Global conservation outcomes depend on marine protected areas with five key features

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Global conservation outcomes depend on marine protected areas with five key features

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In line with global targets agreed under the Convention on Biological Diversity, the number of marine protected areas (MPAs) is increasing rapidly, yet socio-economic benefits generated by MPAs remain difficult to predict and under debate[1,2]. MPAs often fail to reach their full potential as a consequence of factors such as illegal harvesting, regulations that legally allow detrimental harvesting, or emigration of animals outside boundaries because of continuous habitat or inadequate size of reserve[3–5]. Here we show that the conservation benefits of 87 MPAs investigated worldwide increase exponentially with the accumulation of five key features: no take, well enforced, old (>10 years), large (>100 km^2), and isolated by deep water or sand. Using effective MPAs with four or five key features as an unfished standard, comparisons of underwater survey data from effective MPAs with predictions based on survey data from fished coasts indicate that total fish biomass has declined about two-thirds from historical baselines as a result of fishing. Effective MPAs also had twice as many large (>250 mm total length) fish species per transect, five times more large fish biomass, and fourteen times more shark biomass than fished areas. Most (59%) of the MPAs studied had only one or two key features and were not ecologically distinguishable from fished sites. Our results show that global conservation targets based on area alone will not optimize protection of marine biodiversity. More emphasis is needed on better MPA design, durable management and compliance to ensure that MPAs achieve their desired conservation value.

A multitude of socio-economic and biological factors influence the responses of species to protection within MPA networks, adding considerable uncertainty when making specific predictions regarding the conservation benefits of new MPAs. Even within well-designed MPAs, populations of marine species can respond quite differently to prohibitions on fishing as a consequence of species-specific factors such as mobility, larval dispersal, fecundity, longevity, indirect interactions among species, environmental context, and overall level of exploitation before protection[5,6]. To assess the extent to which MPAs fulfil their ecological potential, we used a database unprecedented in geographic scale to investigate how conservation value, characterized by ecological response of fish communities within MPAs, is affected by the cumulative effects of five key planning and management features: (1) degree of fishing permitted within MPAs; (2) level of enforcement; (3) MPA age; (4) MPA size; and (5) presence of continuous habitat allowing unconstrained movement of fish across MPA boundaries[6–10]. Although previous studies have considered these factors independently, this is the first study, to our knowledge, that considers them simultaneously, using data collected globally with standardized methods.

Observations from the subset of MPAs that seem to work effectively—that is, they include at least four of five 'NEOLI' (no take, enforced, old, large and isolated) features—are additionally used to infer ecological condition associated with unfished reefs. For this aspect, we used the global network of MPAs as a vast ecological experiment, where effective no-take areas represent human predator exclusion plots within a matrix of fished coasts[11].

Eight community-level metrics were assessed using data from 40 nations on shallow reef fish densities and sizes provided by researchers and trained volunteer divers participating in the Reef Life Survey (RLS) programme[12]. A total of 964 sites in 87 MPAs were surveyed (Extended Data Fig. 1a), with data aggregated into 121 MPA/ecoregion groupings for analysis. MPA means were compared with statistical predictions for fished coasts using data from 1,022 non-MPA sites surveyed in 76 of the 232 Marine Ecoregions of the World[13] (Extended Data Fig. 1b and Supplementary Data Table 1). The four community metrics investigated, each widely considered to respond to MPA declaration[14,15], were: (1) total biomass of all fishes; (2) total biomass of large (>250 mm length) fishes; (3) species richness of all fishes (number of species sighted per transect); and (4) species richness of large fishes. We also estimated the total biomass of three commercially important taxa (sharks, groupers and jacks), with unexploited damselfishes providing a control group for effects evident on targeted fishery groups. Effect size was calculated using the log ratio of measured values in MPAs relative to values predicted using global models for fished coasts.

Among 14 environmental and socio-economic covariates used in random forest models[16] to develop predictions for fished coasts, mean sea surface temperature, annual temperature range, photosynthetically active radiation, and latitude consistently exerted the strongest influence on the global distribution of species richness and biomass metrics (Extended Data Fig. 2). Biomass of groupers and jacks was also greatly influenced by human population density, and the biomass of sharks and groupers was influenced by phosphate concentration.

Fish species richness along fished coasts peaked in the southeast Asian 'coral triangle' region (Fig. 1a), as expected[12,17]. However, when only the number of large fishes sighted along transects was considered (Fig. 1b), the global centre of species richness shifted to more isolated locations within the Indo-Pacific region. Overfishing of large predatory fishes presumably contributed to these geographical patterns. Sharks, groupers and other large fishes were present within the coral triangle

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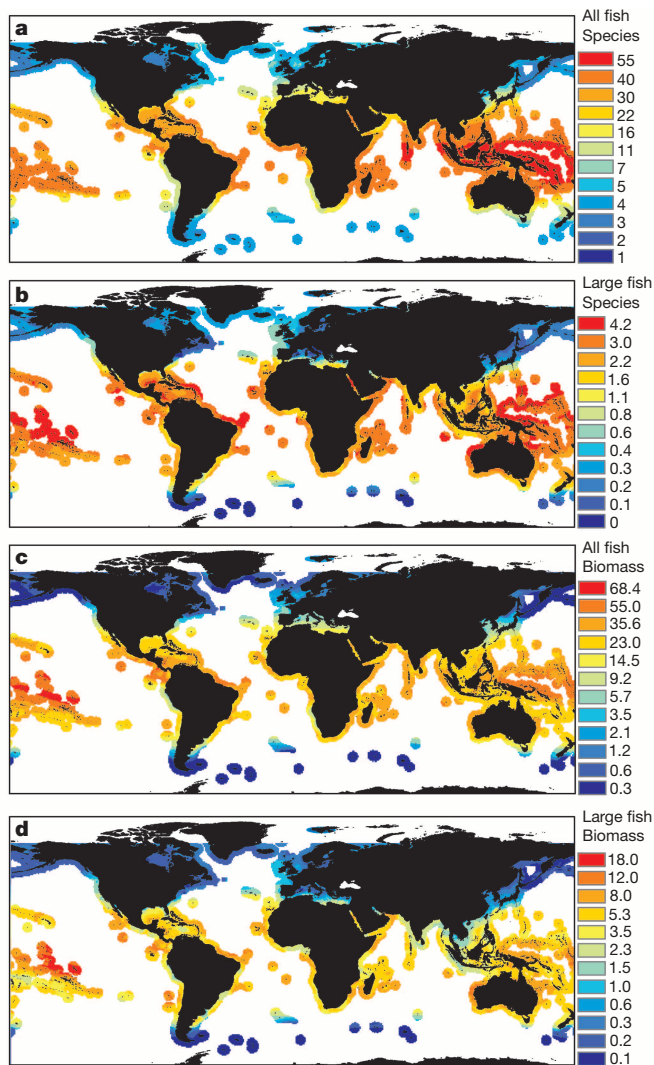
Figure 1 | Predicted global distribution of four community metrics for fishes associated with coral and rocky reefs outside of MPAs. Predictions are from random forest models developed using data from 1,022 sites in fished locations worldwide. **a**, Species richness of all fishes (number of species sighted per 250 m^2). **b**, Species richness of large (>250 mm total length) fishes (per 250 m^2). **c**, Total biomass of all fishes (kg per 250 m^2). **d**, Total biomass of large fishes (kg per 250 m^2).

region but had been exploited to near absence on most reefs, and so were rarely recorded on transects; consequently, observed species richness of large fishes was relatively low.

Our predictive models indicated that total fish and large fish biomass were highest in French Polynesia and the nearby Line Islands (Figs 1c, d), and sharks, groupers and jacks also had disproportionally high biomass in that region (Extended Data Figs 3a–c). Shark biomass on fished coasts was also very high off the Pitcairn Island group, and northeastern and northwestern Australia. Reassuringly, high shark and grouper biomass was accurately predicted for Galapagos, regardless that no data from fished sites in the oceanic tropical eastern Pacific region were used to generate the predictive models. At the time of the surveys, all islands in the region (Galapagos, Cocos and Malpelo) were within MPAs; however, data obtained before fishing restrictions in Galapagos indicate anomalously high shark and grouper biomass for fished coasts in that archipelago (S.B. and G.J.E., unpublished data). Damselfishes occurred in relatively high abundance in all tropical ocean basins (Extended Data Fig. 3d).

Across all 87 MPAs investigated, species richness of large fishes was 36% greater inside MPAs compared to fished areas (95% confidence

interval (CI), 16–60% increase), biomass of large fishes was 35% greater (CI 3–78% increase) and sharks 101% greater (CI 17–239% increase). Nevertheless, for species richness of all fishes and the other four biomass metrics investigated, no significant difference ($P > 0.05$) was found between levels observed in MPAs and those predicted for fished coasts. Moreover, many MPAs possessed fish biomass well below predicted regional averages, as indicated by the large percentage of MPAs with negative log ratios for total biomass, ranging from 25% of MPAs for large fishes to 31% for sharks to 47% for groupers. These negative values indicate considerable site-scale variability in fish densities, with some MPA sites exhibiting low fish biomass due to local habitat variability between survey sites and, in other cases, a bias resulting from stakeholder consultation processes before MPA declaration aimed at minimizing lost fishing opportunity[18].

The poor overall performance of MPAs worldwide in terms of recovery of fish biomass relative to fished sites was due to a high frequency of ineffective MPAs and high spatial variability in fish densities, rather than an absence of recovery in all MPAs. The efficacy of MPAs was strongly influenced by the five NEOLI planning and management features (no take, enforced, old, large and isolated), with MPAs that scored highly with multiple NEOLI features typically having highly elevated biomass of exploitable fishes compared to fished sites (Fig. 2). MPAs with at least four NEOLI features were distributed across six countries in three oceans (Extended Data Fig. 1a) and a range of environmental conditions, indicating that model outputs and conclusions were not strongly regionally biased.

No significant differences were evident between fished sites (zero features) and MPAs with one or two NEOLI features; however, effect sizes rose rapidly when the number of features increased from three to five (Fig. 2 and Extended Data Fig. 4). For example, the measured rises in mean values within MPAs relative to fished areas for total fish biomass, total large fish biomass and shark biomass with three NEOLI features were 30%, 66% and 104%, respectively. These increases were, however, modest compared to values when all five NEOLI features were present, with large increases of 244%, 840% and 1,990%, respectively. Similar marked increases in biomass were evident for groupers (882%) and jacks (864%). Non-fished damselfishes showed a smaller mean increase of 111% at MPAs with five NEOLI features. This increase was on the margins of statistical significance, lying outside the 95% confidence interval (Extended Data Fig. 4) but nonsignificant ($P < 0.05$) when assessed with a t-test, which adjusts for small sample size.

All four MPAs with five NEOLI features were small oceanic islands (Cocos, Costa Rica; Malpelo, Colombia; Kermadec Islands, New Zealand; and Middleton Reef, Australia), raising a potential concern that calculated effect sizes were biased by plankton and pelagic fish subsidies that enlarge food webs at isolated oceanic locations. 'Oceanic island' was, however, included as a categorical covariate in random forest models, therefore model predictions should accommodate small island effects. Regardless, further investigation into the contribution of external subsidies to food webs at isolated MPAs is warranted. Alternative explanations for elevated damselfish numbers in the most effective MPAs compared with poorly protected MPAs include reduced fishing-related habitat deterioration such as dynamite damage to coral, and trophic cascades involving smaller predators that consume damselfishes and are prey to sharks and groupers.
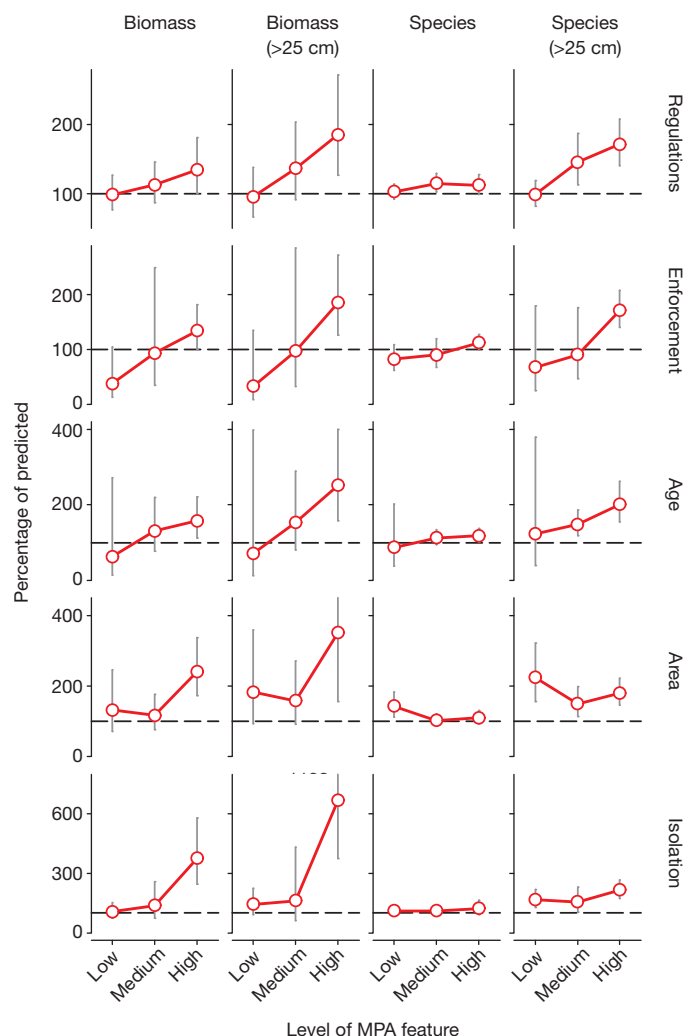
No-take regulations, efficient enforcement, large area (>100 km^2) and old age (>10 years) each contributed similar increases in fish biomass within MPAs (Fig. 2). However, isolation, a categorical factor that distinguished MPAs with reef habitat surrounded by deep (>25 m) water or large expanses of sand from MPAs with shallow reef habitat extending to fished areas, seemed to exert a stronger influence for community-level biomass and richness metrics than the other four features. For example, the mean increase (95% CI) for total fish biomass associated with MPAs with three NEOLI features was 100% (14–252%) when one of the three features was isolation, compared to 14% (−18%–58%) for three NEOLI MPAs when isolation was not included. Compliance
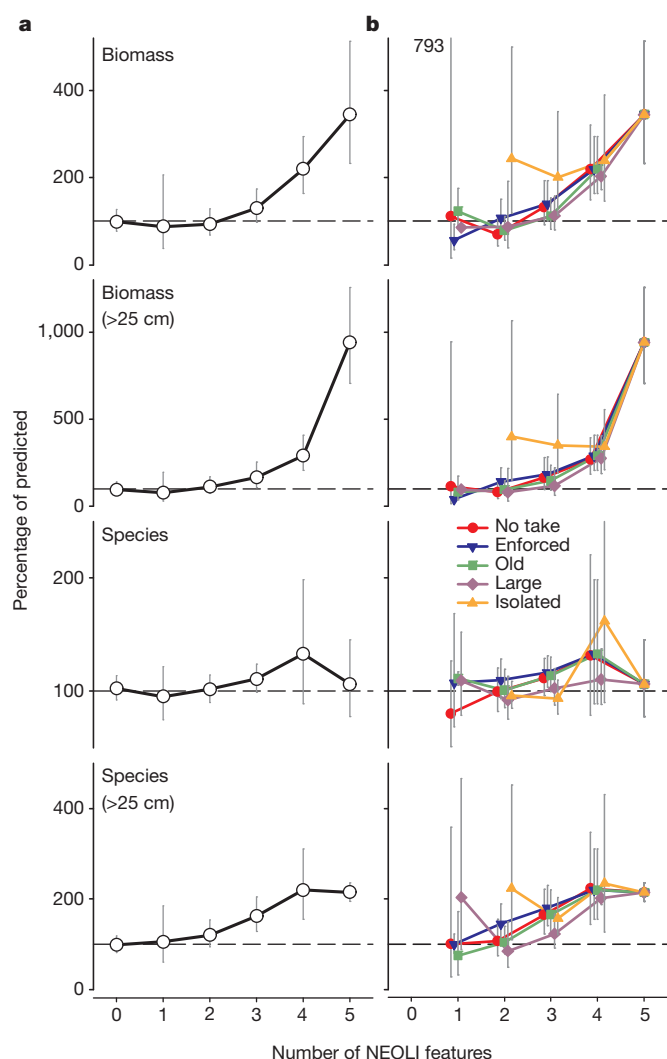
Figure 2 | Mean response ratios for MPAs with different numbers of NEOLI (no take, enforced, old, large, isolated) features. Mean ratio values have been back transformed from logs and expressed as percentages with 95% confidence intervals, with 100% equivalent to fished coasts. Sites on fished coasts have 0 NEOLI features. **a**, Mean response ratios for four community metrics. **b**, Mean response ratios for community metrics where each NEOLI feature was included within the set examined. The 'no-take' plot with two features, for example, depicts the mean response for no-take MPAs with a single other NEOLI feature. 95% confidence limits that lie off-scale are shown by number. Samples sizes are shown in Extended Data Table 1.

Figure 3 | Mean response ratios with 95% confidence intervals for four community metrics and low, medium and high levels of five MPA features. Values have been back transformed to per cent scale, with 100% equivalent to fished coasts. The feature 'regulations' was analysed using data from 82 MPAs with high enforcement; the feature 'enforcement' was analysed using data from 75 MPAs that are no-take; and the features 'isolation', 'age' and 'area' were analysed using data from 52 MPAs that are both no take and well enforced. 95% confidence limits that lie off-scale are shown by number. Samples sizes are shown in Extended Data Table 1.

may have contributed to the isolation effect, in that isolated MPAs are generally well demarcated for control purposes. They are readily recognized by fishers and more easily policed than coastlines with complicated mosaics of no take, restricted take and fishing zones. Although very important, the effect of isolation was similar in magnitude—rather than clearly superior—to other MPA features for biomass of sharks, groupers and jacks (Extended Data Fig. 4).

When MPAs that are no take and well enforced are considered, differences were evident in how the other MPA features affect different components of the fish community (Fig. 3 and Extended Data Fig. 5). Total fish biomass increased significantly from low to high levels for all five MPA features, and these same trends were magnified for large fishes (Fig. 3). Regardless of general concerns that large pelagic species move such great distances that few individuals are fully protected within MPAs[19], sharks and jacks seem to receive considerable protection from fishing mortality within the large, well-enforced, no-take MPAs studied here. The biomass of sharks and groupers rose exponentially when MPAs were fully isolated, and also greatly increased with area and age. The

biomass of jacks showed little isolation and age effects, but rose greatly in MPAs that were large, well enforced and no take. Damselfish biomass did not increase significantly with the accumulation of individual NEOLI features.

The large number of MPAs investigated here has allowed relatively subtle and higher order interactive MPA effects to be detected. Previous studies of MPAs have shown, for example, negligible or weak patterns associated with MPA size[6,9,14,15,20], and those detected here were only evident for MPAs with at least three of the NEOLI features. However, MPA size was very important for such metrics as jack biomass, which showed a stronger response to MPA area than to other metrics (Extended Data Fig. 5). This response probably resulted from time spent by actively-swimming fishes outside park boundaries, which increases probability of capture for fishes associated with small MPAs.

Species richness of large fishes exhibited a highly significant difference between MPAs with five NEOLI features and fished locations (115% increase relative to predicted, CI 95–137%; t-test, P < 0.0001; Fig. 2). By contrast, MPAs with five NEOLI features did not differ significantly in total species richness (6% increase relative to predicted)

from fished locations (*t*-test, $P = 0.42$; Fig. 2), nor did any of the five features individually have a clear effect on species richness (Fig. 3). Thus, total species richness along transects did not detectably increase in effective MPAs, despite the presence of additional large fish species, perhaps because of food web changes in the form of reduced presence of small fish species that comprised prey of the larger predatory species[5,21,22]. Regardless of these transect-scale effects, species richness at regional scales probably increased in areas with a mosaic of fished and effective MPAs because of the additional presence of large fishery-targeted species within the seascape[18].

Of the 87 MPAs investigated, only four possessed all five NEOLI features, whereas five MPAs possessed four features, and 39, 57 and 16 MPAs possessed three, two and one feature, respectively. The low proportion of MPAs possessing four or five NEOLI features (10%), and thus regarded here as effective, probably overstates the true proportion of effective MPAs worldwide. Our survey strategy deliberately targeted well-known and well-regarded MPAs, with most large and long-established MPAs included in this study.

Although only a small subset of MPAs are ever likely to qualify as large, most MPAs could achieve the remaining four NEOLI features. MPAs require additional time to age, and sufficient will among stakeholders, managers and politicians for increased implementation of no-fishing zones, increased levels of compliance, and extension of boundaries past the limits of reef systems or to deep water. If these could be achieved in tandem with current trends for declaration of large remote 'wilderness' MPAs[23,24], then conservation benefits from the global MPA network should increase markedly. However, the current base is very low with only 0.08% of the world's oceans within no-take MPAs in 2008 (ref. 25), and with opportunities for an expanded network diminishing as establishment and opportunity costs for large isolated MPAs escalate in line with human population growth[24,26].

By using effective MPAs as an unfished standard, our study allows the first global assessment of the magnitude of fishing effects on temperate as well as tropical reef communities. Fish biomass was greatly reduced overall, with 63% of all fish biomass, 80% of large fish biomass, 93% of sharks, 84% of groupers and 85% of jacks apparently removed from reefs by fishing.

In spite of their huge magnitude, these estimates are probably conservative because they are based on the assumption that MPAs with four or five NEOLI features provide an accurate non-fished baseline for inferring historical patterns. Yet fish populations are unlikely to have fully recovered from previous impacts of fishing in four NEOLI MPAs, which were found to be less effective than five NEOLI MPAs for some metrics. Moreover, high fishing mortality rates for sharks and wide-ranging predatory fishes outside MPAs will negatively influence total numbers within boundaries through reduced immigration rates, and further recovery of fish biomass within MPAs probably continues over much longer time spans than the 10-year threshold used here to define old MPAs[18]. Our estimates for effective MPAs include uncertainty associated with the low number of effective MPAs surveyed, most notably for sharks, as only five of the nine category 4 and 5 NEOLI MPAs had sharks present. Also, biomass may be overestimated because of diminished flee responses from divers of large fishes in well-enforced no-take MPAs[27]. Regardless, fishing clearly exerts a very large and ubiquitous impact on shallow reefs.

The 80% reduction in biomass of large fishes outside effective MPAs coincides with the threshold value used by the International Union for Conservation of Nature (IUCN) to categorize species as Critically Endangered for Red List assessments[28]. Although recognizing that application of current Red List thresholds to exploited fish stocks remains contentious[28], the high number of large-bodied species that together average 80% decline indicates that innumerable threatened fish species probably exist, and that effective MPAs probably have a large role in safeguarding populations of many of these species[4]. Even nations with relatively well-managed fisheries have few sharks and other large predatory coastal fishes outside well-designed and mature MPAs. Given

the huge scale of fishing impacts, the rate of fish extinctions is likely to increase greatly through this century unless a refugial network of effective MPAs exists to allow persistence of large-bodied species and associated predator-dominated food webs, and broad-scale fisheries management practices significantly improve[29].

METHODS SUMMARY

Surveys were based on Reef Life Survey methodology[12,30], with support from volunteer SCUBA divers trained individually to scientific data collection standards. All fishes observed within $50\,\text{m} \times 5\,\text{m}$ transect blocks were counted, and total fish lengths estimated, during swims on adjoining blocks up one side and down the other side of 50-m lines. Each transect was set along a depth contour, with two depth contours (mean 2.4) generally surveyed at each site. Sites located within 87 MPAs were investigated, with approximately half located in Australia (36) and New Zealand (8). In total, 48 MPAs were complete no take, 18 MPAs allowed limited fishing, whereas 21 MPAs were multi-zoned with interspersed no-take and limited fishing zones. Data were compiled from 171,331 underwater abundance counts of 2,544 species in 9,544 transect blocks at 1,986 sites.

We assessed effects of five MPA features (fishing regulations, enforcement, age, area and isolation), each categorized at low, medium and high levels, on eight fish community metrics (species richness of all fishes and large (>250 mm) fishes; total biomass of all fishes, large fishes, sharks, groupers, jacks and damselfishes). The magnitudes of effects were quantified using the log ratio of observed value within the MPA to predicted value at that location if the MPA did not exist (for example, $\log[B_\text{m}/B_\text{p}]$, where B_m is measured fish biomass and B_p is biomass predicted if the site was fished). Predictions were produced using random forest procedures[16], where each forest was created by generating 2,000 regression trees from a bootstrap sample of the data. Relationships were initially established between 14 covariates (environmental and socio-economic) and measured values of the eight response metrics at fished sites. These relationships were then used, with known covariate values at each MPA, to predict each of the eight community metrics at that MPA location.

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

Author Contributions G.J.E. and R.D.S.-S. conceived the project; G.J.E., R.D.S.-S., M.A.B., A.T.F.B., S.C.B., S.B., S.J.C., A.T.C., M.D., S.C.E., G.F., D.E.G., A.J.I., S.K., D.J.K., R.M., G.S., E.M.A.S. and many others collected the data; G.J.E., R.J.T., T.J.W., S.K. and S.C.E. prepared figures; G.J.E. drafted the initial manuscript; all authors contributed to analyses and interpretation.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to G.J.E. (g.edgar@utas.edu.au).

METHODS

Survey methodology. Standardized visual census counts were made at 1,986 sites using Reef Life Survey (RLS) methodology (see RLS methods manual 'Standardised survey procedures for monitoring rocky and coral reef ecological communities' at http://reeflifesurvey.com/files/2008/09/NEW-Methods-Manual_15042013.pdf). Divers made counts and estimates of total lengths of all fish species observed during swims at ~2 m s^{-1} along the centre of a 5-m-wide swathe up one side and then down the other side of 50-m transect lines. Fishes sighted in transect blocks were recorded on an underwater slate, with abundance estimates made by counting individuals of less abundant species and, in locations with high fish densities, estimating the number of more abundant species. The abundance of schooling fishes was recorded by counting a subset within the school which was combined with an estimate of the proportion of the total school. Nearly all fishes were recorded to species level, with exceptions classified at the highest taxonomic resolution possible. The use of digital photography typically allowed later identification of most unidentified species, with assistance of taxonomic experts as required.

Experienced scientists and skilled recreational divers both contributed data to the RLS programme, all divers having either substantial previous experience in fish surveys or extensive one-on-one training by R.D.S.-S. or G.J.E. To provide a major element of consistency in diver contributions at the global scale, G.J.E. and R.D.S.-S. participated in most surveys, providing 31% of all data analysed. Validation tests indicated no difference in quality or composition of data provided by volunteers participating in this programme when compared to professional biologists[30].

Each transect was set along a depth contour, with two depth contours generally surveyed at each site (mean of 2.4 depths per site; minimum, maximum, mean ± s.d. depth contours surveyed: 0.1 m, 42 m, 7.5 ± 4.1 m, respectively). Sites located within 87 MPAs were investigated, with approximately half located in Australia (36) and New Zealand (8). In total, 48 MPAs were no take where all fishing was prohibited, 18 MPAs allowed limited fishing, whereas 21 MPAs were multi-zoned with interspersed no-take and limited fishing zones. Data were compiled from 171,331 underwater abundance counts of 2,544 species in 9,544 transect blocks (50 m × 5 m).

MPA features and community metrics investigated. We assessed the influence of five MPA features on eight fish community metrics calculated using field survey data. The MPA features investigated were each categorized at three levels: low (L), medium (M) and high (H). (1) Regulations. Extent that regulations restrict fishing at survey site. L, site can be openly fished with no fishing restrictions additional to those generally applied within the state; M, site located within an MPA but with some fishing methods allowed; H, no-take area within an MPA. (2) Enforcement. Extent of compliance to regulations that restrict fishing, both through overt policing and through community support for regulations. Level was decided at the time of surveys after discussion with local park authorities, and on the basis of observations of the extent of infractions while conducting fieldwork. L, little attempt at control, a 'paper park'; M, a moderate level of policing attempted, although infractions were apparent; H, appears to be well enforced, although clandestine poaching may occur. (3) Age. Period between when regulations restricting fishing were first enacted and field surveys undertaken. L, MPA zone <5 years old; M, MPA zone 5–10 years old; H, MPA zone >10 years old. (4) Area. MPA zone area, as described in management plan or documents provided locally to users. L, <1 km^2; M, 1–100 km^2; H, >100 km^2. (5) Isolation. Degree that reef habitat surveyed is isolated by habitat boundaries from adjacent fished reef. L, shallow (<25 m) reef habitat extends continuously across MPA boundary; M, a small (1–20%) percentage of zone boundary breached by continuous shallow reef habitat; H, MPA zone isolated from fishing areas by depth (>25 m) or sand barriers of at least 20 m width.

We investigated eight community metrics. (1) Species richness of all fishes. Total number of all fish species sighted within 50 m × 5 m transect blocks. (2) Species richness of large fishes. Total number of fish species sighted within 50 m × 5 m transect blocks for the set of individuals observed on transects exceeding the 250 mm size class bin (that is, 300 mm size and above). (3) Total fish biomass. Total biomass of all fishes sighted in 50 × 5 m transect blocks. Estimated by combining abundance counts with size estimates using length-weight relationships provided for total length of each fish species (in some cases genus and family) in Fishbase (http://www.fishbase.org). Bias in divers' perceptions of fish size underwater was additionally corrected using relationships presented in ref. 31. (4) Total biomass of large fishes. Total biomass of individuals sighted in 50 × 5 m transect blocks that exceeded the 250 mm size class bin. (5) Total biomass of sharks. Sum of biomass of all fishes in transect that belong to orders Carcharhiniformes, Heterodontiformes, Lamniformes and Orectolobiformes. (6) Total biomass of groupers. Sum of biomass of all fishes in transect that belong to family Serranidae, genera *Dermatolepis*, *Epinephelus*, *Gracila*, *Mycteroperca*, *Paralabrax*, *Plectropomus*, *Trachypoma* and *Variola*. Small serranids such as *Pseudanthias* spp. were not considered. (7) Total biomass of jacks. Sum of biomass of all fishes in transect that belong to family Carangidae. (8) Total biomass of damselfishes. Sum of biomass of all fishes in transect that belong to family Pomacentridae.

Data aggregation. To reduce spatial confounding resulting from highly clumped distribution of sites surveyed, data were aggregated before analyses as means for each ecoregion, MPA and zone type. Thus, fished sites were aggregated as mean values for each of 76 Marine Ecoregions of the World[13], whereas MPA data were aggregated into 121 MPA zones by ecoregion combinations. Multi-zoned MPAs contributed two data points to analyses (no-take sites and restricted fishing sites), whereas very large MPAs that extended across ecoregional boundaries (for example, Great Barrier Reef Marine Park, Galapagos Marine Reserve) were also partitioned with aggregated data from each ecoregion.

Global models. Models were developed using random forest procedures[16], as available in the 'extendedForest' packages for R (https://r-forge.r-project.org/projects/gradientforest), to predict the distribution of the eight community metrics in inshore habitats globally, including the MPA locations investigated. Each random forest consisted of numerous (2,000 in this case) regression trees, where each tree is fit to a bootstrap sample of the biological data using a recursive partitioning procedure. Random forest analyses also contain cross-validation routines based on random subsets of survey sites and covariate predictors that are excluded during development of each tree (the 'out-of-bag' data). Cross-validation using out-of-bag data allows estimation of prediction performance (R^2).

Using random forests, relationships were identified between mean densities of different fish species observed per transect in 76 marine ecoregions[13] and the global distribution of 14 environmental and socio-economic covariates (Extended Data Table 2). Data for each ecoregion were logged after aggregation as a mean of mean values for sites within each ecoregion, with a total of 1,022 fished sites investigated overall. Ecoregions with a value of zero for a particular metric (for example, grouper biomass in temperate locations) were removed from analysis and treated as missing values when generating predictive models associated with individual MPAs. To estimate prediction error, cross-validation was used where observations not selected in the bootstrap sample for a tree were compared to their predictions. The per cent change in accuracy was measured to assess the importance of each predictor variable (Extended Data Fig. 2). This is the change in accuracy of the predictions between models that include or do not include a given covariate, where accuracy was measured by the mean of the residuals squared using the 'out-of-bag' data.

Linear least-squares regression of survey observations at fished sites with random forest predictions indicated that the models provided a reasonable fit. R^2 values for predicted versus observed plots were 63%, 38%, 80% and 64% for total biomass, large fish biomass, species richness and large fish species richness, respectively, whereas the percentages of observations > predictions were 46%, 46%, 53% and 54%, so observed data were well balanced with an even scatter above and below predictions.

Relationships generated between response metrics and environmental covariates were combined with available data on environmental and socioeconomic covariates at 964 sites surveyed in 87 MPAs to predict each of the eight fish community metrics within each unique combination of MPA zone type (no take or restricted fishing) and ecoregion. From generated random forests, predictions were made at new sites by taking the average of response metrics derived from each tree individually. MPA effects for each MPA zone type were then calculated using the log ratio of predicted/observed value (for example, $\log[B_m/B_p]$, where B_m is measured fish biomass and B_p is biomass predicted if the site was fished). When no individuals of one of the four fish groups (sharks, groupers, jacks or damselfishes) were recorded within a particular MPA, then that MPA was excluded from calculations of effect size. Mean effect sizes and confidence intervals thus relate to the subset of sites where each of the various fish groups were observed.

Random forest models were also used to predict values of each metric for fished sites across 5 arcmin grid cells globally, which were then plotted on maps within a coastal buffer. The calculations underlying random forest models used to generate global maps differed from calculations used to predict MPA values in two ways: (1) they were based on 10 rather than 14 environmental covariates, with government effectiveness, corruption, GDP and oceanic island not considered given their small contribution to models (Extended Data Fig. 2) and difficulty in compilation through the full global prediction space; and (2) data for the four fish groups were $\log[x +$ minimum value for metric] transformed before analysis and back transformed post hoc to compensate for the many zeroes associated with global mapping predictions.

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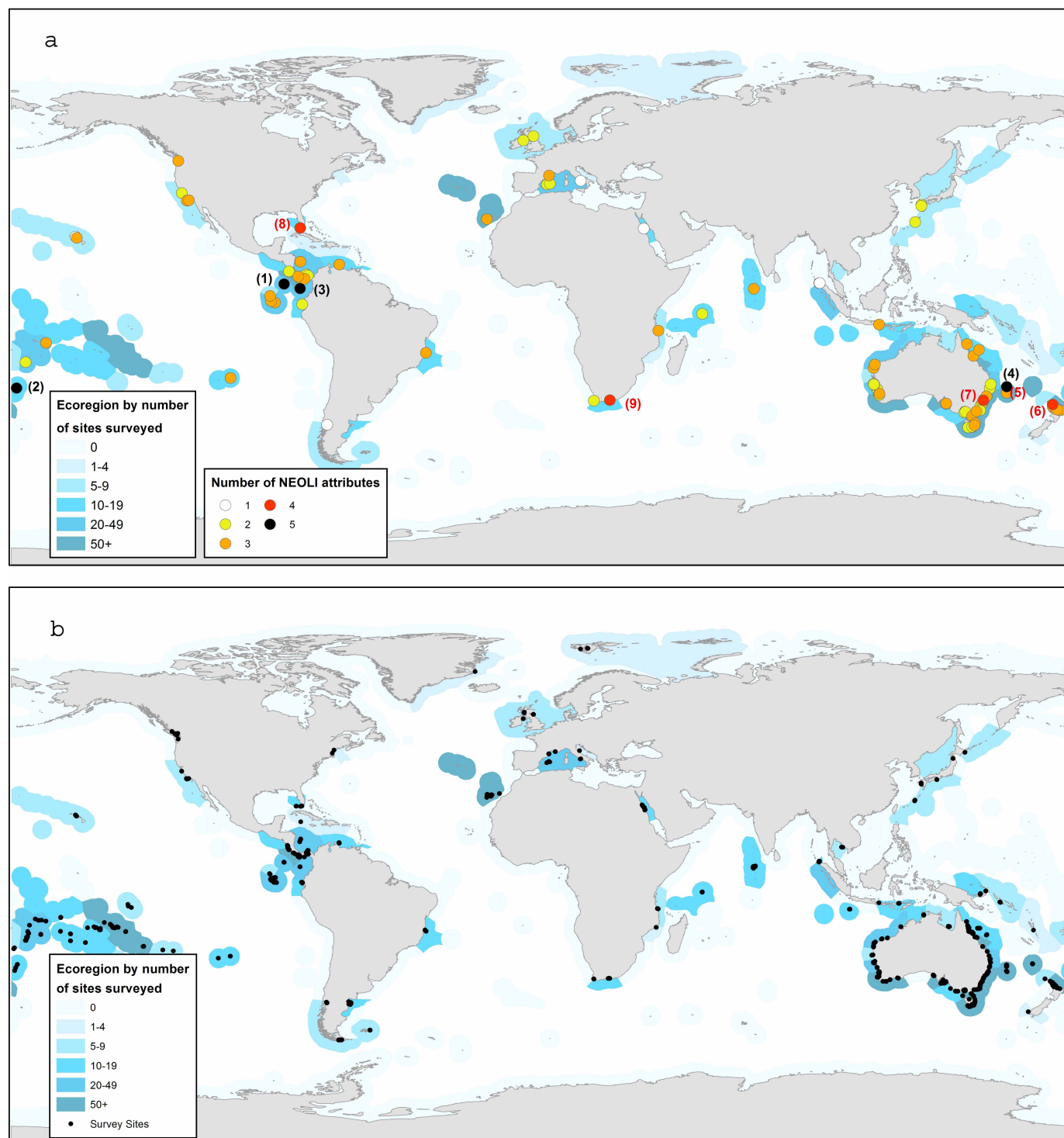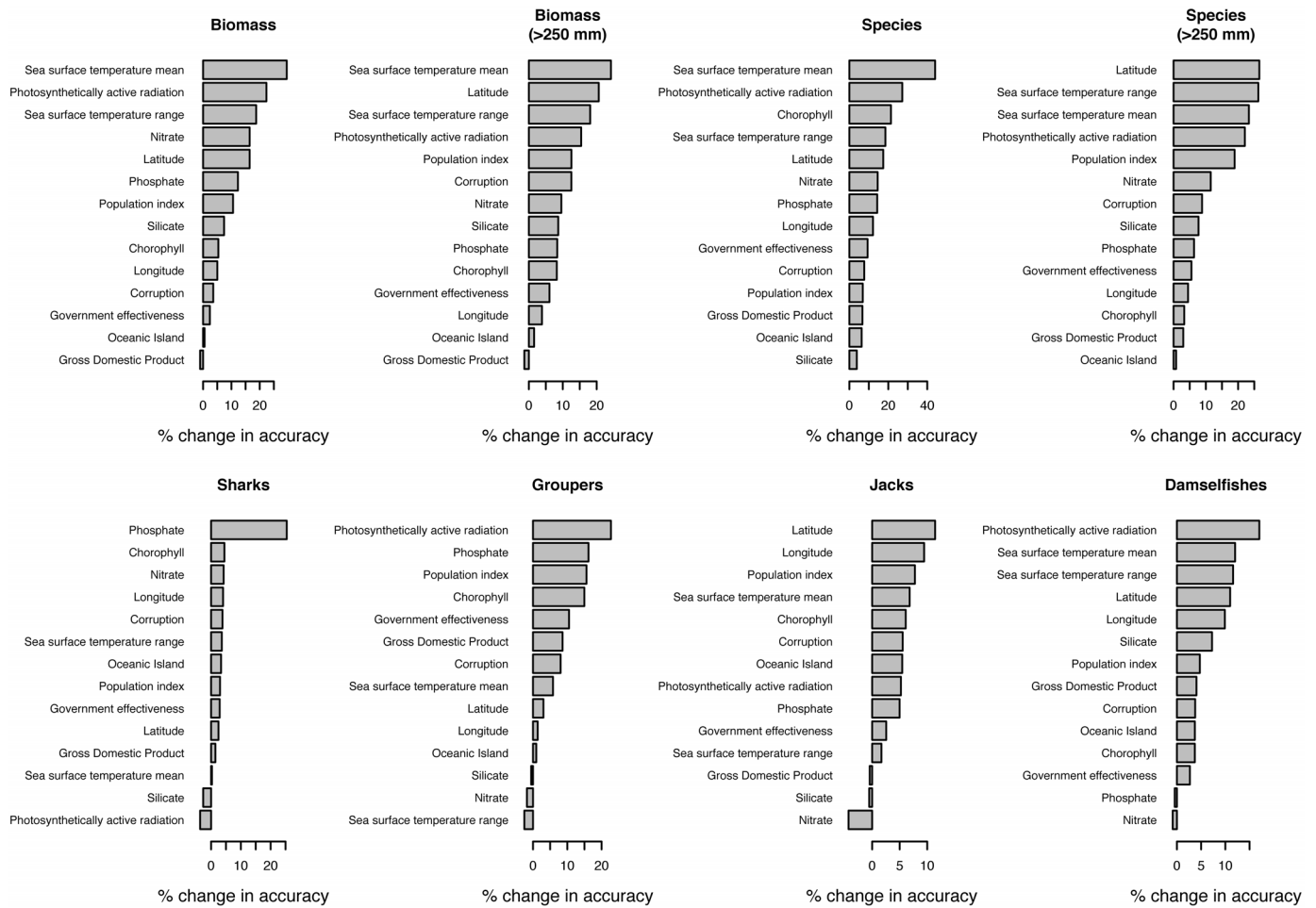
Extended Data Figure 1 | Distribution of sites surveyed. a, Number of NEOLI (no take, enforced, old, large and isolated) features at MPAs investigated (coloured circles). MPAs with most NEOLI features are overlaid on top; consequently numerous MPAs with one and two features are not visible. MPAs with five NEOLI features are (1) Cocos, (2) Kermadec Islands, (3) Malpelo, (4) Middleton Reef; MPAs with four NEOLI features are (5) Elizabeth Reef, (6) Poor Knights Islands, (7) Ship Rock, (8) Tortugas and (9) Tsitsikamma. **b**, All MPA and fished sites surveyed (black circles). Blue shading summarizes the number of sites surveyed within each ecoregion.

Biomass

Sea surface temperature mean	
Photosynthetically active radiation	
Sea surface temperature range	
Nitrate	
Latitude	
Phosphate	
Population index	
Silicate	
Chorophyll	
Longitude	
Corruption	
Government effectiveness	
Oceanic Island	
Gross Domestic Product	

0 10 20
% change in accuracy

Biomass (>250 mm)

Sea surface temperature mean	
Latitude	
Sea surface temperature range	
Photosynthetically active radiation	
Population index	
Corruption	
Nitrate	
Silicate	
Phosphate	
Chorophyll	
Government effectiveness	
Longitude	
Oceanic Island	
Gross Domestic Product	

0 10 20
% change in accuracy

Species

Sea surface temperature mean	
Photosynthetically active radiation	
Chorophyll	
Sea surface temperature range	
Latitude	
Nitrate	
Phosphate	
Longitude	
Government effectiveness	
Corruption	
Population index	
Gross Domestic Product	
Oceanic Island	
Silicate	

0 20 40
% change in accuracy

Species (>250 mm)

Latitude	
Sea surface temperature range	
Sea surface temperature mean	
Photosynthetically active radiation	
Population index	
Nitrate	
Corruption	
Silicate	
Phosphate	
Government effectiveness	
Longitude	
Chorophyll	
Gross Domestic Product	
Oceanic Island	

0 10 20
% change in accuracy

Sharks

Phosphate	
Chorophyll	
Nitrate	
Longitude	
Corruption	
Sea surface temperature range	
Oceanic Island	
Population index	
Government effectiveness	
Latitude	
Gross Domestic Product	
Sea surface temperature mean	
Silicate	
Photosynthetically active radiation	

0 10 20
% change in accuracy

Groupers

Photosynthetically active radiation	
Phosphate	
Population index	
Chorophyll	
Government effectiveness	
Gross Domestic Product	
Corruption	
Sea surface temperature mean	
Latitude	
Longitude	
Oceanic Island	
Silicate	
Nitrate	
Sea surface temperature range	

0 10 20
% change in accuracy

Jacks

Latitude	
Longitude	
Population index	
Sea surface temperature mean	
Chorophyll	
Corruption	
Oceanic Island	
Photosynthetically active radiation	
Phosphate	
Government effectiveness	
Sea surface temperature range	
Gross Domestic Product	
Silicate	
Nitrate	

0 5 10
% change in accuracy

Damselfishes

Photosynthetically active radiation	
Sea surface temperature mean	
Sea surface temperature range	
Latitude	
Longitude	
Silicate	
Population index	
Gross Domestic Product	
Corruption	
Oceanic Island	
Chorophyll	
Government effectiveness	
Phosphate	
Nitrate	

0 5 10
% change in accuracy

Extended Data Figure 2 | Relative importance of the 14 covariates used in global prediction models developed with random forests. Per cent change in accuracy for a given predictor variable is measured by the change between models that include or do not include that predictor variable, with accuracy assessed as the mean of the residuals squared. Residuals are based on a cross-validation technique to avoid bias, and the change in accuracy is divided by the standard error for a given tree then averaged across all trees.
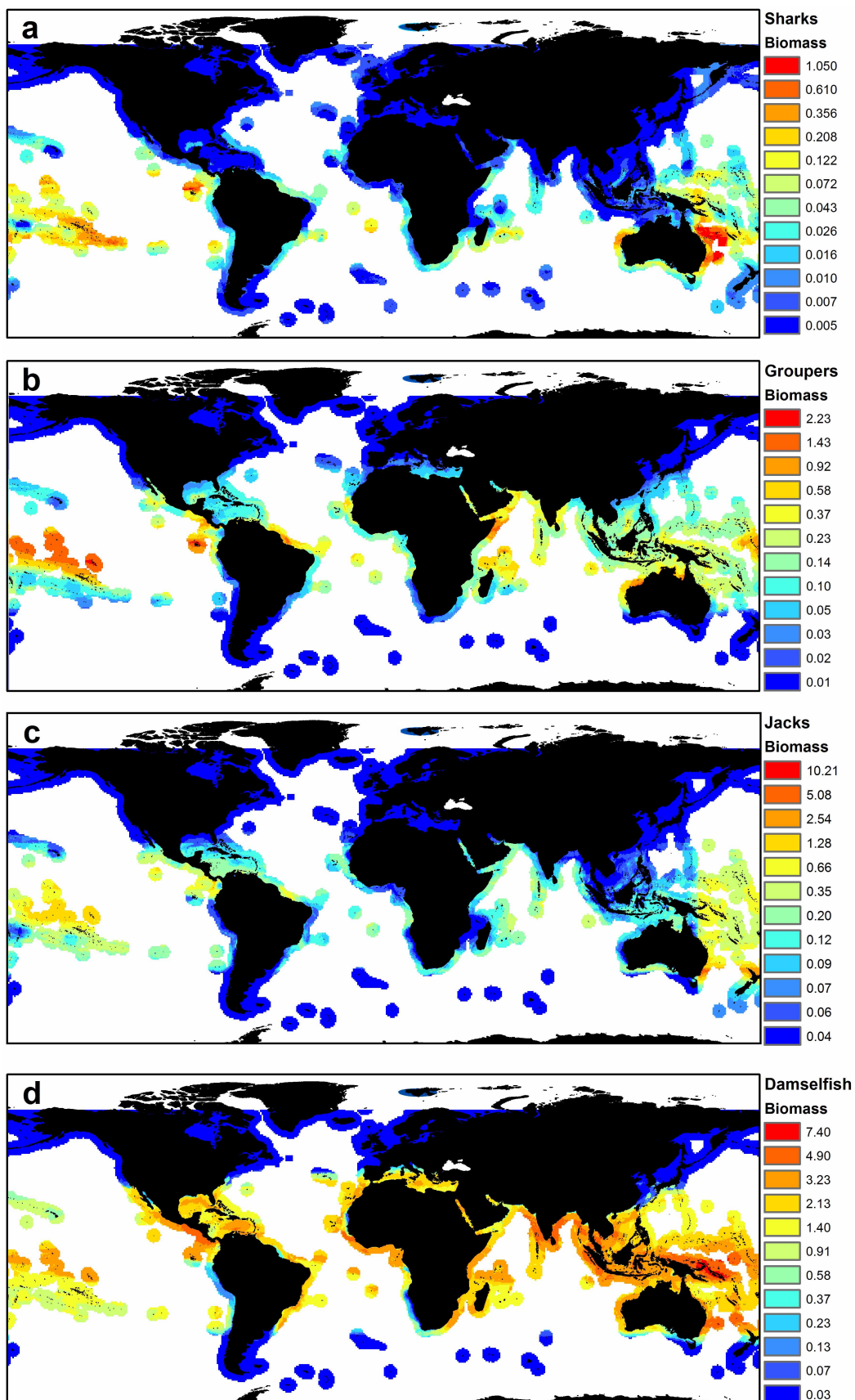
Extended Data Figure 3 | Predicted global distribution of fish biomass (kg per 250 m²) on fished coasts. Predictions are from random forest models developed using data from 1,022 sites in fished locations worldwide. **a**, Sharks. **b**, Groupers. **c**, Jacks. **d**, Damselfishes. Note that scales in colour schemes differ among maps, and numbers represent predicted values represented by each colour after smoothing of log-transformed site-level data.
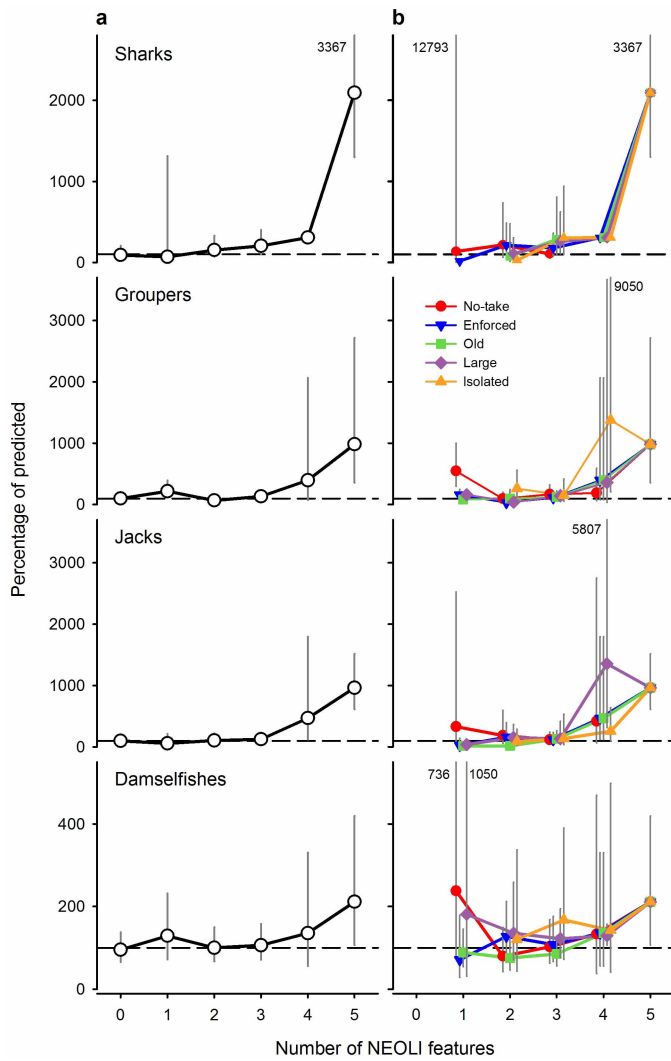
Extended Data Figure 4 | Mean response ratios for MPAs with different number of NEOLI features. Mean ratio values have been back transformed from logs and expressed as percentages with 95% confidence intervals. The number of NEOLI features varies from 0 at sites along fished coastlines to 5 for MPA sites with all NEOLI features. **a**, Plots calculated for sites where sharks, groupers, jacks and damselfishes were present and the subsets of MPAs with different numbers of NEOLI (no take, enforced, old, large, isolated) features. **b**, Mean response ratios for community metrics where each NEOLI feature was included within the set examined. 95% confidence limits that lie off-scale are shown by number. Sample sizes are shown in Extended Data Table 1.
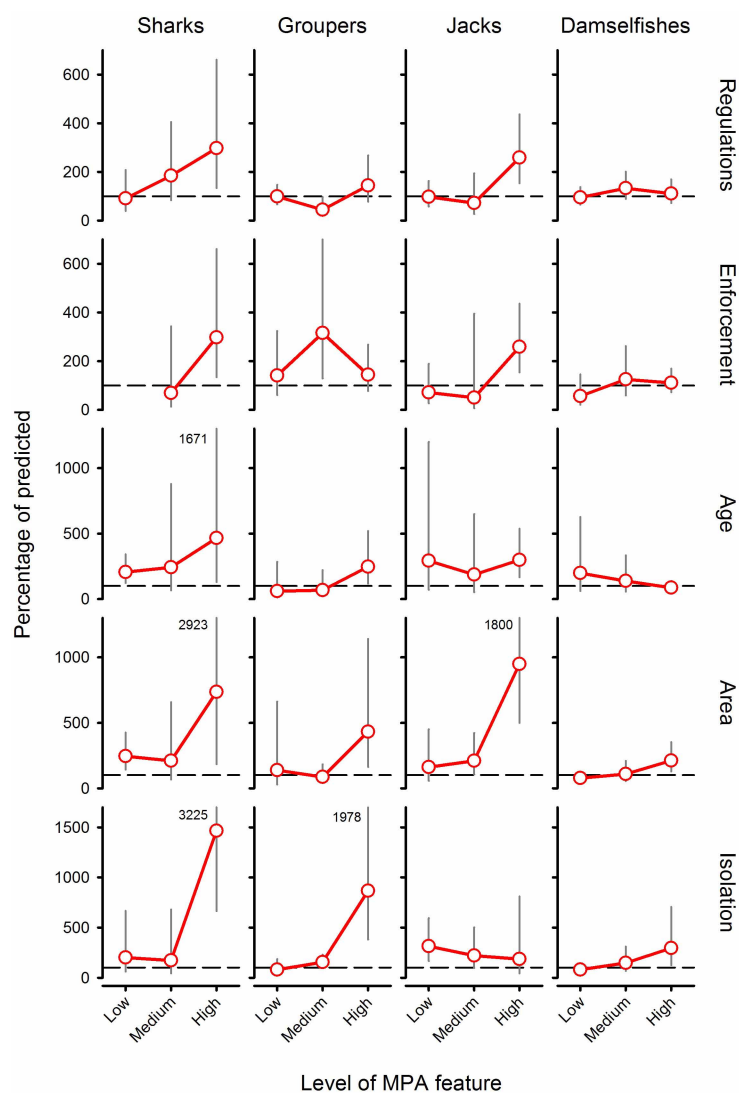
Extended Data Figure 5 | Mean response ratios for the subsets of sites at which sharks, groupers, jacks and damselfishes were observed. Values have been back transformed to per cent, with 100% equivalent to fished coasts, and with 95% confidence intervals. The feature 'regulations' was analysed using data from 82 MPAs that are well enforced; the feature 'enforcement' was analysed using data from 75 MPAs that are no take; and the features 'isolation', 'age' and 'area' were analysed using data from 52 MPAs that are both no take and well enforced. Sharks were not observed in any no-take MPA with low enforcement, so the associated response ratio could not be calculated. 95% confidence limits that lie off-scale are shown by number. Sample sizes are shown in Extended Data Table 1.

Extended Data Table 1 | Sample sizes applied in figures

Figure 2a

Metric	MPA subset	No. of NEOLI features					
		0	1	2	3	4	5
All metrics	All	76	16	57	39	5	4

Figure 2b

Metric	MPA subset	No. of NEOLI features					
		0	1	2	3	4	5
All metrics	No-take		7	31	29	4	4
	Enforced		5	36	32	5	4
	Old		2	22	31	5	4
	Large		2	16	16	3	4
	Isolated			8	9	3	4

Extended Data Figure 4a

Metric	MPA subset	No. of NEOLI features					
		0	1	2	3	4	5
Sharks	All	29	3	26	14	1	4
Groupers	All	46	8	36	22	4	4
Jacks	All	50	6	29	27	4	4
Damselfishes	All	62	12	48	36	4	4

Extended Data Figure 4b

Metric	MPA subset	No. of NEOLI features					
		0	1	2	3	4	5
Sharks	No-take		2	13	9		4
	Enforced		1	22	10	1	4
	Old			5	8	1	4
	Large			9	9	1	4
	Isolated			3	6	1	4
Groupers	No-take		3	19	14	3	4
	Enforced		2	21	16	4	4
	Old		2	14	18	4	4
	Large		1	11	12	3	4
	Isolated			7	6	2	4
Jacks	No-take		2	12	20	3	4
	Enforced		2	21	21	4	4
	Old		1	10	20	4	4
	Large		1	10	11	2	4
	Isolated			4	9	3	4
Damselfishes	No-take		4	25	26	3	4
	Enforced		4	31	29	4	4
	Old		2	17	28	4	4
	Large		2	14	16	2	4
	Isolated			8	9	3	4

Figure 3

Metric	Feature	Level of feature		
		Low	Medium	High
All metrics	Regulations	76	30	52
	Enforcement	9	14	52
	Age	5	19	28
	Area	14	30	8
	Isolation	35	9	8

Extended Data Figure 5

Metric	Feature	Level of feature		
		Low	Medium	High
Sharks	Regulations	29	15	23
	Enforcement	0	5	23
	Age	3	12	8
	Area	3	14	6
	Isolation	12	6	5
Groupers	Regulations	46	20	27
	Enforcement	7	9	27
	Age	3	8	16
	Area	6	14	7
	Isolation	16	6	5
Jacks	Regulations	50	19	33
	Enforcement	2	6	33
	Age	3	10	20
	Area	8	19	6
	Isolation	19	6	8
Damselfishes	Regulations	62	28	44
	Enforcement	8	10	44
	Age	3	17	24
	Area	11	26	7
	Isolation	29	7	8

Extended Data Table 2 | Covariates used as predictor variables in global random forest models

Variable	Variable abbreviation	Units	Scale	Reference (if applicable)
Index of population pressure	POP_index	index	2.46 arcmin (4.6 km)	
Government Effectiveness	Govt Eff	index	country	35
Control of Corruption	Corruption	index	country	35
Per capita GDP	GDP	US$	country	#
Mean nitrate	Bio_nitrate	umol/l	5 arcmin (9.2 km)	36
Mean phosphate	BIO_phosphate	umol/l	5 arcmin (9.2 km)	36
Mean silicate	BIO_silicate	umol/l	5 arcmin (9.2 km)	36
Mean chlorophyll A	BIO_chlomean	mg/m^3	5 arcmin (9.2 km)	36
Photosynthetically active radiation	BIO_parmean	Einstein/m^3/day	5 arcmin (9.2 km)	36
Mean sea surface temperature	BIO_SST_mean	^{o}C	5 arcmin (9.2 km)	36
Range of sea surface temperature	BIO_SST_range	^{o}C	5 arcmin (9.2 km)	36
Oceanic island isolated from continental shelf	Oceanic island	yes/no		
Site latitude	Latitude	decimal degrees	0.0001^o	
Site longitude	Longitude	decimal degrees	0.0001^o	

The index of population pressure was calculated by fitting a smoothly tapered surface to each settlement point on a year 2000 world population density grid[32] using the quadratic kernel function[33]. Populations were screened for a density greater than 1,000 people per 0.04 degree cell, and the search radius was set at 3.959 degrees. This table contains refs 34 and 35.
Per capita GDP was obtained from IMF for 2012 at http://en.wikipedia.org/wiki/List_of_countries_by_GDP_%28PPP%29_per_capita.