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Marine protected areas marginally offset anthropogenic declines in tropical reef fish contributions to nature and people

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Abstract

Human activities are rapidly eroding the biodiversity of most ecosystems, threatening the myriad contributions they provide to nature and people. Protected areas are often seen as key management tools for their conservation. However, the lack of historical baselines hinders our ability to fully assess these declines and the extent to which protected areas can compensate for decades of human-mediated degradation. Using a Bayesian framework, we modeled 22 fish community contributions across 2,800 tropical reefs, and predicted their levels under counterfactual scenarios, to compare the relative benefits of Marine Protected Areas (MPAs) and anthropogenic impacts on unprotected reefs. We show that human activities have significantly reduced fish biodiversity- and biomass-related contributions, with, for example, a 120% decline in piscivore biomass, corresponding to a net loss of 19 kg per hectare of reef. In contrast, the benefits of MPAs appear comparatively low, with conservation efforts potentially offsetting only 5% of this decline. Ultimately, only old and fully protected areas provide marked benefits to nature and people. This suggests that even if we drastically increase our protection efforts across the ocean (30% coverage by 2030), we cannot expect short-term socio-ecological benefits to counterbalance a long history of human footprint. A desirable future for nature and people thus requires a paradigm shift in our relationship with ecosystems and their biodiversity, beyond MPA establishment.

Introduction

In 1962, Rachel Carson warned in her book *Silent Spring*[1] about the serious threats that intensive agricultural practices posed to terrestrial ecosystems. Sixty years later, land-use changes have led to a 75% decline in insect biomass[2] and a loss of at least 25% in the abundance of common European birds[3]. In parallel, most marine ecosystems have been overexploited by fisheries, leading to the collapse of some commercial fish stocks across all oceans[4,5].

It is now clear that changes in terrestrial biodiversity are primarily driven by habitat transformation and direct exploitation, while direct exploitation, climate change, and pollution are the main drivers of changes in marine biodiversity[6,7]. In this context, changing our relationship with nature through sustainable practices is the key strategy for mitigating short-term ecological impacts. Towards this objective, governments implemented extraction management plans before expanding conservation efforts through Protected Areas (PAs) over the past 50 years[8,9]. Today, they aim to protect 30% of Earth’s land and sea by 2030 to safeguard ecosystem integrity[10]. Although controversial[11,12], PAs are prevalent legal management tools for controlling direct anthropogenic pressures[13]. However, the extent to which these conservation efforts have restored ecosystems in their pre-industrialisation state or offset anthropogenic declines is virtually unknown[14,15].

This question is even more critical as humanity and nature depend on a multitude of contributions (*e.g.*, food resources, climate regulation) provided by living organisms[16]. Here, we use the term "contribution" as a more inclusive and plural concept than ecosystem services, encompassing biodiversity benefits both to people well-being[17] and to the functioning of ecosystems[18]. These contributions can be considered within the Nature Futures Framework (NFF) through three complementary perspectives: Nature-for-Nature (centered on nature's intrinsic value), Nature-for-Society (focused on societal benefits), and Nature-as-Culture (linked to cultural values)[18,19]. Considering these perspectives together, the NFF promotes the development of sustainability pathways that envision desirable futures for both nature and people. Yet, while the effects of PAs on biodiversity have been widely studied[20,21], their benefits for each of these NFF perspectives remain underexplored at a large scale[22,23].

Recent studies have explored the benefits of PAs on some key nature's contributions, such as biomass[24,25], aesthetic value[26], or cultural attachment[27]. However, trends in nature's contributions remain difficult to assess due to the scarcity of historical quantitative data, preventing us from having reliable baselines against which to measure conservation gains inside PAs or losses outside them[28,29]. Consequently, the extent to which PAs have mitigated centuries of human footprint on ecosystems is virtually unknown, particularly when considering multiple contributions to nature and people that involve synergies and trade-offs[30,31]. A comprehensive assessment of nature's contributions, within an integrated framework that considers socio-environmental contexts, is essential to better understand the impact of human activities[32], navigate between the multiple values of nature, and explore different pathways towards sustainability[33].

While Before-After-Control-Impact (BACI) studies, based on long-term in situ monitoring, are considered the gold standard for evaluating PA effects[34], they remain local and cannot provide global and historical assessments. In this context, large-scale models using multiple socio-environmental drivers of nature's contributions offer a valuable alternative for evaluating conservation outcomes and human footprints on ecosystems[24,35]. Species Distribution Models (SDMs), traditionally used to predict species' occurrences or abundances based on environmental and socio-economic factors[36,37], can be extended to model ecosystem-level metrics like biodiversity[38]. This approach bypasses the need to reconstruct species communities, reducing biological complexity[39,40], and holds promise for modeling nature's contributions. Yet, modeling interrelated contributions independently with univariate models risks producing unrealistic associations. Joint distribution models (jSDMs) can address this issue by simultaneously modeling several contributions in response to environmental and socioeconomic factors, while accounting for covariations among these contributions[32,41]. Moreover, these models can be used to examine counterfactual scenarios, exploring the effects of 'alternative pasts'[35]. For example, counterfactual scenarios can investigate how ecosystems would appear if no conservation efforts had been implemented[24,35], or if anthropogenic pressures had remained minimal - similar to the conditions observed in 'pseudo-pristine' ecosystems like remote islands[42,43]. The differences between the contributions estimated under current conditions of protection and the simulated scenario without protection can be used to quantify the conservation legacy of PA establishment[35]. Likewise, comparing current anthropized conditions with 'pseudo-pristine' scenarios can help estimate the human footprint on contributions. This framework enables identifying the most impacted contributions, quantifying their decline, and assessing the extent to which conservation efforts have offset anthropogenic declines.

This knowledge gap is particularly critical for tropical reefs. Although they cover only a small fraction of the world's marine surface, these ecosystems provide vital and diverse contributions to millions of people[44], primarily through their fish communities that support livelihoods and nutrient supplies via fisheries, but also cultural heritage and aesthetic value[31,45–48]. However, these ecosystems rapidly degrade due to overfishing, pollution and climate change[48–50], making their preservation a global priority. Understanding the effects of Marine Protected Areas (MPAs) relative to human footprint on fish community contributions to both nature and people is essential to provide strategic guidance for conservation efforts, while promoting a more balanced and sustainable future for tropical and coastal socio-ecological systems.

Here, we leveraged standardized underwater surveys across 2,803 sampled reefs, encompassing 1,695 fish species from tropical and subtropical regions, to estimate 22 different contributions provided by fish communities to nature and people (Table 1). Using a hierarchical Bayesian linear model, we jointly analyzed their relationships with 38 socio-environmental covariates (Table 2), and quantified the relative effects of MPAs and human footprint on these contributions by exploring counterfactual scenarios.

Results

Drivers of fish contributions across tropical reefs

By considering sampled reef identity nested within countries as random effects, our model showed strong explanatory power (Fig. 1), with an average R-squared of 0.67 (± 0.2 s.d.) among all contributions, ranging from 0.32 for calcium content to almost 1 for available fish biomass (Fig. S1). A five-fold cross-validation confirmed reliable predictive performance of the model, with an average R-squared of 0.34 (± 0.2 s.d.), ranging from 0.15 for fish calcium content to 0.89 for endemic fish richness.

Random effects accounted for on average 69% of the total explained variance (Fig. 1) - a portion commonly observed in such large-scale distribution models[51,52] - shared between the country effect (32%) and the sampled reef identity effect (37%). The latter, which mostly influenced fish biomass-related contributions, reflects the unmeasured socio-economic (e.g., fishing gears), habitat (e.g., 3-

dimensional complexity) or environmental (e.g., oxygen content) characteristics, including spatial and temporal effects, as well as residual associations among contributions arising from inherent synergies or trade-offs[31,41,53]. By contrast, fish community contributions such as functional and evolutionary distinctiveness, endemism, and omega-3 content were rather predominantly influenced by the country-level random effect (Fig. 1), reflecting broad geographical patterns shaped by geological history, latitudinal gradients, but also unmeasured covariates such as culture, governance, trades, or infrastructures.

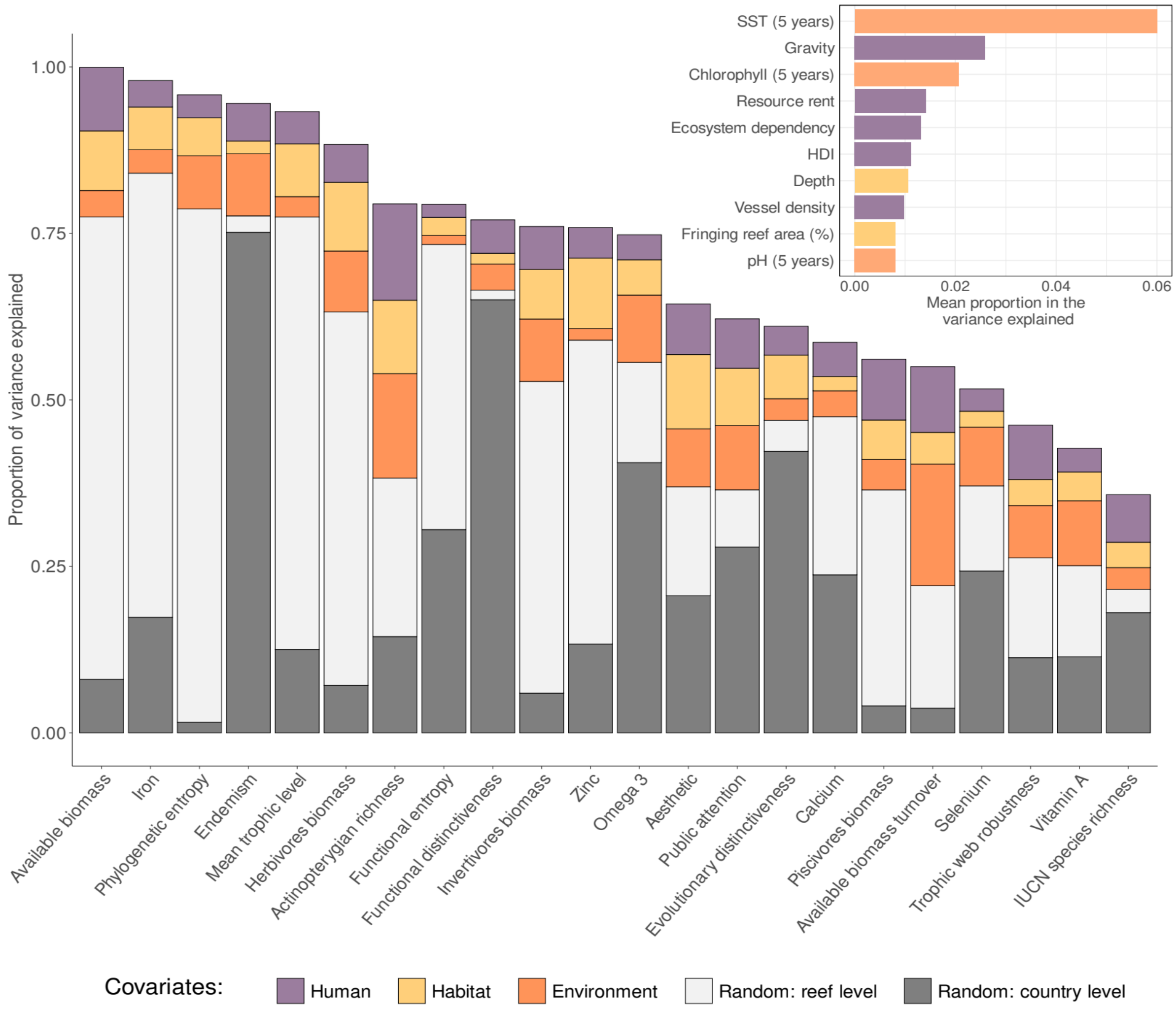

Figure 1 : Importance of human, habitat, and environmental fixed effects along with random effects in explaining 22 forms of fish contributions to nature and people on tropical reefs. *The total height of each bar corresponds to the proportion of the variance explained by the full model (R² for each contribution; see Table S3 for model 1 structure). The importance of each covariate category in the explained variance is represented by the height of the stacked bars. The importance of the random effects is reported in gray tones. The insert in the top right corner displays the average importance of the top-10 fixed effects in the model. The average importance of all fixed effects is shown in figure S2.*

Details on the importance of all covariates within each category for the contributions are shown in figure S3.

Using the Bayesian model, we also quantified the relative importance of fixed effects in explaining observed contributions. Globally, the 38 covariates accounted in total for 31% on average of the explained variance, with environmental covariates (representing physico-chemical conditions) accounting for 12%, human-related covariates (proxies of anthropogenic pressures) for 10%, and habitat covariates (local and surrounding benthic composition, and geomorphic features) for 9% (Fig. 1 and Fig. S2). The most influential environmental covariates were sea surface temperature (SST) and chlorophyll (a proxy for primary production), which strongly affected fish community contributions, notably actinopterygian species richness, biomass turnover, and public attention. Among habitat covariates, depth and fringing reef area predominantly influenced most contributions as they represent habitat availability for fish communities (Fig. 1 and Fig. S3).

Anthropogenic effects on fish contributions

Among the 10% of variance in fish contributions explained by anthropogenic covariates, human gravity - a proxy of local exploitation, pollution and habitat disturbance (see methods)[54] - emerged as the most influential (2.5%; insert Fig. 1). Higher human gravity induced a decrease in piscivore and herbivore biomass, available biomass, food web robustness and threatened (IUCN Red-listed) species richness (Fig. 2). Conversely, gravity increased biomass turnover, calcium content, community aesthetics and evolutionary distinctiveness. These positive associations were mainly influenced by some regions such as Canary islands, where dense human populations coincide with unique evolutionary histories and low biomass that is rapidly renewed under exploitation by fisheries, or highly populated Indonesian reefs that host particularly attractive fish communities on coral reefs[26].

By classifying reef protection status as fully protected (no-take MPAs with medium to high compliance[55]), restricted (other protection statuses) or unprotected (no MPA recorded), we assessed the influence of conservation legacy in shaping fish contributions. On average, protection status accounted for only 0.5% of the explained variance in fish contributions, with significant positive correlations between full protection and community aesthetics, public attention, actinopterygian species richness, the presence of IUCN-threatened species, as well as invertivore and herbivore biomass (Fig. 2). Restricted MPAs showed comparable relationships with contributions but the posterior distribution of estimates displayed wider ranges and weaker statistical support, probably due to the heterogeneity of restrictions and effectiveness conditions (Fig. S4)[56]. On the other hand, the density of vessels (over 10 m long; see Methods) was significantly and negatively correlated with actinopterygian species richness, aesthetic value, public attention and biomass turnover in fish communities, while positively associated with vitamin A and omega-3 content, trophic web robustness and invertivore biomass[57]. Monitoring vessel traffic near tropical reefs - using modern tools such as satellite imagery combined with artificial intelligence to detect untracked vessels[58] - offers a valuable proxy for potential reef disturbances linked to commercial shipping, tourism, or fisheries. However, at present, these activities cannot be distinguished, and their respective effects remain intertwined. As a result, estimated effect sizes likely reflect both the impacts of human activities on fish communities (e.g., artisanal and recreational fishing) and the attraction of biodiverse reefs for leisure activities such as diving, which can blur the association between vessel density and fish biomass. Moreover, part of small-scale and recreational fisheries (vessels <10m) remains untracked while having major impacts on tropical reefs[59]. As a complementary covariate, human gravity can partially account for these hidden pressures, since these small fishing vessels have limited range and are closely linked to the surrounding human populations[60].

Local economic growth, represented by the downscaled Gross Domestic Product (GDP)[61], was negatively correlated with almost all contributions, except calcium content. It mainly impacted IUCN-threatened species richness, trophic web robustness, invertivore biomass, and piscivore biomass (Fig. 2). This is in line with previous studies showing that economic growth contributes significantly to ecosystem degradation and biodiversity loss[62].

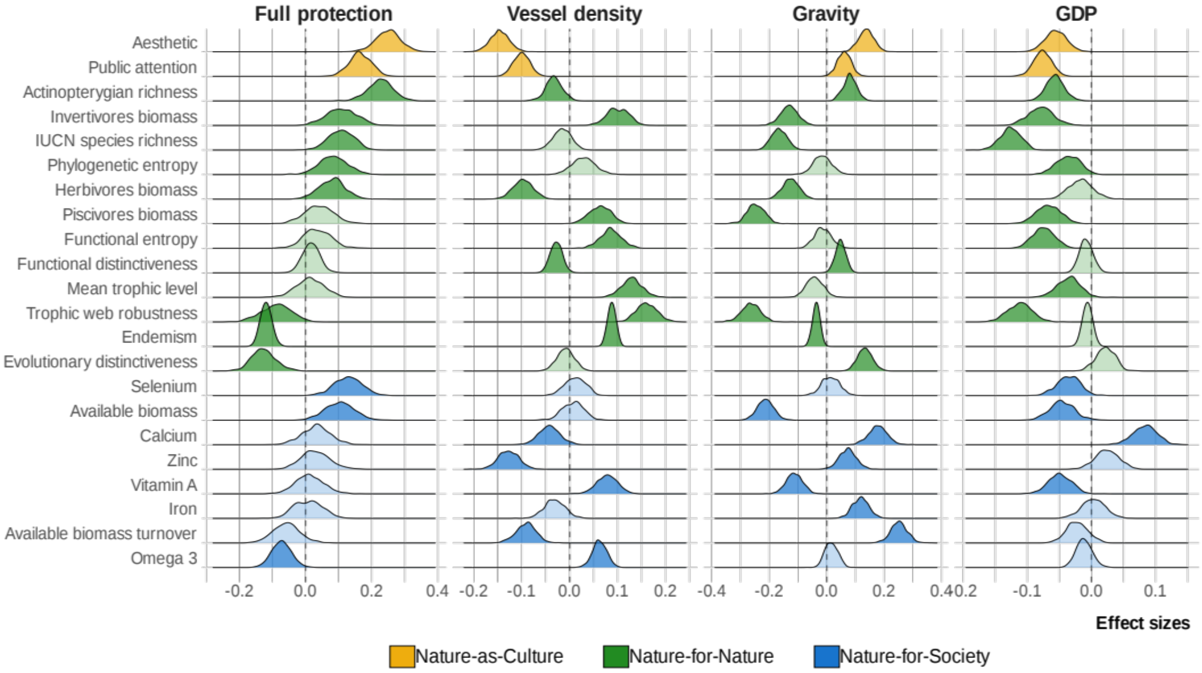

Figure 2 : Effect sizes of four anthropogenic covariates on 22 fish community contributions modelled across tropical reefs. *Density plots show the posterior distributions of the estimated effect*

sizes across the sampled iterations of the Markov chains. "Full protection" corresponds to no-take MPAs with medium to high compliance to restrictions. "Vessel density" is the number of vessels (over 10m long) within a 10 km radius of the reef, detected by satellite imagery. "Gravity" is a proxy of human pressure, accounting for population size and travel time to the reef. "GDP" is the Gross Domestic Product, defined at the local scale; it represents a proxy of the regional economic activity surrounding the sampled reef. The contributions provided by fish communities are colored according to their relevance to one of the three perspectives of the Nature-Futures-Framework, either Nature-for-Nature (centered on nature's intrinsic value), Nature-for-Society (focused on societal benefits), or Nature-as-Culture (linked to cultural values). Effect sizes with a support level greater than 0.95 are displayed in darker colors. While a high support level indicates strong statistical confidence in the covariate effect, it does not reflect its relative importance in explaining community-level contributions, where human-related covariates generally explain little variance (see Fig. 1 and Fig. S2). To see the effect size of each covariate on all contributions, see figure S5.

Human footprint versus conservation legacy

To estimate human footprint on fish community contributions, we used the same trained model (model 1, Table S3) to generate counterfactual predictions under various scenarios. We compared the current state of the 22 contributions on unprotected reefs to a 'pseudo-pristine' state that might have existed without human impacts. This counterfactual scenario was modeled by placing current unprotected reefs under virtual conditions of minimal anthropogenic pressure (pseudo-pristine conditions), characterized by the lowest levels of gravity and vessel density observed in our global dataset, the maximum travel time to the nearest human population, and full protection (Fig. 3-A). By comparing the current values of the 22 contributions and those provided by the counterfactual pseudo-pristine scenario, we found that human footprint generally reduced the value of most reef fish contributions to nature and people, despite heterogeneity among contributions and reefs (Fig. S6). Although human-related covariates explained a relatively small portion of the variance compared to random effects or environmental covariates in our model (Fig. 1), their modification under the counterfactual scenario led to substantial changes in key contributions. The largest declines were found in piscivore biomass (-120% as a median across reefs), herbivore biomass (-47%) and available biomass for fisheries (-38%). Biodiversity contributions were also impacted by humans, with a median footprint of -30% for IUCN-threatened species richness and -3.2% for overall actinopterygian species richness. Cultural values, such as aesthetics (-2.5%) and public attention (-0.8%), also slightly declined with human footprint. Conversely, human footprint enhanced fish biomass turnover (+10%; Fig. 3-B), as fisheries target larger fish, thus sparing smaller and more productive individuals[63].

To assess the conservation legacy of MPAs, we predicted the level of fish community contributions on currently fully protected reefs under a hypothetical unprotected scenario. In this counterfactual, we removed protection and adjusted vessel density to the same level as unprotected reefs in the corresponding country, while keeping all other covariates unchanged (Fig. 3-A). We found that conservation legacy was associated with increases in most reef contributions, with notable gains in IUCN-threatened species richness (+15% as a median across reefs), piscivore biomass (+6.3%), and actinopterygian species richness (+6.6%). A negative effect of -3.7% was observed for fish endemism (Fig. 3-B and Fig. S7), probably due to fewer conservation efforts on islands that generally host more endemic species[64].

To determine the restoration potential of MPAs, we compared the magnitude of the effects between the two counterfactual scenarios. Our results indicated that conservation legacy could only marginally offset human footprint on biomass-related contributions. For example, MPAs counterbalanced human footprint by only 29% and 5%, for available biomass and piscivore biomass (Fig. 3-B), respectively, highlighting the limited capacity of MPAs to offset anthropogenic declines for these two major nature's contributions on tropical reefs. While MPAs had a significant positive effect on IUCN-threatened species richness, they can only offset up to 51% of losses resulting from historical human footprint. In contrast, some contributions – such as selenium content, phylogenetic entropy – could be almost entirely compensated for by MPAs, with a restoration potential close to 100% of the human footprint. This is likely due to the limited human footprint on these contributions or because their effects are not detectable at this scale (*e.g.*, compensated by species turnover). In addition, we observed a greater increase in actinopterygian species richness and aesthetic value inside MPAs compared to the decrease induced by human footprint (restoration potentials of +290% and +268%, respectively). This is likely due to the role of MPAs as refuges for many species[37], which contribute to a higher aesthetic value[26], and the relatively low human footprint on these contributions. Some contributions (*e.g.*, zinc and calcium content, functional distinctiveness) have been affected similarly by both conservation and human footprint. In these particular cases, MPAs tend to amplify the effects of anthropogenic pressures, albeit these changes remain minor (<3% variation in these fish contributions). Overall, despite strong response heterogeneity across contributions, human footprint drastically reduced nature-for-nature contributions (-19% on average) and to a lesser extent nature-for-society contributions (-3%). MPAs only partially offset these losses suggesting undercompensation. However, conservation legacy showed a comparatively greater impact than human footprint on nature-as-culture contributions (+4.1% versus -1.6%, insert Fig. 3-B).

To visualize these effects, we projected reef fish communities into a multidimensional contribution space using a Principal Component Analysis (PCA). Each country was then represented by the centroid of its sampled reefs in this space, under three conditions: (*i*) current contributions, and contributions predicted under (*ii*) pseudo-pristine and (*iii*) no conservation effort counterfactual scenarios (Fig. 3-C). The sampled reefs were distributed along two major structuring axes: the first PCA axis (PC1, 29%) mainly reflected biomass and actinopterygian species richness, while the second axis (PC2, 26%) was shaped mainly by trophic structure, piscivore biomass, zinc and aesthetics. All countries, except Indonesia, showed consistent responses to anthropogenic pressures and conservation efforts. Although the magnitude of change varied slightly depending on the degree of anthropogenic pressures, *e.g.*, stronger shifts in the Canary Islands (Spain) and the USA compared to the Cook Islands, the magnitude of human footprint systematically overwhelmed the magnitude of conservation legacy worldwide on reef fish contributions regardless of the country. Human footprint and conservation legacy mainly influenced reefs along the first PCA axis, with opposite outcomes. In contrast, on the second axis, human footprint slightly shifted reefs towards lower PC2 values, reflecting a decline in available biomass and piscivore biomass, while conservation legacy did not counteract this effect, also pushing reefs towards lower PC2 values by increasing aesthetic value, herbivore biomass and actinopterygian species richness.

Although relative changes allow for a simultaneous comparison of human footprint and conservation legacy across all contributions, examining the absolute effects of human activities can provide more tangible perspectives (Fig. 4). Conservation legacy in full MPAs have resulted in a median increase of +64 kg/ha in available fish biomass, with values ranging from +8.5 kg/ha (5th percentile) to +331 kg/ha (95th percentile). In contrast, human footprint resulted in a median decrease of -159 kg/ha in available biomass at unprotected reefs, with effects ranging from -950 kg/ha (5th percentile) to -26 kg/ha (95th percentile). Considering that the median of available biomass observed in tropical reefs is ~550 kg/ha (Fig. 4), the scale of these changes highlights the substantial impact of human activities on this key contribution. For piscivores, fully protected areas have induced a median gain of only +0.9 kg/ha, albeit with a wide variability (5th–95th percentiles: -51 to +58 kg/ha). By comparison, human footprint was twenty-fold greater on piscivore biomass, resulting in a median loss of -19 kg/ha, with effects of varying magnitude among reefs, but all negative (5th–95th percentiles: -430 to -1 kg/ha). Although human footprint had an overall negative effect on herbivores (-50 kg/ha on median), some unprotected reefs showed biomass increases of ~20kg/ha (Fig. 4-A), probably due to indirect benefits from degraded environments or a release from piscivores predation[65]. Similarly, while the median human footprint on fish aesthetics was negative (-76 in score value), some reefs showed slight positive effects, possibly due to biodiversity turnover that may favor highly aesthetic species. Fully protected areas showed a median increase of +4.1 species in actinopterygian richness per 500 m2 transect area, with a narrow distribution around this value. In contrast, human footprint had more variable effects on IUCN-threatened species richness, with an overall median negative effect (-0.2 species per sampled reef; Fig. 4). Importantly, MPA attributes such as age or size are well known to influence conservation outcomes[55,66]. As a complementary analysis, we separated fully protected areas into those being older or younger than 10 years, and found that older MPAs tended to exhibit stronger conservation legacy, particularly on biomass-related contributions (Fig S9). For example, old fully protected areas showed a median available biomass gain of +81 kg/ha, compared to +30 kg/ha in young ones (Fig. S9). Interestingly, the positive effects on piscivore biomass (+5 kg/ha in old MPAs) and IUCN-listed species appear to be strongly age-dependent, with little effect detected in young MPAs.

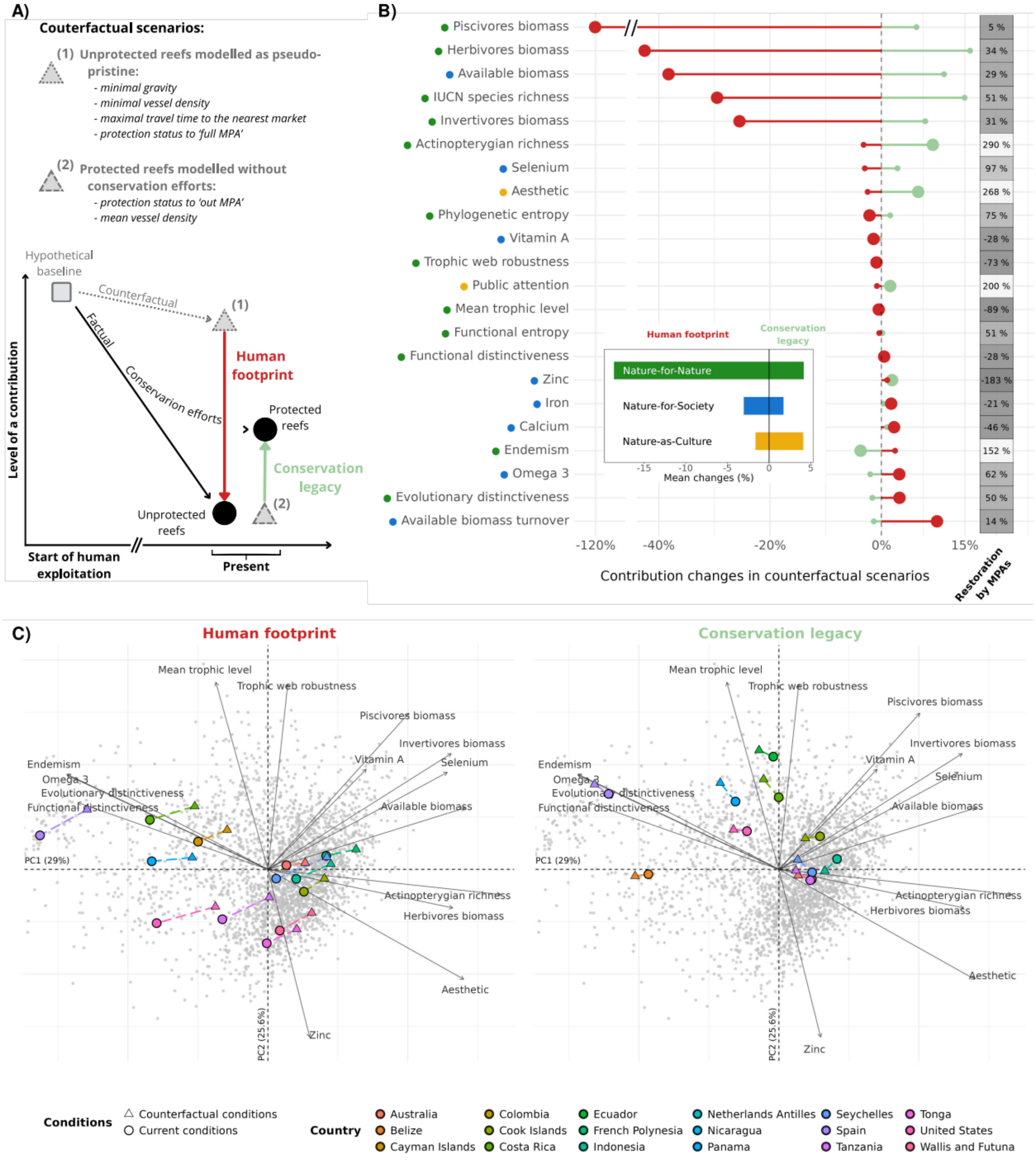

Figure 3: Relative changes in fish contributions on tropical reefs under counterfactual scenarios of pseudo-pristine conditions or no conservation efforts. (A) *Conceptual framework representing*

counterfactual scenarios. Currently unprotected reefs were modeled under pseudo-pristine conditions, characterized by low human gravity, low vessel density, high travel time to the nearest human population, and full protection. Conversely, reefs currently under full protection were modeled as unprotected ('outside MPAs') and subject to the same vessel density as unprotected reefs of their country. The differences between these counterfactuals and the current situations were considered respectively as human footprint and conservation legacy. The magnitude of conservation legacy in relation to human footprint illustrates the potential of MPAs to bend the curve of fish contribution losses. ***(B)*** *Median percentages of changes in reef contributions for both counterfactual scenarios. In each reef and for each contribution, the percentage of change was calculated as the difference between the modeled contribution under current and counterfactual conditions, divided by the modeled contribution under current conditions. For a given contribution, a larger dark-red dot means that the loss due to human footprint is significantly greater than the gain from conservation legacy, or vice versa for larger light-green dots. The shaded column on the right represents the ratio between the human footprint and the conservation legacy for each contribution. This percentage reflects the potential of restoration by MPAs, e.g., on average, MPAs have the potential to compensate for 5% of piscivore biomass loss due to human footprint. Each contribution is identified in the three perspectives of the Nature Future Framework (NFF; see Fig. 2) by a colored dot to its left. The insert corresponds to the average effects of the counterfactuals on the 3 perspectives of the NFF, among the contributions. See figure S6 and figure S7 to see the details of contribution changes.* ***(C)*** *In the multidimensional space of nature's contributions obtained by Principal Component Analysis, we plotted for each country, the barycenters of reefs in their current state (circles) and in the counterfactual scenarios (triangles). The distance between the circle and the triangle corresponds to the magnitude and direction of the changes resulting from human footprint (left) or conservation legacy (right) in the contributions space. Contributions with* $\cos^2<0.3$ *in this PC1xPC2 space were not represented in these plots for visibility purposes. Only countries with >20 sampled reefs used in the counterfactuals are displayed.*

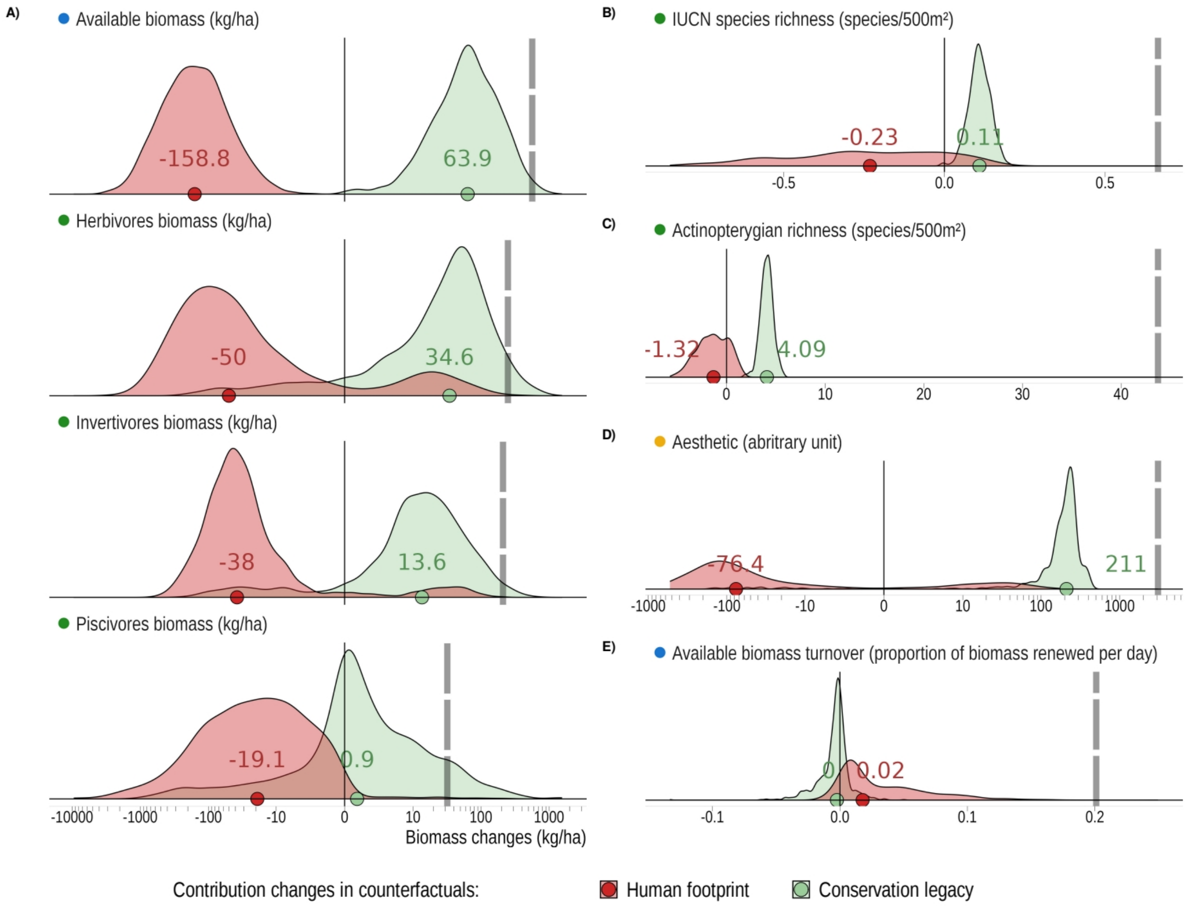

Figure 4: Extent and variability of human footprint and conservation legacy on eight fish contributions across tropical reefs. *Each unprotected reef has been compared to its virtual equivalent under a counterfactual pseudo-pristine scenario. The difference between contributions between both represents the human footprint on these contributions. A value of 0 indicates no difference between predicted values under current and counterfactual conditions. The distributions of human footprint effects, calculated across 1,132 unprotected reefs, are shown in red. Conversely, the distributions of conservation legacy effects, calculated across the 869 protected reefs, are shown in light green. Associated colored dots indicate the median value of each distribution, while grey dashed lines represent the median of modeled contributions under current conditions. For instance, human footprint induced an average loss of piscivore biomass comparable in magnitude to current observed values in reefs, whereas the negative effect of human footprint on actinopterygian species richness remains relatively small compared to observed richness. The x-axis has been log-transformed for biomass and aesthetic to improve visualization. Each contribution is identified in the three perspectives of the Nature Future Framework (NFF; see Fig. 2) by a colored dot to its left. Only the contributions for which we had substantial relative changes in figure 3-B have been represented here, see figure S8 for the other contributions.*

Discussion

Despite anthropogenic pervasive impacts on most ecosystems on Earth[16], assessing the extent to which conservation efforts can compensate for or even bend the curve of ecological degradation over the last decades remains challenging. Using counterfactual scenarios, we explored the contributions of tropical reef fish communities in various alternative scenarios of human pressure, while accounting for local social-environmental contexts. By comparing scenarios of modeled anthropogenic pressures and conservation efforts on fish community contributions, we demonstrated that conservation legacy to date has provided only limited offset to the human footprint for biomass-related contributions and IUCN-threatened species richness, with a restoration potential ranging only from 5% for piscivore biomass, to 51% for IUCN-threatened species richness. In contrast, several contributions - such as nutrient content, trophic structure and functional or phylogenetic diversity - show comparatively less sensitivity to human influence at the community scale. This limited sensitivity may reflect either a genuine stability in the face of anthropogenic pressures, or highly variable and context-dependent responses that do not produce consistent large-scale trends. Finally, we reveal that MPAs are particularly effective in enhancing cultural contributions, such as aesthetic value, as well as actinopterygian fish richness among nature's contributions to nature, by generating a net surplus of these contributions within protected areas. These results should be considered in the light of the moderate predictive power of our model (mean marginal $R^2 = 0.34$), which reflects the inherent difficulty of embracing the complexity of ecological communities at the global scale. Indeed, the high idiosyncrasy of tropical reefs challenges global interpretation[67], and several fine-scale covariates - such as wave exposure, habitat complexity, or socio-cultural practices - remain poorly documented and/or difficult to quantify at the global scale. Consequently, a substantial share of the variance is explained by random effects rather than fixed effects. Since our counterfactual scenarios only modify fixed effects while keeping random effects constant, this assumes that random effects mainly capture structural or environmental heterogeneity (e.g., reef geomorphology, wave exposure) that remains unchanged under alternative human-pressure scenarios. However, if part of the variance explained by random effects corresponds to unmeasured anthropogenic influences (e.g., local pollution, fishing gear), these would not vary in the counterfactuals, potentially leading to conservative estimates of both human impacts and conservation benefits. Thus, while the inclusion of random effects strengthens model realism by accounting for unobserved spatial structure, it may also attenuate the magnitude of predicted anthropogenic effects. Although our model revealed consistent global patterns, it cannot fully capture local-scale variability, which is critical for site-specific management decisions. Yet, the significant and ecologically meaningful changes observed in response to modifications of human-related covariates support the usefulness of this modeling framework for demonstrating general patterns of conservation effectiveness in the face of anthropogenic pressures.

By using this counterfactual approach, we demonstrated that while conservation efforts can benefit many fish community contributions, MPAs have the potential to compensate for only a minor fraction of what has been lost due to human impacts. Specifically, conservation benefits resulted in approximately +64 kg/ha in available biomass on fully protected reefs compared to unprotected reefs, which aligns with previous findings[24,25]. However, this gain must be balanced against the median loss of -159 kg/ha on unprotected reefs compared with pseudo-pristine conditions, with many reefs experiencing drops of several hundred kilograms per hectare. In addition, the modeling of conservation legacy is based on the observed effectiveness of current MPAs. To avoid underestimating their impact, we focused here on fully protected areas only, defined as no-take zones with medium to high level of compliance. Yet, many MPAs remain paper parks or are located in areas that are already too badly degraded[22] to provide substantial benefits. Indeed, conservation legacy estimates on available biomass showed a large variability in MPA effectiveness (Fig. 4). Notably, when separating fully protected areas by age, we found that old MPAs (>10 years) show a stronger conservation legacy, with a median gain of +81 kg/ha in available biomass (Fig. S9), compared to younger MPAs. This highlights that only the oldest and/or most restrictive MPAs could compensate for the median human footprint on fish biomass - yet such highly effective MPAs are far from the norm[11,24] and, even if massively implemented in a near future, will require many years to reach their full ecological potential. This emphasizes that globally, current conservation legacy on tropical reefs largely undercompensates human footprint on most fish community contributions, even in fully protected areas[68,69]. However, our study could not account for governance and management, which are known to influence MPA effectiveness[11,66], as comprehensive and standardized indicators remain limited across global MPAs. Including such covariates would likely enhance our ability to explain MPA effectiveness, but also underlines the challenge of scaling up such high levels of investment in protection globally. Our results are in line with existing literature, suggesting that remoteness from human populations is the most important factor for preserving the functional or phylogenetic diversity of tropical fish communities[38,70]. Similarly, in terrestrial ecosystems, although PAs are beneficial to biodiversity, they cannot fully counteract the increasing human footprint and still experience wild population declines[14]. PAs can play an essential role in mitigating anthropogenic pressures and biodiversity erosion[9], but they only marginally bend the degradation curve and are far from inducing a restoration pathway.

A key challenge in conserving ecosystems and their myriads of contributions remains the identification of a reliable baseline. Given the scarcity of long-term monitoring data, the effectiveness of protection is often assessed by comparing the state of ecosystems within and outside protected areas[71,72]. However, this approach cannot account for long-term biodiversity losses and reduced contributions compared to previous conditions. As pointed out as early as the 1990s[73], humans tend to shift their baseline over time, defining their reference conditions on the basis of past personal experience. The use of archival documents could be a potential option for finding older references.

For example, the movie Silent World (1956)[74] by J.Y. Cousteau depicts a striking picture of flourishing marine life with fish abundances that have since been severely reduced by human exploitation and appear now impossible to retrieve, even in the most effective MPAs. Although such archival records are informative, extracting high-quality quantitative data suitable for modeling ecosystems and their contributions remains a promising yet challenging avenue[28]. Counterfactual scenarios, although unable to reconstruct truly pristine historical states, offer an alternative tool for assessing conservation baseline shifts[35]. By simulating fish communities in the most pristine reef conditions observed today (i.e. under human footprint counterfactual scenario), we were able to compare the effects of protected areas not only with surrounding degraded ecosystems, but with what might exist on each reef in the near absence of anthropogenic pressures. In this way, model-based counterfactuals aim to approximate what long-term before-after-control-impact (BACI) studies achieve[34,35], balancing the socio-ecological gains of PAs against losses observed outside. While BACI approaches remain the gold standard for assessing the effects of anthropogenic activities and management actions - due to their ability to take into account local specificities - model-based counterfactuals can provide a more flexible and operational complement.

However, counterfactual approaches rely on the hypothesis of space-for-time substitution to model reef conditions in the absence of baseline data[75,76]. These models can be confounded by systematic biases on a global scale, such as non-random placement of no-take MPAs which are frequently established on the basis of prior ecological value and/or lower economic costs[77]. Furthermore, the counterfactual approach is based on the assumption that drivers operate independently, which is a simplistic view of reality. For example, in real-world conditions, establishing MPAs can reduce direct human pressures such as anchoring or fishing, which in turn may improve habitat complexity and indirectly benefit reef fish communities - a cascading effect not explicitly taken into account by the *"all else being equal"* assumption of counterfactual models. In addition, “pristine” conditions used to inform counterfactual scenarios often rely on sites from particular ecoregions or ecosystems (e.g., remote islands), which may not be fully representative of other socio-ecological contexts, where reference sites no longer exist (e.g., Great Barrier Reef, Florida). Our results should therefore be considered as one line of evidence, ideally complemented by *in situ* temporal studies (e.g., BACI designs) or spatial comparisons (e.g., inside/outside MPAs), which better account for local or regional specificities (e.g., fishing gears, culture) while reducing model simplification biases. To address this issue, we compared our model-based estimates of conservation legacy with empirical differences estimated between 122 protected reefs and nearby (50 km buffer) unprotected reefs (see Methods). Despite the limited sample size and coarse matching, we found qualitatively consistent results between both approaches (Fig. S10). Yet, the high variability observed in fish community contributions between matched pairs limits the reliability of this spatial comparison in our dataset, and highlights the need for future studies comparing alternative methods using more tailored data and seeking causality[78].

In addition, the reliability of counterfactual predictions is highly dependent on data quality and representativeness within the training dataset, both in terms of ecological observations and the ability of covariates to account for factors shaping fish community contributions, particularly for reefs under minimal human pressure. Such quasi-pristine conditions of low anthropogenic pressure are generally found on remote pacific islands, such as the Coral Sea in Australia, Malpelo or the Galapagos[42,79]. Yet human activities are so ubiquitous across the oceans that even remote areas are not truly pristine anymore[80,81]. Consequently, as our model is based on modern data, it cannot reconstruct a truly pristine state, which leads us to believe that the extent of human footprint might here be underestimated. The observed effect could therefore be considered as the lower limit of anthropogenic impacts on reef fish contributions. This approach highlights the importance of protecting pseudo-pristine areas, such as remote atolls of western New Caledonia[82], to preserve these regions as last refuges for biodiversity and as living examples of minimally disturbed ecosystems that help maintain a low-bias comparative baseline.

Our study, albeit empirical and non-causal, enables a global comparison of the magnitude between conservation legacy and human footprint on 22 reef fish contributions, providing a quantitative perspective on the impact humans have had on reefs and the extent to which conservation efforts can potentially offset these impacts. Given the limited conservation legacy compared to the pervasive human footprint we found on most fish contributions (Fig. 3), our results suggest that expanding protection to 30% of reefs, with only 10% under strict protection[10], is unlikely to offset broad anthropogenic impacts. This challenges the expectation that MPAs alone could restore ecosystems to their pre-industrial state, or even maintain current conditions, without a substantial reduction in anthropogenic pressures both inside and outside protected areas[83]. A few well-protected and closely monitored MPAs, such as Malpelo[42], Chagos[84], or Galapagos[85], demonstrate the effectiveness of such strict measures in limiting the degradation of reef ecosystems, but similar efforts remain hardly achievable on a global scale for ethical and operational reasons[86]. Importantly, designating reefs as no-take zones inherently reduces material contributions, such as food supply, to zero. Yet, effective MPAs may benefit surrounding reefs through spillover effects[87] and represent potential assets for future dynamic management (e.g., rotational closures)[88,89] and a legacy for future generations As an alternative, well-managed partially protected areas may also support benefits for both nature and people [11,90], though their effectiveness remains variable and requires further investigation[38,56].

Although local GDP accounted for only a small proportion of the variance in our models, it was negatively correlated with almost all contributions. This could suggest that current socio-ecosystems driven by economic growth are incompatible with sustaining ecosystem integrity. This finding resonates with a growing body of literature emphasizing the urgent need to explore post-growth scenarios that redefine our relationship with nature[19,62] and prioritize human well-being - taking ecological footprints into account - as a development goal, rather than relying on measures based on GDP or HDI (Human Development Index)[91,92].

To better protect ecosystems and prepare resilience to future disturbances, it appears essential to foster awareness of our profound and pervasive impact on ecosystems regarding our limited capacity to restore them. This is even more critical as human population growth[93], along with expanding infrastructure and transport[94], will inevitably increase human gravity on reefs. Because human population gravity is one of the strongest drivers of losses in fish community contributions, it appears crucial to decouple demographic growth from ecosystem degradation, by reducing our extractive and damaging activities on tropical reefs.

As societies become increasingly disconnected from nature[95,96] - pushing us toward a likely sixth mass extinction[97] and unprecedented warming in recent millennia[98] - tropical reefs can emerge as a pivotal focus for action. Being a biodiversity hotspot and supporting the well-being and livelihoods of a large part of humanity, these ecosystems exemplify where we must bend the declining curve of most nature's contributions. This multidimensional approach pleads for a paradigm shift in the way we perceive and interact with our planet, moving beyond protecting isolated fragments of nature far from human populations as a means of "balancing" our pervasive negative footprints.

Methods

Methods summary

We used standardized Reef Life Survey data from 2,803 tropical reefs, including biomass for 1,600 ray-finned fish species and presence data for 60 elasmobranchs[99]. Across these reefs, whether fully protected, partially protected, or unprotected, we quantified 22 contributions that fish communities make to nature and human populations (Table 1).

We fitted a Bayesian hierarchical community model (HMSC)[100] including 38 environmental, social, and habitat covariates as fixed effects (Table 2), and sampling units nested within countries as random effects (model 1, Table S3). This framework jointly models all contributions and accounts for their covariation as well as unmeasured local reef characteristics.

Using the trained model, we generated counterfactual scenarios by altering human-related covariates while keeping environmental conditions constant[35]. For protected reefs, we simulated the absence of protection to estimate conservation legacy. For unprotected reefs, we simulated pseudo-pristine conditions (full protection, minimal human presence) to quantify the human footprint. Percentage differences between observed and counterfactual predictions were used to assess the relative effects of MPAs and anthropogenic pressures.

Fish community data

We used fish data from the Reef Life Survey (RLS) database (https://reeflifesurvey.com/), which consists of standardized underwater visual censuses of fish abundance and size distribution on worldwide reefs[99]. Conducted from September 2006 to August 2024, these surveys covered 50 m transects with two 5 m x 5 m belts assessed on either side. Only reefs with a minimum monthly sea surface temperature (SST) above 17°C were included, encompassing tropical and subtropical reefs where tropical species occur[63,101]. We excluded anguilliformes (Muraenidae, Ophichthidae, Congridae, Anguillidae) and cryptobenthic families (Aploactinidae, Apogonidae, Blenniidae, Bythitidae, Callionymidae, Chaenopsidae, Creediidae, Dactyloscopidae, Gobiesocidae, Gobiidae, Grammatidae, Labrisomidae, Opistognathidae, Plesiopidae, Pseudochromidae, Syngnathidae, Tripterygiidae) due to inconsistent visual quantification[102,103]. Then, we converted fish abundance counts and size estimates to individual biomass in each survey using length-weight relationships[104] (https://fishbase.mnhn.fr/). To minimize juvenile identification bias, we excluded individuals < 3.75 cm for species with a maximum body size < 25 cm, and individuals < 6.25 cm for species with a maximum body size ≥ 25 cm[105]. For elasmobranchs, we combined their presence data with that of actinopterygians to calculate the number of IUCN-threatened species. However, elasmobranchs were not included in the assessment of other contributions, as their specific behaviors and high mobility (e.g., divers avoidance, transient occurrence in reef areas, etc.) may bias local biomass estimates and make them less reliable indicators of site-level ecosystem functioning[106,107]. Surveys with abnormal fish sizes (*i.e.*, > 2*the maximum length of the species, or > maximum length + 50 cm) were removed to address possible diver or data entry errors. The 72 surveys with biomass greater than 500 kg/500m² or abundance greater than 10,000 individuals, likely indicating temporary aggregations of large schools, were also excluded. The final dataset comprised 4,398 surveys, conducted in 1,497 RLS sites (unique GPS positions). Surveys conducted at the same RLS site on the same day were aggregated, as described below in the “ Contributions assessment ” section, to obtain fish community contributions on 2,803 ‘sampled reefs’ (i.e. unique GPS positions at a given sampling date; Fig. S11).

Species traits

We compiled the species list from the selected reefs and standardized each species name to the currently accepted scientific name using the rfishbase::synonyms() function (rfishbase v4.1.2[108]) to avoid taxonomic mismatches. For the 1,637 actinopterygian and 58 elasmobranch species, we extracted 18 species-specific traits from FishBase (rfishbase v4.1.2[108], https://www.fishbase.se/) and other sources (Table S1) to calculate individual contributions. To maximize species coverage and reef diversity, we supplemented this dataset with additional information. The IUCN categories were filled in with inferred data from Loiseau et al.[109], and we added aesthetic scores for 141 species following the methods of Langlois et al.[47]. The list of traits used to assess fish contributions and their description is available in Table S1. Although we had a high level of completeness for known traits (from 85.4 to 99.9% of known values; see Table S1), a few missing values for some species could have excluded several diverse reefs from the dataset. To address this, we chose to impute the missing values using random forest via the missForest R package (missForest v1.5[110]). This method was applied to the species-specific traits: ‘Length’, ‘K’, ‘Trophic_guild’, ‘Calcium’, ‘Iron’, ‘Omega-3’, ‘Selenium’, ‘Vitamin A’, ‘Zinc’, ‘Geographic_range_Albouy_2019’, ‘Public attention’ and ‘ Aesthetic’. To improve the model's ability to predict these missing data, the random forest was applied to a dataset containing the additional species-specific traits: fishing, aquaculture, and aquarium importance, trophic level, water column position, schooling behavior, IUCN category, fishing vulnerability (source: FishBase), morphological characteristics[111], bathymetric range[112], and climatic vulnerability[113]. In addition, we incorporated species taxonomy into random forest by summarizing taxonomic positions using Multiple Correspondence Analysis (FactoMineR::MCA(), FactomineR v2.11[114]). Imputation performance was highest when the taxonomy was included in this form and when the first 35 axes of the MCA were added to the random forest dataset.

We applied 50 independent iterations of the missForest imputation model (missForest::missForest(), ntree = 100, max_iter = 10) and retained the median or the most frequent item of imputed values across the iterations. Categorical values were retained if at least 80% of the models converged to the same result, while the median of numerical values were retained if the coefficient of variation (CV = standard deviation/mean) was < 0.2. Otherwise, we kept the trait values as ‘NA’. To evaluate these imputations, we generated 50 datasets in which 20% of the trait known values were randomly masked and used the missForest function to predict these pseudo-missing values. Prediction performance for categorical traits was assessed using the proportion of correct predictions, while numerical traits were assessed using R-squared correlations. The prediction performance for species traits - ranging from 0.47 for selenium to 0.83 for trophic guild (Fig. S12) - was considered satisfactory for imputing the 1,269 missing trait values among the total 34,300 values in the species trait dataset.

In addition, we classified species according to their potential use in fisheries. Due to the limited availability of species-level data (Table S1) and the low accuracy of the random forest model (Accuracy = 0.58), we shifted a family-level approach. Using the FishBase ‘*Importance’* trait, which classifies species according to their commercial fishing interest, we classified families as ‘*targeted’*, ‘*targeted if species exceed 20 cm’*, or ‘*non-targeted’*, following the decision tree described in Fig. S13. This classification (Table S2) enabled us to separate the exploitable or potential biomass available to local fisheries from the observed biomass.

Contributions assessment

We calculated 22 fish-based nature contributions in each tropical reef, following the methods from Flandrin et al.[31] (see Table 1). Regarding the nutrient cycling contribution of fish, we excluded estimations of phosphate and nitrogen recycling, as well as carbonate excretion due to excessive missing data at the species level. Additionally, these contributions are mainly determined by biomass at the community level[31]. For each contribution, we retained only surveys where species with known (or inferred) trait values accounted for more than 80% of both biomass and abundance, resulting in the removal of 211 surveys. Each reef fish community contribution was calculated as the average of the fish contributions across all the surveys at a given sampled reef (unique GPS point at a given date). Despite the dissimilarity in sample size among sampled reefs, we consider that averaging the values limits the over-sampling bias of more studied reefs by giving equal weight to all of them. Ultimately, we ended up with 2,803 'sampled reefs', which were identified by their GPS position and sampling date. Correlations between contributions are shown in Figure S14.

Table 1: Nature contributions used in this study. *All metrics were calculated at the reef fish community level using data from standardized reef fish surveys (RLS). The 22 fish-based contributions have been separated into the three perspectives of the Nature Future Framework: Nature-for-Nature (NN), -for-Society (NS), and -for-Culture (NC). This categorization is used for visualization purposes in figure 2 and 3-B, but does not alter analyses. Contributions identified by (*) have been log-transformed to limit the effect of asymmetric and high-magnitude distributions. This table has been adapted from Flandrin et al.*[31]*, see this research article for calculation details.*

	Contribution	**Description**
Nature-for-Nature	Actinopterygian richness	Number of actinopterygian species per reef (500 m^2)
	IUCN-threatened species richness	Number of actinopterygian and elasmobranch species listed as ‘Critically Endangered’, ‘Endangered’, or ‘Vulnerable’ in the IUCN Redlist
	Endemism	Average of species endemism on the reef. Species endemism is assessed from species geographic range[115]
	Functional distinctiveness	Average of species functional trait distinctiveness at the reef level. The functional distance between each species was assessed in a (Length x Diet x Trophic level x Water position x Growth constant x Schooling behaviour) trait space[116]
	Evolutionary distinctiveness	Average of species evolutionary distinctiveness[117] at the reef level
	Biomass per trophic guild* (3 trophic groups)	Total biomass of reef fish split into herbivores, invertivores and piscivores trophic guilds. Species trophic guild was extracted from Parravicini et al.[118]
	Functional entropy	Sum of pairwise functional distance between species, weighted by their relative biomass on the reef[119]
	Phylogenetic entropy	Sum of pairwise phylogenetic distances between species, weighted by their relative biomass on the reef[120]
	Trophic web robustness	Allometric coefficient between the number of trophic interactions and species richness, as a proxy of trophic robustness to local extirpations[121]. The trophic metaweb between tropical species was assessed by applying a body size niche model described by Albouy et al.[122]
	Mean trophic level	Average of species trophic level weighted by their relative biomass on the reef. Used as a Proxy of the biomass stability through time in empirical food web[123]
Nature-for-Society	Available biomass*	Total biomass of reef fish belonging to fishable families. Fishable families were classified using the fishery ‘importance’ trait from FishBase (https://www.fishbase.se/), following the method described in figure S13.
	Turnover of available biomass	Biomass turnover of fishable species in the reef. Biomass turnover is determined as the proportion of biomass produced per day (total production per day / total biomass)[63]
	Available nutrients in fish flesh *(Calcium, Iron, Omega 3, Selenium, Vitamin A, Zinc)*	Nutrient quantities contained in an average 100g food portion (wet weight) of fish on the reef (*i.e.*, nutritive quality relative to the fishing effort)[46]
Nature-as-Culture	Aesthetic value	Estimation of fish community aesthetic value of the reef, by accounting for species richness and aesthetic composition effect (individual species aesthetic effects, weighted by their relative abundance)[26]
	Public attention	Public attention of species is obtained by combining the number of views of Wikipedia articles, photos on Flickr and mention on X[124]. Reef public attention is the 3rd quartile of public attention scores for species recorded on this reef, to reduce the influence of high outliers and species richness, following Flandrin et al. (2024)[31].

Reef covariates

We extracted environmental, habitat and human-related covariates for each reef at its sampling dates. We calculated the median, 5th and 95th percentile of each covariate over three temporal windows: five years, one year and seven days before sampling. To use informative predictors, we removed highly correlated covariates (Pearson correlation > 0.7 or < -0.7), and then performed an analysis of variance inflation factor (VIF), retaining only those with a VIF < 5 (Fig. S15). Of the 38 covariates selected, those with a right-skewed distribution were log-transformed, before all covariates were scaled to standard units (mean = 0, s.d. = 1; see details in Table 2).

We classified the sampled reefs according to their protection status at the sampling date. The 1-5 protection score of the sampled reefs was first extracted from Protected Seas (https://navigatormap.org/methodology/) based on their GPS position, and supplemented by on-site expert opinion. Data providers classified each MPA into a high to low compliance category, based on their on-site expert opinion. We considered no-take MPAs (scored 5 in the Protected Seas classification) with high or medium compliance as fully protected, while those with low compliance and all other protection statuses were classified as under restricted protection. We classified all other sampled reefs, as well as reefs sampled before MPA establishment as ‘out’ of MPAs. Of the 2,803 sampled reefs, 869 were under strong protection, 802 were restricted and 1,132 were outside MPA.

To estimate boat-related disturbance (combined effect of fishing activity, tourism, pollution, and noise), we used the new Global Fishing Watch dataset based on Sentinel-2 satellite imagery (https://globalfishingwatch.org/). With a 10 m resolution, Sentinel-2 imagery coupled to artificial intelligence allows the detection of vessels ≥10 m in length, regardless of AIS vessel tracking, thereby capturing both tracked and untracked fleets. For each RLS site (GPS position), we extracted the number of vessels detected within a 10 km radius and standardized detections by the number of satellite images over the area. We excluded detections classified as infrastructure, those with cloud coverage >0.5, and those with a detection probability <0.5. Vessel density per site was averaged over the 2020–2024 period. This metric was considered as a proxy for anthropogenic disturbance associated with vessel presence, including fishing activity, tourism, pollution, and noise.

For habitat variables, we used two data sources providing information at different spatial scales. The "Allen Coral Atlas" (https://www.allencoralatlas.org/) maps the world’s coral reefs by coupling high-resolution satellite imagery with deep learning algorithms[125], offering data on substrate types and benthic organism cover. These data were extracted for each coordinate by averaging data over a 500 m radius around the sampling location. While these data are static, they provide estimates of habitat composition and condition in the area surrounding the sampling points. We also used data on benthic composition collected through photo-quadrats during Reef Life Survey counts, providing finer spatial and temporal insights than those from the Allen Coral Atlas. Within each 50 m survey, 20 photo-quadrats were evenly spaced and then analyzed using the SQUIDLE+ software (https://squidle.org/). Randomly overlaid points on the photos were identified to the finest possible functional or taxonomic groups, providing percentage cover data at the survey scale. To standardize the data globally, these groups were aggregated into nine categories: corals, algae, coralline algae, seagrass, sessile invertebrates (*e.g.*, sponges), coral rubble, rock, sand, and microalgal mats (*e.g.*, cyanobacteria). Benthic cover data were then transformed using an arcsine transformation (inverse sine of square-root transformed values) to account for the 0–1 range and the right-skewed distribution of this type of data[126].

As the benthic cover data (derived from photo-quadrat surveys) contained 36% missing values, we imputed them using the same random forest imputation algorithm applied to species traits (see above). This imputation was based on the other environmental, habitat, and anthropogenic covariates and allowed us to maximize the diversity of reefs included in our models. We assessed the imputation accuracy by applying a cross-validation procedure. We randomly removed 30% of the data, imputing them, and compared the predicted results to the initial data. The best predictive power was achieved when we reduced the dimensionality of the covariates, excluding latitude, longitude, and depth, to 20 dimensions using principal coordinates analysis (PCoA). These 20 dimensions, combined with spatial variables (latitude, longitude, and depth), served as the basis for the random forest imputation model. The predictive power was strong for algal and coral cover ($R^2 \sim 0.7$) and moderate for other categories ($R^2 = 0.4–0.7$; Fig. S16). We explicitly verified that imputing these data did not overly bias the models by running a Bayesian model including only reefs with observed benthic composition data (n = 1829). This reduced model showed similar performance (average $R^2 = 0.71$), and the fixed-effect trends identified in this study remained unchanged (Fig. S17).

Ultimately, we modeled fish contributions using 38 covariates, including 8 environmental, 22 habitat, and 8 human-related covariates. To ensure that the large number of habitat covariates did not bias the results, we ran an alternative model with a reduced set of habitat-related components (model 2, Table S3). This simplified model yielded results consistent with the full version, showing no differences in performance, covariate importance ranking, or the study's main conclusions (Fig. S18).

Table 2: Environmental, habitat and anthropogenic covariates used to model the contributions of fish communities on tropical reefs. *Covariates identified by (*) have been log-transformed to limit the effect of right-skewed distributions. Covariates identified by (**) have been transformed using an arcsine transformation, which is more appropriate to right-skewed distribution within the 0–1 range*[126].

	Covariate name	**Source**	**Scale**	**Description**	**Rationale**
Environment	SST (5 years)	https://coralreefwatch.noaa.gov/product/5km/index.php	Resolution of 0.5° latitude × 0.5° longitude, daily resolution	Average Sea Surface Temperature (SST) over the 5 years before the sampling	Major driver of species distributions and fish biomass[105]
	Chlorophyll (5 years)*			Average sea water chlorophyll-a concentration over the 5 years before the sampling	Proxy for primary production,and energy available to consumers, conditioning fish biomass[127]
	Chlorophyll (7 days)*			Average sea water chlorophyll-a concentration over the 7 days before the sampling	Proxy for recent algal bloom events during sampling
	pH (5 years)	https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_BGC_001_029/description	local, monthly resolution	Average sea surface pH over the 5 years before the sampling	Influences fish physiology and coral calcification; may shape fish distribution and coral habitat[128,129]
	DHW_quantile95 (5 years)*	https://coralreefwatch.noaa.gov/product/5km/index.php	local, daily resolution	Degree Heating Weeks (DHW), defined as the accumulation of temperature anomalies exceeding the maximum monthly mean SST over a 12-week period for a given region[130]. 95% quantile of the DHW index over the 5 years before the sampling	Proxy for the intensity of the strongest heatwaves in recent years. Heatwaves can degrade reef habitat by coral bleaching[131], and impact reef fish biodiversity and productivity[132]
	DHW (1 year)*			Average DHW index over the year before the sampling	Proxy for the last potential bleaching event
	DHW (7 days)*			Average DHW index over the week before the sampling	Proxy for ongoing or very recent thermal stress during sampling
	DHW (5 years)*			Average DHW index over the 5 years before the sampling	Indicator of chronic thermal stress in recent years
Habitat	Depth	RLS diver	Survey	depth of the survey	Strong predictor of fish community structure and composition[133]
	Rock ; Coral ; Coralline algae ; Coral rubble ; Sand ; Other sessile invert (photo-quadrat)**	RLS photo-quadrats	Survey	Mean percent cover of each benthic component in the survey, assessed with 20 photo-quadrats along the 50m line	Proxy for the local benthic habitat, structural complexity, benthic health, and degradation. Linked to biodiversity and biomass[134]

	Fringing reef area (“Terrestrial reef flat” in Allen coral atlas) ; Rubble ; Inner reef flat ; Sand ; Coral algae ; Seagrass ; Microalgal Mats ; Back reef slope ; Deep lagoon ; Sheltered reef slope ; Reef slope ; Reef crest ; Plateau ; Patch reefs ; Rock (%)*	Allen Coral Atlas (https://www.allencoralatlas.org/)	GPS position (RLS site; 7.5 m^2 resolution)	Global maps of coral reef habitats by coupling high-resolution satellite imagery and deep learning algorithms (Kennedy et al. 2020). Proportion coverage of geomorphologic or benthic components within a 500-m radius around the RLS site	Proxy for the surrounding reef habitats, broad benthic and geomorphic context of the sample[133]
Anthropogenic	Gravity*	Cinner et al. 2018[54]	local, based on 2010 assessment	Human population density divided by the square of the travel time	Proxy for the local human impact by exploitation, pollution, habitat disturbance, or other sources[54]
	HDI	https://hdr.undp.org/data-center/country-insights#/ranks	country, estimated between 2001 and 2021	Human development index: summary measure of average achievement in key dimensions of human development: a long and healthy life, being knowledgeable and having a decent standard of living	Proxy for the way of life of people living in the country; may affect nature relationship and exploitation practices[92]
	Natural resource rent*	Selig et al. 2019[135]	country, estimated in 2019	Amount of resources available within a territory	Reflects economic reliance on resource extraction[135]
	Marine ecosystem dependency (MED)*			Dependence of the country on marine resources in terms of nutrition, economy and coastal protection	Indicates national dependence on marine resources[135]
	Vessel density*	https://globalfishingwatch.org/data-download/datasets/public-sentinel2-vessel-detections%3Av1.0	GPS position (RLS site; 10 km radius), 2020-2024	Density of vessels larger than 10 m around reef (10 km buffer) including the untracked dark fleet	Proxy for anthropogenic disturbances caused by vessels (commercial shipping, tourism, fishing) in the surrounding waters[58]
	GDP*	Kummu, Taka, and Guillaume	regional	Local Gross Domestic Product (total monetary value of goods and	Reflects economic intensity; potentially relate to habitat disturbances[91]

		2018[61]		services produced) downscaled at the regional scale	
	Protection status	Protected Seas (https://navigatormap.org/), on-site expert opinion	GPS position (RLS site)	Categorical protection status: - “full”: No-take MPAs (scored 5 in the Protected Seas classification) associated with high or medium compliance (expert opinion) - “restricted”: no-take MPAs with low compliance and all other protection statuses - “out”: no restriction measures	Indicates degree of restriction on extractive activities
	Travel time*	Maire et al. 2016[136]	GPS position (RLS site), based on 2010 assessment	Travel time in minutes between the reef and the nearest populated pixel within a 500 km radius	Proxy for reef accessibility and potential human use[136]

Bayesian models

We used a Hierarchical Modeling of Species Communities (HMSC)[100] Bayesian model to analyse the contributions of tropical fish communities to people and nature in 2,803 sampled reefs, using 38 environmental, habitat and human-related covariates, along with two random effects: sampled reef (unique IDs) nested within countries.

To address the computational demands of Bayesian model computation, we used the ‘HMSC-HPC’ framework for GPU deployment[137]. By integrating Python and TensorFlow into its core while retaining the user-friendly R interface, this enhanced framework partially addressed the dataset's computational constraints and achieved substantial speed-ups compared to the original ‘Hmsc-R’ package.

We fitted HMSC models with four Markov chains Monte Carlo (MCMC) of 200,000 iterations each, removing the first half as burn-in. Posterior distributions were obtained from 800 posterior samples, with 200 samples per chain separated by a thinning interval of 1,000 (*i.e.*, one sample is collected every 1,000 iterations). We calculated the support levels for the fixed effects as the proportion of posterior samples above or below zero, according to the direction of the mean effect, providing statistical evidence of the observed effects. Due to the hierarchical nature of the dataset, we incorporated in the model the sampled reef ID (corresponding to a GPS position at a given date; 2,803 levels) nested within the country (33 levels) as a random intercept. We visually inspected the convergence and mixing of chains using the R package ‘ggmcmc’ version 1.5.1.1[138]. Convergence was deemed satisfactory when the effective sample size equaled the number of posterior samples[139], and the potential scale reduction factors were below the 1.1 threshold[139]. The thinning interval was selected by observing the convergence of the models for increasing thinning values. We observed good convergence with a thinning interval of 1,000 (Fig. S19), while larger thin did not improve convergence quality although increasing computation time. Similarly, 200 samples per chain resulted in an effective sample size close to 800 (Fig. S19), and reasonably normal posterior distributions of estimates (Fig. 2), while maintaining acceptable computation times. A burn-in of half the iterations was sufficient to ensure sampling inside the target distribution, without introducing bias into the conserved samples (Fig. S20). We also ensured that the four independent MCMC chains were mixed properly (Fig. S20). Default priors were used following Tikhonov et al.[139].

All covariate effects on contributions were modeled as linear (model 2, Table S3). Quadratic terms were tested but did not improve model performance, and no pronounced quadratic effect with surface temperature (SST) was detected in the linear model (Fig. S21). Contributions were fitted to normal distributions (Fig. S22), which provided the best performance measures.

We assessed model quality by evaluating both explanatory and predictive power. Explanatory power was estimated using the R-squared between observed and predicted values from a model trained on the full dataset. Predictive power was measured through five-fold cross-validation, where five models with the same structure as the full model were trained on 80% of the data and tested on the remaining 20%, ensuring no overlap of coordinates (RLS sites) between training and test sets. This approach allowed for predictions across the entire dataset, with predictive power quantified by the R-squared from this cross-validation procedure. The full model, which included fixed effects, outperformed the null model containing only random effects (model 3, Table S3), with an average predictive power of 0.24 versus 0.34. The relatively small difference between the two is due to random effects compensating for the missing fixed effects: for example, 'SST (5 years)' is partially structured along countries, but including it as a fixed effect will allow the model to capture more variability within countries. In addition, we tested the influence of the chosen random level structure by fitting a model without random effects (Model 4) and a model with only country as a random effect (Model 5; Table S3). We found that Model 1 (random effect: sample_unit/country) had similar predictive performance to Model 5 (predictive $R^2 = 0.34$) but a higher explanatory power (explanatory $R^2 = 0.67$ vs. 0.38; Table S3), leading us to select Model 1 for the study. The importance ranking of covariates and the size effects of human-related variables remained consistent across all models (Fig. S23).

Residual correlations among contributions after accounting for fixed effects were estimated at the sampling unit (*i.e.*, each sampled reef) and country scales (Fig. S24). Conditional predictions were applied to explicitly test the informative nature of these residual associations. We tested the predictive power of the models trained on 80% of the dataset, either by predicting the remaining 20% for a single contribution (marginal prediction), or by predicting the same 20% while knowing the values of other contributions (conditional prediction). The conditional predictions clearly outperformed the marginal predictions (Fig. S1), highlighting the informative nature of the residual associations. Random effects at the sampled reef level took into account the ecological and historical specificities of each reef, including spatial features. In addition, HMSC introduces latent factors associated with the random levels to capture residual covariance among response variables that is not explained by the fixed effects. These latent factors can reflect unmeasured ecological or spatial processes, and the model determines how many of them are useful based on the residual structure present in the data. In our case, we examined the first three latent factors because they explained the largest share of the residual variation, but they did not reveal any broad-scale spatial pattern (Fig. S25). Local contingencies, such as ecological history or localized interactions, therefore appeared to have a strong influence on the contributions.

All analyses were performed using the R package ‘Hmsc’ version 3.1.2[139].

Counterfactual scenarios

Using the trained full model (model 1, Table S3), we generated counterfactual scenarios by modifying human-related covariates to simulate two theoretical conditions: (i) the absence of conservation efforts (“Conservation Legacy” scenario) and (ii) pseudo-pristine conditions (“Human Footprint” scenario).

(i) In fully protected reefs, we simulated the absence of conservation efforts by setting their protection status to "out" and adjusting vessel density to match the average observed in unprotected reefs within the same country. This allowed us to estimate reef contributions as if no protection measures had been implemented, *i.e.*, if the current protected reef had experienced the same exploitation trends as the surrounding unprotected reefs. For this analysis, restricted MPAs were excluded in order to focus specifically on fully protected areas, where the potential conservation effects are expected to be higher. We calculated the ‘Conservation Legacy’ as the difference between the contributions predicted under current conditions and those predicted under counterfactual conditions. To standardize comparisons across reefs and contributions, this difference was expressed as a percentage change of the current contribution–calculated as the difference between the modeled contribution under actual and counterfactual conditions, divided by the modeled contribution under actual conditions. The distributions of these percentage changes are shown in figure S7.

(ii) Conversely, in unprotected reefs, we simulated pseudo-pristine conditions by applying full protection, setting vessel density and human presence ('gravity') to the lowest observed levels, and increasing travel time from the reef to the nearest human population to the highest level currently observed. The difference between predicted contributions under pseudo-pristine and current conditions quantified the "Human Footprint" on reef contributions. The percentage change distributions are shown in figure S6.

This model-based counterfactual approach relies on two key assumptions. First, it assumes that the model has been trained on a sufficiently representative range of covariate combinations. Second, it is based on the hypothesis of absence of covariance between human-related variables and environmental or habitat variables - i.e. we estimated the contributions under new human conditions, assuming that all else remains equal, which may underestimate long-term effects (e.g., habitat degradation). To test the first assumption, we tested the plausibility of the counterfactual scenarios by projecting both observed and counterfactual reef conditions into a multivariate covariate space using a Factor Analysis of Mixed Data (FAMD). We found that counterfactual conditions fall within the range of observed conditions in the training data (Fig. S26), indicating that the model does not extrapolate beyond realistic environmental or human conditions. The second assumption is more difficult to evaluate in the absence of long-term empirical data, and we further discuss its implications and limitations in the Discussion section.

To compare the magnitude of the conservation legacy on protected reefs and the human footprint on unprotected reefs, we tested whether the distributions of changes in these two counterfactual scenarios were significantly different using a Wilcoxon Rank Sum test. As we performed 22 independent comparisons (one per contribution), we applied a Bonferroni correction to control for multiple hypothesis testing, setting the significance threshold at $\alpha = 0.05 / 22$. By comparing changes in the human footprint with the opposite of changes in the conservation legacy, we illustrated in figure 3-B which counterfactual scenario resulted in a significantly larger magnitude of change for each contribution.

To assess the robustness of our model-based counterfactual estimates of conservation legacy, we performed a complementary analysis based on a spatial design-based comparison. We identified a subset of 122 fully protected reefs for which at least one unprotected reef had been sampled within a 50 km buffer and within 60 days. For each of these protected reefs, we (i) estimated the conservation legacy using our model-based counterfactual approach, and (ii) calculated the observed difference in community contributions between the protected reef and its matched unprotected site(s), following an inside/outside MPA comparison. We found qualitatively consistent results between both approaches, supporting the credibility of our model-based predictions (Fig. S10). However, the in/out design-based method yielded a wider spread of estimated changes, with higher conservation legacy in biomass compared to those predicted by the model. This high variability may reflect the small size and heterogeneity of the subset that limits the detection of clear patterns, and the ecological differences that are difficult to control for in global predictive models. Moreover, because our spatial matches were based on coarse criteria (i.e., proximity in space and time), some paired reefs likely differ substantially in habitat conditions. A more rigorous matching procedure would require a context-specific selection, with appropriate covariates and statistical matching methods, in a tailored dataset[140].

Finally, to explicitly test whether the much greater impact of the human footprint compared to conservation legacy is not merely a modeling artifact - since the human footprint was estimated by altering four human-related covariates, whereas conservation legacy was based on only two changes - we conducted an additional comparison. Specifically, we recalculated the human footprint under a reduced-impact scenario, where only gravity was set to its minimal value and protection status was set to full, while travel time and vessel density remained unchanged. Although this adjustment led to a slight reduction in the magnitude of the human footprint, the overall results remained virtually unchanged (Fig. S27), reinforcing the robustness of our approach in modeling the human footprint using four covariates.

Data availability

Raw fish data are publicly available through a live data portal accessible via www.reeflifesurvey.com. All data required for this study are also available from the associated Zenodo repository (10.5281/zenodo.17602130)[141].

Code availability

All relevant codes to reproduce all the analyses and figures are available from the associated Zenodo repository (10.5281/zenodo.17602130)[141].

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Author Contributions Statements

Conceptualization: U.F., D.M., N.M. Methodology: U.F., D.M., N.M, L.S, E.M., N.L., M.M. Data Curation: U.F., C.H., L.S., E.C. Data analysis: U.F., D.M., N.M. Visualization: U.F. & NM. Writing – original draft: U.F. Writing review & editing: All authors.

Competing Interest Statement

The authors declare that they have no competing interests.

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