



ECOLOGY

Low human interest for the most at-risk reef fishes worldwide

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Human interest in biodiversity is essential for effective conservation action but remains poorly quantified at large scales. Here, we investigated human interest for 2408 marine reef fishes using data obtained from online public databases and social media, summarized in two synthetic dimensions, research effort and public attention. Both dimensions are mainly related to geographic range size. Research effort is also linked to fishery importance, while public attention is more related to fish aesthetic value and aquarium trade importance. We also found a strong phylogenetic bias, with certain fish families receiving disproportional research effort and public attention. Most concerningly, species at the highest risk of extinction and those most vulnerable to future climate change tend to receive less research effort and public attention. Our results provide a lens through which examining the societal attention that species garner, with the ultimate goals to improve conservation strategies, research programs, and communication plans.

INTRODUCTION

Human activities are eroding biodiversity (1, 2) and strongly disrupt ecosystem functioning (3), which not only have marked consequences on the direct goods nature provides to humanity but also degrade our experience of nature (4). To halt this widespread biodiversity decline, more effective and ambitious conservation policies and practices are needed, which, in turn, require a better knowledge of biodiversity and reliable sources of information for the public. Our knowledge of biodiversity has been formed largely around how humanity interacts with nature (5). Such interactions date back to our earliest history and have not been limited to the acquisition of food and resources but also relate to medicine, art, myths, and traditions (6, 7). Yet, these ancestral interactions have changed during our history and are rarely now as direct and intimate. Public interest tends now to be mainly focused on domestic uses, with also disproportionate focus on emblematic and charismatic species (8, 9). The study of natural history has similarly changed, from the early work by Pliny the Elder and the natural philosophers in the 18th and the 19th centuries (i.e., Carl Linnaeus, Jean-Baptiste Lamarck, and Charles Darwin) to a very different era of modern science in the 2000s. As the study of natural history was evolving toward a modern biodiversity science, it was becoming further disconnected from the public interest/attention.

The more recent emergence of a global biodiversity culture founded on the internet as a main source of information has accelerated this decoupling, particularly through the intensive use of social media (10, 11). The result is that human attention is incredibly biased on a very small swathe of species across the Tree of Life, a trend that is clear among the scientific community as well as the broader public

(12–16). A marked bias in conservation support and actions toward particular taxa (17–19) is more worrying given that public awareness could be a key factor in our willingness to engage in collective conservation actions (20, 21); scientific knowledge is essential to our ability to build effective conservation strategies (22). These biases of perception on the intrinsic value of species, regardless of their contributions to people, both in the scientific community and the broader public, result in biases in how ecosystems are valued and prioritized for conservation.

In the marine realm, particularly for the world's reef fishes, these biases are critical. Reef fishes play fundamental roles in the functioning of the world's most vulnerable ecosystems like coral reefs (23, 24). They hold important value for a considerable portion of the global human population (25) and support various livelihoods for economically disadvantaged communities reliant on fishing as a means of survival and to attract tourists (26, 27). They are sought after for their beauty (28, 29) and renowned for their remarkable morphological diversity and aesthetic value (15, 30, 31). Yet, our knowledge about the importance of reef fishes has largely been focused on a small proportion of species targeted by fishers (32). However, fishing importance represents only a single component among a number of dimensions by which reef fishes are of value to humans and is even not connected to the intrinsic values of fishes to reef ecosystems.

The study of human interest in reef fishes should shed light on how societal perceptions and scientific research contribute to increased knowledge and conservation efforts. While the dimensions of human interest in nature are multiple and intricate (5, 33, 34), we foresee two dimensions of interest in reef fishes that could be compared and measured globally. The first dimension, public attention, encompasses the collective views, attitudes, and perceptions of the general public. Public attention is known to play a pivotal role in shaping conservation initiatives, as it influences public support, awareness, and funding for conservation efforts (35, 36). Understanding the factors that drive public attention in reef fishes, such as their aesthetic appeal, cultural significance, or economic value, may provide valuable insights into how to engage and motivate

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the public toward conservation actions. The second dimension, research effort, represents the body of research on reef fishes generated by scientists. Research effort occurs across various fields, including taxonomy, genetics, behavior, biogeography, fisheries science, and ecology. Much of this knowledge is crucial for effective conservation strategies in identifying vulnerable species, setting reference points for sustainable yields, tracking the achievement of conservation targets, and assessing the impacts of human activities on reef ecosystems (37, 38). It is likely that these two dimensions of human interest will covary with some species' intrinsic factors such as diel activity or trophic level and more flexible extrinsic factors linked to human uses such as price or aquarium trade (Fig. 1). If the latter factors drive human interest, then some levers may be found to alleviate pressure on some species and reinforce attention toward neglected ones. More broadly, investigating how the two dimensions of human interest are related and how they connect to species threats can also shed light on potential synergies and trade-offs between the feasibility of conservation programs and public engagement, both of which are key to conservation success.

Here, we used data from the worldwide and standardized Reef Life Survey (RLS) program (39) to select 2408 fish species found on the world's coral and rocky reefs. We evaluated human interest by collecting a massive amount of data from online public databases as well as major social media (Fig. 1). Our study presents a synthetic approach that summarizes these multiple sources of information into two simple dimensions related to research effort and public attention (16). We then revealed how research effort

and public attention were related to species attributes and human uses. We mapped these two dimensions of human interest across the Tree of Life and lastly used the International Union for Conservation of Nature (IUCN) threat categories and a climate risk index (40) to highlight the potential implications of human interest biases for reef fish conservation and future management (Fig. 1). We found a strong bias in human interest toward a small portion of reef fish biodiversity which is primarily driven by geographical range, human uses, and aesthetic value, emphasizing the need for targeted efforts to (re)balance attention and resources across reef fish species.

RESULTS

The two dimensions of human interest

We used a total list of 2408 ray-finned fish species (Actinopterygii) from 140 families, mostly (2271 species) extracted from the RLS database (31, 39, 41) and complemented with 137 species mentioned as reef-associated by FishBase and classified as threatened (TH) by IUCN (but not present in the RLS database). This species list captures the ecological, scientific, and social significance of the diverse array of reef fishes across all major ocean basins and reef areas covering all vulnerability classes.

To measure human interest, we built upon recent advances in the emerging fields of iEcology (10, 42, 43). These approaches analyze data available from digital sources and offer unique insights for a large number of species and taxa. We focused on major online resources from which a massive amount of quantitative data could be collected online (Fig. 1): occurrences in generalist scholar databases, National Center for Biotechnology Information (NCBI) genomic information, FishBase information, Wikipedia views, Twitter, and Flickr. We summarized the eight metrics used to capture human interest in Table 1 (see Materials and Methods for more details).

We analyzed covariations between the different metrics of human interest in fish species using a principal components analysis (PCA) and found that the first and second PCA axes explained 57.7 and 11.8% of the total variance, respectively (Fig. 2A). The first axis was strongly associated with species' geographic ranges; fishes with the highest human interest metrics being those with the largest distributions (Fig. 2A). The eight metrics of human interest were clearly split between two groups along the second PCA axis (Fig. 2A) with fishes that have received more public attention, such as the Mandarinfish (*Synchiropus splendidus*), having positive values (Wiki_views, Flickr, and Twitter) and those subject to more research effort, such as the Orange-spotted grouper (*Epinephelus coioides*), having negative values (Sci_Fields, H_index, Tot_pubs, NCBI, and FishBase). Other PCA axes did not show any clear pattern between the different metrics of human interest and were not considered further (fig. S2). Despite their positive correlation (Fig. 2B; $r = 0.65$, $P < 0.001$), aggregated metrics of research effort and public attention (see Materials and Methods) clearly differentiate species with high public attention and low research effort, such as the Eastern blue devil (*Paraplesiops bleekeri*), or those with high research effort but low public attention, such as the Dwarf round herring (*Jenkinsia lamprotaenia*). The species that attracts the highest human interest of those considered (averaged research effort and public attention) is the European sea bass (*Dicentrarchus labrax*).

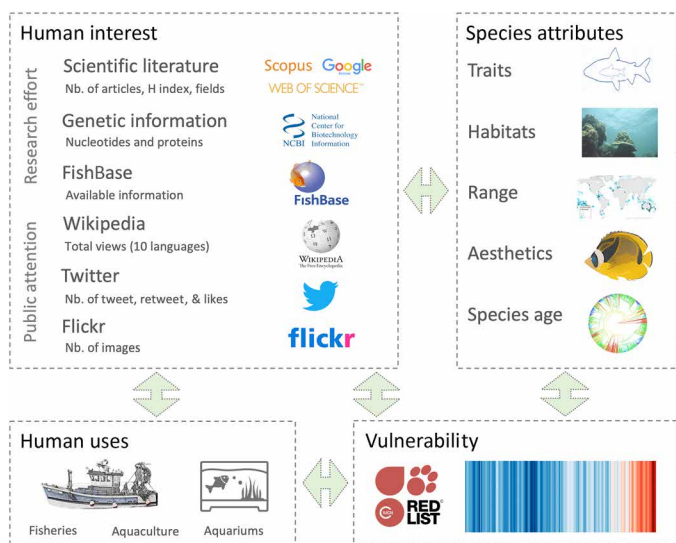


Fig. 1. Workflow of our analysis pathway. We collected data on research effort and public attention from online databases and major social media platforms. This information was summarized in two dimensions and compared to key species attributes and human uses metrics and mapped across the Tree of Life. Last, the two dimensions of human interest were compared for each species to their conservation status (IUCN red list) and climate risk vulnerability (40). See Materials and Methods for a complete description of these steps. The drawings of fish boat and aquarium are CC0 1.0 and provided from www.publicdomainpictures.net and www.uwxing.com. The picture of reef is CC0 1.0, (https://commons.wikimedia.org/wiki/File:Hen_Chicken_reef_1999.jpg). The world map of RLS sites was provided by R. D. S. Smith and is CC0 1.0. The fish in the box "species attributes" is *Chaetodon lunula* and was digitally created by N.M. (CC0 1.0).

Table 1. Synthetic metrics used to assess the two dimensions of human interest. All these metrics (see also Fig. 1) are \log_{10} -transformed (except Sci_fields) and normalized between 0 and 1. See Materials and Methods for a complete description. ASJC, Scopus All Science Journal Classification.

| Metrics | Description |
|-------------------------|---|
| Research effort | |
| FishBase | Variables in FishBase with attributed values. |
| H_index | Species Hirsch index which combines the number of publications and the number of citations each species received in Scopus. |
| NCBI | Occurrences in the Nucleotide and the Proteins NCBI databases. |
| Sci_fields | Spread of publication records across scientific fields according to the ASJC system. |
| Tot_pubs | Publications found in Web of Science and Google Scholar. |
| Public attention | |
| Flickr | Digital photographs available on Flickr. |
| Twitter | Tweets, likes, and retweets on Twitter. |
| Wiki_views | Views in the 10 most-viewed languages on Wikipedia (ISO 639-1; codes: en, es, fr, de, ru, pl, nl, it, and pt). |

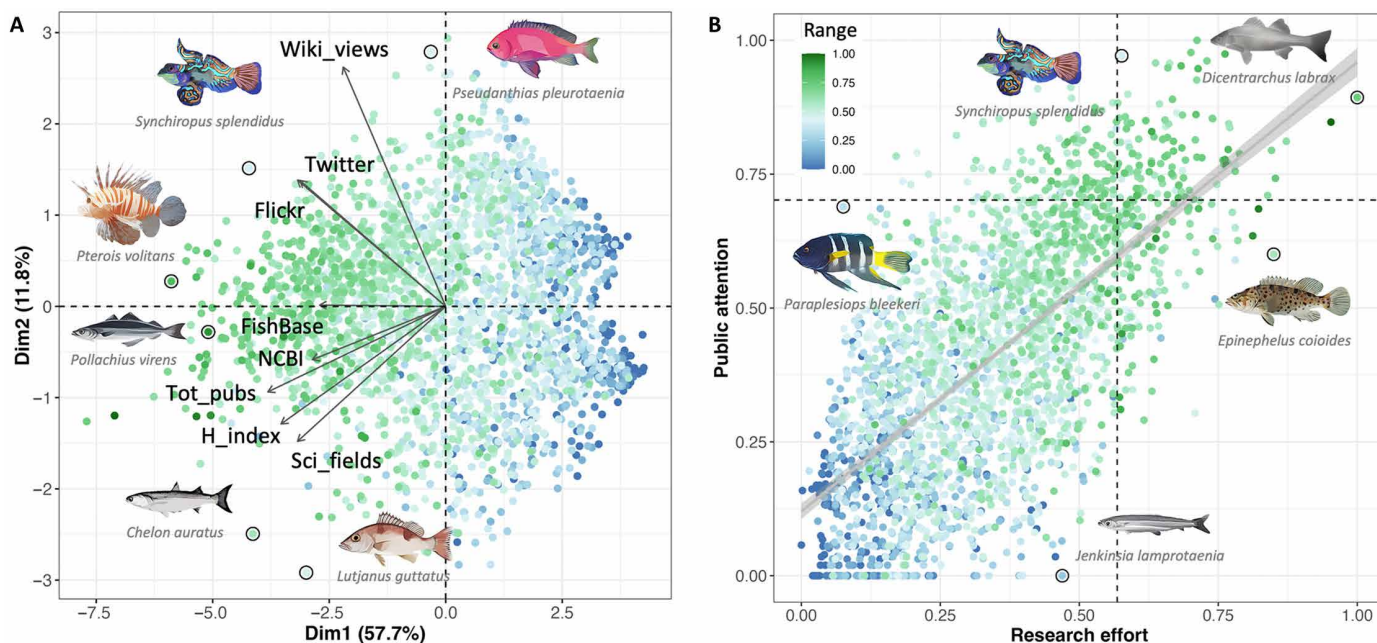


Fig. 2. The two dimensions of human interest for global reef fishes. (A) Two first axes of the PCA between the eight metrics used to capture human interest (Table 1). Dots represent the distribution of 2408 reef fish species within this space. Examples include the Squarespot anthias (*Pseudanthias pleurotaenia*) and Mandarinfish (*Syngnathus splendidus*) with high public attention, the Golden gray mullet (*Chelon auratus*) and Spotted rose snapper (*Lutjanus guttatus*) which have high research effort, and the Saithe (*Pollachius virens*) and Red lionfish (*Pterois volitans*) which scored highly on both public interest and research effort. (B) Research effort and public attention synthetic indices (see Materials and Methods) are positively correlated ($r = 0.65$) but highlight outliers with particularly high values for one or both dimensions of interest. The gray line shows the linear fit with 95% confidence intervals. The horizontal and vertical dashed lines represent the 90% quantiles (111 species fit above the intersection of the two lines). The European sea bass (*Dicentrarchus labrax*) show both the highest research effort and public interest. For both (A) and (B), dot colors reflect species global geographic ranges (\log_{10} transformed and scaled between 0 and 1); color legend is given in (B). The drawings used to represent fishes were digitally created by N.M. and are CC0 1.0.

Species attributes driving research effort and public attention

We then used Boosted Regression Trees (BRT) to measure the importance of species attributes and human uses in explaining variation in research effort (Fig. 3A) and public attention among reef fishes (Fig. 3B). Beyond species' range size, which is the main correlate of human interest (representing 50.4 and 47.2% of variables' importance

for research effort and public attention, respectively), research effort was positively related to fishery importance (11.8%). Research effort was also biased toward species of importance for aquaculture (8.1%), with lower temperature preference (7.9%) and importance for aquarium trade (4.9%). Public attention showed a strong positive bias toward species of high aesthetic value (21.4%) and was, to a lesser extent, biased toward species used in aquarium trade (13.1%), belonging to

old evolutionary lineages (5%) and being important for fisheries (4%). Research effort and public attention were also biased toward species with larger body size (5.3 and 3.6%, respectively). For both research effort and public attention, we found only a weak effect of other variables tested, including most ecological traits (except body size and species age) or habitat preferences (except temperature preference for research effort).

Research effort and public attention across the Tree of Life

We observed a strong phylogenetic bias for research effort ($\lambda = 0.58 \pm 0.01$, P value < 0.001) and a moderate bias for public attention ($\lambda = 0.43 \pm 0.01$, P value < 0.001) across the phylogeny of reef fishes (Fig. 4). A high proportion of scientific research has targeted very few families, particularly commercial species from the Carangidae, Scombridae, Serranidae, Lutjanidae, and Lethrinidae families. Public attention appears to be spread more broadly across the Tree of Life, although partly concentrated not only among species in families receiving high research effort (except Lethrinidae) but also including species with high aesthetic scores from the Pomacanthidae, Chaetodontidae, Acanthuridae, and Balistidae families. Some families show contrasting patterns for the two metrics, with high research effort but low public attention (e.g., Lethrinidae) or low research effort but high public attention (e.g., Muraenidae). Cryptobenthic families of reef fishes such as Blenniidae, Gobiidae, and Tripterygiidae show both very low research effort and public attention. Other (large) families such as the Pomacentridae and Labridae show a more variable distribution of research effort and public attention between species.

Implications for reef fish conservation and future management

We found that threatened (TH) fish species, i.e., those most at risk of extinction (IUCN Red List), and those not evaluated (NE) by the IUCN had lower average values for research effort and public attention than data deficient (DD) and least concern (LC) species (Fig. 5A). Yet, the TH group proportionally contains more species in the top 90% quantiles of research effort and public attention than other groups (Fig. 5B), indicating that while most TH species receive very little attention, like the Shortfin minidartfish (*Aioliops brachypterus*), some get high attention, such as the well-known Atlantic goliath grouper (*Epinephelus itajara*) or the Haddock (*Melanogrammus aeglefinus*).

Using the climate risk index (40), we analyzed the relationships between both dimensions of human interest and species' predicted vulnerability to climate change for two contrasting Intergovernmental Panel on Climate Change (IPCC) shared socioeconomic pathways (SSPs; SSP5-8.5 and SSP1-2.6). We found that both research effort and public attention are negatively correlated with the climate risk index ($r = -0.3$ for both dimensions, $P < 0.001$), suggesting that the species predicted to be most at risk of being adversely affected by climate change also receive the least research effort and public attention (Fig. 6, SSP5-8.5). Species geographic range size was the main driver of this relationship (see dots color gradient on Fig. 6) as the negative correlation was lost when accounting for species range. We also found that the relationship between species risk index and both research effort and public attention was disproportionately stronger when considering only species classified as TH by IUCN (Fig. 6; $r = -0.57$ for research effort and $r = -0.53$ for public attention,

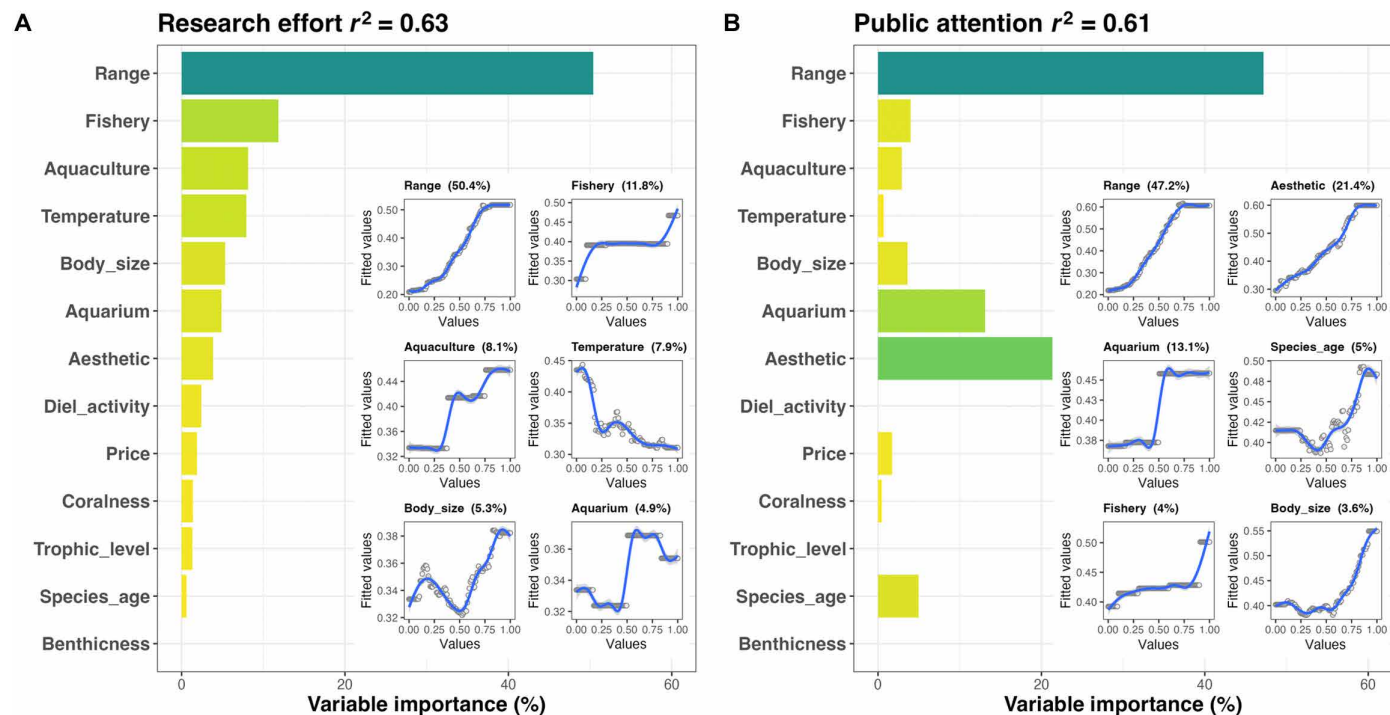


Fig. 3. Drivers of human interest for global reef fishes. Importance of species attributes and human uses (see Fig. 1) in Boosted Regression Tree models explaining (A) research effort ($r^2 = 0.63$) and (B) public attention ($r^2 = 0.61$). Complete description of species attributes and human uses variables are given in Materials and Methods. Both panels show variable importance expressed as relative percentages and associated partial dependence plots for the six most important variables. Variables are ordered according to their decreasing importance in the model for research effort in both panels to ease comparison.

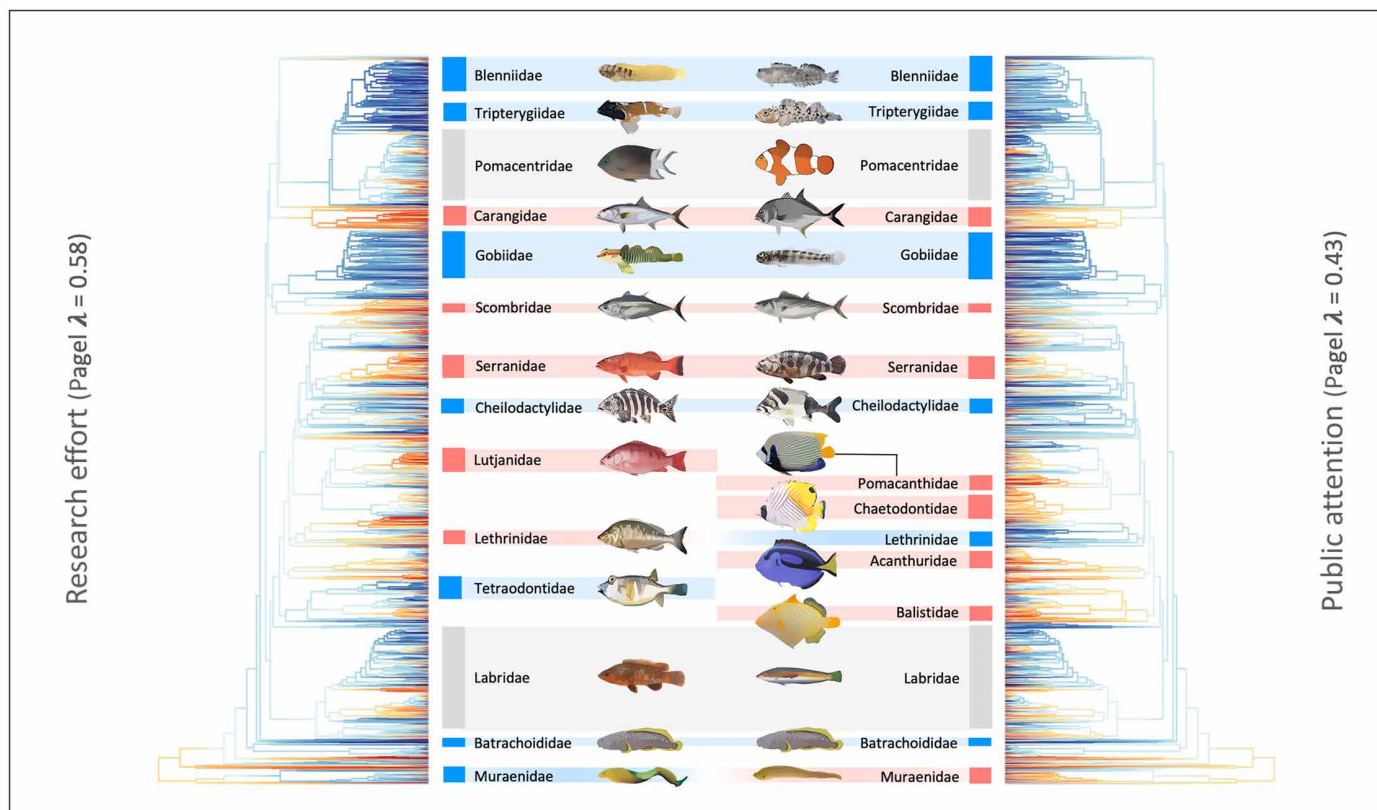


Fig. 4. Mapping the two dimensions of human interest for global reef fishes across their Tree of Life. Research effort (left) and public attention (right) are mapped over the phylogenetic tree with a color gradient obtained by estimating states at internal nodes with maximum likelihood (91) from low (blue) to high (red) values. Pagel's λ coefficient, which measures the importance of phylogenetic clustering, is given for both research effort and public attention (see Materials and Methods). For illustration, we highlighted families (using color bands in the middle of the figure) with contrasted research effort and public attention values (families with high values in red, low values in blue and contrasted values in gray). We provide illustrations of example fish species for each family (to illustrate higher, lower, or average values of human interest depending on which family was considered). In alphabetical order: Acanthuridae (*Paracanthurus hepatus*), Balistidae (*Balistapus undulatus*), Blenniidae (left, *Omobranchus aurosplendidus*; right, *Entomacrodus solus*), Batrachoididae (*Daector schmitti*), Carangidae (left, *Seriola lalandi*; right, *Caranx ignobilis*), Chaetodontidae (*Chaetodon auriga*), Cheilodactylidae (left, *Goniistius rubrolabiatus*; right, *Cheilodactylus plessisi*), Gobiidae (left, *Tigriogobius harveyi*; right, *Gobiosoma hildebrandi*), Labridae (left, *Labrus bergylta*; right, *Coris julis*), Lethrinidae (*Lethrinus nebulosus*), Lutjanidae (*Lutjanus campechanus*), Muraenidae (left, *Gymnothorax funebris*; right *Gymnothorax javanicus*), Pomacanthidae (*Pomacanthus imperator*), Pomacentridae (left, *Acanthochromis polyacanthus*; right *Amphiprion ocellaris*), Scombridae (left, *Rastrelliger kanagurta*; right, *Sarda sarda*), Serranidae (left, *Plectropomus leopardus*; right, *Epinephelus itajara*), Tetraodontidae (*Omegophora cyanopunctata*), Tripterygiidae (left, *Enneapterygius larsonae*; right, *Trianectes bucephalus*). The drawings used to represent fishes were digitally created by N.M. and are CC0 1.0.

$P < 0.001$). These results were robust for the two contrasting IPCC SSPs (see fig. S3 for SSP1-2.6).

DISCUSSION

Our study introduces a comprehensive approach to evaluate two crucial but unassessed nonmaterial dimensions of human interest toward biodiversity: public attention and research effort. These dimensions are integral parts of Nature's Contribution to People, which poses challenges and offers opportunities in biodiversity research (33, 44). By harnessing the power of online platforms, we were able to tap into a vast reservoir of data reflecting a wide range of human interests across multiple metrics and species. Previous studies have applied similar online data extraction methods to quantify these dimensions independently for certain taxa, ecosystems, or biodiversity-related trends, including research effort for Australian mammals (13), public sentiment for the Great Barrier Reef (45), and public attention toward endangered animals (46) or invasive amphibians, birds,

and mammals (47). Our study integrates these two dimensions into a single framework and relates them to species attributes, human uses, and extinction risks (Fig. 1), revealing marked biases in human interest that appear related to a relatively small number of important factors. Such online data sources are continuously updated, cover an extensive range of taxonomic groups, and might even reflect real-time shifts in human interest (42, 48). This broad applicability opens up exciting avenues for future research, making it a powerful tool for understanding the dynamics of human interest for biodiversity into the digital age (16).

Our findings shed light on how certain species attributes and human uses can elevate reef fish species' profile in science and public consciousness. We show that reef fish species with large geographical ranges tend to gather more scientific and public attention. Easier accessibility and visibility provide researchers and the public with more opportunities for interaction and observation. Moreover, their frequent overlap with human activities expose them to more research effort while simultaneously triggering public concern. In

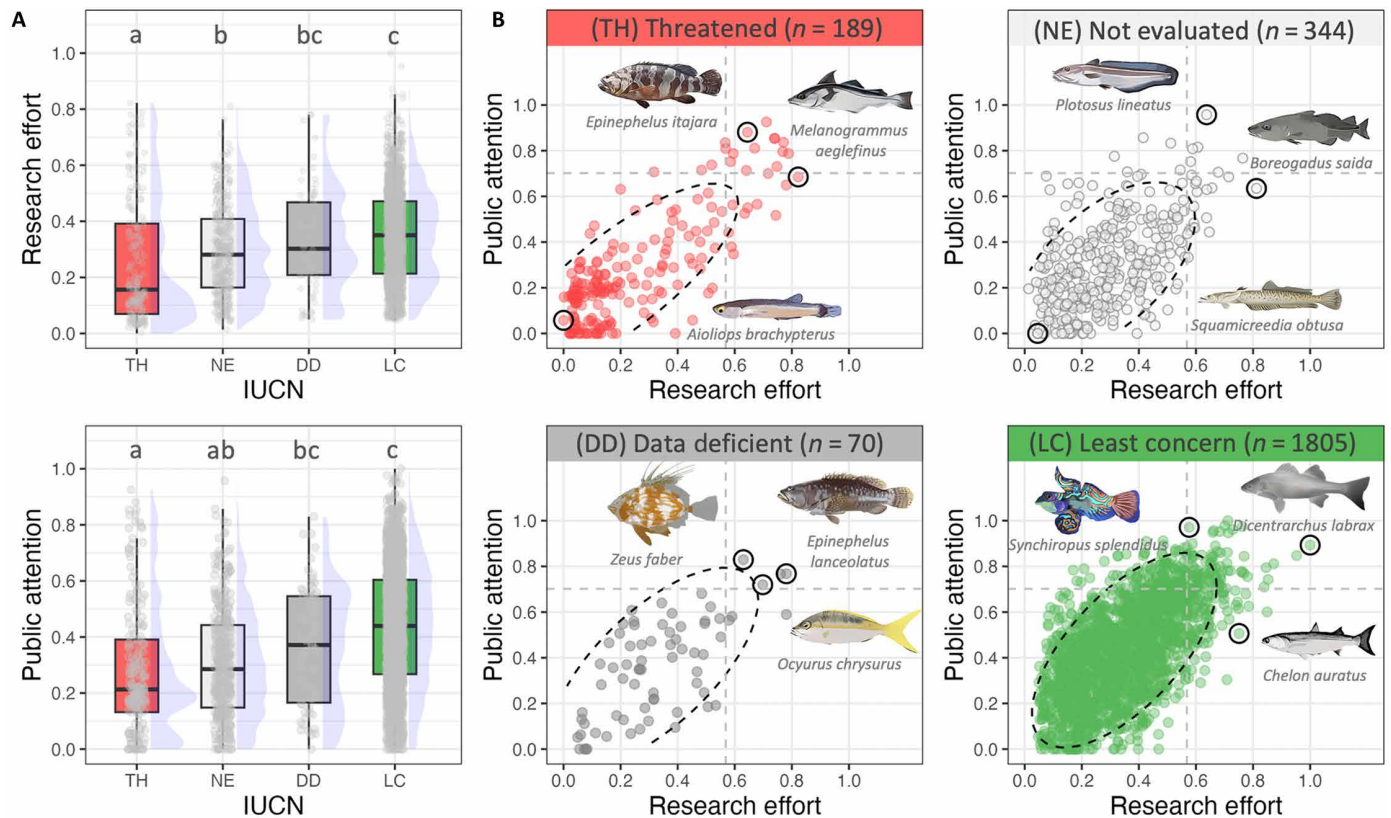


Fig. 5. Human interest among IUCN categories for reef fishes. (A) Box plots of the research effort (top) and public attention (bottom) among the four IUCN categories (TH comprising critically endangered, endangered, and vulnerable species; NE; DD; and LC including LC and near-threatened species). Letters indicate significant differences between the IUCN groups for both research effort (Dunn's test P values are, respectively, $P < 0.01$ between TH and NE, $P < 0.01$ between TH and DD, $P < 0.001$ between TH and LC, and $P < 0.001$ between NE and LC) and public attention (Dunn's test P values are, respectively, $P < 0.05$ between TH and DD, $P < 0.001$ TH and LC, and $P < 0.001$ between NE and LC). (B) Relationship between research effort and public attention for the species belonging to the four IUCN categories. The dashed ellipses represent 90% of the data (distance from the centroid). The horizontal and vertical dashed lines represent the 90% quantiles for both dimensions of human interest (computed on all species). For category TH, 12 species fit above the intersection of the two quantiles lines (6.3%); NE, 6 species (1.7%); DD, 4 species (5.7%); and LC, 89 species (4.9%). Examples of fishes are given within each subpanel. The drawings used to represent fishes were digitally created by N.M. and are CC0 1.0.

addition, broad distributions expose these species to a variety of cultural contexts, fostering public attention and inspiring scientific interest due to their acquired symbolic significance. This “mass effect” of species commonness on human interest could also lead to a kind of “Matthew effect” (49), where the few emblematic or commercially valuable species attract more attention and resources, which, in turn, leads to more discoveries and recognition, further increasing their popularity than others. The flip side of this effect is a potential increased disregard toward many important but lesser-known species. This calls for concerted and directed initiatives to reallocate attention and resources toward less conspicuous or regionally overlooked species.

We observed discrepancies between research effort and public attention for many species, raising questions about how these two dimensions of human interest intersect and diverge. Research effort showed a marked skew toward commercially important species, highlighting the utilitarian bias in scientific research. In many ways, this likely reflects the importance of industry funding for science, where “fundamental” research is far less resourced than “applied” research. This bias in research effort was also present for species with larger body sizes, lower temperature preferences, and those of interest to

aquaculture and aquarium trade. On the other hand, our study revealed that aesthetic appeal and importance for aquarium trade are major catalysts for capturing public attention. Overall, the two dimensions of human interest were only weakly related or unrelated to most of the species ecological attributes we tested (with the exception of body size, temperature preference, and species age). This suggests that fish’ ecological traits, which are mostly related to their role in ecosystem functioning and resilience, are not driving either research effort or public attention. Taken with previous research showing that the most ecologically original reef fish species tend to be considered the least attractive to people (30, 31) or that yellow fishes receive far more research effort than by chance (15), our results strongly advocate for a more ecologically oriented balance of research effort (and funding) and communication campaigns.

The phylogenetic analysis revealed that certain evolutionary lineages of reef fishes receive disproportionate research effort and public attention, mostly due to their commercial importance (such as Carangidae, Scombridae, and Serranidae) or aesthetic appeal (such as Pomacanthidae, Chaetodontidae, and Acanthuridae). The clustering of scientific interest and public attention within the Tree of Life arises from a simple interplay of biological characteristics

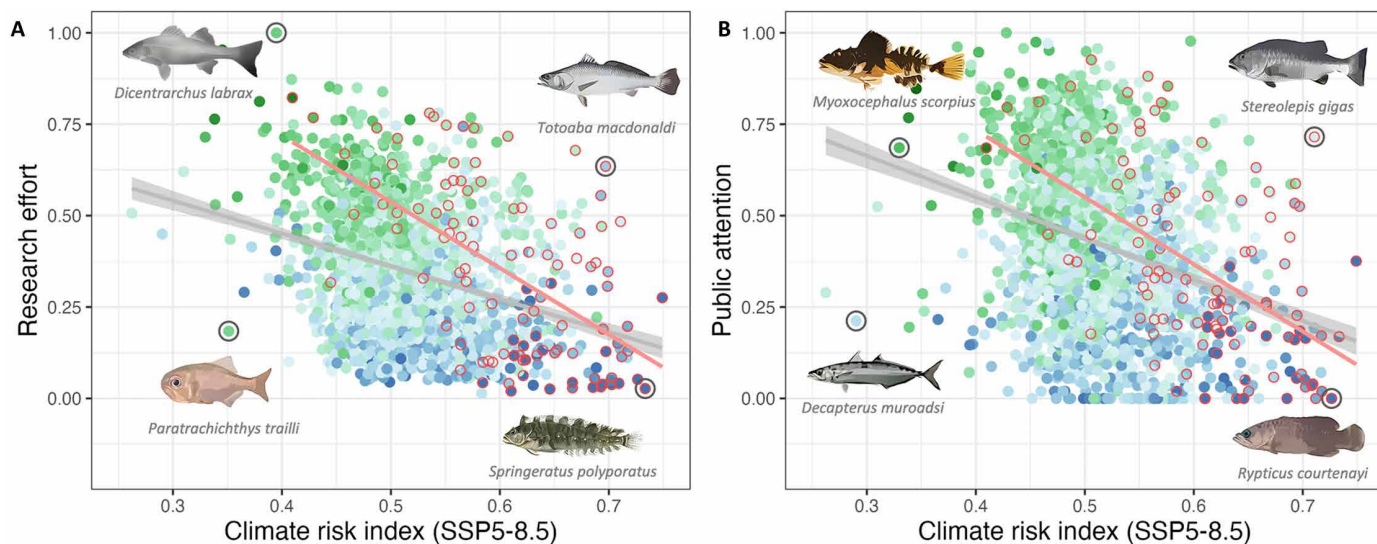


Fig. 6. Climate risk and human interest for global reef fishes. Relationship between research effort and public attention with climate risk index as computed in (40) under the IPCC SSP5-8.5 scenario. For both (A) and (B), dot colors reflect species geographic ranges [\log_{10} transformed and scaled between 0 and 1; from large (green) to narrow (blue) ranges; as in Fig. 2]. The gray lines show linear model regression with 95% confidence intervals ($n = 2094$, $r = -0.3$ for both research effort and public attention, $P < 0.001$). Dots surrounded by red circles are species considered as TH by the IUCN. The red lines show linear model regression for TH species ($n = 106$, $r = -0.57$ for research effort and $r = -0.53$ for public attention, $P < 0.001$). Examples of fishes are given at the four corners of the human interest and climate risk relationship. The drawings used to represent fishes were digitally created by N.M. and are CC0 1.0.

and human perceptions (16). Species within certain families often exhibit shared traits and characteristics, such as larger body sizes and importance for fisheries or aesthetic value that attracts attention. Public attention might also be influenced by frequent media or cultural representations of certain families, essentially based on aesthetic values.

Other influential factors in the clustering of interest on certain parts of the Tree of Life include the accessibility and visibility of certain families. Cryptobenthic fishes (50) such as Blenniidae, Gobiidae, and Tripterygiidae, for instance, show very low research effort and public attention which are likely due to their small size and cryptic nature making them less visible and more difficult to study. Further, the taxonomy of many of these cryptobenthic fishes is poorly resolved, meaning that few researchers or members of the public can identify them, let alone study or appreciate them (50). Despite these challenges, cryptobenthic fishes play important ecological roles, including for trophodynamics (51) and reef functioning (23). They are crucial components of coral reef ecosystems and underline the importance of increasing research efforts and public attention toward them.

Our findings have also important implications for the conservation of TH and climate vulnerable species. First, the results from the IUCN Red List assessment indicate that species now at the highest risk of extinction receive limited attention in terms of public interest and research effort. Some flagship species such as the Atlantic goliath grouper (*Epinephelus itajara*) are TH and receive a relatively high level of attention, but most of the IUCN TH reef fishes are lacking the level of attention necessary to fuel effective conservation measures. Urgent actions are thus required to prioritize the research effort and to raise public attention toward these overlooked TH species. Our results echo with a recent study that found an increase in Google searches for TH mammals only for large species (52), which are the most popular (53). We also found that some

species that are actually categorized as DD by the IUCN show relatively high research effort, such as the John Dory (*Zeus faber*), the Giant grouper (*Epinephelus lanceolatus*), and the Yellowtail snapper (*Ocyurus chrysurus*). It is therefore possible that more information may be available to IUCN working groups for assessment of threat status than presently realized. Our index of research effort could prove valuable for assisting in the prioritization of data-deficient species evaluation. This prioritization could also be used for the NE species, but as they are more numerous than DD, a combination between an extinction probability risk based on species range and the research effort index might here be a better strategy. Overall, our results illustrate how digital information gathered online could help speed up the process of IUCN status assessment (11).

Our study also found that species with higher risk to climate change, potentially facing major risks in the future, receive lower attention. By focusing on the worst-case greenhouse gas emission scenario (SSP5-8.5), which unfortunately appears to be the more likely scenario at present (54), our findings underscore the need for immediate and proactive measures to safeguard these reef fishes from the future impacts of climate change. We found our results robust to a less marked greenhouse gas emission scenario (SSP1-2.6), suggesting that, even in the unlikely future with an emphasis on sustainable development and reduced greenhouse gas emissions, the species gathering the least human attention will still be under substantial risk from climate change. Although we acknowledge that the climate risk index provides only an indication of vulnerability for any given species and outcomes which will likely be highly context dependent, our results still point to a general gap in research and public attention that will likely grow in importance for some of these species. We also acknowledge that the IUCN indicators of species threats and the climate risk index are, by construction, highly correlated to species' range sizes. Range size is also the main driver of human interest and so appears to play a central role in the

relationship between species' interest and vulnerability. This does not rule out the resulting small interest that humans have on rare (and thus vulnerable) species, but it questions the policy levers available to increase human attention for these neglected species. Overall, our research highlights the need to prioritize the research effort toward species that have small ranges and are potentially vulnerable to climate change. This also implies deeply modifying how we assess extinction risk to face the need for more comprehensive assessments. Integrating advanced techniques, such as environmental DNA metabarcoding (55), machine learning models (56), or other automated calculations (57), could greatly enhance our understanding of species' threat status, facilitating more informed conservation prioritization and enabling evidence-based, rather than human-biased, decision-making.

Our study underscores the potential biases in conservation actions driven by public perceptions on certain species. Public perception, reflecting society's collective view, plays a pivotal role in influencing species conservation, including environmental attitudes, awareness, funding, promotion, and research efforts (17, 18, 58). We show here that public attention is mostly focused on common, beautiful, and large species so it urges to further investigate the influence of public perception on conservation decision-making to ensure that biases are identified and addressed, ultimately promoting more inclusive and effective conservation strategies. By gaining a deeper understanding of public perceptions and the factors that drive them, conservation practitioners can develop targeted communication and outreach strategies to engage diverse stakeholders and garner support for conservation initiatives. Moreover, it is critical to address potential biases in scientific research and funding allocation to ensure that species conservation efforts are guided by a comprehensive understanding of the entire Tree of Life and its value to nature and people (59).

We also found that fishery importance was driving most of the research effort and that some entire branches of the Tree of Life were mostly ignored by the scientific community, including cryptobenthic fishes. From a fisheries perspective, unequal research effort across species also reduces opportunities for ecosystem-based fisheries management (60) and potential nutritious but unexploited species like herbivores (61). Ultimately, by integrating multiple perspectives and considering a broader range of species, research programs and conservation actions would become more equitable and aligned with the goals of biodiversity conservation. This integration would not only enhance the relevance of conservation actions but also foster greater public participation and ownership of conservation initiatives, leading to more sustainable and effective outcomes.

Our integrative measures of public interest and scientific knowledge rely on digital data sources, such as scientific literature, online databases, and social media platforms that introduce potential biases associated with data availability, accessibility, and representativeness. It is thus important to acknowledge the existence of other important dimensions and scales of integration. For instance, in our study, the public attention metric likely captures some aspects of the so-called cultural values (62) as platforms like Flickr, Twitter, and Wikipedia, which are sources of our data for public attention, include user-generated content related to recreational activities, aesthetic appreciation, educational content, and more. Yet, cultural values are complex and multifaceted and cannot be fully captured only by online behavior and data. For example, certain symbolic or

spiritual values may not be widely discussed or depicted online. It is also likely that cultural values will depend on people's origins. For instance, people disconnected from nature may pay more attention to flagship species than people living in contact with nature (8, 63). As some of the online platforms can provide some georeferenced data, an interesting future direction would be to compare public attention metrics computed from people who live close to a species of interest with those from people geographically distant or simply with people living close to the ocean. Coastal populations, in particular, often have a stronger connection and dependence on reef ecosystems compared to continental populations, and this should be integrated to further understand the drivers of local population interest in reef fishes.

Striking a balance between local context and global relevance will thus be crucial in effectively addressing public interest for reef fishes, but we believe that our study provides important insights and a basis from which more subtle measures of public attention or cultural values can be derived. Note also that using species scientific names to measure public attention may have resulted in increasing the observed correlation between public attention and research effort (beside the effect of species geographic range). We would expect less correlation if we had used common names to measure public attention, but that was impractical for our study. An extraordinarily large range of common names (many often inaccurate or misleading) can be applied for individual species, which can vary geographically or by people's level of education or hobbies. In particular, double meanings (overlapping common names applied to multiple species) would have made the data unreliable.

We consider our measure of research effort to be stronger. Research is highly international, and we included a large number of publications not referenced in mainstream scientific databases [such as Web of Science (WOS)], by using the total number of publications found on Google Scholar. These included gray literature (books, reports, etc.), which are important sources of information, increasingly so in an era in which natural history studies are rarely published in mainstream journals (64). Last, we also acknowledge that our measure depends highly on who has access to online resources, inducing a bias toward the "Western" public, a tendency exemplified by the negative relationship we found between research effort and fish preferred temperatures which point out toward temperate zones. We missed the so-called local knowledge (65) on biodiversity. We could thus also use our metrics as a benchmark against which to measure the western bias [e.g., (58)] for particular reef fish species, as was recently suggested for crop plants (66). We see these different points as opportunities for further research, to refine measures of human interest for biodiversity.

Another limitation of our study is the exclusion of Chondrichthyan (cartilaginous fishes), which represent a diverse group of species including sharks, rays, and skates. Our analysis focused specifically on Actinopterygii (ray-finned fishes) for which aesthetic value, which is a strong component of human interest, was available from previous work (31). Chondrichthyans play critical ecological roles in marine ecosystems and often elicit unique public perceptions and conservation concerns due to their emblematic nature and conservation status. Particularly, sharks and ray have been shown recently to be under severe threat of extinction (1). Given their large body size and importance for fisheries, it is likely that they should attract high human interest. For these emblematic species, public attention

would probably be based on body size and cultural values rather than aesthetic value per se as shown for birds (67). We would thus need more subtle measure of public attention, as they trigger a complex cultural response, being both feared and revered (68). Future research should aim to incorporate Chondrichthyans into our analyses to provide a more comprehensive understanding of the interplay between human interest, scientific knowledge, and conservation priorities across the full spectrum of reef fish biodiversity.

The biased popularity of particular species can result in unequal scientific resource allocation and inadequate consideration in conservation efforts (5, 12, 13, 18). While excluding subjectivity from biodiversity agendas seems challenging or even impossible to achieve, understanding the role of utilitarian needs and emotional factors in this bias may contribute to developing less biased approaches across the Tree of Life (16). Here, we show that reef fish species with a broader geographic range capture more human interest across a spectrum of metrics, encapsulated in two primary dimensions—public attention and research effort. Our study suggests that research effort is mainly motivated by utilitarian considerations, while public attention is biased toward aesthetically appealing and large species. Notably, species with a higher extinction risk and climate vulnerability attract less scientific effort and public attention, highlighting a knowledge gap that could be detrimental to face the ongoing biodiversity erosion with appropriate future conservation strategies. Looking forward, the insights and methodology we present have the potential to extend how we approach and study human interest in biodiversity. By identifying the factors driving both public attention and research effort, we can target areas where these interests are misaligned with conservation needs. This in turn will aid in crafting strategies that balance public sentiment, research effort, and species' conservation statuses, ultimately leading to more effective and equitable biodiversity conservation outcomes (19).

Human interest in biodiversity is dynamic. An important challenge is to identify which of the human interest drivers are most amenable and could be used as levers to increase attention toward species with low actual interest. For example, we show that public attention is highly dependent on species' range size; thus, it should be a priority to inform about species small range size and range decline (69) to avoid these species to get even less attention (8). We also show that aesthetic value is one of the main drivers of public attention, which requires a strong effort in communication campaigns toward less attractive species to counteract the aesthetic debt paid by the less attractive species (31). For research efforts, there is an urgent need to ask research agencies, whose decisions shape the world research agenda, to put more emphasis on neglected species with ambitious funding programs. In conclusion, this study underscores the value and necessity of integrative approaches to evaluate and understand the myriad ways humans interact with and value biodiversity. Only by fully accounting for these complex relationships can we hope to navigate the challenges of biodiversity conservation in the Anthropocene. By doing so, we can foster stronger engagement and support for biodiversity conservation, leading to more effective and sustainable management practices. Recognizing our biases of perception in biodiversity, which are mainly driven by their contributions to people, is a first step in acknowledging the inherent worth of species and that they should be given more fair consideration. Ultimately, this would help shift our interest to be in greater alignment with the needs and demands of endangered ecosystems which we are part of.

MATERIALS AND METHODS

Analyses were carried out using R v.4.2.2 (70). All relevant code and data are available from the associated repository (see Data and materials availability).

List of species

We used the list of species previously analyzed in (31) to evaluate reef fish aesthetic values on 2417 species. They used the RLS database (39), which contains thousands of standardized and quantitative visual surveys conducted by scuba divers on rocky and coral reef habitats in shallow waters (0- to 20-m depth) worldwide. These underwater visual surveys, conducted between September 2006 and May 2019, consist of 50-m belt transects (each with two 5-m-wide blocks). All fish species encountered by divers are recorded rather than only those from a particular list of families or groups (i.e., species are not excluded or included based on color, shape, or size). Langlois *et al.* (31) focused specifically on ray-finned fishes (Actinopterygii) and excluded Pleuronectiformes (14 species) and Syngnathiformes (31 species) to streamline their morphological analysis. They also supplemented their list of species with 137 reef-associated species from FishBase classified as TH (but not present in the RLS database) to ensure that their final dataset encompassed more TH fishes listed on the IUCN Red List. We removed seven species that show up in the RLS data as being found on reefs but are clearly not primarily reef species: *Elagatis bipinnulata*, *Euthynnus affinis*, *Euthynnus lineatus*, *Gadus morhua*, *Mola mola*, *Salmo salar*, and *Thunnus albacares*. Taxonomic names were checked using the function `validate_names()` from the R package `rfishbase` v.4.1.2 (71). This resulted in removing two species as *Kyphosus analogus* was synonyms of *Kyphosus vaigiensis* and *Pseudocaranx georgianus* was synonyms of *Pseudocaranx dentex*. The final total species number was 2408 reef fish species from 140 families, which provide a broad representation of fishes observed on the world's reefs (across all major ocean basins). Lists of accepted synonyms for each species were obtained using the function `synonyms()` from the R package `taxise` v.0.9.100 (72) according to the World Register of Marine Species database (73).

Measuring human interest

We gathered information online (Fig. 1) for scientific literature, genomic information, FishBase available information, Wikipedia views, Twitter, and Flickr. We recorded data for each accepted and synonym species name (results were summed at the species level) except for FishBase and Wikipedia where only accepted names were used as the searches with synonyms often redirect to the accepted names pages.

WOS, Scopus, and Google Scholar are the three major bibliographic databases used by researchers. WOS and Scopus focus on scientific literature, offering comprehensive citation data. Google Scholar indexes scholarly publications across more various sources. WOS was used to identify all the articles published on each species (`Wos_tot`) using the functions `wos_search()` and `wos_get_records()` from the R package `rwoslite` (<https://github.com/FRBCesab/rwoslite/releases/tag/v0.0.1>; search in title, abstract, and keywords). We assembled a dataset of 45,687 articles (published before 31 January 2023) and tallied the number of citations for each article recorded on Scopus with the function `scopus_search()` from the R package `rscopus` v.0.6.6. We assessed the scientific field of each journal using the Scopus All Science Journal Classification (ASJC)

system that categorizes journals into 333 scientific fields. We also recorded the number of total occurrences on Google Scholar (Gscho_tot), before 31 December 2019, with a built-in function using the R package R Selenium v1.7.4. Gscho_tot is higher than Wos_tot as it includes gray literature (books, reports, etc.) that are important source of information for biodiversity science (64). For each species, we then computed a suite of indices that we all normalized between 0 and 1: (i) the total number of publications (Tot_pubs), calculated as the average of log₁₀-transformed and normalized (between 0 and 1) Wos_tot and Gscho_tot; (ii) the Hirsch index (hereafter H_index), which combines both the number of articles found in WOS and the number of citations (found in Scopus) those articles received [e.g., (74)], log₁₀ transformed; and (iii) an index measuring the spread of publication records across scientific fields (hereafter Sci_fields) by summing for each species the number of different ASJC fields weighted by the number of articles found in WOS within each field (we used the Simpson index which is a power function and gives less weight to fields with low numbers of articles).

The NCBI hosts databases such as GenBank, PubMed, and Basic Local Alignment Search Tool (BLAST), supporting genetic data analysis. We used the function *entrez_global_query()* of the R package *rentrez* v.1.2.3 (75) to get the number of occurrences in the Nucleotide and the Proteins databases that contain among the most frequently entered data in NCBI for each species. Both values were log₁₀-transformed, normalized, averaged, and normalized again (between 0 and 1) to provide an index summarizing the effort of genomic and protein sequencing (hereafter NCBI).

FishBase is an online database that provides comprehensive information about various fish species from around the world (>35,100 fish species compiled from >59,800 references). It is a valuable resource for researchers and conservationists (76). We used the functions *ecology()*, *ecosystem()*, *estimate()*, *reproduction()*, *species()*, and *stocks()* from the R package *rfishbase* v.4.1.2 (71) to collect all the information available on FishBase for each species (441 variables) and count the number of variables with non-attributed (NA) values. FishBase index (hereafter FishBase) was simply the total number of variables minus the number of NAs, which could reasonably be linked to the amount of scientific information available for each species, log₁₀-transformed and normalized (between 0 and 1).

Wikipedia is a free online encyclopedia that allows users to collaboratively create and edit articles on a wide range of topics. It has become one of the largest and most popular sources of general knowledge for the public worldwide with 61,240,562 articles published in 324 languages (77). We used the function *article_pageviews()* from the R package *pageviews* v.0.5.0 to record the number of views in the 10 most-viewed languages on Wikipedia (English, German, Spanish, Russian, Japanese, French, Polish, Dutch, Italian, and Portuguese), which account for 81.3% of page views on Wikipedia (43). This restriction to the 10 most-viewed languages brings a bias as we do not include all of the mother tongues of most of humanity; but we believe that, given the weight of the 10 most-viewed languages (81.3% of total page views) adding more language would not have drastically changed our results. The time frame considered was 1 October 2015 to 31 January 2023. The total number of views in the 10 most-viewed languages (hereafter Wiki_views) was log₁₀-transformed and normalized (between 0 and 1).

Twitter is a social media platform that enables users to post and interact with short messages known as “tweets.” It has become a hub for social discussions with a global audience (hundreds of millions

of tweets are sent each day). We recorded for each species all the tweets posted on Twitter before 31 December 2019 with a built-in function using the R package R Selenium v1.7.4. We curated the resulting dataset by removing the messages that were not linked to fishes (some fish names could lead to misleading tweets; such as with the species *M. mola* for instance, as “mola” is a term of approval or enthusiasm commonly used in Spanish) and ended with a list of 40,836 tweets. The number of tweets, number of likes, and retweets for each species were log₁₀-transformed, normalized, averaged, and normalized again to provide an index (between 0 and 1) summarizing the popularity on Twitter (hereafter Twitter).

Flickr is an online platform designed for hosting, sharing, and organizing digital photographs. It provides users with a space to showcase their images and connect with a community of photographers from around the world: It hosts over 500 million photos from 112 million users as of 2022 (78). We used the Flickr application programming interface (<https://flickr.com/services/api/>) with the function *get()* from the R package *httr* v.1.4.6. The time frame was from 1 January 2010 to 31 February 2023. We recorded for each species the total number of digital photographs available on Flickr. We curated the result for aberrant values (for instance, the fish named *Boops boops* unfortunately does not lead only to images of fishes on Flickr and we had to correct for this). These values (hereafter Flickr) were log₁₀-transformed and normalized (between 0 and 1).

Ecological traits and habitat

We used the RLS trait database (79) that covers body size (maximum length), feeding ecology (trophic level), behavior (water column position and diel activity pattern), and habitat. Preferred temperature was the midpoint of the thermal range (80). Full traits were available for most species, and missing values were completed using the R package *missForest* v1.4 (81); methods and descriptions are available in (31). All continuous variables were normalized between 0 and 1. Nominal variables were transformed into numerical variable as follow: (i) We performed a multiple correspondence analysis (MCA) with both the variable habitat (coral, sand, rock, and water column) and water column (demersal, benthic, pelagic site attached, and pelagic) using the *MCA()* function of the R package *FactoMineR* v.2.8 (82). We found that the axis 1 of the MCA (33.1%) was mostly driven by position in the water column (fig. S1) and that the axis 2 of the MCA (21.1%) clearly differentiated fish species associated with coral and demersal habitats from species associated with sand and benthic habitats (rock habitat being intermediate). We thus used the axis 1 to define an index of “Benthicness” (normalized between 0 and 1) and the axis 2 to define an index of “Corallness” (normalized between 0 and 1); (ii) the trait diel activity was scored 0 for the modality “night” and 1 for the modality “day.” This resulted in a set of six ecological traits, Body_size, Trophic_level, Temperature, Corallness, Benthicness, and Diel_activity, all between 0 and 1.

Species geographical ranges

Fish geographic ranges were computed using the Global Biodiversity Information Facility (GBIF), which is a global network that facilitates free and open access to more than 2.3 billion biodiversity records (83). (i) We first used the R package *rgbif* v.3.7.7 to extract species occurrences: Accepted names were used to retrieve the GBIF species identifier (taxonKey) with the function *name_backbone()*, and total occurrences recorded were downloaded with the function

`occ_download()`. We selected only occurrences that had coordinates without any geographical issue and that mentioned “Human_observation,” “Observation,” “Occurrence,” and “Machine_observation” as a basis of record status between the years 1960 and 2022. We ended up with a dataset of 2,459,981 occurrences for 2332 species (96.8% of our species list). (ii) To compute range size, we used a world grid of $0.05^\circ \times 0.05^\circ$ resolution (approximately 5.5×5.5 km at the equator) and recorded for each species the number of grid cells with at least one GBIF occurrence. We ran spatial analyses under the Behrmann projection system. The 76 species without GBIF occurrences were attributed 0. These values (hereafter range) were \log_{10} -transformed and normalized (between 0 and 1).

Aesthetic values

Fish aesthetic values were obtained from Langlois *et al.* (31). They were computed by combining assessment of fish photographs by humans with predicted values generated through machine learning techniques. These values (hereafter aesthetic) were normalized (between 0 and 1). See (31) for full methodological details.

Phylogenetic tree, species evolutionary age

The phylogenetic tree using the list of accepted species names was computed with the R package `fishtree` v0.3.4 (84, 85). Among the 2408 reef fish species, 2300 species from 140 families were retrieved (using FishBase accepted names) given the taxonomy used in the package `fishtree` v0.3.4, and we used this subset (95.5% of our dataset) to build the phylogenetic tree. The tree incorporates grafted species without direct genetic information by using data from other published phylogenies or inferred from taxonomic positions, resulting in instances where multiple branches stem from a single node, deviating from the ideal dichotomous divisions of a phylogenetic tree. To address these polytomies, a stochastic polytomy resolver was used, generating 100 realizations that placed missing speciation events (86). We extracted the evolutionary species age of the species as the length of the branches from the first node of the tree to the species’ leaf averaged over the 100 trees generated. These values (hereafter `Species_age`) were \log_{10} -transformed and normalized (between 0 and 1).

Human uses

We used the R package `rfishbase` v.4.1.2 (71) to obtain several metrics of human fish uses: importance for fisheries, for aquaculture, for aquarium trade and price categories (respectively referred as “Importance,” “UsedforAquaculture,” “Aquarium,” and “PriceCateg” in FishBase). We gave numerical values to each modality of these four variables and normalized all resulting metrics between 0 and 1. Importance for fisheries (hereafter fishery) is as follows: “Highly commercial” was scored 6 ($n = 38$), “commercial” 5 ($n = 371$), “minor commercial” 3 ($n = 415$), “subsistence fisheries” and “of potential interest” 2 ($n = 88$), and of “no interest,” “unknown,” and NAs 1 ($n = 1496$). Importance for aquaculture (hereafter aquaculture) is as follows: Commercial was scored 4 ($n = 60$), “experimental” and “likely future use” 2 ($n = 9$), “never/rarely” 1 ($n = 2261$), and NAs 0 ($n = 78$). Importance for aquarium trade (hereafter aquarium) is as follows: Commercial was scored 3 ($n = 851$), “public aquarium” 2 ($n = 104$), never/rarely and “potential” 1 ($n = 1160$), and NAs 0 ($n = 293$). Price categories (hereafter price) are as follows: “Very high” was scored 4 ($n = 636$), “high” 3 ($n = 334$), “medium” 2 ($n = 371$), “low” 1 ($n = 81$), and unknown and NAs 0 ($n = 986$).

IUCN status and climate risk

Global IUCN status of fish was extracted from the FishBase data we collected above (see the “Measuring human interest” section). For ease of interpretation, we categorized the species into four groups based on their IUCN status: “TH” comprising critically endangered, endangered, and vulnerable species ($n = 189$); “LC” including LC and near-threatened species ($n = 1805$), “DD” ($n = 70$), and “NE” ($n = 344$).

Climate risk was extracted from Boyce *et al.* (40) who evaluated climate risk for 24,975 marine species using 12 climate indices across their native distributions considering two contrasting IPCC SSPs: SSP5-8.5, representing fossil-fuelled development, and SSP1-2.6, representing a future with an emphasis on sustainable development and reduced greenhouse gas emissions (87). Using $1^\circ \times 1^\circ$ grid cells, they computed the climate risk index over each species’ geographic distribution and averaged the values to obtain a synthetic vulnerability index. Boyce *et al.*’s (40) climate risk index thus captures ecological responses and evaluates vulnerability based on sensitivity, future exposure, and proxies for adaptive capacity (values are between 0, low vulnerability, to 1, high vulnerability). We could extract climate risk for 2094 species (86.9%) of our dataset for both SSP5-8.5 and SSP1-2.6 scenarios.

Statistical analysis

To disentangle the different dimensions of human interest, we computed a PCA on the eight human interest metrics gathered (see the “Measuring human interest” section): FishBase, Flickr, `H_index`, NCBI, `Sci_fields`, `Tot_pubs`, Twitter, and `Wiki_views` (Table 1) using the function `dudi.pca()` of the R package `ade4` v1.7-22 (88). Visualization was performed with the R package `factoextra` v1.0.7. As the metrics relative to public attention (Flickr, Twitter, and `Wiki_views`) were separated from the metrics relative to the research effort (FishBase, NCBI, `Tot_pubs`, `H_index`, and `Sci_Fields`), we computed two separate PCA analyses with both groups of metrics and used the species coordinates on each first axis of the PCAs as a measure of both research effort and public attention. This method allowed us to obtain simple metrics for each dimension of human interest that took into account the correlation between each constitutive variable. The resulting values were normalized between 0 and 1. The relationship between research effort and public attention was measured with a Pearson correlation test using the `cor.test()` function of the base-attached `stats` R package (70).

The influence of species attributes (range, ecological traits, habitat preferences, species ages, and aesthetics) and human uses (fishery, aquaculture, aquarium, and price) on both research effort and public attention was measured using a BRT model that combines decision tree algorithms (as in random forest) with boosting methods, which represent the effect of each predictor after accounting for the effects of other predictors and are robust to missing values and outliers. We used the function `gbm()` of the R package `gbm` v.2.1.8.1 with 2000 trees and a learning rate of 0.01. Importance of each variable has been measured by removing them individually from the general model and comparing the resulting r^2 to the r^2 of the model with all variables.

To examine how both research effort and public attention were clustered within the phylogenetic tree, we used Pagel’s λ coefficient (89), which quantifies the association between the similarity of a trait (here research effort or public attention) and the phylogenetic distance between species. Pagel’s λ assesses the feasibility of reconstructing

the tree solely based on the trait value, where a λ of zero indicates a single polytomy at the root node (no phylogenetic pattern) and a λ of one indicates an exact replication of the tree (strong phylogenetic pattern). Pagel's λ for both research effort and public attention were computed on each of the 100 phylogenetic trees generated (see the "Phylogenetic tree, species evolutionary age" section) using the function `phylosig()` from the R package `phytools` v1.5-1 (90) and averaged.

To compare research effort and public attention across the four IUCN categories, we performed a Kruskal-Wallis test and Dunn's test multiple pairwise comparisons using the functions `kruskal_test()` and the `dunn_test()` of the package `rstatix` v0.7.1. The relationship between both research effort and public attention with climate vulnerability (for both SSP5-8.5 SSP-8.5 scenarios) was measured with a Pearson correlation test using the `cor.test()` function of the base-attached `stats` R package (70).

Fish illustrations

Figures 1, 2, 4, 5, and 6 show drawings of fish that were digitally created by the lead author and are free of copyright (CC0 1.0). These drawings should be solely regarded as "representative" for illustrative purposes as they may deviate from the actual characteristics of the respective fishes. The fishes chosen to illustrate the figures were chosen as they were the most characteristic of the different cases presented in our results.

Supplementary Materials

This PDF file includes:

Figs. S1 to S3

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