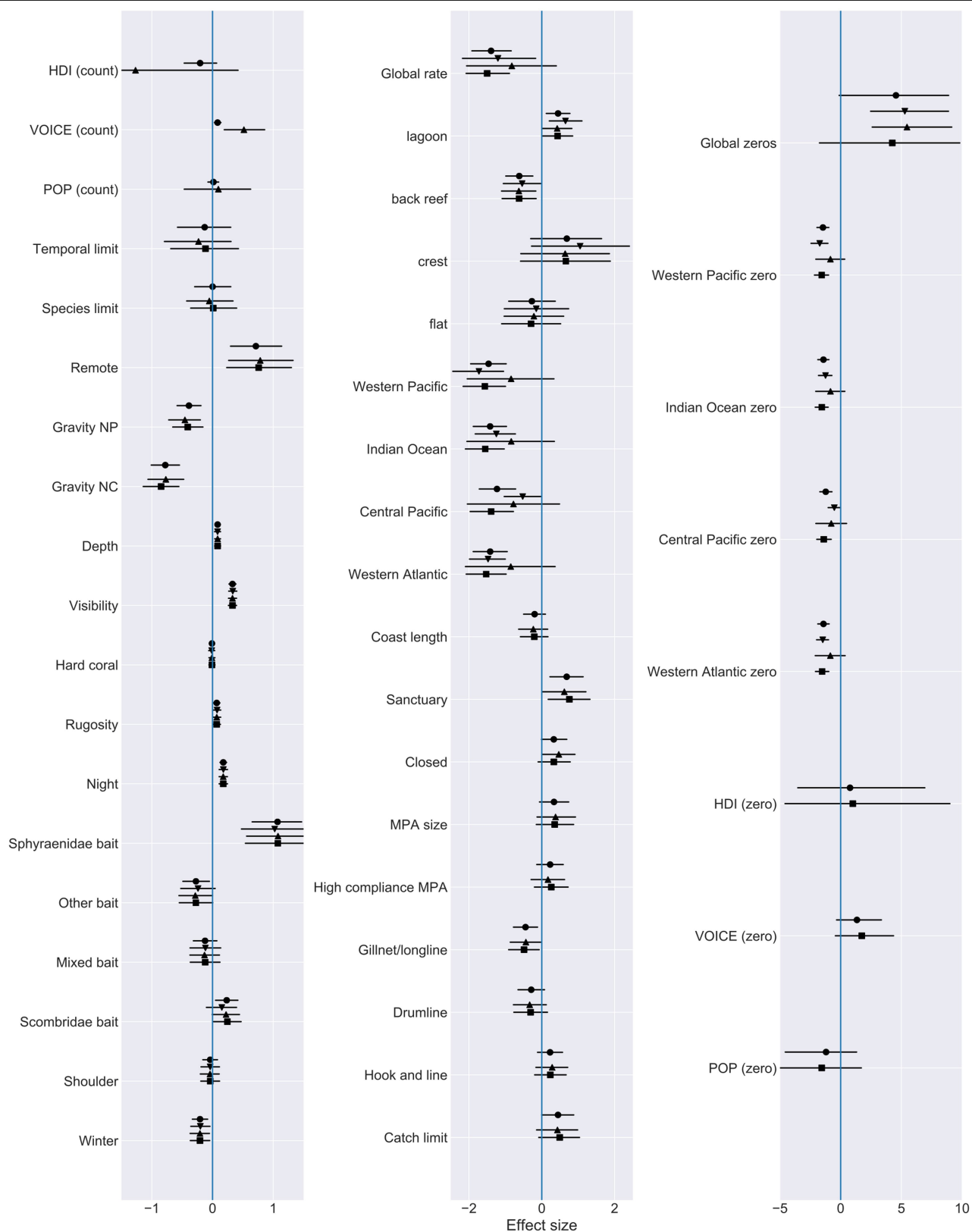
in **a**, with estimates of 1.26 (0.29–2.67) (intercept) and 3.17 (1.89–6.49) (slope), using the OLS function of the `scipy statsmodels` package in Python. The wider variability in **b** is because lines were estimated from using five data points with replacement. **c**, Bootstrap-based power analysis results showing the number of observations required to have a 95% probability of the estimated linear slope being  $> 0$ ; probabilities on the y axis are the proportion of bootstrap replicates (with replacement) for which the 95% confidence intervals of the estimated slope do not overlap zero.



#### Extended Data Fig. 2 | Expected probability of sharks being observed.

Expected probabilities for BRUVS sets from 58 national jurisdictions surveyed by Global FinPrint. The number of reefs surveyed is indicated in parentheses. Among the eight lowest-ranked nations there is estimated to be less than 0.1% chance of a shark being present any time a BRUVS is deployed, suggesting that sharks are functionally extinct on these survey reefs. Functional extinction in this study means that reef sharks are essentially absent from the ecosystem,

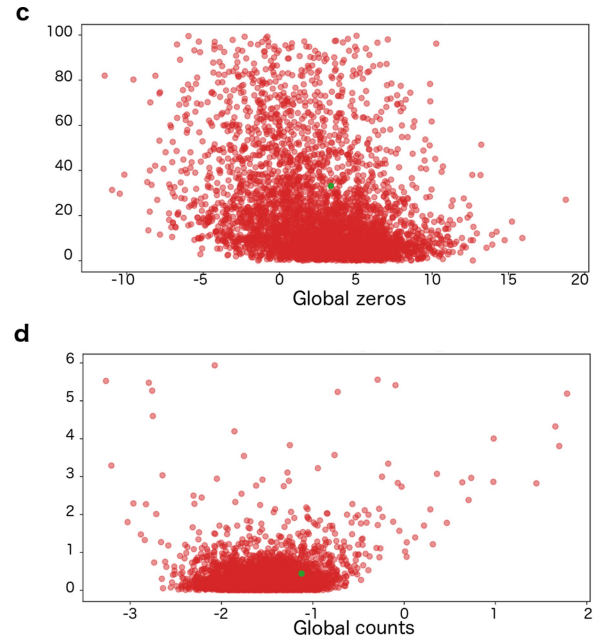
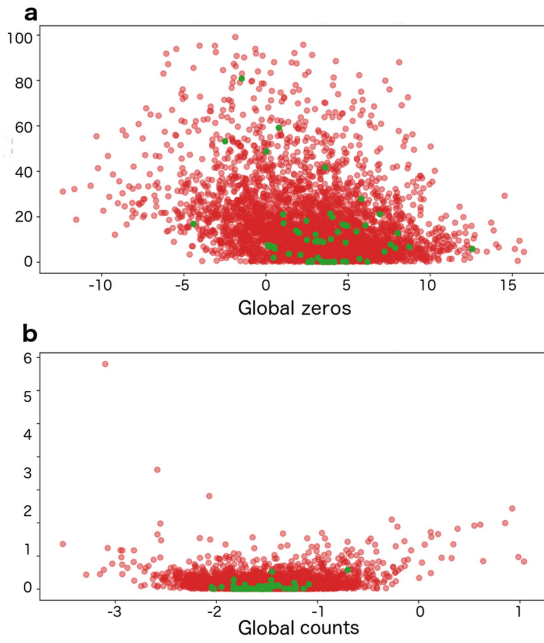
and have little to no functional role in structuring the surrounding reef fish community through predation or fear-based effects<sup>43</sup>. Symbols are median (circles), 50% (wide horizontal lines) and 95% (thin horizontal lines) highest posterior density (credible) intervals. Note that although there are more reefs observed from jurisdictions such as Australia, the hierarchical model explicitly accounts for such imbalances.



**Extended Data Fig. 3 | Forrester plot of ZINB posterior distribution effect sizes for candidate models.** Left and centre columns, covariates present in the count component of the model. Right column, covariates present in the zero-inflation component of the model. The median (circles) and 95% (thin horizontal lines) highest posterior density (credible) intervals for four independent Markov chain Monte Carlo chains (left) are shown. Models with

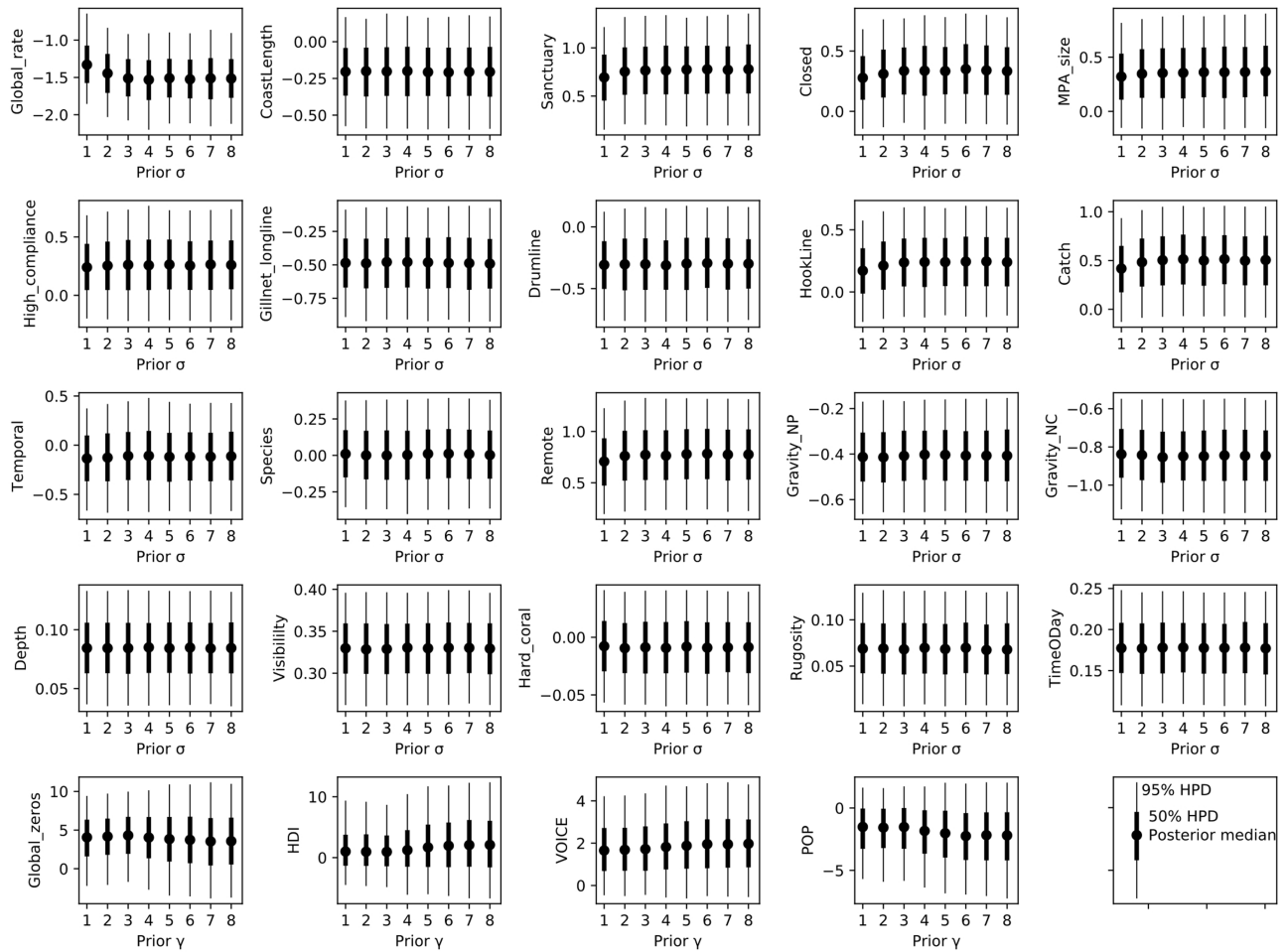
PSIS-LOO-based weights  $>0$  include the ZINB full model (77% weight; squares), the ZINB full count model (16% weight; upwards pointing triangle) and ZINB partial null (7% weight; downwards pointing triangle); circles indicate model-weighted estimates used for inference. R-hat values for all parameters were between 1.01 and 1, suggesting no evidence that models failed to converge. Note the differences in the scale along the x axes.





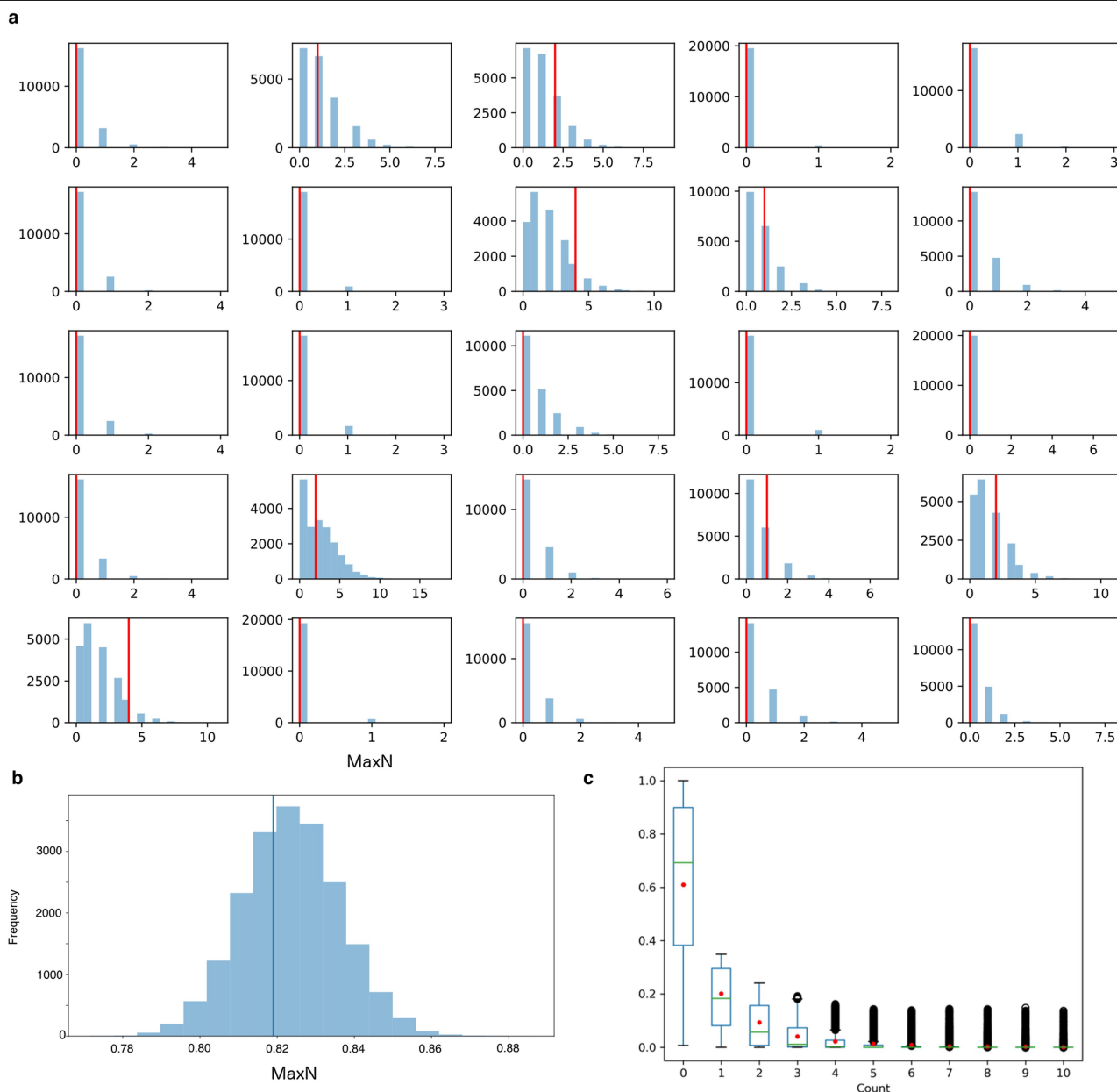
**Extended Data Fig. 4 | Diagnostic plots for Hamiltonian Monte Carlo analyses. a–d**, Bivariate plots of posterior traces (red dots) of global zero slopes versus region-level zero variances for a centred parameterization (**a**); global count slopes versus region-level count variances for a centred parameterization (**b**); global zero slopes versus region-level zero variances for a non-centred parameterization (**c**); and global count slopes versus

region-level count variances for a non-centred parameterization (**d**). Green dots highlight potentially divergent transitions in NUTS samples. **a, b**, A high number of clustered divergent transitions are clustered, indicative of pathological parameter space. **c, d**, These problems are eliminated using a non-centred, re-parameterization<sup>39</sup> of the original full zero-inflated hierarchical model, which had 77% of posterior PSIS-LOO model weight.



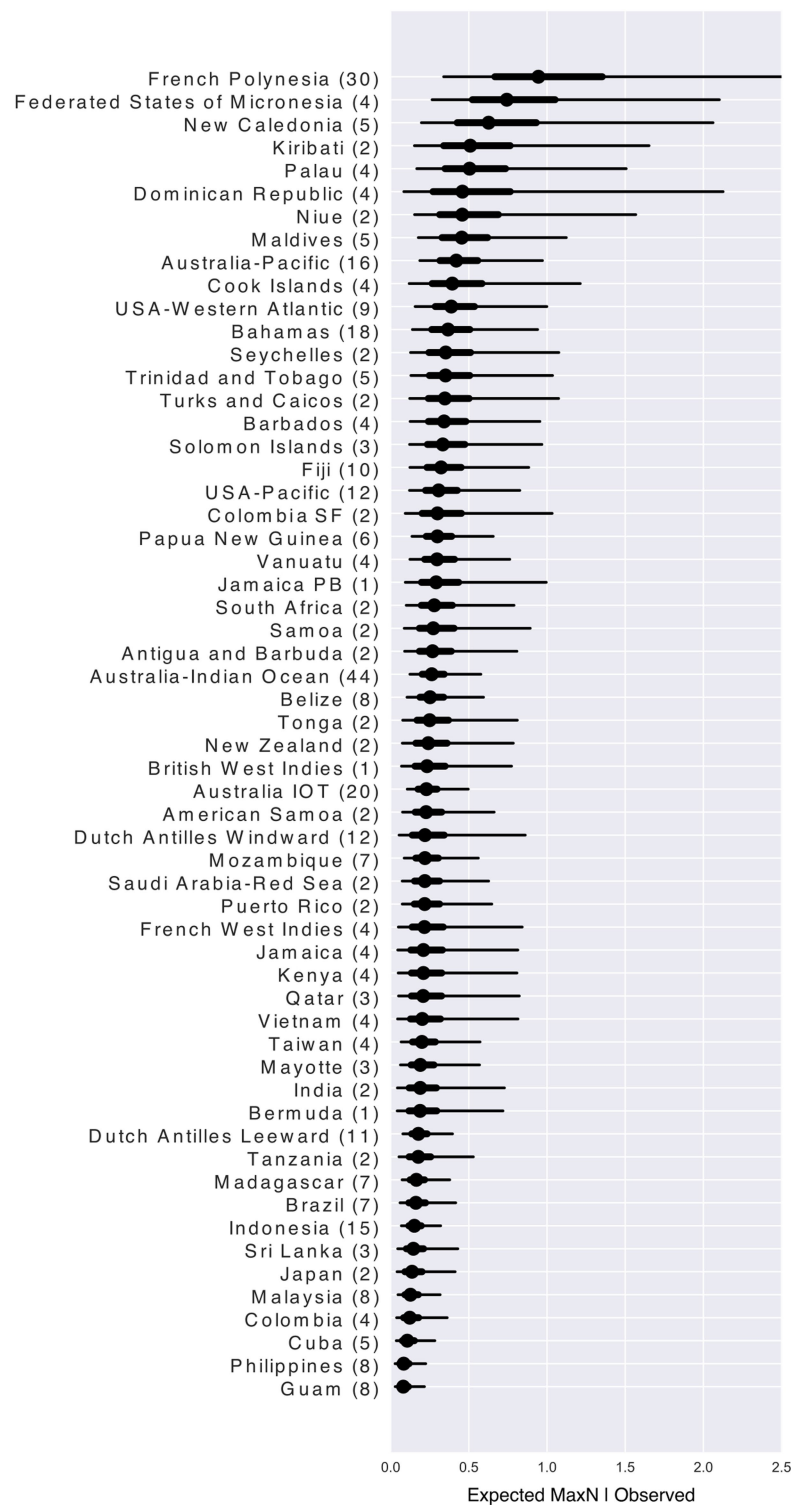
**Extended Data Fig. 5 | Sensitivity plot for the effects of  $N(0, \sigma)$  or  $C(0, \gamma)$  prior standard deviations ( $\sigma$ ) and scales ( $\gamma$ ).** Selected posterior parameter estimates are shown for the full zero-inflated negative binomial model (77% of PSIS-LOO weight) of reef shark MaxN observations in Global Fingerprint. Symbols

are median (circles), 50% (wide horizontal lines) and 95% (thin horizontal lines) highest posterior density (credible) intervals. Results show minor effects of prior specification on the global rate, with small changes to Cauchy prior scale values for HDI, VOICE and POP.



**Extended Data Fig. 6 | Posterior predictive distributions. a, b,** Distributions (blue) are shown for the full model, which had the majority (77%) of posterior model weight, of observed MaxN (vertical red lines) for 25 (of >15,000) randomly selected BRUVS sets from Global FinPrint (**a**) and the observed overall mean MaxN (vertical blue line) (**b**). Distributions that consistently overlap observed values are taken as evidence that the full ZINB model is consistent with the observed data. **c,** Frequency distribution of posterior

predictive densities (box plots) and observed mean MaxN values (red dots) for 15,176 BRUVS sets observed as part of Global FinPrint. Note, in **a**, only 4.3% of observations were outside their 95% highest posterior predictive density, suggesting that there is no evidence that the full model is inconsistent with the observed data. Note, the plot in **c** was truncated at MaxN = 10 (representing >99% of observed MaxN) for clarity.



**Extended Data Fig. 7 | Expected relative abundance (MaxN) conditional on an excess zero not occurring.** Data are shown for BRUVS sets from 58 national jurisdictions surveyed by Global FinPrint. The number of reefs surveyed is

indicated in parentheses. Symbols are median (circles), 50% (wide horizontal lines) and 95% (thin horizontal lines) highest posterior density (credible) intervals.

Extended Data Table 1 | Model selection

Model	Description	LOO (SE)	$\Delta$ LOO	Weight
ZI full ('Full model' in the text)	Zero-inflated hierarchical model with select covariates in both the count and zero components of the model	27583.7 (283)	0	0.77
ZI full – count only	Zero-inflated hierarchical model with all covariates in the count component of the model	27588.3 (247)	4.6	0.16
ZI Partial Null	Zero-inflated hierarchical model with only sampling-related covariates in the count component of the model	27594.7 (247)	11.0	0.07
Non-ZI - full	Includes all covariates and hierarchical structure but without zero-inflated component	27738.8 (248)	155.0	0
Non-ZI Partial Null	Adds national and reef-scale hierarchical structure to the model without covariates; no zero-inflation present	27739.6 (248)	155.9	0
Null	Estimates only Poisson ( $\mu$ ) and gamma ( $\alpha$ ) distribution parameters	37081.4 (247)	9497.7	0

Model selection for the candidate negative binomial models used for the estimation of the relative abundance of reef sharks (MaxN) within the Global FinPrint dataset. The negative binomial model used was parameterized as a Poisson random variable for which the rate parameter is gamma-distributed. ZI, zero-inflated; LOO, leave-one-out cross-validation; SE, standard error of the LOO;  $\Delta$ LOO, the net difference in LOO scores relative to the LOO for the lowest-scoring model; weight, the probability of each model being equivalent to the lowest-ranking LOO model (ZI full), based on the standard error of the difference in LOO scores (see Methods).

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- ☐ ☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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- ☐ ☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- ☒ ☐ For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted  
*Give  $P$  values as exact values whenever suitable.*
- ☐ ☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- ☐ ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- ☐ ☒ Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection

Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure (www.seagis.com)

Data analysis

All analysis was done in Python 3.7.1

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

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Data and code used to reproduce the analysis – except for geolocations – can be accessed at <https://github.com/mamacneil/FinPrint>.

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# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We surveyed 371 coral reefs in 58 nations using 15,176 individual Baited Remote Underwater Video Stations, primarily between 2015 and 2018. The study was hierarchically structured, with sets made within reefs, reefs within nations, and nations within regions.
Research sample	Study reefs were selected to correspond as closely as possible to those surveyed by Cinner et al. 2018 Nature 535:416-419.
Sampling strategy	Nearly all (> 98%) BRUVS were deployed during daylight hours (07:00-17:00) and the initial deployment coordinates for each day were determined using a randomly generated position within the sampling area. The first BRUVS were then deployed as close as possible to these coordinates and the remainder were then set at least 500 m away from previous sets, at depths of 2-40 m. This spacing was designed to reduce the likelihood of individuals occurring on multiple cameras. Bottom depth and sea surface temperature were recorded at deployment.
Data collection	Visibility, substrate complexity, and substrate type were estimated for each deployment using a still frame from the footage after the BRUVS settled to the bottom in the Benthobox software ( <a href="http://www.benthobox.com">www.benthobox.com</a> ) BRUVS were retrieved after at least 70 minutes to ensure a standard 60 minutes of data collection from the time of settlement. Videos were reviewed by at least two trained and independent readers at normal play speed and reviewed by a master annotator to ensure accuracy in species identification. Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure ( <a href="http://www.seagis.com">www.seagis.com</a> ) to record species present and the number of individuals observed. Sharks were recorded as MaxN, which is the maximum number of individuals of each species seen on any given frame of a BRUVS video set.
Timing and spatial scale	Surveys were conducted haphazardly, as partner investigators became available and logistical constraints permitted, between July 2015 and 2018
Data exclusions	We excluded one national-scale estimate for Fiji in Figure 4, due to differential targeting of reef sharks in this nation.
Reproducibility	<i>Describe the measures taken to verify the reproducibility of experimental findings. For each experiment, note whether any attempts to repeat the experiment failed OR state that all attempts to repeat the experiment were successful.</i>
Randomization	Sampling was systematic (50 target replicates per reef), covering most or large-swaths of survey reefs. Reefs were selected haphazardly due to location availability and correspondence with Cinner et al 2016 Nature 535:416-419.
Blinding	N/A
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Field conditions were generally good, consistent, and had no-impact on remote samples made below the water surface.
Location	Global
Access and import/export	N/A
Disturbance	N/A

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

### Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging