Towards process-oriented management of tropical reefs in the anthropocene

Raphael Seguin, David Mouillot, Joshua Cinner, Rick Stuart Smith, Eva Maire, Nicholas Graham, Matthew Mclean, Laurent Vigliola, Nicolas Loiseau

▶ **To cite this version:**

HAL Id: hal-03858373

https://hal.umontpellier.fr/hal-03858373v1

Submitted on 9 Oct 2024

Towards process-oriented management of tropical reefs in the anthropocene

Raphael Seguin [1,2] ✉, David Mouillot[1], Joshua E. Cinner [3],
Rick D. Stuart Smith[4], Eva Maire [5], Nicholas A. J. Graham [5],
Matthew McLean[6], Laurent Vigliola [2,7] and Nicolas Loiseau [1,7]

Tropical reefs and the fish relying on them are under increasing pressure. Shallow-reef fish provide important ecological information in addition to sustaining fisheries, tourism and more. Although empirical metrics of fish biomass are widely used in fisheries management, metrics of biomass production—how much new biomass is produced over time—are rarely estimated even though such production informs potential fisheries yields. Here we estimate fish standing biomass (B), biomass production (P, the rate of biomass accumulation) and biomass turnover (P/B ratio, the rate of biomass replacement) for 1,979 tropical reef sites spanning 39 tropical countries. On the basis of fish standing biomass and biomass turnover, we propose a conceptual framework that splits reefs into three classes to visualize ecological and socio-economic risk and help guide spatial management interventions (for example, marine protected areas) to optimize returns on conservation efforts. At large scales, high turnover was associated with high human pressure and low primary productivity, whereas high biomass was associated with low human pressure and high primary productivity. Going beyond standing fish biomass to consider dynamic ecological processes can better guide regional coral reef conservation and sustainable fisheries management.

Severe impacts on ecosystem functioning are among the most widespread ecological consequences of the Anthropocene, occurring as a direct result of resource overexploitation, habitat degradation and defaunation[1–3]. Tropical reefs are no exception, with degraded states and processes projected to worsen in the long term due to escalating human pressures[4–6]. Given the diverse and essential contributions to people provided by tropical reefs, such degradation will have overwhelming consequences for human livelihood and welfare, primarily in developing countries[7].

Marine protected areas (MPAs) are a key management tool to counteract deleterious human impacts on tropical reefs[8–10]. MPAs, and in particular no-take or fully protected marine reserves (which

ban extractive activities), can increase the abundance and biomass of fish species within their boundaries[11,12] and even benefit fisheries by improving catches in adjacent areas through the spillover of both adults and larvae[13–15]. In some cases, MPAs can improve human well-being, but in others they can be deleterious to people and become a source of conflict[16]. As alternatives, partially protected areas, locally managed MPAs and other effective area-based conservation measures[17] can maintain the provision of livelihoods to people[18] but sometimes to the detriment of ecological benefits[19].

A critical challenge for marine conservation is therefore to sustain nature's contributions to people while protecting marine biodiversity by preventing ecological decline. Thus, to be sustainable and fair,

[1]MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Montpellier, France. [2]ENTROPIE, IRD, UR, UNC, CNRS, IFREMER, Noumea, France. [3]ARC Center of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia. [4]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia. [5]Lancaster Environment Centre, Lancaster University, Lancaster, UK. [6]Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada. [7]These authors contributed equally: Laurent Vigliola, Nicolas Loiseau. ✉e-mail: raphaelseguin@protonmail.com

management actions must be both context-specific and inclusive[18], which entails a trade-off between objectives such as maintaining fisheries, ecosystem functioning and biodiversity[20,21]. Even though these objectives are not systemically antagonistic[20,21], they are rarely considered together since MPAs may not be successful across both biodiversity and socio-economic objectives[22]. A range of management options and fisheries restrictions adapted to the local context may thus be necessary to reach several Sustainable Development Goals synergistically. However, the scientific basis or rationale to define and classify local contexts where different management options can be the most appropriate is unclear.

Here we suggest that examining tropical reefs along gradients of both fish biomass and biomass turnover (that is, the ratio between biomass production (P) and standing biomass (B), or P/B ratio) can inform on which reefs are at risk both ecologically and socially and can guide possible regional-scale conservation strategies on tropical reefs. Indeed, fish standing biomass is closely related to several ecological states and processes and has also often been used to manage coral reef fisheries[23,24]. However, fisheries yield also depends on the dynamics of biomass production (g m^{-2} d^{-1}), a flow-based rate measuring biomass accumulation in a place over time, and biomass turnover (P/B ratio), the rate at which biomass is produced and stored[25]. Both metrics can provide complementary information for improving the local management of resources as they inform on the stability of fisheries yields, but they have less often been calculated due to data deficiency[26–28]. Furthermore, the relationship between biomass and biomass production is generally nonlinear, which may lead to increased biomass turnover with increasing fishing pressure across some range of biomass[29]. Indeed, a given reef can exhibit high turnover with a low to intermediate biomass, suggesting that fishing activities could be sustainable and that partial protection (for example, restrictions on fishing gears or effort) could promote a compromise between exploitation and conservation[30,31]. Other reefs can host a very high fish biomass but with low biomass turnover. In this case, if these reefs are not already under some kind of protection, preserving the ecological states, processes and contributions associated with high fish biomass by placing a no-take or no-entry MPA may be appropriate when socially feasible or acceptable[24,32]. Using 1,979 tropical reef sites from a global database on fish community composition and size structure, we calculated fish biomass, biomass production and biomass turnover (Supplementary Fig. 1). We split reef sites into three different management classes: high standing biomass, high biomass turnover and low standing biomass/turnover (Fig. 1). More precisely, we split reef sites by lower (25%) and upper (75%) quartiles for low versus high biomass turnover, and by 25% and 95% percentiles for low versus high biomass, on a logarithmic scale for both metrics. We then used environmental and human variables to model and understand the roles of social and environmental contexts in determining which of these classes each site belonged to.

Results

Prediction of species growth rate
We used standardized and quantitative reef fish counts from the Reef Life Survey (RLS) database[33], among which we selected tropical and subtropical reefs (showing a minimum monthly sea surface temperature of 17 °C) spanning all tropical ocean basins (Supplementary Fig. 1). Following a previously published procedure, we used a broader definition of 'tropical' oceans, including locations between 17 °C and 20 °C where tropical species are present. Even though these included subtropical reefs, we hereafter refer to these reefs as tropical[34]. We used an existing framework and its associated rfishprod package to estimate fish growth trajectories (K_{max}) using fish individual body size and sea surface temperature (the two drivers of fish growth variation across reef fish species[35]) and mortality rates using fish individual size, maximum size and growth coefficients[36], for the 1,400 species in our database[25]. The predicted growth coefficients (K_{max}) for the 1,400 species based

on maximum length and temperature ranged from 0.02 to 8.71 (Supplementary Fig. 2), decreased according to the maximum observed body size and increased with temperature, as expected (Supplementary Fig. 3).

Reef fish biomass, biomass production and biomass turnover
We calculated fish standing biomass on the basis of our predicted growth trajectories, daily fish biomass production and biomass turnover (P/B ratio) for each transect, and we averaged these metrics across transects within each site, resulting in values for 1,979 sites spanning 39 countries. Across the 1,979 reef sites, fish standing biomass ranged from 1.36 g m^{-2} to 816 g m^{-2}, and fish biomass production ranged from 0.002 g m^{-2} d^{-1} to 2.74 g m^{-2} d^{-1}. Although biomass outliers (>99% of all values) were removed, sites with very high biomass still remained. These sites were mainly characterized by observations of important schools of large fish (for instance, a school of 120 *Naso hexacanthus* that were 40 cm long on one transect). Fish biomass turnover (the ratio between standing biomass and biomass production) ranged from 0.018% per day to 0.635% per day. Overall, standing biomass and biomass production exhibited a strong positive correlation ($r = 0.76$, $P < 0.001$). However, we observed only a weak, albeit significant, negative relationship between fish standing biomass and biomass turnover ($r = -0.15$, $P < 0.001$), confirming that these two latter metrics provide different and complementary information relevant to fisheries potential and management on tropical reefs (Supplementary Fig. 4).

Distribution of reef sites in management classes
Of the 1,979 sites, our thresholds resulted in 90 sites (4.5%) classified as low standing biomass/turnover, where both fish biomass and biomass turnover were below 25% of the observed values. We identified 91 high biomass sites, with fish biomass above 95% and turnover values below 75% of the observed values, and 495 high biomass turnover sites, where biomass turnover was above 75% of the observed values. Almost every class was present across all sampled geographical areas, with no area showing sites of only one class (Fig. 4 and Supplementary Fig. 5).

We calculated the mean relative percentage of each class as the average percentage of biomass in each of the six trophic-level bins (using trophic-level values from FishBase[37,38]) (Fig. 2). Low turnover/biomass sites were dominated by intermediate trophic levels (3/3.5), mainly benthic invertivores and planktivores, and had the lowest proportion of biomass at low trophic levels (2/2.5, mostly algal farming fish) and higher trophic levels (3.5–5). In contrast, high turnover sites had the highest relative biomass of primary consumers compared with sites in the other classes (2/2.5, mostly scraping and browsing herbivores). High turnover sites and high biomass sites both had higher proportions of biomass in the top trophic levels (predators) than sites in the low biomass/turnover class (Fig. 2).

For each site, we calculated the mean relative biomass and fish body size per diet category. Overall, mean carnivore and herbivore fish sizes were significantly higher in high biomass sites than in other sites ($P < 0.001$). The overall mean fish size regardless of diet was significantly lower in high turnover sites than in other sites ($P < 0.001$), and mean carnivore and herbivore fish sizes were also significantly lower in high turnover sites than in others ($P < 0.001$). The relative biomass of herbivores was significantly higher in high turnover sites than in other sites ($P < 0.05$, Fig. 2).

Environmental and socio-economic drivers
The mean accuracy of our random forest model (Methods) classifying reef sites into management classes using nine environmental and socio-economic variables was 73% over 100 iterations. Sea surface temperature, human gravity (a proxy of human impact calculated as the ratio between population estimates of a place and the squared travel time to the reefs[9]) and primary productivity had the strongest predictive capacity, with relative contributions (evaluated by permutation; Methods)
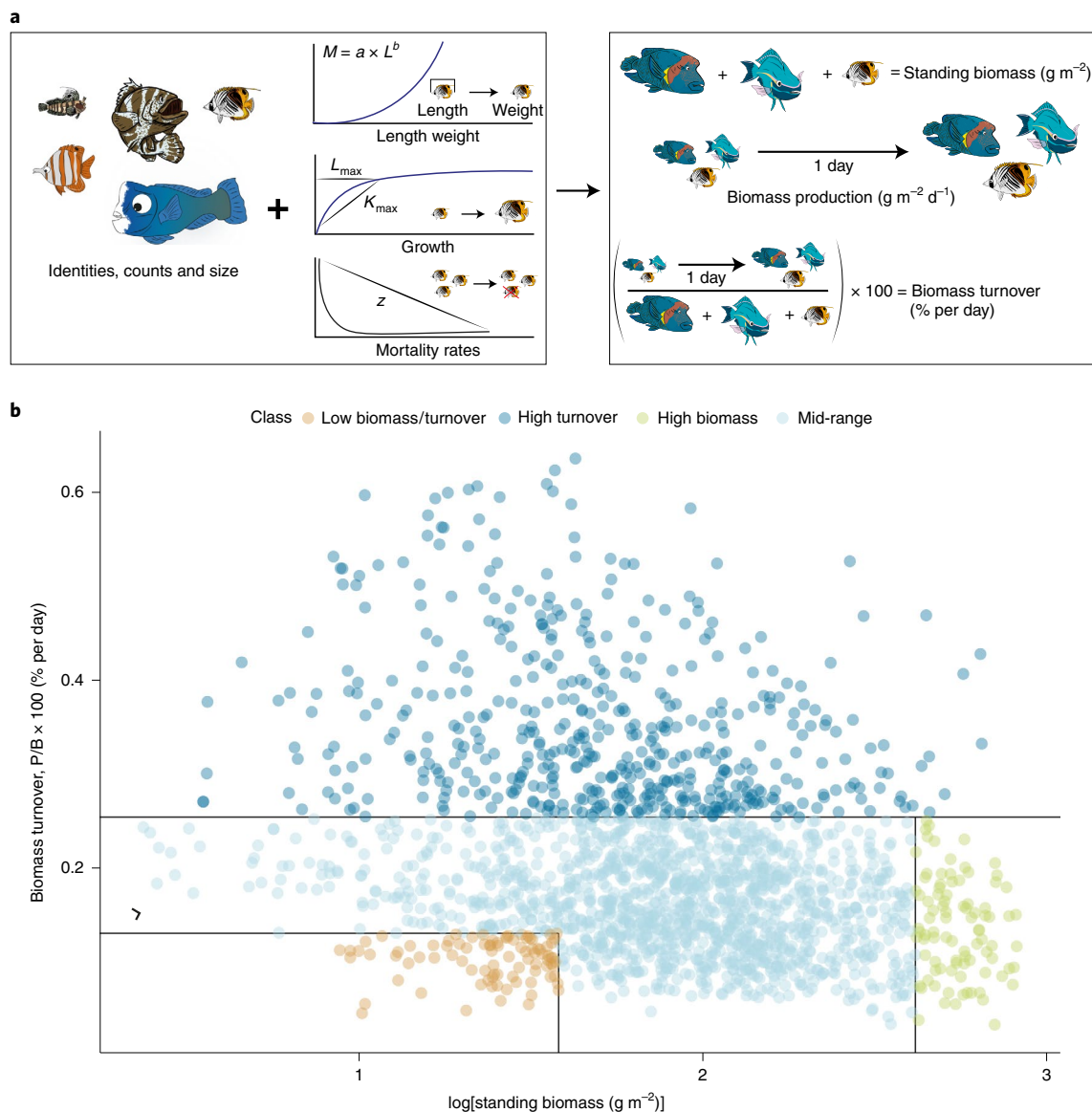
Fig. 1 | Standing biomass, biomass production and turnover calculations for tropical reef fishes. a, We used the rfishprod package to estimate growth trajectories and mortality rates for the 1,400 fish species in the RLS database, and then to estimate standing biomass (g m^{-2}), biomass production (g m^{-2} d^{-1}) and biomass turnover (the P/B ratio multiplied by 100, expressed as % per day) for the 1,979 sites spanning 39 countries (Supplementary Fig. 1)[25,33,35,68]. M is fish body mass in grams, L is fish body length in centimeters, a is the coefficient of the power function, b is the allometric coefficient and z is the species-specific mortality coefficient. **b**, According to fish standing biomass and biomass turnover, we classified the reef sites into three management classes and one 'base' class: high biomass (green), high turnover (dark blue), low biomass/turnover (orange) and mid-range sites (light blue, the base class). Tropical reefs in our case include those with a monthly sea surface temperature >17°C[34]. Panel **a** adapted with permission from ref.[25], Springer Nature Limited.

of 24.6%, 14.7% and 12.7%, respectively. Other parameters such as the human development index (a measure of socio-economic development that incorporates wealth, life expectancy and education[39]), degree heating weeks and the presence of non-governmental organizations (acting as potential levers towards the achievement of conservation targets) also influenced the classification, with relative contributions of 11.4%, 10.2% and 10%, respectively (Supplementary Table 1 and Supplementary Fig. 6). Surprisingly, dependency on marine ecosystems and MPA management had weak predictive capacity (with relative importance of 7.6% and 5.7%, respectively; Supplementary Figs. 6–8). We conducted a sensitivity analysis by modifying these thresholds by ±5% and ±15%. We also conducted a sensitivity analysis by removing transects that had individuals larger than 95% of all other individuals and transects that had schools with a number of individuals higher than 95% of all other schools, to account for potential high variability

between transects. While necessarily changing the number of sites in each management class, all these sensitivity analyses did not change model performance or variable importance in subsequent analyses (see below, Supplementary Figs. 9 and 10 and Supplementary Table 1).

Partial dependence plots, showing the marginal effect of each covariate on the predicted outcome (that is, its independent effect if all other variables were held static), revealed that sites with high fish biomass were characterized by low human gravity and intermediate to high primary productivity (Fig. 3). Even though high biomass sites were characterized by overall low human gravity, the levels of human gravity and dependency on marine resources were highly variable among management classes (Fig. 4). High turnover sites were characterized by high temperature, high human gravity and low primary productivity. Of note, the low primary productivity observed in the high turnover class may be linked to biases in the method used to estimate primary
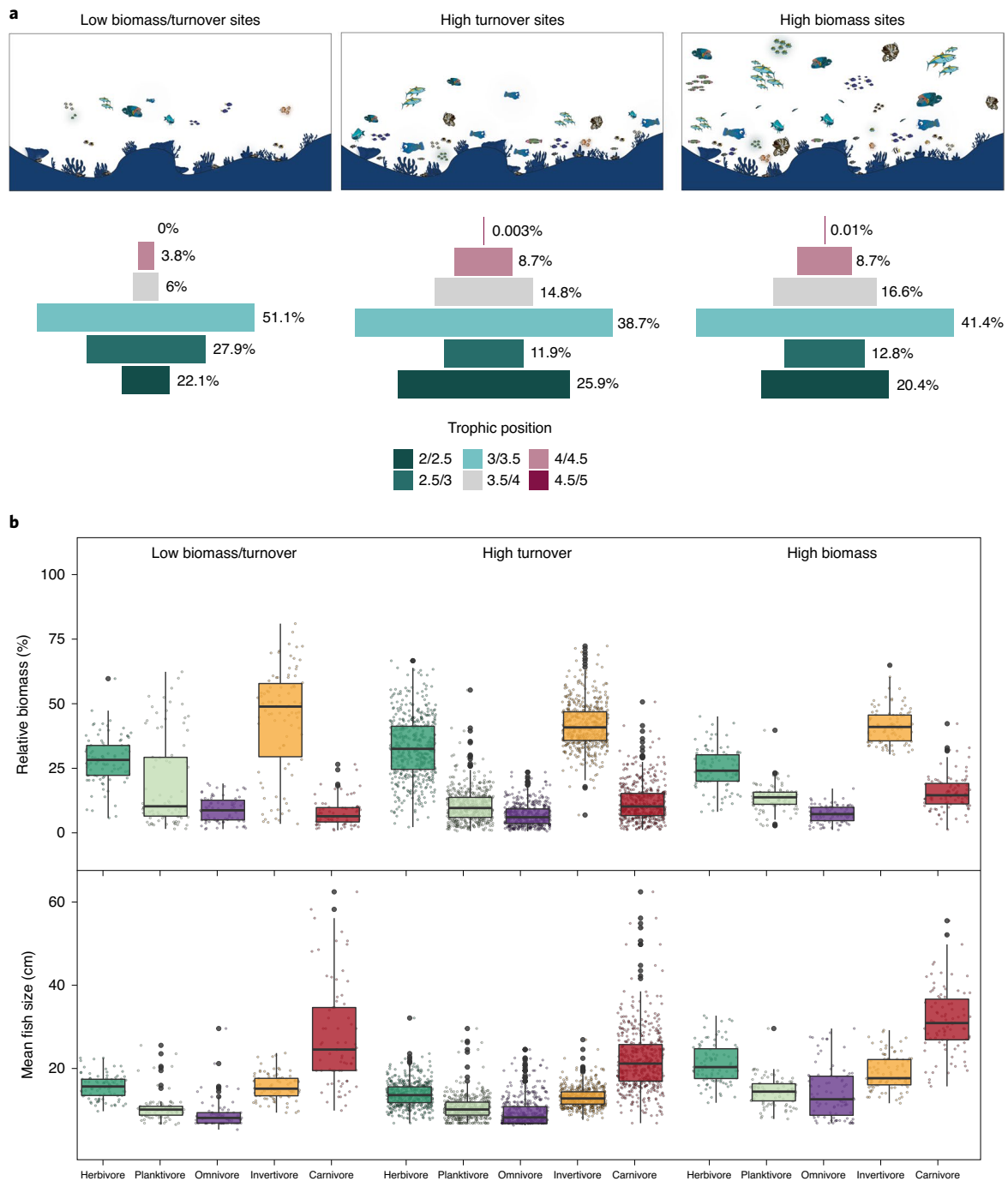
Fig. 2 | Trophic composition, relative biomass and mean size of fish communities for each management class. a, The trophic pyramids were calculated using the relative biomass of each trophic category following a previously published procedure[37]. **b**, The box plots represent site-level relative biomass and mean size per diet across management classes. Each dot represents one site, the black horizontal bars correspond to the median and the upper and lower hinges are the 25% and 75% quantiles. Upper whisker is the largest observation less than or equal to upper hinge + 1.5 * IQR (inter-quartile range), and lower whisker is the smallest observation greater than or equal to lower hinge - 1.5 * IQR. (n = 1,979).

production given that it does not account for spatial subsidies, which have been shown to drive biomass production[40]. In contrast, low biomass/turnover sites were characterized by high human gravity, high primary productivity and colder temperatures (Fig. 3).

Discussion

Process-based metrics such as biomass production provide important information on fisheries yields and biomass build-up and consequently need to be incorporated into decisions about where and how to manage

tropical reefs[5]. Several studies show the decoupling of biomass turnover, a dynamic ecosystem rate, from standing stock biomass, which presents new opportunities to improve and adapt conservation strategies[29,30,41]. We propose a conceptual framework accounting for both fish standing biomass and biomass turnover to guide the incorporation of ecological processes into the management of tropical reefs.

High biomass sites are characterized by more biomass in higher trophic levels, a higher relative biomass of upper trophic levels, and higher fish size of lower and upper trophic levels (Fig. 2), consistent
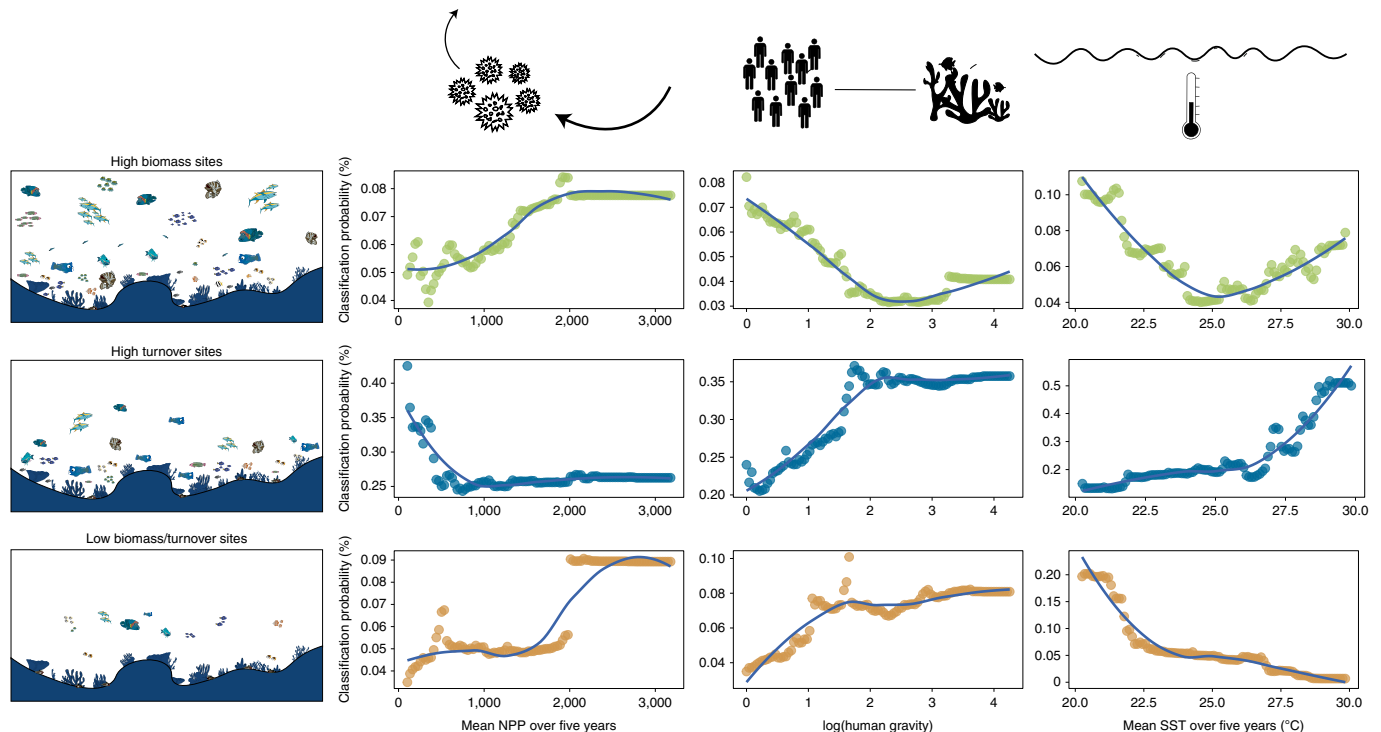
Fig. 3 | Relative contributions of sea surface temperature, human gravity and primary productivity to classification probability. Partial dependence plots showing the relative contributions of sea surface temperature (SST), human gravity and net primary productivity (NPP, expressed in mg C / m² / day) to the classification probability of each management class according to the random forest model using the partial function from the pdp package (v.0.7.0.9000). We excluded mid-range sites because they did not represent a management class but served as a base class. The blue lines were fitted using the locally estimated scatter-plot smoothing method of the geom_smooth function from the ggplot2 package (v.3.3.5), a non-parametric approach in which least squares regression is performed to fit a smooth curve through points in a scatter plot.

with the U-shaped trophic structure of vertebrate assemblages[42]. This U-shape ensures a high energy transfer efficiency (that is, a high proportion of production of lower trophic levels is converted into production at the upper trophic levels), a critical factor shaping marine ecosystem functioning but also sustainable fishing rates[43]. These sites are mainly located in areas with low human gravity, confirming their status as intact reefs with low anthropogenic pressures. We suggest that these remote sites with high fish biomass, if they are not already under some kind of protection, can be seen as the locations most suited to establishing no-entry or no-take marine reserves. Prioritizing conservation efforts towards areas with low economic and social costs is an increasingly used policy to rapidly and easily achieve conservation goals such as Aichi target 11, which aimed to protect "at least 17% of terrestrial and inland water areas and 10% of coastal and marine areas" by 2020, or Sustainable Development Goal 14, which aims to "conserve and sustainably use the oceans, seas and marine resources for sustainable development"[44]. These so-called 'residual' conservation efforts have come under criticism because they target locations where human impacts are already low and reducing resource extraction is assumed to make little difference in both ecological and socio-economic outcomes[44]. However, when considering multiple ecological goals simultaneously (fisheries, biodiversity and ecosystem functioning), marine reserves can provide substantial gains, including in areas with moderate to low human impact[21]. Furthermore, high fish biomass is shown to support key ecosystem functions (such as predation) and associated contributions to humanity, which justifies the urgent protection of these sites[23,24]. Although these high biomass reefs are in remote locations far from human uses, they can constitute important sources of larvae and juveniles that allow the replenishment of depleted stocks in other areas through dispersal corridors, if sufficiently connected[45]. Furthermore, the accumulation of large individuals of commercial species inside well-protected MPAs can benefit fisheries outside MPA boundaries through adult spillover, thereby contributing to food security and human livelihoods[14].

In contrast, low biomass/turnover sites not only have little biomass overall but also lack a solid base at the bottom of the food web, with a low biomass of primary consumers (herbivorous fishes, Fig. 2), suggesting that benthic primary productivity may be low or that fishing pressure may be extremely high. These sites also exhibit a high relative biomass of mid-trophic-level generalists, consistent with high fishing pressure which can induce the replacement of herbivorous fish by herbivorous sea urchins[37]. These sites are at risk of ecological collapse given their low biomass as well as their low rate of biomass renewal; they should therefore benefit from conservation efforts when possible. However, it remains unclear how these sites would react to protection given their low regenerative and reproduction potential. Previous studies show that heavily depleted sites may need 35 years on average to recover[23], and recovery could be impaired by low biomass turnover, meaning that protection efforts on these sites may only promote uncertain long-lasting benefits. However, further research is needed to understand the consequences of this low biomass/turnover state for local fisheries and how these sites can react to fishing restrictions to provide locally informed management decisions. Indeed, given that conservation operates on a tight budget[46], the strategic placement of MPAs must avoid conservation failures, which may lead to an erosion of trust, increasing risk of conflicts[15,46] and hindering future conservation endeavours[47]. However, this class exhibits high inter-site variability, with certain sites hosting higher fish size of carnivores, which may explain their low turnover (Fig. 2). This calls for detailed analyses of the trophic and size structures of these sites before considering appropriate management measures.
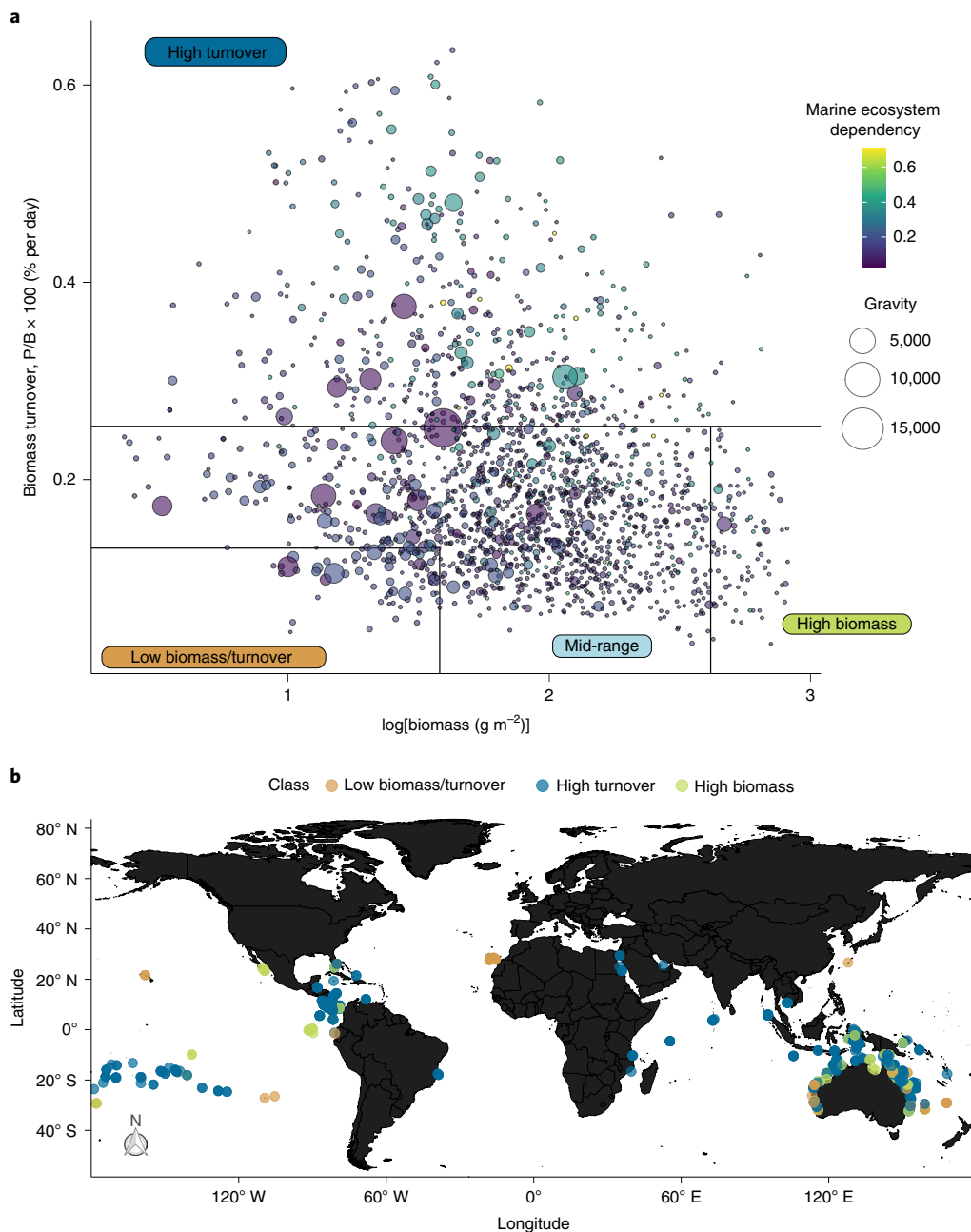
Fig. 4 | Standing biomass, turnover and management classification of tropical reef sites. a, Relationship between standing biomass and turnover for the 1,979 tropical reef sites. The dot sizes represent human gravity, and the colours represent the dependency on marine ecosystems[69]. **b**, World map showing the sites classified as high biomass (green), high biomass turnover (blue) or low biomass/turnover (orange).

The high biomass turnover sites are usually located in areas with high human pressure, concurring with previous findings that turnover is positively associated with exploitation rate[29] (Fig. 3). Indeed, this suggests that fishing pressure removes large species contributing to high biomass and therefore increases biomass turnover, boosted by small species. This widespread exploitation of reefs is altering species composition and ecosystem functioning towards novel ecosystems[48]. However, several studies report that fisheries catches have maintained or even increased in heavily fished sites[29]. These artisanal fisheries are mostly sustained by an increase in herbivorous fish biomass such as parrotfish (Scaridae) or rabbitfish (Siganidae), which show high growth rates and therefore contribute to high biomass production[29,49]. In accordance with these previous observations, this management class

was characterized by a higher relative biomass of herbivorous fishes than of the other management classes, as well as overall smaller fish size (Fig. 2). High biomass turnover has been identified as a compensatory ecological mechanism whereby fish populations characterized by high growth rates (such as herbivores) positively respond to size-selective fishing gears and biomass collapse through increased biomass turnover[29,41]. However, this compensatory mechanism may be only short term, as intensive degradation may eventually also lead to a decrease in herbivore biomass[49]. Indeed, we observe a lower mean fish size at lower and upper trophic levels than in other levels, suggesting that intensive degradation disrupted the U-shaped trophic structure of these high turnover sites (Fig. 2)[42]. Accounting for and monitoring reef fish biomass production and turnover appears key to understanding

the responses of tropical reefs to future degradation and choosing the most appropriate management strategy.

Given the highly variable socio-economic context of these high turnover sites (Fig. 4), our framework suggests locally informed spatial management, where protection intensity needs to consider local ecological and social contexts[18]. When human gravity and dependence on marine ecosystems are high, we suggest concerted and co-managed local restrictions on these sites (for example, relating to industrial activities or destructive fishing practices) through the establishment of partially protected MPAs, locally managed MPAs or other effective conservation measures that can still sustain local fisheries and other well-being outcomes[15,18]. Other effective conservation measures may be of particular relevance here given their importance for Indigenous and Community Conserved Areas and ecosystem-based management[50]. In most instances, partial protection would not achieve the same ecological outcomes as full protection that is complied with[19,51]. However, in many coral reef countries, compliance with fully protected MPAs is low[52], so better ecological outcomes can come from partial protection[53]. Additionally, socio-economic outcomes from partial protection (such as sustaining livelihoods and cultural connections) are mainly positive[19,54], and this type of management may enable traditional practices[55] and improve the food security of local communities[15]. We argue that these protection measures should be prioritized where dependency on reefs is high and when the total exclusion of extractive activities is not feasible or socially appropriate. In some instances, access restriction can be combined with no-take areas, whereby access restrictions can act as the incentive for establishing no-take areas when communities might not otherwise be willing to give up areas for conservation[54,55].

According to our thresholds, mid-range sites do not fit in any of the management classes and exhibit neither high biomass turnover nor high biomass. Here management should focus on avoiding the shift towards the ecological trap of low fish biomass and biomass turnover. A range of management strategies may help achieve this goal depending on local socio-economic, cultural and environmental contexts.

Overall, our framework and associated results remain conceptual and, given their global scale, do not necessarily represent any real-life implications or guides regarding specific sites that were studied. Our framework is intended as a heuristic means of considering both stable-state and dynamic measures of reef functioning to inform management. Our results may serve as a demonstration that both metrics are differently affected by environmental and socio-economic parameters, which in turn shape the state of reefs worldwide. Applications for management should be refined at a local scale, tailoring each strategy to local priorities, needs and contexts, while complementing this framework with other important measures of tropical reef state such as habitat complexity, size structure and number of endemic species[56,57]. Furthermore, we acknowledge that our defined classes are based on thresholds that are, to some extent, arbitrarily chosen. Yet, our sensitivity analysis shows that changing thresholds did not change model performance or variable importance. Finally, even though migratory fish made up only a small portion of the studied species, we ignored potential gains and losses in biomass production due to migratory fish. Planners will always be faced with hard choices[21], but clearer trade-offs and frameworks may assist them in achieving biodiversity conservation priorities while considering socio-economic constraints. The decoupling between fish biomass and biomass turnover and the contrasting information they provide allow for context-dependent local management and provide crucial information for MPA placement or restrictions and the ecological and socio-economic outcomes they aim to achieve.

Methods
RLS
The RLS database is a global dataset of underwater visual transects that has monitored the abundance and size distribution of temperate and tropical fish species globally. According to the RLS protocol available at https://www.reeflifesurvey.com, a survey consists of a 50 m transect line on which two methods are applied. Method 1 monitors fish composition, abundance and size classes observed in two five-metre-wide by five-metre-high bands. Method 2 monitors invertebrates and cryptic fishes in two one-metre-wide by two-metre-high bands on either side of the transect line. We restricted our analyses to warm-water reefs by selecting sites that experience minimum monthly sea surface temperatures of 17 °C[34]. Although the present study focused on the tropics, whose sea surface temperature limit is usually set at 20 °C, we decided to use a broader definition of tropical oceans, thereby including locations where species of tropical affinity are present. We removed sharks, rays, seahorses, cryptobenthic fish families and fishes smaller than 5 cm, given the unreliable estimates of small and cryptic assemblages via underwater visual censuses[58,59]. Finally, we removed biomass outliers by filtering out transects with biomass and biomass turnover values 99% higher than all other values. In this study, we worked at the site scale, averaging our metrics across all transects in a given site, which may lead in some cases to variance due to different sample sizes (Supplementary Table 2). However, averaging values between transects at the site level allows us to limit sampling bias at the transect scale. At this global scale, there is a temporal gap between all the studied sites that cannot be avoided. However, within each site, all transects were carried out the same day, so the averaged values are only spatial and not temporal.

Fish biomass production and biomass turnover
The sum of all individual growth trajectories determines the energy flux at the community level, leading to changes in biomass production. Estimating growth trajectories at the individual level is thus the first step to estimating biomass production and establishing predictions at ecosystem levels. We used the abundance, body size and temperature reported by the surveys to estimate standing biomass, growth trajectories and mortality using a previously published framework and its accompanying package, rfishprod (v.0.01)[25].

Briefly, we modelled growth trajectories using the two main drivers of reef fish growth, body size and temperature[35]. For this, we used the species-specific maximum length and the temperature at which the observations were made. We then obtained species-specific length–weight relationships using parameters obtained from FishBase[38]. From this information, we computed a species-specific growth coefficient, K_{max}, a standardized growth parameter under a von Bertalanffy growth model. This coefficient represents the von Bertalanffy growth coefficient (K) scaled to apply to a theoretical population where L_{inf}, the species-specific asymptotic maximum length, is equal to the species L_{max}, the maximum observed length, and has previously been used to estimate growth trajectories[4,25,29,41]. Biomass production, expressed as the accumulated biomass of an assemblage in a day, was obtained by subtracting the modelled weight gained by a fish after one day from the observed fish weight, calculated using the length–weight coefficients. Daily mortality rates were estimated stochastically by calculating the probability of a fish dying, taking into account individual growth trajectories, size and age, and removing fish that were expected to die, using previously published predictive models and the rfishprod package[25,36]. We estimated standing biomass and biomass production at the transect level by summing both metrics for each transect, and we calculated biomass turnover, the ratio between biomass production and standing biomass (P/B ratio)[25,26,60,61]. Site-level information was obtained by averaging all metrics across all transects of a given site.

Management classes
We divided the sites into three classes of standing biomass (<25%, 25–95% and >95%—low, medium and very high biomass) and biomass turnover (<25%, 25–75% and >75%—low, medium and high biomass turnover) to partition tropical reefs into three different management

classes: (1) high biomass sites, (2) high biomass turnover sites and (3) low biomass/turnover sites. Sites that fit in none of these three management classes were classified as mid-range sites. These thresholds were defined on the basis of quantiles of observed data, except for high biomass, where we used the 95% threshold to define sites with high biomass[21]. For each of these classes, we calculated the relative biomass of each trophic-level group, following a previously published procedure[37], and we calculated relative biomass and mean fish size per site and diet (herbivore, invertivore, omnivore, planktivore and carnivore)[42]. We statistically compared these metrics between management classes using the one-way analysis of variance test implemented with the aov function in R[62] (version 4.2.1), and we performed multiple pairwise comparison using Tukey multiple comparison of means with the TukeyHD function in R. We conducted a sensitivity analysis to test the influence of the choice of these thresholds on model performance and the influence of environmental and socio-economic covariates on the management classes by changing the thresholds determining the different classes to ±5% and ±15%. To account for high size variability between transects, we conducted a secondary sensitivity analysis by removing individuals whose size was higher than 95% of all other individuals and removing schools for which the number of fish was higher than in 95% of all other schools. The results show that the model performance and outcomes are robust to the choice of the thresholds (Supplementary Methods). We then modelled the effects of human and environmental variables on these classes on the RLS dataset.

Modelling management classes

We selected a set of four environmental and five socio-economic variables with the potential to explain the standing biomass and biomass turnover of fish communities. The environmental variables included net primary production, mean sea surface temperature, degree heating weeks and depth. The socio-economic variables included human gravity (a proxy of human impact considering human population size and accessibility to the reef[9]) and management, as well as dependency on marine ecosystems, the human development index and the number of non-governmental organizations at the country scale. Since human rights and environmental protection are interdependent, we also included violence and freedom of speech at the country scale[63]. The human development index and dependency on marine ecosystems inform on the socio-economic context, which is a key correlate to illegal fisheries, overexploitation and the establishment of protected areas[5,46,63–65]. Although a proxy of fisheries management agencies or cooperatives would have been more related to fisheries management, finding standardized data at this scale was challenging; we therefore chose the number of non-governmental organizations, which acts as a potential lever towards the achievement of conservation strategies[66]. To select only uncorrelated explanatory variables, we first computed the pairwise correlation between variables within each group of variables. For each pair of variables with a correlation higher than 0.7, we removed the variable involved in several high correlations and kept the other variable, until all pairwise correlations were less than 0.7. The uncorrelated selected variables were depth, primary productivity, human gravity, management, sea surface temperature, degree heating weeks, the human development index and the number of non-governmental organizations. All selected variables were log-scaled prior to analysis to reduce skew and improve model fit. A full description of the covariates, data sources and rationale can be found in the Supplementary Methods.

Modelling drivers of management classes

To understand the potential drivers of these management classes, we examined how key environmental and socio-economic drivers were related to the probability that a site was in any of the management classes. To model management classes according to our nine selected drivers, we used a random forest classification algorithm using the

ranger package (v.0.12.1)[67]. We tested our model performance using 100-fold cross-validation. The drivers' importance was estimated using permutation, which is calculated using the percent increase in the mean square error after randomly permuting a given predictor for every tree in the model, averaging the error of the models and then determining the difference relative to the accuracy of the original model. The model parameters were num.trees = 1,000 and mtry = 3.

Reporting summary

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

Data availability

The biomass production and turnover data that support the findings of this study are available on Figshare with the identifier https://doi.org/10.6084/m9.figshare.20368932.v1.

Code availability

All analyses were performed in R, and the relevant codes are available from the GitHub repository at https://github.com/LoiseauN/Predict_productivity.

References

1. McCauley, D. J. et al. Marine defaunation: animal loss in the global ocean. *Science* **347**, 1255641 (2015).
2. Hoegh-Guldberg, O., Poloczanska, E. S., Skirving, W. & Dove, S. Coral reef ecosystems under climate change and ocean acidification. *Front. Mar. Sci.* **4**, 158 (2017).
3. Ceballos, G., Ehrlich, P. R. & Raven, P. H. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc. Natl Acad. Sci. USA* **117**, 13596–13602 (2020).
4. Brandl, S. J. et al. Extreme environmental conditions reduce coral reef fish biodiversity and productivity. *Nat. Commun.* **11**, 3832 (2020).
5. Hughes, T. P. et al. Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
6. Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J. & Graham, N. A. J. Coral reef ecosystem services in the Anthropocene. *Funct. Ecol.* https://doi.org/10.1111/1365-2435.13331 (2019).
7. Pereira, P. H. C. et al. Effectiveness of management zones for recovering parrotfish species within the largest coastal marine protected area in Brazil. *Sci. Rep.* **12**, 12232 (2022).
8. Campbell, S. J. et al. Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. *Conserv. Lett* **13**, e12698 (2020).
9. Cinner, J. E. et al. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl Acad. Sci. USA* **115**, E6116–E6125 (2018).
10. Edgar, G. J. et al. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
11. Mumby, P. J., Steneck, R. S., Roff, G. & Paul, V. J. Marine reserves, fisheries ban, and 20 years of positive change in a coral reef ecosystem. *Conserv. Biol.* **35**, 1473–1483 (2021).
12. Harrison, H. B. et al. Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* **22**, 1023–1028 (2012).
13. Kerwath, S. E., Winker, H., Götz, A. & Attwood, C. G. Marine protected area improves yield without disadvantaging fishers. *Nat. Commun.* **4**, 2347 (2013).
14. Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A. & Claudet, J. Assessing spillover from marine protected areas and its drivers: a meta-analytical approach. *Fish Fish.* **21**, 906–915 (2020).

15. Ban, N. C. et al. Well-being outcomes of marine protected areas. *Nat. Sustain.* **2**, 524–532 (2019).

16. Cinner, J. E. et al. Winners and losers in marine conservation: fishers' displacement and livelihood benefits from marine reserves. *Soc. Nat. Resour.* **27**, 994–1005 (2014).

17. Gurney, G. G. et al. Biodiversity needs every tool in the box: use OECMs. *Nature* **595**, 646–649 (2021).

18. Smallhorn-West, P. F. et al. Hidden benefits and risks of partial protection for coral reef fisheries. *Ecol. Soc.* **27**, art26 (2022).

19. Turnbull, J. W., Johnston, E. L. & Clark, G. F. Evaluating the social and ecological effectiveness of partially protected marine areas. *Conserv. Biol.* **35**, 921–932 (2021).

20. Sala, E. et al. Protecting the global ocean for biodiversity, food and climate. *Nature* **592**, 397–402 (2021).

21. Cinner, J. E. et al. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**, 307–311 (2020).

22. McShane, T. O. et al. Hard choices: making trade-offs between biodiversity conservation and human well-being. *Biol. Conserv.* **144**, 966–972 (2011).

23. MacNeil, M. A. et al. Recovery potential of the world's coral reef fishes. *Nature* **520**, 341–344 (2015).

24. McClanahan, T. R. et al. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc. Natl Acad. Sci. USA* **108**, 17230–17233 (2011).

25. Morais, R. A. & Bellwood, D. R. Principles for estimating fish productivity on coral reefs. *Coral Reefs* **39**, 1221–1231 (2020).

26. Lindeman, R. L. The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–417 (1942).

27. Pauly, D. & Froese, R. MSY needs no epitaph—but it was abused. *ICES J. Mar. Sci.* **78**, 2204–2210 (2021).

28. Rindorf, A. et al. Strength and consistency of density dependence in marine fish productivity. *Fish Fish.* **23**, 812–828 (2022).

29. Morais, R. A., Connolly, S. R. & Bellwood, D. R. Human exploitation shapes productivity–biomass relationships on coral reefs. *Glob. Change Biol.* **26**, 1295–1305 (2020).

30. Kolding, J., Bundy, A., van Zwieten, P. A. M. & Plank, M. J. Fisheries, the inverted food pyramid. *ICES J. Mar. Sci.* **73**, 1697–1713 (2016).

31. Morais, R. A. et al. Severe coral loss shifts energetic dynamics on a coral reef. *Funct. Ecol.* **34**, 1507–1518 (2020).

32. Sala, E. & Giakoumi, S. No-take marine reserves are the most effective protected areas in the ocean. *ICES J. Mar. Sci.* **75**, 1166–1168 (2018).

33. Edgar, G. J. & Stuart-Smith, R. D. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci. Data* **1**, 140007 (2014).

34. Parravicini, V. et al. Global patterns and predictors of tropical reef fish species richness. *Ecography* **36**, 1254–1262 (2013).

35. Morais, R. A. & Bellwood, D. R. Global drivers of reef fish growth. *Fish Fish.* **19**, 874–889 (2018).

36. Gislason, H., Daan, N., Rice, J. C. & Pope, J. G. Size, growth, temperature and the natural mortality of marine fish: natural mortality and size. *Fish Fish.* **11**, 149–158 (2010).

37. Graham, N. A. J. et al. Human disruption of coral reef trophic structure. *Curr. Biol.* **27**, 231–236 (2017).

38. Froese, R. & Pauly, D. (eds.). FishBase. Version 06/2022. https://www.fishbase.org (2022).

39. Cochrane, K. L. Reconciling sustainability, economic efficiency and equity in marine fisheries: has there been progress in the last 20 years? *Fish Fish.* **22**, 298–323 (2021).

40. Morais, R. A., Siqueira, A. C., Smallhorn-West, P. F. & Bellwood, D. R. Spatial subsidies drive sweet spots of tropical marine biomass production. *PLoS Biol.* **19**, e3001435 (2021).

41. Hamilton, M. et al. Climate impacts alter fisheries productivity and turnover on coral reefs. *Coral Reefs* https://doi.org/10.1007/s00338-022-02265-4 (2022).

42. Cooke, R. et al. Anthropogenic disruptions to longstanding patterns of trophic-size structure in vertebrates. *Nat Ecol Evol.* **6**, 684–692 (2022).

43. Eddy, T. D. et al. Energy flow through marine ecosystems: confronting transfer efficiency. *Trends Ecol. Evol.* **36**, 76–86 (2021).

44. Devillers, R. et al. Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? *Aquat. Conserv. Mar. Freshw. Ecosyst.* **25**, 480–504 (2015).

45. Fontoura, L. et al. Protecting connectivity promotes successful biodiversity and fisheries conservation. *Science* **375**, 336–340 (2022).

46. Gill, D. A. et al. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543**, 665–669 (2017).

47. Agardy, T., di Sciara, G. N. & Christie, P. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar. Policy* **35**, 226–232 (2011).

48. Robinson, J. P. W. et al. Habitat and fishing control grazing potential on coral reefs. *Funct. Ecol.* **34**, 240–251 (2020).

49. Robinson, J. P. W. et al. Productive instability of coral reef fisheries after climate-driven regime shifts. *Nat. Ecol. Evol.* **3**, 183–190 (2019).

50. Dudley, N. et al. The essential role of other effective area-based conservation measures in achieving big bold conservation targets. *Glob. Ecol. Conserv.* **15**, e00424 (2018).

51. Zupan, M. et al. How good is your marine protected area at curbing threats? *Biol. Conserv.* **221**, 237–245 (2018).

52. Pollnac, R. et al. Marine reserves as linked social–ecological systems. *Proc. Natl Acad. Sci. USA* **107**, 18262–18265 (2010).

53. McClanahan, T. R., Marnane, M. J., Cinner, J. E. & Kiene, W. E. A comparison of marine protected areas and alternative approaches to coral-reef management. *Curr. Biol.* **16**, 1408–1413 (2006).

54. Smallhorn-West, P. F., Weeks, R., Gurney, G. & Pressey, R. L. Ecological and socioeconomic impacts of marine protected areas in the South Pacific: assessing the evidence base. *Biodivers. Conserv.* **29**, 349–380 (2020).

55. Cinner, J. E. et al. Sixteen years of social and ecological dynamics reveal challenges and opportunities for adaptive management in sustaining the commons. *Proc. Natl Acad. Sci. USA* **116**, 26474–26483 (2019).

56. Wilson, S. K. et al. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* **20**, 442–451 (2010).

57. Nash, K. L. & Graham, N. A. J. Ecological indicators for coral reef fisheries management. *Fish Fish.* **17**, 1029–1054 (2016).

58. Brandl, S. J., Goatley, C. H. R., Bellwood, D. R. & Tornabene, L. The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol. Rev.* **93**, 1846–1873 (2018).

59. Willis, T. J. Visual census methods underestimate density and diversity of cryptic reef fishes. *J. Fish. Biol.* **59**, 1408–1411 (2001).

60. Allen, K. R. Relation between production and biomass. *J. Fish. Res. Board Can.* **28**, 1573–1581 (1971).

61. Leigh, E. G. On the relation between the productivity, biomass, diversity, and stability of a community. *Proc. Natl Acad. Sci. USA* **53**, 777–783 (1965).

62. R Core Team. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, 2020).

63. Cinner, J. E., Daw, T. & McClanahan, T. R. Socioeconomic factors that affect artisanal fishers' readiness to exit a declining fishery. *Conserv. Biol.* **23**, 124–130 (2009).

64. Cinner, J. E. et al. Linking social and ecological systems to sustain coral reef fisheries. *Curr. Biol.* **19**, 206–212 (2009).

65. Hicks, C. C., Crowder, L. B., Graham, N. A., Kittinger, J. N. & Cornu, E. L. Social drivers forewarn of marine regime shifts. *Front. Ecol. Environ.* **14**, 252–260 (2016).

66. Espinosa-Romero, M. J., Rodriguez, L. F. F., Weaver, A. H., Villanueva-Aznar, C. & Torre, J. The changing role of NGOs in Mexican small-scale fisheries: from environmental conservation to multi-scale governance. *Mar. Policy* **50**, 290–299 (2014).

67. Cutler, D. R. et al. Random forests for classification in ecology. *Ecology* **88**, 2783–2792 (2007).

68. Edgar, G. J. et al. Establishing the ecological basis for conservation of shallow marine life using Reef Life Survey. *Biol. Conserv.* **252**, 108855 (2020).

69. Selig, E. R. et al. Mapping global human dependence on marine ecosystems. *Conserv. Lett.* **12**, e12617 (2019).

Acknowledgements

Author contributions

R.S. and N.L. conceived the study with support from D.M., J.E.C., N.A.J.G., R.S.S., E.M., M.M. and L.V. All authors contributed to data collection and/or compilation and made substantive contributions to the text.

Competing interests

The authors declare no competing interests.

Additional information

nature portfolio

Corresponding author(s): Raphael Seguin

Last updated by author(s): Sep 1, 2022

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	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	Open Reef life survey dataset
Data analysis	R statistical language version 4.2.1

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 and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The biomass production and turnover data that support the findings of this study are available in figshare with the identifier 10.6084/m9.figshare.20368932.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data where this information has been collected, and consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*
Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

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

Study description	1979 tropical reef sites over 31 countries
Research sample	We used the Reef life Survey Dataset, an international open source dataset of underwater visual transects on coral reefs.
Sampling strategy	Underwater visual surveys over 50m transect lines and 10 meters width
Data collection	Diver team from Reef Life Survey
Timing and spatial scale	Surveys started in 2008 and span out across 31 countries in our dataset of tropical and subtropical reefs.
Data exclusions	We excluded data from where minimal temperatures over the past 5 years were under 17 degress to focus on tropical and subtropical reefs.
Reproducibility	We conducted sensitivity analyses on the thresholds used to define the management categories and the samples
Randomization	We aggregated surveys at the site level by averaging metrics across surveys. We then defined thresholds at quantiles of data to define management categories, except for upper biomass where the threshold was set at 95% to account for the degraded state of reefs worldwide. Model performances was estimated using cross-validation by randomly creating a training and testing dataset.
Blinding	We used an already existing dataset of underwater visual surveys, locations are chose by the divers from this dataset.

Did the study involve field work?   ☐ Yes   ☒ No

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
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology and archaeology
☒	Animals and other organisms
☒	Clinical data
☒	Dual use research of concern

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging