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Conserving the beauty of the world's reef fish assemblages

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On shallow rocky and coral reefs, cultural and recreational values, like aesthetics, are critical aspects of Nature's Contributions to People (NCP) that support human well-being and provide billions of dollars in tourism revenue. Quantifying the aesthetic value of reef ecosystems and uncovering the conditions that enhance it could support NCP-based management. Here, we combine a global dataset of reef fish surveys, species-level aesthetic values, and causal modeling to assess the global status and drivers of reef fish assemblage aesthetic value. We find that aesthetic value is inherently linked to species richness, displaying a latitudinal gradient with peaks in the tropics, but varies strongly with the presence of exceptionally beautiful or less-beautiful species. Sea surface temperature, primary productivity, human gravity, and protection status are the strongest drivers of assemblage-level aesthetic value. Protection against human impacts consistently enhances aesthetic value by boosting taxonomic and phylogenetic diversity, and this effect is greatest in species-rich, tropical ecoregions. Economic development has little influence, indicating that low-income countries are not constrained from maintaining beautiful fish assemblages. Our results therefore suggest that marine protected areas (MPAs) can support multiple NCPs simultaneously, particularly in developing tropical countries. While we highlight the effectiveness of MPAs, given the low level of marine protection globally and the sensitivity of aesthetic value to environmental conditions, the beauty of the world's reefs appears severely threatened. Aesthetic value should be immediately integrated into reef conservation and management plans.

ecology | ecosystem services | conservation | causal inference

Significance

Ecosystems provide critical services to human societies, the most well-known including food provisioning and coastal protection. However, ecosystems also provide cultural services that are essential to human well-being and economic livelihood. The aesthetic value of ecosystems creates an intimate connection between people and nature and supports tourism. We evaluated the distribution and drivers of the aesthetic value of fish assemblages on shallow reefs worldwide. We found that protected areas enhanced aesthetic value by harboring greater species richness and exceptionally beautiful species, which was strongest in tropical regions. We also found that aesthetic value was not related to countries' level of wealth. Protected areas can therefore support fisheries, tourism, and human well-being simultaneously, and tropical, developing countries can benefit most.

Evaluating how and where ecosystems support human livelihood is critical for achieving sustainable development goals. Nature's Contributions to People (NCP) is a growing framework for assessing links between ecosystems and human society. While NCP encompasses the whole spectrum of interactions between nature and people (1, 2), previous studies have focused mainly on material goods, ecosystem productivity, or invasive species resistance. Few studies have quantified nonmaterial dimensions like cultural importance, well-being, or the perceived aesthetics of biodiversity (3). However, such nonmaterial NCP can have a substantial role in conservation biology (4, 5). Society's willingness to engage in conservation action is not solely driven by what nature can offer in terms of material benefits but also by how people experience the natural environment (6). Conservation values often stem from the emotional connection that humans have with nature (7), as there is a clear association between affective factors (emotions that impact human decision-making) and people's willingness to safeguard species and ecosystems (8, 9).

Nonmaterial value refers to the cultural relationship people have with nature and the impact nature has on people's mental state, creativity, and overall sense of well-being (2). This underscores the importance of preserving and promoting natural environments for the benefit of human health and happiness. Among nonmaterial NCP, aesthetic value is one of the most direct links people have with nature (5). Quantitative measures of perceived species aesthetics (hereafter "aesthetics") are now becoming available, making comparisons possible with other NCP metrics (10, 11). Yet estimates of aesthetics at the biological assemblage level (a relevant scale for conservation) are still scarce (5) and do not account for the spatial distribution of organisms or environmental characteristics (12, 13). To include biodiversity aesthetics in the NCP agenda and to increase our capacity to understand its drivers and protect it, we need broad-scale assessments across diverse social and environmental conditions.

Shallow rocky and coral reef fish assemblages offer a unique opportunity to quantify aesthetics. Among ecosystems emblematic for their aesthetic value, reefs host exceptional biodiversity, including over 6,000 fish species (14), many that have evolved vivid coloration

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and body shapes used in camouflage and communication (15, 16). Reef fishes provide at least two key NCPs: i) their aesthetic value is highly important to human cultural heritage and is an iconic example of how biodiversity can be experienced as beautiful, and ii) they have strong economic importance as a vital food source (17) and by supporting aquarium and tourism industries (18). Shallow reefs are indeed important destinations for scuba diving and snorkeling, attracting millions of tourists worldwide and generating an estimated $36 billion per year in revenue (18). Although quantitative aesthetic values are now available for more than 2,000 rocky and coral reef fish species, how these values scale up to fish assemblages around the world has not yet been assessed. Moreover, the environmental and human conditions that enhance (or degrade) fish assemblage aesthetic value have not been identified.

Here, using global, standardized data from the Reef Life Survey (RLS) program (19), we estimated and mapped the aesthetic value of fish assemblages from 3,526 sites worldwide and identified aesthetic hotspots and coldspots. We then assessed the potential environmental and anthropogenic drivers of aesthetic value using causal inference and Bayesian regression models. Finally, we disentangled the pathways by which marine protected areas (MPAs) may affect aesthetic value and analyzed geographic variability in MPA effectiveness. Our study provides a quantitative evaluation of the potential to conserve the aesthetics of these iconic and endangered ecosystems, providing direction for future management.

Results

From Fish Species to Assemblage Aesthetic Values. Our assemblage-level estimates of aesthetic value are indirect and based on previous work by Tribot et al. (13) and Langlois et al. (10) These authors directly quantified reef fish assemblages' aesthetic values through online surveys with >2,000 respondents who ranked fish assemblages by their perceived beauty. The authors similarly quantified individual species' aesthetic values based on >10,000 survey respondents (5, 13). These studies found no influence of sociocultural backgrounds of survey respondents, allowing a robust estimation of species and assemblage aesthetic values. Using linear models, Tribot et al. (13) showed that assemblages' aesthetic values are primarily determined by the combination of species richness and species aesthetic values—assemblages with more species are considered more beautiful, however, certain species can increase or decrease the overall value (13). Using model coefficients from ref. 13, we calculated 1) the aesthetic value of each fish assemblage—the total aesthetic value based on both species richness and species aesthetic values (weighted by species abundances), and 2) the deviation from the value expected based purely on species richness—how much higher or lower an assemblage's aesthetic value is than expected given how many species there are (*Material and Methods*). We weighted species aesthetic values by abundances because highly beautiful species will not contribute importantly to human perception of aesthetic value if they are not commonly observed, and vice versa. Worldwide, we found that assemblage-level aesthetic values increase with species richness as expected (Fig. 1*B*) but that assemblages with the same species richness vary over fivefold due to compositional differences (Fig. 1*C*). Even though species-rich assemblages are more likely to contain species with high aesthetic values, assemblage-level aesthetic values are unevenly distributed along the species richness gradient, with most values being below predictions at low species richness (Fig. 1*B*).

Global Distribution of Fish Assemblage Aesthetic Values. Assemblage aesthetic values closely mirrored global patterns in species richness, increasing toward the equator and decreasing toward the poles (Fig. 2*A*). The Maldives, Seychelles, Vanuatu, Ningaloo, and Western Sumatra ecoregions are aesthetic hotspots with the highest average values (Fig. 2*A*). Conversely the ecoregions with the lowest average values were the North and East Barents Sea, East Greenland Shelf, Channels and Fjords of

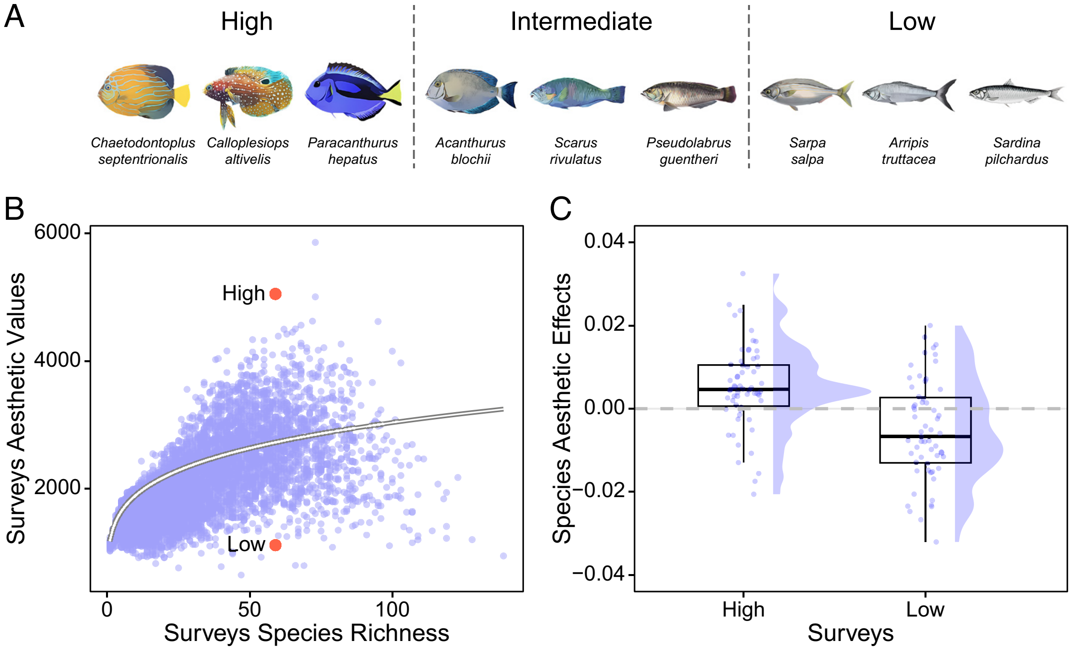

Fig. 1. Evaluating the aesthetic values of RLSs. (*A*) Aesthetic effects were computed for the 2,270 fish species in the RLS dataset. Digitally created drawings of three sets of species with high, intermediate, and low aesthetic values are shown as examples (CC0 1.0). (*B*) Relationship between the number of species in each survey (n = 7,013 surveys across 3,526 sites) and the estimated assemblage aesthetic values. The thick line represents the expected aesthetic values computed with species richness only (*Material and Methods*). Two surveys with the same species richness but high or low assemblage aesthetic values are highlighted in red. (*C*) Distribution of the aesthetic effects among the species present in the two highlighted assemblages in panel (*B*). Boxplots show the median, 50%, and 75% quantiles.

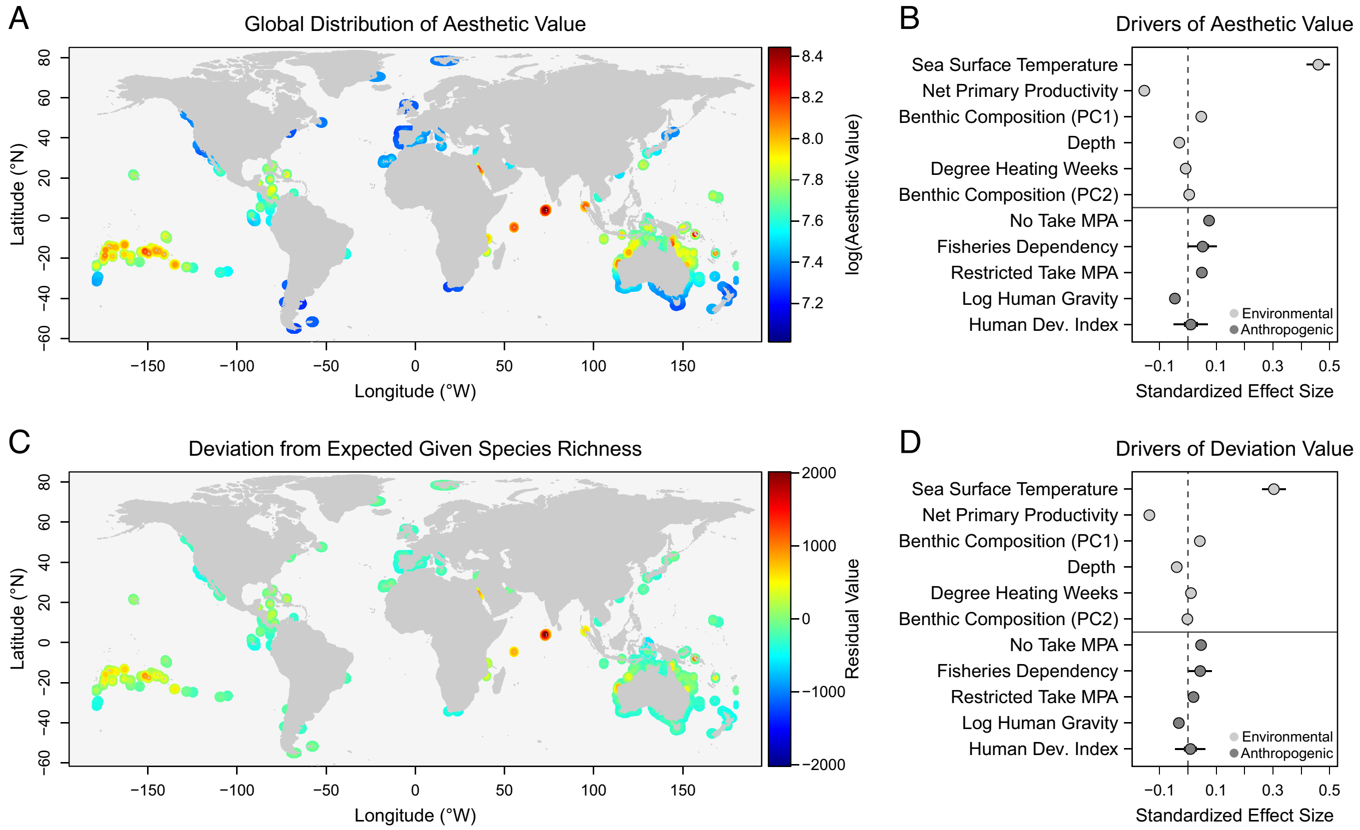

Fig. 2. Global distribution and drivers of fish assemblage aesthetic value. (*A*) Global map of assemblage aesthetic value. (*B*) Forest plot showing the effect sizes, 50% credible intervals (thick lines), and 90% credible intervals (thin lines) for all predictor variables of assemblage aesthetic value. (*C*) Global map of the deviation from the expected aesthetic value given species richness. (*D*) Forest plot showing the effect sizes, 50% credible intervals (thick lines), and 90% credible intervals (thin lines) for all predictor variables of the deviation value. In both panels (*B* and *D*), environmental variables are plotted in light gray and anthropogenic predictors are plotted in dark gray.

Southern Chile, Oyashio Current, and North Patagonian Gulfs (Fig. 2*A*). The deviations from the values expected given species richness (i.e., residual aesthetic values not explained by species richness), followed a similar pattern (r = 0.76 between assemblage aesthetic values and residual values across all ecoregions; Fig. 2*C*). However, several ecoregions deviated significantly in both positive and negative directions. For instance, Vanuatu and the Banda Sea both contained ~70 species per site on average, yet Vanuatu had a much higher average aesthetic value than expected while the Banda Sea had a much lower value than expected. Interestingly, there was also high variation within many tropical ecoregions, meaning that neighboring sites could have contrasting aesthetic values, likely driven by local variation in species composition. The Great Barrier Reef (GBR) had many sites with aesthetic values both substantially lower and higher than expected based on species richness (Fig. 2*C*). Looking closer revealed that GBR sites with high aesthetic values were more characterized by Acanthuridae, Cirrhitidae, and Balistidae, whereas low-value sites where more characterized by Caesionidae, Carangidae, and Lutjanidae (*SI Appendix*, Fig. S1).

Drivers of Fish Assemblage Aesthetic Values. Following the structural causal model [SCM (20)] framework, we generated a Directed Acyclic Graph (DAG) that was used to guide statistical model building (*Material and Methods*). We built individual Bayesian regression models for each anthropogenic and environmental predictor variable, controlling for necessary covariates through the SCM selection framework. From each model, we extracted the posterior distribution (effect size) for the predictor variable of interest and then aggregated all posterior distributions into a single visual plot. Several predictor variables in this study were assessed using ordination axes (*Material and Methods*). Benthic composition was assessed by applying a Principal Components Analysis to benthic substrate proportions recorded from the survey transects and using the first two PC axes as predictor variables (which primarily characterized gradients in live coral vs. macroalgal cover; *SI Appendix*, Fig. S2). In total, we assessed 10 potential predictor variables (*SI Appendix*, Table S1), resulting in 10 regression models. All models had excellent performance, with R^2 values of ~0.88 (for all) when considering both random and fixed effects (of which fixed effects accounted for up to 0.58).

Assemblage aesthetic values were primarily driven by environmental gradients in sea surface temperature (SST) and net primary productivity (NPP) (Fig. 2*B*), with temperature having a strong positive effect (effect size and 90% credible interval = 0.46 [0.42, 0.50]), and productivity having a strong negative effect (−0.15 [−0.17, −0.14]). Assemblage aesthetic values were also influenced by benthic composition (PC1 axis) and depth, with higher aesthetic values being associated with a higher proportion of live coral cover (PC1: 0.046 [0.033, 0.059]; *SI Appendix*, Fig. S2), and shallower depths (−0.030 [−0.038, −0.023]). Beyond environmental factors, aesthetic values were also shaped by human pressure and conservation status. Human gravity had a negative impact on aesthetic values (−0.047 [−0.061, −0.034]), while restricted-take (0.049 [0.038, 0.060]) and no-take (0.075 [0.063, 0.086]) MPAs had positive effects. At the country level, Human Development Index (HDI) did not have an important influence, but countries with higher fisheries dependency had higher aesthetic values, although this effect was variable (Fig. 2*B*). It is important to note, however, that alternative model structures (that included a spatial Gaussian Process) provided slightly weaker effects for some variables (*SI Appendix, Supporting Methods* and Figs. S3 and S4).

We also examined the drivers of the deviation from the values expected based on species richness. Across nearly all predictor variables, we found similar results, but with lower effect sizes (Fig. 2 *B* and *D*). This means that environmental and anthropogenic factors largely influenced aesthetic value through species richness, but not exclusively. SST, NPP, benthic composition, and no-take MPAs remained the most influential drivers (Fig. 2*D*).

Effect of No-Take MPAs on Fish Assemblage Aesthetic Value. After identifying the overall positive effect of no-take MPAs on assemblage aesthetic value, we examined whether this effect varied among ecoregions (*Material and Methods*). We found that the effect of no-take MPAs varied predictably across ecoregions, with a clear unimodal latitudinal pattern (Fig. 3). Tropical ecoregions, with much higher species richness, had substantially stronger MPA effect sizes than temperate regions. Thus, the capacity for MPAs to enhance fish assemblage aesthetic value increases toward the equator with increasing regional species richness.

To disentangle the effects of MPAs, we also tested the strength of each potential causal pathway one by one by blocking each pathway and quantifying the subsequent decrease in the overall MPA effect (*Material and Methods*). We expected MPAs to affect aesthetic values through fish diversity (taxonomic, phylogenetic, or functional), taxonomic composition, trophic composition, and benthic composition, with the sum of these effects approximating the total effect of MPAs. We found that the positive effect of MPAs on aesthetic values was primarily explained by increasing taxonomic diversity, with secondary contributions from phylogenetic diversity and taxonomic composition. Functional diversity, trophic composition, and benthic composition had nearly no contribution to the positive effect of MPAs on aesthetic value (Fig. 4). However, the individual contributions did not account for the entire MPA effect, meaning MPAs also enhance aesthetic values through other mechanisms.

Family Contributions to the MPA Effect. The previous analysis revealed that taxonomic diversity was the main pathway by which MPAs enhanced assemblage aesthetic values, with less contribution by taxonomic composition. Although aesthetic values depend highly on taxonomic composition (10), this is not the primary mechanism by which MPAs enhance aesthetic values. To fully understand this result, we examined how the abundance of each family varied between fished sites and no-take MPAs alongside families' average aesthetic values. We found that among families that dominated in MPAs, there was a mix of both high and low aesthetic values (Fig. 5). For instance, families considered less beautiful such as Latridae (Trumpeters), Lethrinidae (Emperors), and Carangidae (Jacks and Pompanos) were more dominant in MPAs than fished sites, which would reduce aesthetic values below expectations based on species richness (Fig. 5). However, MPAs were also characterized by some highly beautiful families such as Acanthuridae (Surgeonfishes, Unicornfishes, and Tangs), Zanclidae (Moorish Idols), and Pomacanthidae (Angelfishes) (Fig. 5). Hence, MPAs protect families considered both beautiful and less beautiful, so altering taxonomic composition is not the primary pathway by which MPAs increase aesthetic values of fish assemblages.

Discussion

Combining a global dataset of reef fish surveys with species-level aesthetic values, we assessed the global status and drivers of aesthetic value in reef fish assemblages. We found that aesthetic value is intrinsically linked to species richness but varies among reefs of similar richness due to differences in species composition, i.e., from species individual aesthetic effects. Some species have exceptionally high aesthetic values (e.g., Blue-striped Angelfish, Comet), and their presence increases assemblage aesthetic value well above the value expected from species richness alone. As previously highlighted (10), these species cluster in families and phylogenetic lineages found primarily on species-rich tropical reefs. This is a result of the evolution of color and signaling (i.e., through social behavior and camouflage) being an important driver of the richness of highly colorful fish species (15, 16). Consequently, assemblages with aesthetic values substantially higher than expected occur in species-rich tropical regions hosting families such as Chaetodontidae (Butterflyfishes), Pomacanthidae (Angelfishes), and Acanthuridae (Surgeonfishes) associated with the exploitation of coral reef niches. Temperature and productivity had the

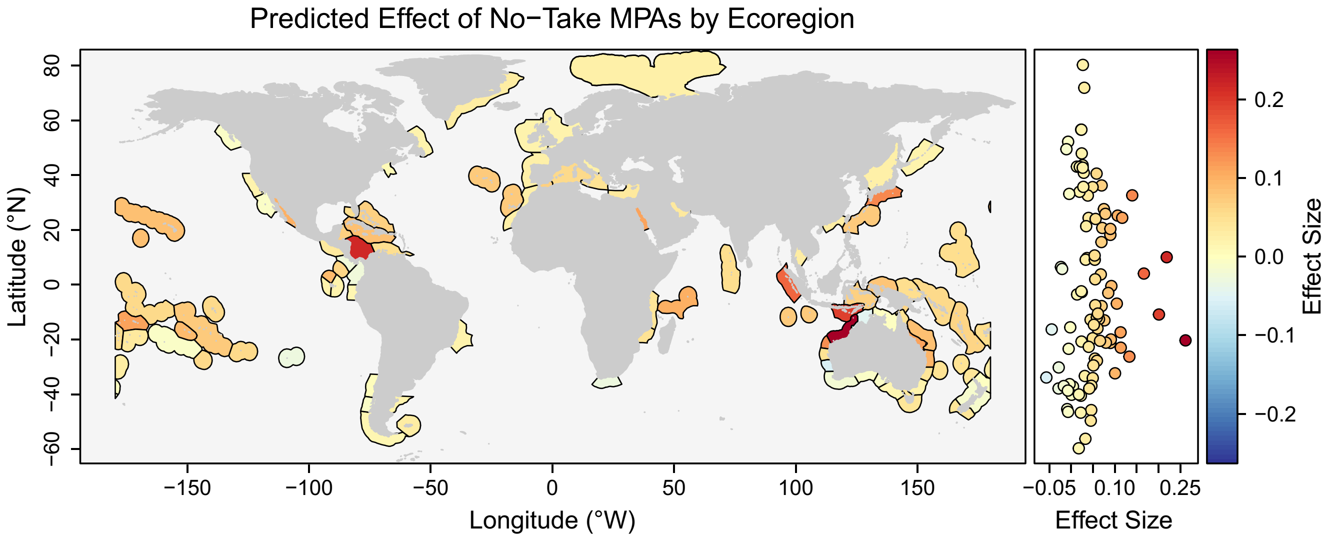

Fig. 3. Geographic variation in the effect of no-take MPAs on fish assemblage aesthetic value. Ecoregions are plotted on the global map and colored by their no-take MPA effect size as predicted from the varying slope model (see *Material and Methods* for details). Effect sizes for each ecoregion are also plotted against latitude (average latitude among sites within each ecoregion).

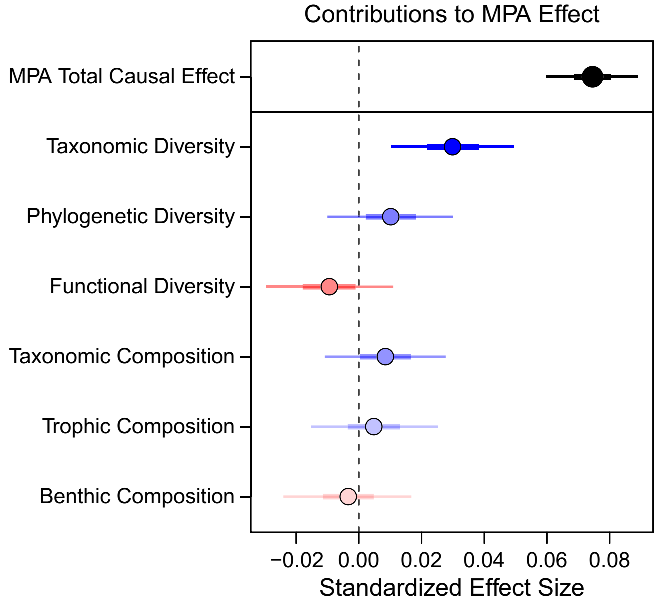

Fig. 4. Contributions of the potential pathways by which no-take MPAs enhance fish assemblage aesthetic value. Forest plot showing the effect sizes, 50% credible intervals (thick lines), and 90% credible intervals (thin lines) for the total causal effect of no-take MPAs and the contributions of each pathway to the total causal effect of no-take MPAs. Red points indicate negative effects, blue points indicate positive effects, and color intensity is scaled to effect size.

strongest effects on aesthetic value, which is unsurprising given their role in shaping biogeographic patterns in species richness (21). However, we also reveal that human gravity and protection status had important effects on assemblage aesthetic values, meaning conservation actions can enhance and preserve the overall beauty of shallow reefs, which is key for Nature's Contribution to People (NCP).

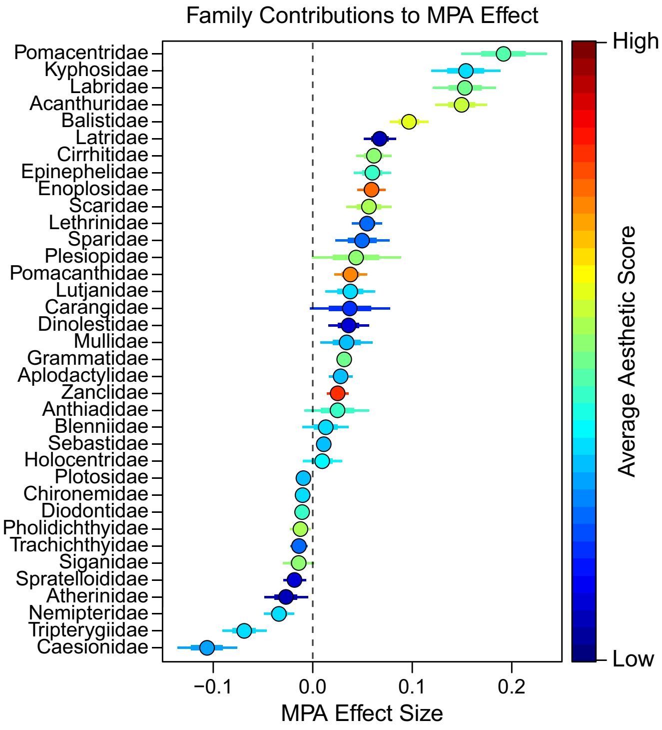

Fig. 5. Family contributions to the effect of no-take MPAs on fish assemblage aesthetic value. Forest plot showing the effect sizes, 50% credible intervals (thick lines), and 90% credible intervals (thin lines) for the influence of MPA status on family abundances. Only the families with the highest absolute MPA effects (top 25%) are shown. Families are colored by the average aesthetic value of their species.

Although aesthetic values depend highly on species composition, we highlight that MPAs primarily enhance fish assemblage aesthetic values by increasing taxonomic diversity. People's perceptions of aesthetic value are known to depend strongly on species richness, with greater preference for more diverse assemblages (13). Assemblages with higher taxonomic and phylogenetic diversity are also more likely to host species considered exceptionally beautiful (Fig. 1). Yet, differences in taxonomic composition did not contribute strongly to the positive effect of MPAs on aesthetic value. Many heavily fished families such as Carangidae (Jacks and Pompanos), Sparidae (Sea Breams and Porgies), and Lutjanidae (Snappers) have low average aesthetic values, and these groups benefit from protection against fishing (22, 23). Although MPAs also host many beautiful families, the fact that protection benefits species considered less beautiful implies that differences in taxonomic composition are not the primary means by which MPAs enhance fish assemblage aesthetic values. This is an intuitive result, but it has important implications for conservation, because it demonstrates that MPAs can potentially serve multiple NCPs simultaneously. MPAs have the potential to boost populations of fished species, while simultaneously creating hotspots of beauty by supporting greater species diversity. We thus find important support for MPAs as broad conservation tools that can potentially benefit both fisheries and tourism simultaneously.

We also found that fish assemblage aesthetic value is higher on reefs with greater coralline algae and live coral cover. Coral cover creates complex three-dimensional habitat that can enhance fish species diversity through greater niche availability, as well as by increasing refuge for juveniles and prey species (24, 25). Many exceptionally beautiful species are also facultative or obligate coral users/feeders, notably butterflyfishes and wrasses (26). The positive relationship between live benthic habitat and aesthetic value is particularly important because it means that managers can potentially enhance the beauty of reef fish assemblages by protecting living coral or through coral restoration, albeit at very localized scales. Unfortunately, the influence of benthic habitat also means that future coral mortality will strongly degrade fish assemblage aesthetic value, and major declines in overall reef beauty are to be expected in the coming years. Surprisingly, benthic composition was not identified as a major pathway by which MPAs increase aesthetic value. However, it is important to recognize that this is the average result across all reefs surveyed worldwide, and results are context-dependent at the local scale. In many cases, MPAs and openly fished sites have similar benthic composition, and MPAs may be deliberately placed in degraded areas to promote recovery (27). However, given that live coral cover boosts the aesthetic value of reef fish assemblages, managing for coral-dominated reefs is a key way managers can indirectly conserve aesthetic value, and placing MPAs around thriving coral is likely to produce the greatest overall aesthetic benefits (28).

Interestingly, countries' HDI had no influence on fish assemblage aesthetic value, while those wither greater fishing dependency hosted more beautiful assemblages. This is another important result, because it indicates that the ability to protect and enhance aesthetic value is not constrained by wealth or socioeconomic development. Wealthier countries could have greater capacity and infrastructure to create and enforce MPAs, yet both high and low-income countries can host exceptionally beautiful fish assemblages. Moreover, given the greater potential for MPA benefits in species-rich, tropical regions and the fact that human development and GDP decrease toward the equator (29), MPAs are promising tools to safeguard multiple NCPs in developing tropical countries where socioeconomically viable or acceptable.

Although our results highlight the effectiveness of MPAs in conserving the beauty of the world's reef fish assemblages, only 7% of global coral reefs are partially or fully sheltered by MPAs (30). Moreover, previous studies have shown that most MPAs are ineffective due to illegal fishing, poor management, improper placement, or other issues (31). Given the low level of marine protection globally and the sensitivity of aesthetic value to environmental conditions and coral cover, the beauty of the world's reefs appears severely threatened, and immediate action is needed to integrate aesthetic value into reef conservation and management plans. Biodiversity worldwide is deteriorating at rates unprecedented in human history, yet humans continue to depend on biodiversity for recreation, cultural inspiration, and material goods. In response to this challenge, the Kunming-Montreal Global Biodiversity Framework set out to ensure that by 2030 at least 30% of marine and coastal areas of particular importance for biodiversity and ecosystem functions are conserved and managed through protected areas and that 30% of degraded areas are under effective restoration. Our findings suggest that investments in expanding and strengthening MPAs or restoration will pay off, particularly when effectively protecting reef systems where both material (e.g., fish biomass for consumption and nutrition) and nonmaterial (aesthetic value) contributions can be secured.

Despite the importance of our findings, our study had several important limitations. First, we only considered fish assemblages, which are one component of reef ecosystems. Other organisms from hard corals and seaweeds to crabs and nudibranchs all contribute directly to reef aesthetic values. Given the aesthetic appeal of hard and soft corals themselves and the invertebrates that live within them, many reefs with depauperate fish assemblages are likely to still be considered beautiful by many people. Comparing patterns in aesthetic values across taxa should reveal important insights into the covariation of beauty and whether beautiful fish species are associated with beautiful species of coral or other organisms. We also removed Pleuronectiformes (Flatfishes) and Syngnathiformes (Seahorses and Pipefishes) that could contribute importantly to aesthetic value, particularly species like Pygmy Seahorses, which are highly sought after by recreational divers (32). Additionally, by only considering ray-finned fishes (Actinopterygii) we miss the potential contributions of sharks and rays, which also attract major tourism enthusiasm (11, 32). The disproportionate presence of very large fishes within MPAs should also add to the aesthetic values quantified here and should be incorporated into more comprehensive estimation of people's perception of reef fish assemblages. People may also be drawn to large schools of fishes, and although we weighted aesthetic value by abundance, we cannot fully capture this effect, but this is an interesting avenue for future research. It has also been demonstrated that some taxonomic groups are more likely to avoid divers (33), and diver surveys do not account for uneven species detectability. However, identical protocols are used in all RLS surveys and because human interest in reef fish aesthetics is mainly through diving and snorkeling, our data truly reflect the potential human perception of beauty. We also acknowledge that appreciation of beauty can be subjective and vary from person to person depending on sociocultural background (e.g., ref. 34). However, despite these potential differences, the studies on which we based our aesthetic evaluation (refs. 10, 13) found no effect of the public's sociocultural background on their aesthetic preferences (despite using very large pools of more than 2,000 and 13,000 participants, respectively, although it should be noted that these surveys were only available in two languages). While we did not assess water clarity in this study, realized aesthetic appeal will also depend highly on visibility, and assemblages in clear, oligotrophic waters likely have greater potential for aesthetic value. Finally, while we find that taxonomic diversity is the main pathway by which MPAs boost aesthetic value, the absolute difference in richness between fished sites and MPAs is low (~five species on average), and evidence for MPAs enhancing richness at local scales is mixed (35). the causal pathways we tested did not fully account for the total effect of MPAs, and the importance of taxonomic composition may vary regionally. For instance, higher aesthetic value in MPAs could be driven by greater abundances of Acanthurids in one region but by Pomacanthids in another region, and a broad assessment of taxonomic composition may not fully account for this. The finding that benthic composition was not a primary pathway by which MPAs enhance aesthetic value is also likely influenced by the limited and simplified habitat data available for this study. Further study, particularly at local scales, is needed to verify whether MPAs have the potential to boost aesthetic value by harboring greater coral habitat.

By shifting toward a NCP framework, we can recognize the critical role that aesthetic value plays in shaping our relationship with nature. This recognition can help us develop more comprehensive conservation and management strategies that recognize and enhance the full range of benefits that shallow reefs provide to people. By conserving and restoring the aesthetic value of shallow reefs, we can not only protect these ecosystems but also contribute to the well-being of the people that rely on them.

Materials and Methods

RLS Data. We used fish assemblage data from the RLS—a monitoring program that uses standardized protocols to assess the composition and diversity of fishes, invertebrates, and benthos on shallow rocky and coral reefs worldwide (19). During RLS surveys, trained divers identify, count, and estimate the sizes of all fishes encountered along two 50-m × 5-m blocks per transect. The fundamental survey unit in RLS is therefore the individual transect. Usually, two transects are surveyed within the same patch of reef (within 200 m of each other), an area referred to as a site. To maximize spatial coverage and avoid repeat surveys, we selected the most recent surveys conducted across RLS sites (2006 to 2019). This resulted in 7,013 surveys from 3,526 sites, encompassing 2,655 fish taxa. Fish taxa included unidentified families and genera, for which precise aesthetic values are not available. We then filtered out such taxa for which we did not have aesthetic information. The final list of species used in this study is based on ref. 10 and included the ray-finned fishes (Actinopterygii) from the RLS database, minus the orders Pleuronectiformes (14 species) and Syngnathiformes (31 species) that were removed because of their unusual morphologies that did not fit with the protocol used by Tribot et al. (5). After filtering the RLS fish assemblage data to species for which we had aesthetic information, we ended up with a total of 2,270 fish species.

Aesthetic Value of Fish Assemblages. The next step was to estimate the aesthetic value of the 7,013 surveys in our dataset. To do so, we relied on three previous studies. Tribot et al. (13) conducted an online survey to directly quantify the aesthetic values of coral reef fish assemblages along a gradient of species richness. They then determined the influences of species richness and species composition on assemblage-level aesthetic value using a multiple regression model. In this model, species composition was included as the presence/absence of each species (0 or 1). This model showed that richness and species composition together explained nearly all variation ($R^2 = 0.94$) in assemblage-level aesthetic value. The authors were then able to assess the contribution of each species to assemblage-level aesthetic value based on species individual regression coefficients, which they referred to as species "aesthetic effects" (i.e., how much species presence or absence increased or decreased overall aesthetic value). In a separate study, Tribot et al. (5) also directly quantified individual species aesthetic values based on an online survey where respondents ranked individual species by their perceived beauty. Finally, Tribot et al. (13) showed that there was a strong correlation between species aesthetic effects at the assemblage level (coefficients from the regression model) and species individual aesthetic values from the survey rankings.

To quantify aesthetic values for our 7,013 surveys, we therefore needed i) species richness and ii) species aesthetic effects. Species richness was simply calculated as the number of species per survey. However, because we were working backward (trying to predict assemblage-level aesthetic value), we did not have aesthetic effects for each species. Fortunately, because Tribot et al. (13) showed that species aesthetic effects were strongly correlated to species individual aesthetic values, we were able to estimate species aesthetic effects using species aesthetic values from ref. 10. Our procedure for estimating aesthetic value for each survey was therefore i) convert species aesthetic values from ref. 10 to species aesthetic effects using the fitted model from ref. 13, ii) input species richness and species aesthetic effects into the regression model from ref. 13, i.e., Aesthetic Value ~ Sp. Richness + Sp. Aesthetic Effects. To account for uncertainty in the models fitted by Tribot et al. (13), we regenerated their original models as Bayesian regressions and used the resulting posterior distributions to generate predictions. For each parameter (i.e., regression coefficient), we extracted 4,000 posterior draws, ran predictions, and took the median value of the resulting prediction distribution. However, while Tribot et al. (13) focused on species' occurrences only, we integrated species abundances, which can strongly influence assemblage-level patterns. To do so, we weighted species' aesthetic effects in the regression model by their log-transformed abundances. Thus, highly beautiful species would contribute less to assemblage aesthetic value if they are rare, etc. This procedure provided estimates of the total aesthetic value of all 7,013 surveys in the dataset.

We also calculated the expected aesthetic value based purely on species richness, which was simply calculated by inputting species richness only (without species aesthetic effects or abundances) into the model from ref. 13. Finally, we calculated the deviation in total aesthetic value from the value expected based purely on species richness, which was a measure of how much higher or lower each assemblages' total aesthetic value was due to compositional effects (e.g., hosting an abundance of exceptionally beautiful or nonbeautiful species). To make this clear for the reader, the total aesthetic value of each survey can be visualized as the value of each dot along the Y-axis in Fig. 1*B*. Again, this is the value predicted by the combination of species richness and species abundance-weighted aesthetic effects. The aesthetic value expected based purely on species richness can be visualized as the fitted white curve in Fig. 1*B* (the value predicted by species richness alone). The deviation from the value expected based on species richness can be visualized as the residuals between the fitted white curve and the actual blue dots in Fig. 1*B* (i.e., how much higher or lower each dot is along the Y-axis in comparison to the fitted white curve).

Global Maps. RLS contains over 3,000 sites, many of which are grouped within a few kilometers. Visualizing these data on maps is difficult because many points are superimposed, which can mask important values and trends. To generate a global map that accurately depict aesthetic value across sites without superimposition, we used Inverse Distance Weighted spatial interpolation (IDW), following ref. 36. IDW functions by assuming that similarity between locations diminishes with increasing distance. We first created a 1,000 × 1,000 cell raster grid and assigned existing sites to cells. We then created a 150-km buffer around all empty cells and calculated the distance to existing sites within the buffer. For each empty cell, the value was interpolated as the average of all corresponding sites weighted by the inverse distance raised to the power of 1.6 (power values between 1 and 2 are recommended, with higher values decreasing the influence of faraway points). This produced a 1,000 × 1,000 cell grid of aesthetic value that was then mapped in base R with the center point of each grid cell plotted as a point.

Causal Inference Theory and DAGs. It is often accepted that cause-and-effect relationships can only be derived from randomized experiments where confounding variables are carefully controlled and only variables of interest are manipulated (20, 37). Consequently, studies based on observational data usually conclude that they can identify correlations, but that correlations do not necessarily represent cause-and-effect relationships. However, recent integration of causal inference theory within ecology and biodiversity science has improved our ability to estimate cause-and-effect relationships from observational data (20, 38).

Here we apply a recently emerging and widely applicable causal inference framework, the SCM (20, 37), to determine the global drivers of aesthetic value in reef fish assemblages. SCM uses DAGs to visualize the causal structure of a system under study, and subsequently guide covariate selection required to answer causal queries. DAGs are used to represent a researcher's assumptions about the causal structure of a system or process under study, and must be justified, for example, through published literature, expert opinion, and/or scientific consensus. A DAG consists of a set of nodes (variables) that are connected to each other by arrows. These arrows represent hypothesized causal relationships between variables, pointing from cause to effect, with causes preceding their effects. Importantly, DAGs must include all variables (both measured and unobserved) required to depict a system or process under study, including common cause variables, defined as variables that affect two or more variables already included in a DAG (37).

During a series of meetings with reef ecology experts from around the world (BiodivERsA REEF-FUTURES consortium), we constructed a DAG depicting hypothesized cause-and-effect relationships between several anthropogenic and environmental covariates (*SI Appendix*, Fig. S5 and Tables S1 and S2). First, we included all variables of interest (i.e., predictors), that is, those for which we wished to assess the potential causal effect on fish assemblage aesthetic value. Next, we added common cause variables, which are variables that affect two or more of the variables already in the DAG. For example, although we were not interested in the causal effect of latitude on aesthetic value, we included it in our DAG as we hypothesized that latitude influences several variables of interest such as SST, NPP, and the HDI. We further scrutinized our DAG for potential missing links and added these links where necessary to depict the overall causal structure of our study system. We continued to discuss and modify the DAG until the majority of participants reached a consensus and were satisfied with the links and structure.

Once the DAG was finalized, we tested DAG-data consistency. Simply put, a DAG usually implies many independencies (e.g., X is independent of Y) and conditional independencies (e.g., X is independent of Y, given Z) that should be consistent with the observational data, given that both the observational data and DAG are representative of the data-generating process. If DAG-data consistency is ensured, this provides support for the asserted structure of the DAG itself. On the other hand, failed independencies indicate potential incorrect or missing links. The Dagitty framework, and the corresponding R package *dagitty* (39), conveniently tests DAG-data consistency via a series of partial correlations and allows users to specify the threshold for determining whether an independence has passed or failed. This threshold can be specified according to either p-values or Pearson correlation coefficients. We chose to use a Pearson correlation coefficient of 0.30, which most literature defines as a "weak" relationship (40). We opted against *P*-values because our database has over 7,000 observations, and a Pearson correlation as low as 0.03 will yield a "significant" *P*-value with a sample size this large. Our DAG resulted in 170 conditional independencies. Initial DAG-data consistency tests revealed some failed independencies that we scrutinized and used to update and improve the DAG, i.e., the failures indicated we had missed important links that we then added. For example, we initially included a link from latitude to HDI (on the basis of refs. 29 and 41), but no link from SST to HDI. DAG-data checks indicated that a correlation existed between SST and HDI, even after accounting for their potential cocorrelation with latitude. Thus, we added a direct link from SST to the HDI, which is supported by refs. 41–43. We continued to scrutinize and refine our DAG until all conditional interdependencies were validated.

It is important to note that results from our DAG-based approach to causal inference are dependent on the structure of the DAG and the underlying causal assumptions. Other DAGs are possible that could lead to slightly different results. However, a key strength of this approach is that our DAG is based on a synthesis of scientific literature and discussions among reef ecology experts. Additionally, our causal assumptions are transparently published in our DAG, and readers can directly see how our assumptions translate to our models and results. Thus, readers can appreciate our results in the context of these assumptions, whereas most analyses in ecology do not follow a formal procedure for selecting control variables that remove statistical biases, including confounding and overcontrol bias.

Anthropogenic and Environmental Factors. We extracted data for all available anthropogenic and environmental factors depicted in our DAG. Full details on all variables, such as their scale, their source, and whether they were included as a predictor or control is provided in *SI Appendix*, Table S1. Briefly, survey depth was recorded in situ during RLS data collection using a diver depth gauge. SST data came from the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch Daily 5 km Satellite Heat Stress Monitoring database (44), which provides mean, minimum, and maximum daily SST values from 1985 to the present. We selected mean annual SST for each site over the last 5 y. Degree Heating Weeks (DHW) is an indicator of acute heat stress that combines duration (number of weeks) and intensity (degrees C above local expected maximum monthly temperature) and is expressed as number of heating weeks (1 wk at 1 °C over expected = 1 DHW). We selected mean annual DHW over the last 5 y. DHW data also came from the NOAA Coral Reef Watch Database. NPP came from the Vertically Generalized Production Model that estimates NPP using satellite-derived surface chlorophyll concentrations, daytime SST, and photosynthetically active radiation and is available from 2002 to 2019 (45). We selected the mean annual NPP for each site over the last 5 y. Human gravity is a proxy for anthropogenic pressure expressed as a function of human population size and travel time to a reef and examines the amount of human pressure within the surrounding 500 km of a reef (46). MPA status was classified as either no-take, where all fishing and extraction activities are prohibited, restricted-take, where certain fishing gears or species removals are permitted, or openly fished, where no regulations are in place. MPA status in the RLS database is usually recorded at the time of surveys, although in some cases has been added using boundaries from local MPA maps or based on local advice. HDI is an integrative metric that reflects the level of human health, education, and wealth within a country, and ranges from 0 to 1 (low to high). HDI data (from 2017) came from the United Nations Human Development Indicators database (https://hdr.undp.org/data-center). Fisheries dependency data came from ref. 47, which integrates quantitative indicators of the contribution of coastal fisheries to a country's 1) economy, 2) employment, or 3) food security.

Benthic composition is assessed during RLS surveys using photoquadrats of the substrate. Twenty evenly spaced photos are recorded along the survey transect and later processed using SQUIDLE+ software (https://squidle.org/). Points are randomly overlaid on photographs, and users identify the organisms the points land on into broad functional groups or to the lowest taxonomic resolution possible. This provides percent cover data for benthic organisms such as corals, macroalgae, sponges, etc. Here, we binned the groups into nine broader benthic groups that can be consistently applied globally: coral, algae, coralline algae, seagrass, other sessile invertebrates (e.g., ascidians, sponges), coral rubble, rock, sand, and microalgal mats (e.g., cyanobacteria, encrusting algae films). Although we worked at the global scale, benthic data were primarily available for tropical sites (benthic data had not been processed and analyzed for many RLS locations at the time of analyses). We therefore only considered benthic composition from tropical sites, and statistical models were adjusted to account for this (see *Bayesian Regression Models* below). We defined tropical sites as those that experience minimum monthly SSTs of 17 °C (48). Although the tropical SST limit is usually defined at 20 °C, we used this broader definition of tropical oceans, thereby including locations where species of tropical affinity are present (48). Because we were interested in overall benthic composition across all categories, we used an ordination analysis. We first applied an arcsine transformation (inverse Sine of square-root transformed values) to the proportional benthic cover data, which were highly right skewed. This is similar to a log transformation but more appropriate for proportional data, which are bounded between 0 and 1 (49). We then applied a Principal Component Analysis (PCA) to the resulting transformed data. We then used the first two PCA axes as indicators of overall benthic composition and included them as predictor variables in our drivers' models. Unfortunately, benthic data were unavailable for 36% of tropical surveys. A typical approach would be to delete all surveys where benthic data are unavailable. However, this would throw away a substantial amount of valuable surveys where data for all other covariates are available. Second, removing missing data can induce bias, for instance, if missing data share common characteristics, e.g., missing data come from the most remote locations. In this case, removing surveys with missing data would systematically bias subsequent analyses. Therefore, we chose to impute missing values using random forest, through the R package missForest (50). Full details for this procedure are detailed in the *SI Appendix*.

Species Traits. To calculate the functional diversity of reef fish assemblages, we compiled a trait database of six categorical traits that describe the ecological lifestyle of the 2,270 species included in this analysis. The traits selected were body size, diet, trophic level, gregariousness, substrate preference, and water column position. Body size was categorized into six ordered size bins: 0 to 7 cm, 7.1 to 15 cm, 15.1 to 30 cm, 30.1 to 50 cm, 50.1 to 80 cm, and >80 cm. Diet was classified into seven categories: piscivores, invertivores, corallivores, omnivores, microphages, and grazers. Trophic level was binned into five ordered categories of >2.5, 2.51 to 3.0, 3.01 to 3.5, 3.51 to 4.0, and >4.00. Gregariousness, which describes schooling behavior, was classified into three ordered categories: solitary, pairing or forming small schools, and schooling. Substrate preference was classified into four categories: sand, coral, rock, or water column. Finally, water column position was categorized into four ordered categories: benthic, benthopelagic, pelagic site-attached, and pelagic-mobile (moving between reefs). Trait data were sourced from ref. 51, FishBase (52), and expert knowledge. These methods resulted in a trait database of 2,460 species, where 90.16% of the data were complete (2,218 species). For the 9.84% of missing trait data (242 spp.), we imputed the missing values using missForest. To increase imputation accuracy, we included phylogenetic position captured by the first four axes of a Principal Coordinates Analysis applied to the ray-finned fish phylogeny, fishtree (53, 54) using pairwise cophenetic distances (55). For all imputations, body size and trophic level were converted to their continuous forms. The trait database was then filtered to 2,270 species based on the availability of aesthetic value information for the analysis.

Assemblage Metrics. We assessed taxonomic composition at the family level through an ordination analysis. We first calculated the average abundance of each family in each site and then log-transformed and Hellinger-transformed the abundances. The log transformation reduces skew and dampens the influence of extremely abundant taxa, while the Hellinger transformation reduces the influence of double zero similarity in ordination analysis. We then applied a PCA to the transformed abundance data and used the first four axes as indices of taxonomic composition among sites (*SI Appendix*, Fig. S6).

We also assessed trophic composition through an ordination approach. We first calculated community-weighted mean values of trophic guild categories for each survey using log-transformed abundances. This results in a matrix of proportions of abundance composed of each trophic guild for each site, e.g., 40% invertivores, 30% herbivores, 20% planktivores, 10% piscivores, etc. We again applied an arcsine transformation to the proportions because they were highly skewed and then applied a PCA (*SI Appendix*, Fig. S7). We used the first four PCA axes as indicators of overall trophic composition.

Because assemblage-level aesthetic values were calculated using both species richness and abundance, we used taxonomic, phylogenetic, and functional entropy to assess assemblage diversity. We applied the common mathematical framework based on Hill numbers, which generalizes diversity measures to allow for sensitivity to species abundances based on the parameter q. For all entropy analyses, we set $q = 1$, which weights species, functional groups, or phylogenetic lineages by their relative abundances. This corresponds to the exponential of Shannon entropy for taxonomic diversity, Rao's entropy for functional diversity, and Faith's PD for phylogenetic diversity (56, 57). For functional diversity, the parameter τ was set to the mean functional distance between all pairs of species (56). Phylogenetic diversity was calculated following ref. 57 using the phylogenetic fishtree from ref. 54 with updates by ref. 53.

Bayesian Regression Models. To estimate the potential causal influences of anthropogenic and environmental factors on fish assemblage aesthetic value, we used a series of hierarchical Bayesian regression models. In following with causal inference theory, we did not build one single statistical model to assess the potential influences of all predictor variables simultaneously, but rather built one individual model for each predictor variable. For each predictor variable, we used the DAG to determine the structure of the regression model. To do this, we used the online DAGitty interface (http://www.dagitty.net/). We individually set each predictor variable to the "exposure" in the DAG with aesthetic value set as the "outcome." We identified the minimum adjustment set necessary to obtain the total causal effect of each predictor variable (*SI Appendix*, Fig. S8). The minimum adjustment set provides the list of additional covariates that must be included in a regression model to satisfy the backdoor criterion and account for potential statistical biases. For each individual regression model, although multiple covariates were often included, we extracted only the effect size for the variable of interest. For instance, when estimating the total causal effect of SST, the DAG indicated the minimum sufficient adjustment set must include latitude as a covariate. Hence, our regression model for SST took the basic form: aesthetic value ~SST + Latitude, yet only the effect of SST was derived from this model, with latitude included purely as a statistical control. For some variables, the DAG provided multiple options for minimum adjustment sets. Among the candidate sets, we chose the set that i) included the fewest covariates, and/or ii) included covariates for which we believed that data quality was the highest (e.g., measured in situ or derived from robust remote sensing products at high spatial resolution). This approach was chosen to minimize potential error associated with high collinearity among covariates or variable measurement error.

Because each regression model had the same response variable (aesthetic value), the same model structure was always used. Aesthetic value is bounded between 0 and infinity and is highly log-skewed (many small and few large values). The maximum entropy distribution for modeling such data is either log-normal (equivalent to Gaussian applied on log-transformed values) or Gamma (58). All models therefore used the log-transformed values of aesthetic value as the response with a Gaussian likelihood distribution and an identity link function. All models included transect nested in site and site nested in country as random effects to account for the hierarchical structure of the RLS data (transect surveys are nested within sites and those sites are nested within countries), to account for the nonindependence and spatial autocorrelation of observations belonging to the same site or country, and to allow for predictor variables at different spatial levels. For instance, depth is measured at the transect level, temperature is measured at the site level, and HDI is measured at the country level. Random effects ensure these predictor variables are assessed at the relevant spatial scale within the model. Additionally, each model included climatic zone–tropical or temperate–as a fixed effect. This fixed effect was included for two reasons: i) to account for the large intrinsic differences that exist in aesthetic value and anthropogenic/environmental factors between tropical and temperate locations, and ii) to account for the fact that benthic composition data were not available in temperate locations. Setting all benthic composition observations to 0 in temperate locations and including climatic zone as a fixed effect rather than a random effect prevented temperate observations from contributing to the overall effect size of benthic composition. The full model structure and Bayesian notation are shown in the *SI Appendix*.

We additionally ran a second set of models in which the effect of species richness was "removed," meaning the contribution of species richness to the total causal effect of any given predictor variable was deleted. This was done simply by including species richness as a control variable within each regression model. This assessed how anthropogenic and environmental conditions contribute to the residual value of aesthetic value not accounted for by species richness, i.e., the degree to which aesthetic value is higher or lower than expected for a given level of species richness. This approach is synonymous to first running a model of aesthetic value ~species richness and extracting the residuals of that model to be used in a second series of models, but is the proper method for achieving this goal (see ref. 59 for an explanation on the misuse of residuals as data).

All models were built using the R package *brms* (60) and were run with four chains of 4,000 iterations. As indicated in the equations above, the prior distribution for all slope coefficients and intercepts was a normal distribution with mean 0 and SD 3. This distribution was chosen to be noninformative yet regularizing–constraining the potential slope and intercept values to a realistic range to improve model running time (58). However, priors have little influence with very large datasets and sensitivity tests confirmed that our results were robust to both weakly informative and flat priors (*SI Appendix*, Fig. S9).

After each model was run, the posterior distribution for the variable of interest was extracted, and finally, all posterior distributions were regrouped to generate forest plots. All models were run until sufficient effective sampling size was achieved and Gelman–Rubin diagnostic statistics converged to 1.0. Model performance was checked for each model using the function check_model in the R package *performance* (61), which provided diagnostic plots of i) posterior predictive check, ii) linearity, iii) homogeneity of variance, iv) influential observations, v) collinearity, vi) normality of residuals, and vii) normality of random effects. All model diagnostic plots are provided in *SI Appendix*, Figs. S10–S19. Model checking revealed high Variance Inflation Factors (VIF) for the SST, NPP, DHW, and HDI models due to multicollinearity with latitude. Unfortunately, given our DAG, no alternative minimum adjustment sets were available that did not include latitude as a control variable. Therefore, to test the degree to which multicollinearity influenced model results, we ran sensitivity tests where we reran the models without latitude as a control variable. In all cases, effect sizes showed zero or very little change whether latitude was included, and the test models had low VIF, indicating that multicollinearity had little influence on model results (*SI Appendix*, Figs. S20–S23).

Finally, we tested alternative model approaches. While we used random intercepts for sites nested in countries, an alternative approach would be to include random slopes. We tested models with random intercepts for country and site and random slopes for country (however, sites could not be nested in countries in this configuration within the brms modeling package). However, we found that some models produced singular fits, meaning that the data did not support meaningful variability for the random effects and that these random slope models were potentially too complex for our data, which are sparse in some locations. Thus, random intercepts models were more parsimonious in that they accounted for spatial patterns and heterogeneity in the data without being overly complex and causing convergence issues. We also tested models that included a spatial Gaussian Process to explicitly model spatial dependence in the data. These models provided very similar results to our original models, although with some variables having weaker or more uncertain effect sizes. These models and their results are fully detailed in the *SI Appendix*.

Estimating Geographical Variation in the Effect of No-Take MPAs. To examine regional variation in the effect of MPAs, we reran the regression model for the total causal effect of MPAs with the same minimal adjustment set as previous, but we allowed the slope (i.e., effect size of MPA) to vary by ecoregion. This way, we obtained an estimated effect of no-take MPAs for each ecoregion. The full model structure and Bayesian notation are shown in the *SI Appendix*. After running the model, we plotted the relationship between latitude (i.e., average latitude of sites) and the estimated effect size of no-take MPAs across ecoregions (Fig. 3).

Disentangling the Influence of No-Take MPAs. We hypothesized that MPAs could enhance fish assemblage aesthetic value by boosting diversity (taxonomic, phylogenetic, or functional), containing benthic substrates more likely to host beautiful species (benthic composition), containing trophic groups characterized by beautiful species (trophic composition), or containing beautiful species that are sensitive to human impacts (taxonomic composition). To disentangle these potential pathways, we again used our DAG to run a mediation analysis. We ran a series of regression models where we blocked each corresponding pathway individually and calculated by how much the total causal effect of MPAs declined. For instance, to calculate the contribution of taxonomic diversity to the MPA effect, we reran the same model for the total causal effect of MPAs, but this time with taxonomic diversity included as a control. We then extracted the new effect size of MPAs and subtracted this from the original (by subtracting the second posterior distribution from the first). We did this for each pathway and recorded the resulting value, which was considered the pathway's contribution to the overall MPA effect.

Examining How Families Differ Between Fished Sites and No-Take MPAs. We examined how family abundances varied between fished sites and no-take MPAs (i.e., MPA effect for each family) alongside the average aesthetic value of each family. We first calculated the average abundance of each family at each site. To calculate the MPA effect per family, we then ran an individual regression model for each family. These models all had the same structure and used a Gaussian likelihood distribution applied to log-transformed abundance values. Because abundances were site-level averages, values were continuous and not integers, therefore permitting a Gaussian distribution rather than a Poisson or Negative Binomial. Each model also included Ecoregion as a random effect, under the assumption that sites within Ecoregions were nonindependent, particularly fished sites and MPAs. (see ref. 62 for details on the Marine Ecoregions of the World). Ecoregion was also used in lieu of country in these models, as no country-level predictor variables were included, and ecoregion provided a finer-scale and more geographically balanced resolution. The full model structure and Bayesian notation are shown in the *SI Appendix*. We then calculated the average aesthetic value of all species in each family. To understand how different families contribute to overall aesthetic value in MPAs, we then identified the families with the greatest positive or negative MPA effects (top 25% highest absolute effect sizes) and plotted them in descending order and colored them by their average aesthetic values.

Finally, while our results focus heavily on the potential influence of MPAs on aesthetic value, we would like to clarify that our global scale analysis does not compare spatially paired (i.e., adjacent) MPAs and fished sites. While we do consider random effects for sites, countries, and ecoregions (which account for the spatial distribution and nonindependence of sites), our analyses assess average patterns across all no-take MPAs in the RLS database. A truly paired analysis would require a high number of directly adjacent MPA and fished sites, which is unfortunately not available at the global scale.

Data, Materials, and Software Availability. All data required to recreate the analyses and figures used in this study are available on a dedicated GitHub repository (63), which has been archived as a publication release on Zenodo (64).

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