

Human targeting of morphologically unique fishes amplifies the risk of functional erosion

Received: 8 December 2025

Accepted: 24 September 2026

Published online: 19 October 2026

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Human societies are drawing on wild species for food, fuel, medicines, and recreation. Yet, it remains unclear whether different types of human use target species with common or unique ecological roles. Here we show that humans use a fourth (26%) of the freshwater fish species and these species occupy almost half (45.2%) of the global spectrum of fish morphological diversity. Yet, used species harbour unique trait combinations, that differ according to the way humans use the species such as fisheries, aquaculture, game fish and aquarium. Moreover, the species targeted by humans are characterised by traits that are predominantly associated with threatened species. By simulating the extinction of threatened species used by humans, we revealed a pronounced and non-random erosion of the morphological spectrum. Understanding the trait-based impacts of human use is thus essential to buffer human impact on natural resources. Conservation should therefore safeguard threatened species but also preserve irreplaceable trait combinations that support unique ecological strategies.

For millennia, human societies have drawn on wild species for food, fuel, medicines, ornamentation, recreation, and tradition^{1,2}. This deep and ongoing reliance spans all major taxonomic groups, influencing both human societies and the evolutionary paths of the species human societies use^{3–5}. The human uses of biodiversity have rarely been random; across plants, animals, and fungi, exploited species disproportionately share traits such as large body size⁶, rapid growth⁷, conspicuous appearance^{8,9}, or high nutritional value¹⁰. These traits enhance their utility, accessibility, or appeal and thus make them prime targets for harvest, trade, or domestication.

Yet, traits are also strongly linked to species' ecological roles¹¹, influencing how organisms move, feed, interact, and shape their environments. As a result, exploitation of species driven by culture or economy has ecological consequences for the functioning of ecosystems¹². For instance, the disappearance of large mammals due to human pressure in Europe has drastically modified ecosystems, shifting them from megafauna-rich landscapes with extensive grazing and nutrient redistribution to more homogenised forests and simplified food webs¹³.

Today, harvest and trade of more than 50,000 wild species sustain the livelihoods of hundreds of millions of people over the

world^{2,14}. But as demand rises and exploitation intensifies, concerns are growing over the sustainability of these interactions, their ecological impacts, and the urgent need to align conservation efforts with development goals and human well-being^{15,16}. Understanding the ecological role of the species used by humans is hence becoming a key issue for both biodiversity conservation and sustainability of human societies.

With the rise of trait-based approaches and the availability of large databases, it is now possible to assess the functional diversity of major taxa of interest for humans^{17,18}. However, it remains unclear whether the functional traits targeted by humans for food, ornament or recreation are supported by a large range of species or only a few ones, and if those species are currently threatened. This represents a critical blind spot, as most conservation frameworks—including the IUCN Red List¹⁹, CITES regulations²⁰, and IPBES assessments²—primarily evaluate species' threat status or trade volumes, but rarely account for their functional roles²¹. Yet, exploiting species with unique trait combinations might increase extinction risks for species playing key roles in ecosystems. Integrating trait-based perspectives into conservation frameworks is therefore requested to provide a robust basis for identifying priority species and ensuring that conservation efforts

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safeguard not only biodiversity itself, but also the ecological strategies essential for human well-being.

Here, we focus on freshwater fishes, which number over 18,000 species²² and are intensively used by humans for protein supply, recreation and ornament^{23,24}. We adopt a macroecological perspective to capture the global footprint of human uses on freshwater fish functional diversity, necessary to identify broad, cross-continental patterns. We combine morphological traits from FishMORPH²⁵, the most accurate database on morphological traits of freshwater fish worldwide and FishBase²⁶ for human uses, to investigate whether humans target species with particular morphological traits. We then investigate if these traits are commonly shared or specific to a few morphologically distinctive species. We finally use simulations to quantify to what extent the extinction of threatened species used by humans could reshape the morphological spectrum of freshwater fishes over the globe. We here expect that humans select a non-random subset of the global fish morphological spectrum and that this subset differs according to human uses. If this is true, testing whether species that support unique trait combinations—that are often threatened^{27–29}—are used by humans is of particular importance, as human pressure on those species could trigger extinction risks.

Results

Here we show that the 2334 species used by humans occupy almost half of the volume (Fric = 45.2%, Fig. 1), a proportion that did not significantly differ from expectation (SES = 1.10, $P = 0.863$) when the trait combinations were randomly assigned among all freshwater fish species. This indicates that the volume of morphospace occupied by human-used species is neither larger nor smaller than would be expected if traits were randomly assigned among all freshwater fish species.

However, each type of human use selectively targeted distinct areas of the morphospace, resulting in significant and use-specific trait clustering (Fig. 1). Compared to random expectations (i.e., morphological traits of species randomly assigned within the morphospace), the 1505 species recorded as aquarium trade showed the strongest trait clustering (SES = -7.17, $P = 0.001$). Conversely, the 237 species recorded as aquaculture were more morphologically diverse than expected (SES = 2.83, $P = 0.998$). Fisheries species spanned a broad extent of the morphospace (35.81%), which did not significantly differ from random expectations (SES = 0.32, $P = 0.618$). However, the location of fisheries species within the morphospace was shifted toward higher PC1 scores compared to the global species pool (SES = 15.45, $P = 0.999$, Fig. 2 and Supplementary Table 1), reflecting an overrepresentation of large-bodied species. Similarly, game fishing species occupied a restricted region of morphospace and showed a similarly high proportion of large-bodied, large-mouthed species compared to the global species pool (SES = 31.75, $P = 0.999$, Fig. 2 and Supplementary Table 1); however, the volume did not significantly differ from random expectations (SES = -0.10, $P = 0.458$, Fig. 1f).

The morphological overlaps (i.e., the proportion of morphospace shared by two usages) were highly variable across human uses (Table 1), indicating each human use targeted a specific portion of the morphospace. For instance, game fishing shared minimal overlaps with other categories (overlaps ranged from 0.20 to 0.59, Table 1). Contrastingly, species used in fisheries encompassed a broader trait spectrum, with high overlap with aquaculture, sharing species with similar morphological traits (overlap = 0.81, Table 1).

However, our model indicated that the probability of being used increased with the morphological distinctiveness up to intermediate values and then declined for the most morphologically distinct species (Fig. 3). This result suggests a non-linear, trait-based filtering of species used by humans. When decomposing by usage, we found contrasted patterns depicting different selection pressures according to the type of usage. For aquaculture and game fish, morphological

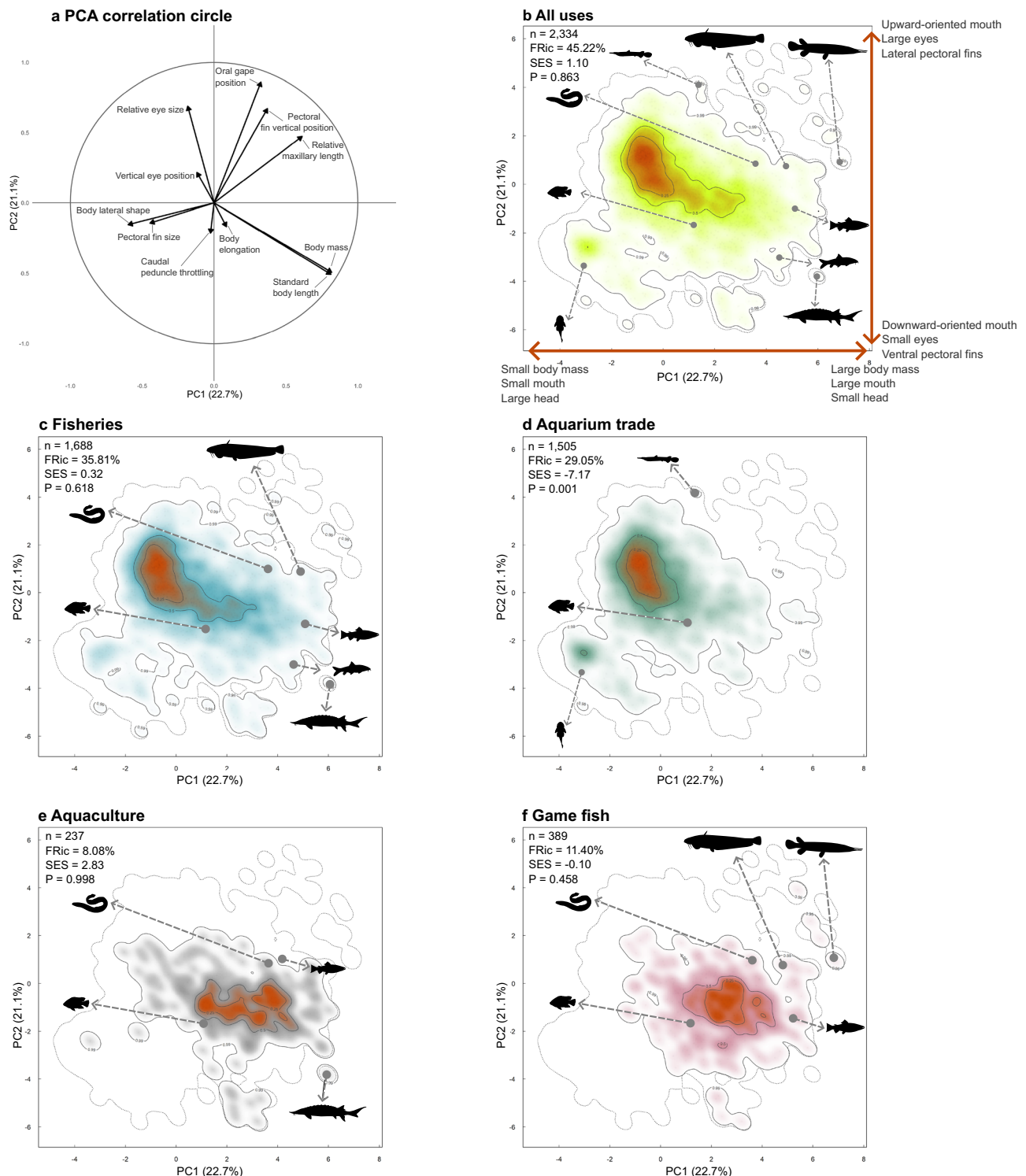
distinctiveness contributed positively to the probability of being used (9.7% and 9.8%, of explained deviance, respectively), indicating a selective pressure toward species with distinctive trait combinations for these types of usage. In contrast, for fisheries and aquarium trade, morphological distinctiveness hardly increased the probability of being used (explained deviance of 1.4% and 0.8%, respectively, Fig. 3), consistent with a selection toward species with common trait combinations.

To evaluate whether the extinction of species that are both used by humans and threatened with extinction would also disproportionately erode the morphological diversity, we simulated sequential species loss scenarios based on IUCN threat levels and calculated the loss of morphological richness following the potential extinction of threatened freshwater fish species used by humans. There, negative values indicate a decrease in the relative abundance of trait values associated with a given region of morphospace. Consequently, the positive values indicate a relative increase arising purely from this mathematical property of quantile differences. From an ecological point of view, those areas cannot be interpreted as an increase of species with such ecological strategies, since no species are introduced. However, they reflect a relative increase in the proportional representation of those trait combinations among surviving species, as losses elsewhere mathematically elevate their dominance within the post-extinction trait spectrum. In addition, we identified morphospace cells that became empty following extinctions and expressed this lost space as a proportion of the total morphospace occupied by the IUCN-assessed used species spectrum.

The loss of both used and threatened species (Table 2) would strongly affect the global morphological diversity with a loss of 4.70 % under the scenario NT (i.e., removing all threatened (i.e., CR, EN, and VU) and near threatened (NT) species. This loss of morphological diversity substantially exceeded the mean loss expected under the null model (1.12%, Supplementary Table 2) if only threatened species (i.e., CR, EN, and VU) and near threatened (NT) species were randomly removed (SES = -24.78, $P = 0.001$, Fig. 4). This pattern was consistent across all usages and scenarios but varied in terms of intensity. The loss of morphological diversity was particularly marked for species occupying peripheral regions of the morphospace (Fig. 4). These findings indicated that species which were both threatened and subject to human exploitation tended to occupy irreplaceable positions in the morphospace. Their extinction would not only reduce species richness but would also disproportionately collapse the morphological diversity of freshwater fish communities by removing trait combinations that no other species can compensate for.

Discussion

Freshwater fish species used by humans do not represent a random sample from the global spectrum of morphological diversity. Instead, they are disproportionately selected for their unique morphological trait combinations. Although the fish species used by humans represent a fourth (26%) of the freshwater fish species, they occupy 45.2% of the total morphospace. These results highlight how human activities draw on a wide array of functional strategies to meet various needs. Since the use of species by humans is considered a major threat to biodiversity^{30,31}, targeting species with unique trait combinations can thus amplify the risk of losing ecological strategies that no other species can replace. This was confirmed by simulating the extinction of threatened species used by humans. This resulted in a pronounced and non-random erosion of the global morphological spectrum, with potential implications for the ecological integrity and functional resilience of freshwater ecosystems worldwide. Since the distinct uses of fish by humans target different regions of the morphospace, conservation actions should be directed toward specific human activities to safeguard the ecological strategies that underpin both Nature's Contributions to People¹⁴ and the long-term resilience of ecosystems³².



Broad evidence across taxa demonstrates specific use by human societies of large-bodied mammals⁶, slow-growing trees³³, or brightly coloured birds⁷. Human societies use a broad range of fish morphologies, because fish are used for a wide array of purposes spanning from fisheries to aquaculture and recreation through angling (game fish) and ornament (aquarium). Yet, considering those four main usages independently disentangles the links between fish morphology and human uses, with each human use targeting a distinct area of the morphospace (Fig. 1). Aquarium trade distinctly targeted species with

upward-facing mouths and large eyes (e.g., guppy, *Poecilia reticulata*). Such preferences, driven by aesthetic considerations³⁴, are not only based on colouration patterns but also on morphology, as suggested for reef fishes by Langlois et al. (2022)³⁵. In addition, human selection was also driven by practicality for aquarium keeping³⁶, and thus preferentially selects small-bodied and small-mouthed species (Fig. 2c) (e.g., Loricariids such as *Ancistrus dolichopterus*, or goldfish, *Carassius auratus*). These morphological profiles often correspond to low trophic-level guilds—omnivores, planktivores, and insectivores^{12,37}—

Fig. 1 | Morphospace of freshwater fish species used by humans. **a** Correlation circle depicting the loadings of the traits in the PCA for PC1 and PC2.

b–f Morphospace of species encompassing all species used by humans. **c–f** Morphospaces of species considering each type of usage. Usage is indicated above each panel. Freshwater fish morphospace was obtained from a PCA on 11 log-transformed morphological traits available for 8970 freshwater fish species (FishMORPH, Brosse et al. 2021). Probabilistic species distributions in the morphospace were represented by multivariate kernel density estimates defined by the two first principal components (PC1 and PC2) of PCA. The colour gradient indicates species density within the morphospace, with dark orange tones denoting higher concentrations of species of each type of usage whereas lighter colours indicate lower densities of species of each type of usage. Black lines represent 0.99, 0.5, and 0.25 quantiles of the morphospace for all usages (**b**) and each type of usage (**c–f**). The dotted grey line shows the 0.99 quantile envelope of the 8,970 freshwater fish species. For each panel, we provide the number of species considered in each usage (*n*), the morphological volume occupied by the species for each usage (FRic), the

standardised effect size (SES) and its associated P value (see Methods for details on SES computation). Statistical significance was assessed using two-sided permutation tests based on 999 randomisations. Morphological volumes were computed across four axes. Morphospaces for the axes 3 and 4 of the PCA are provided in Supplementary Information (Supplementary Fig. 1). To aid interpretation, morphological gradients are annotated directly on the PC axes 1 and 2 of the panel **b** (orange arrows). A correlation between each PC axis and morphological traits is provided in Supplementary Fig. 2. Silhouettes are sourced from PhyloPic and illustrate freshwater species in clockwise order from top left: *Anguilla anguilla*, *Dermogenys pusilla*, *Wallago attu*, *Atractosteus spatula*, *Salmo trutta*, *Luciobarbus brachycephalus*, *Huso huso*, *Oreochromis mossambicus* and *Ancistrus dolichopterus*. Where no species-level silhouette was available, a congeneric silhouette was used. Silhouettes were scaled to relative body size using three classes: > 80 cm (large), 40–80 cm (medium), and <40 cm (small). Silhouettes in panels **c–f** correspond to the same set of species as in (**b**), with those highlighted indicating species associated with each specific usage.

but do not exclude other strategies, such as some predatory species that often attract fish hobbyists due to their unusual colour or morphology (e.g. knife fishes such as *Chitala blanci* represented on the Fig. 1). Conversely, aquaculture targeted preferentially large-bodied benthivores, with downturned mouths (e.g., African sharptooth catfish, *Clarias gariepinus*) and demersal predators such as the Indian knifefish (*Chitala chitala*) (Fig. 2d). Game fishing similarly selected for large-bodied species, with large mouths (e.g., largemouth bass, *Micropterus salmoides*, lake trout, *Salvelinus namaycush*) (Fig. 2e). Aquaculture and game fishing therefore select large species, with traits related to high growth rates and efficient resource utilisation^{38,39}. Such selection of particular morphologies for species used for ornament, recreation and aquaculture contrasts with the morphology of the fish species exploited by fisheries, which have a broad morphological diversity. Fisheries target small-bodied prey species, such as the silver cyprinid (*Rastrineobola argentea*) in Lake Victoria⁴⁰ or the vendace (*Coregonus albula*) in Northern hemisphere⁴¹. Their abundance and small size facilitate easy handling and widespread use⁴². Conversely, large-bodied predators, such as northern pike (*Esox lucius*), are also prized targets for their substantial meat yield and economic importance⁴³. The coexistence of these morphologically distinct species within fisheries underscores the multifaceted nature of human harvesting strategies, which span trophic levels and ecological roles, reflecting varied dietary, cultural and economic demands²³. At the same time, the prominence of small-bodied species in fisheries may also reflect a “fishing down the food web” process, whereby the depletion of large, high-trophic-level species leads to increased exploitation of smaller, lower-trophic-level species⁴⁴. It also underscores the exploitation of the full range of available species in commercial fisheries, which is particularly true in the southern half of the globe^{45,46}.

Moreover, whatever the fish use, we here show that freshwater fish species exhibiting unique morphological trait combinations were preferentially used by humans (Fig. 3). The foregoing implies that exploited species might play critical roles in ecosystems, not insured by other species gathering similar trait comparisons⁴⁷. Therefore, the less insured functions appear to be the most used by humans. This is particularly marked for the species used in aquaculture and game fishing, as these two human uses preferentially target morphologically distinct species that carry unique ecological strategies³⁰. Those activities indeed target a few large species and that are for most of them morphologically unique²⁷. The overexploitation of such specialised species could modify the functional structure of fish assemblages and potentially skew ecosystem processes such as nutrient cycling and trophic interactions^{48,49}. For instance, largemouth bass (*Micropterus salmoides*) is heavily cultured and a popular game fish, but its overexploitation has been shown to downgrade lake food webs and fundamentally change associated ecosystem processes by reducing its

control effect on lower trophic levels⁵⁰. This is also the case for other species targeted by anglers, that are often large-bodied and top predators, playing a key role in ecosystems through top-down effects⁵⁰.

Simulating the extinction of the threatened species used by humans resulted in a marked erosion of the freshwater fish morphological diversity across the globe (Fig. 4, Supplementary Table 2). The sequential removal of species from the most threatened (CR) to the least threatened (NT) categories was designed to reflect a realistic temporal gradient of extinction risk, whereby the most critically endangered species are expected to disappear first, followed by species of progressively lower threat status²⁸. This erosion was not caused by a particular use of fish, and the extinction of threatened fish, whatever the usage, will result in a higher-than-expected decline in fish functional diversity over the globe. Such extinction will disproportionately affect regions of the morphospace occupied by species with specific ecological strategies, such as large-bodied species with predatory (e.g., Boal fish, *Wallago attu*) or benthivorous (Sturgeons, *Acipenser spp.*, *Huso huso*) habits (Fig. 4), that are known to represent the most threatened regions of the morphospace²⁷. Thus, species that are simultaneously used by humans and threatened require particular attention, not only to ensure the sustainability of the species, but also to ensure food security, livelihoods, and ecosystem health across the globe⁵¹.

Our results underscore a dual effect. On one hand, humans disproportionately target morphologically irreplaceable species, amplifying the risk of losing unique ecological functions. This threat was, for instance, mentioned for marine fish in the northern Atlantic region, where sharks represent functionally unique large-bodied predators overexploited by benthic trawls⁵². This was also observed in mammals and birds, where the most functionally distinct species tend also to be the most threatened according to the IUCN categories⁵³. But on the other hand, the species used by humans—particularly in managed systems like aquaculture or through cultural and economic value—may provide some level of protection or conservation incentive. That is the case for common carp (*Cyprinus carpio*), which is threatened in its native range, but globally propagated by aquaculture, making it one of the most common freshwater fish across the globe and even a potential pest for native faunas⁵⁴. Species valued for food, trade, or recreation may hence benefit from propagation, habitat protection, or legal safeguards, acting as a buffer against extinction. Recreational fishing, when stringently regulated, can be managed sustainably and even foster population recovery^{55,56}. Such “trophy hunting” activity could be viewed as a way to protect target species from overfishing by providing more money income than fisheries⁵⁷. Likewise, community-based management has proven successful for high-value species like Arapaima (*Arapaima gigas*) in Brazil, where protecting lakes for subsistence fisheries led to a 193% population increase and improved household incomes⁵⁸. Beyond this win-win outcome, Arapaima plays

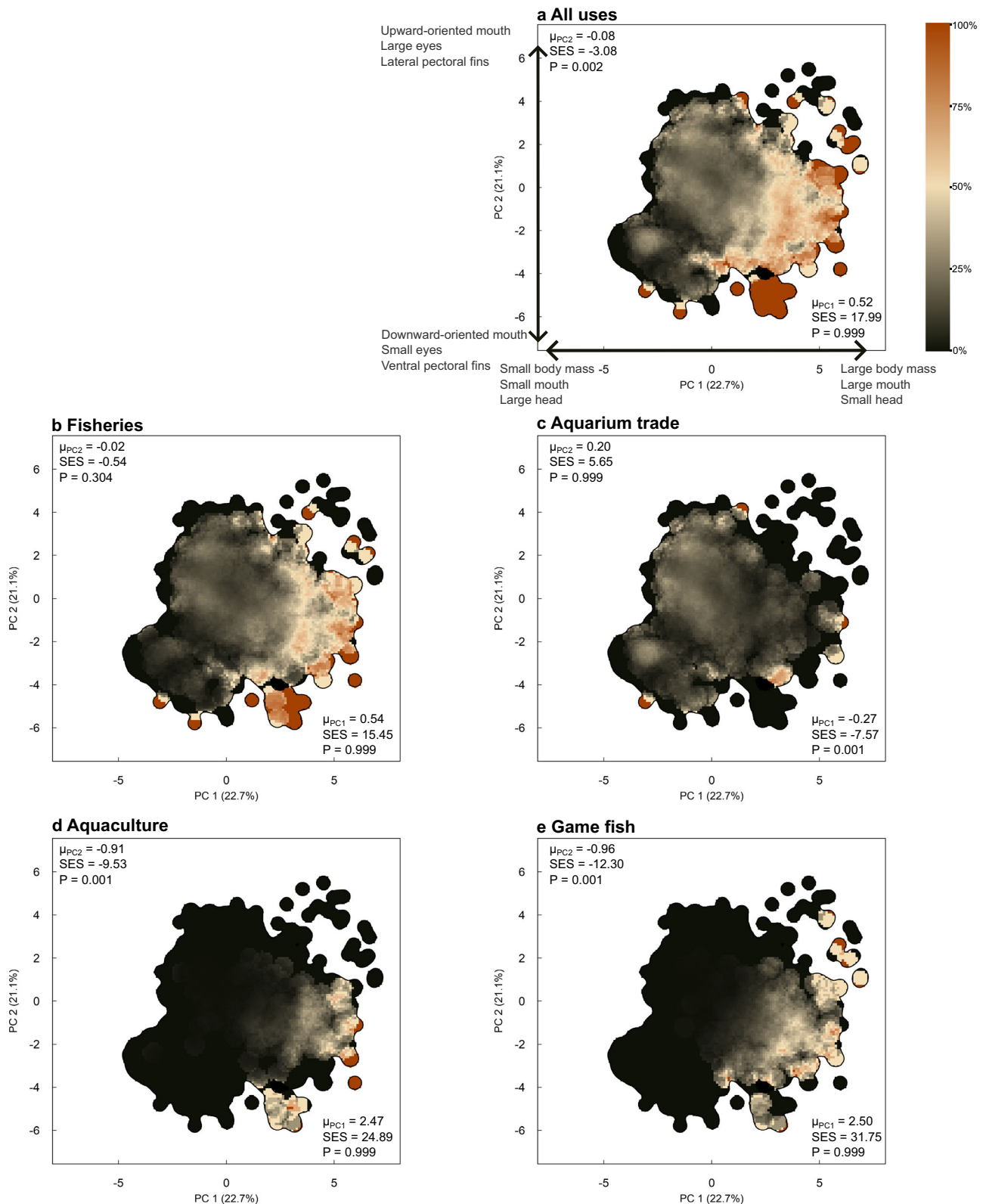


Fig. 2 | Proportion of species used by humans across the fish morphospace. Each panel shows the proportion of species that are used by humans, for all uses (a) and for each category (b–e) over the first two axis of the morphological space (PC1, PC2). The morphospace was discretised into 810,000 cells spanning four retained axes (PC1–PC4; 30 bins per axis). For every cell we computed the ratio of species belonging to the focal usage to all species present. The colour gradient represents this proportion from dark (0% – the cell is occupied by species but none is used) to

dark orange (100% – all species in the cell are used). For each panel we reported the mean scores of the used species along each axis (μ_{PC1} , μ_{PC2}), the standardised effect size (SES) of their occupancy relative to the null expectation, and its associated P value (see Methods for SES computation). Statistical significance was assessed using two-sided permutation tests based on 999 randomisations. Morphological gradients underlying PC1 and PC2 are annotated on panel a (dark brown arrows); gradients for PC3 and PC4 are given in Supplementary Fig. 3.

an umbrella species role, and its management also benefits other threatened species, including turtles and caimans⁵⁹. Although human use can support conservation⁶⁰, we still need to stay cautious about the possible overreliance on utilitarian

approaches, which risks excluding species and habitats with no obvious human value⁶¹. Conservation cannot depend solely on market-based incentives, and protection must extend beyond use; utilitarian logic alone cannot resolve ecological crises⁶¹. In this context, human use considerations complement, but cannot replace intrinsic, non-instrumental reasons to conserve. Trait-based approaches are thus providing a framework to identify functionally irreplaceable species that are disproportionately exposed to human use. The foregoing approaches offer complementary information to traditional conservation assessments that have largely focused on species richness and extinction risk, overlooking the erosion of functional traits that underpin ecosystem resilience. Yet, evidence of global functional homogenisation in freshwater fish faunas highlights the urgent need to complement taxonomic indicators with functional metrics⁶². Integrating functional diversity into conservation planning consistently improves the spatial efficiency⁶³ and robustness of priority areas⁶⁴. Similar insights have emerged from reef systems, where high species richness does not necessarily guarantee functional

Table 1 | Morphological overlap among the four human usages

	Aquaculture	Aquarium	Fisheries	Game fish
Game fish	0.32	0.20	0.59	-
Fisheries	0.81	0.56	-	-
Aquarium	0.27	-	-	-
Aquaculture	-	-	-	-

Overlap was calculated as the proportion of shared volume in 4-dimensions between two groups using ‘TPD’ package. Values range from 0 (no shared volume) to 1 (complete overlap, identical volume).

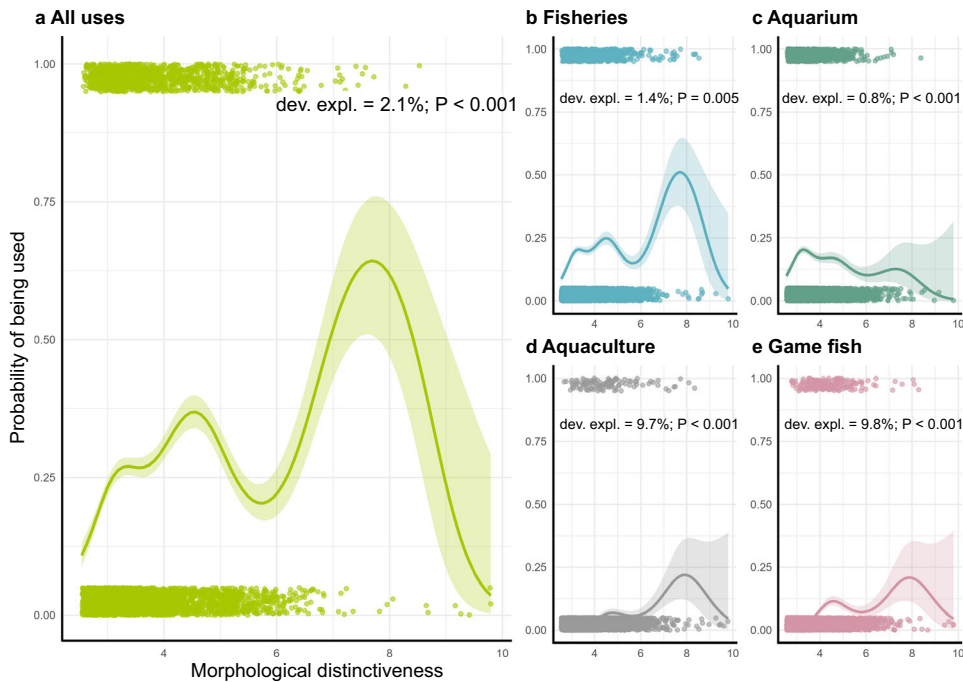


Fig. 3 | Relationship between morphological distinctiveness and the probability of being used across human usage categories. a All uses, **b–e** Each type of uses, indicated in the panel title. Morphological distinctiveness was computed as the average morphological distance within the morphological space in 4-dimensions of each species to all other species in the global pool, using the ‘funrar’ package. Dots represent species (1 = used, 0 = non-used). Colour accounts for distinct usages. Coloured lines depict predicted probabilities of being used

from binomial generalised additive models, with shaded areas indicating 95% confidence intervals of these fitted values. Text annotations report for each panel the percentage of deviance explained (dev. expl.), which quantifies the improvement in model fit relative to the null model (intercept-only), and the P value of the smooth term, assessed using the approximate two-sided test implemented in the ‘mgcv’ package. Exact statistics are reported in Supplementary Table 7.

Table 2 | Number of threatened species for each human use category and threatened category

	Total	CR	EN	VU	NT	DD	LC	Threat.	% Threat.
Fisheries	1688	52	84	86	66	107	1222	288	17.1
Aquaculture	237	11	11	13	18	13	162	53	22.4
Aquarium	1505	35	74	75	44	93	1133	228	15.1
Game fish	389	7	19	33	30	16	276	89	22.9
All uses	2334	65	117	121	93	139	1703	396	17.0
All fish	8970	253	467	514	339	1052	5728	1573	17.5

Threatened species are all species recorded in the IUCN Red List as CR Critically Endangered, EN Endangered, VU Vulnerable, and NT Near Threatened. The “All uses” category refers to the combination of all human uses. The “All fish” category includes all species with morphological information, both used and non-used. Use categories are not mutually exclusive. Species can be associated with more than one use, such that counts within uses are non-independent and can sum to more than the total number of unique species reported under “All uses”.

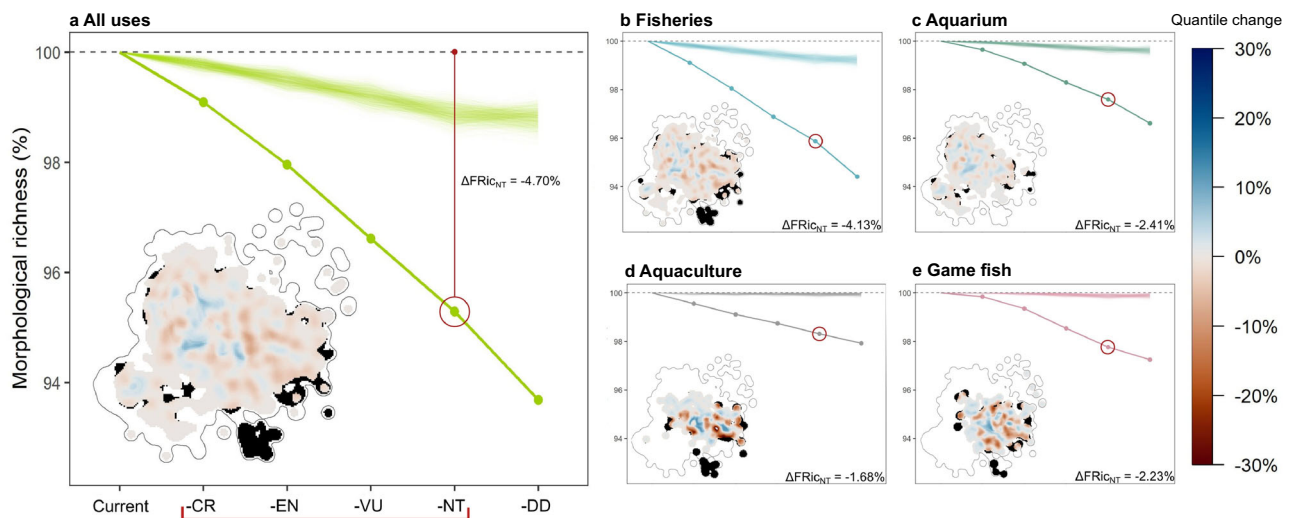


Fig. 4 | Loss of morphological richness following the potential extinction of threatened freshwater fish species used by humans. For **a** All uses and **b–e** each human use category (indicated in the panel title), the percentage of morphological richness loss (ΔFRic) is shown. Morphological richness loss was assessed following a stepwise removal of species used by humans and classified as threatened by IUCN (CR Critically Endangered, EN Endangered, VU Vulnerable, NT Near Threatened, and DD Data Deficient). For each scenario, the observed loss of morphological richness (solid lines) was compared to the expected loss of morphological richness calculated from a random subset of threatened species (fuzzy lines). Dots refers to the significance of the standardised effect size calculated between the observed and randomised values obtained with the null model (see Methods for details).

Filled dots denote significant differences ($P < 0.025$); open dots indicate non-significant differences ($P > 0.025$). $\Delta\text{FRic}_{\text{NT}}$ corresponds to the loss in morphological richness if CR, EN, VU, and NT species are removed and called scenario NT. Within each panel, we illustrated the shift in morphospace following extinction of used and threatened species according to the scenario NT. Black parts of the morphological space indicate the areas that would disappear from the global spectra after extinctions (trait combinations that go completely extinct), brown tones reflect areas in which the TPD quantiles decrease after extinctions (i.e., trait combinations that become less densely occupied), and blue tones reflect areas in which the TPD quantiles increase (see Methods), thus indicating higher proportion of certain trait combinations following species extinctions.

insurance, underscoring that conserving diversity hotspots alone is insufficient when the goal of conservation prioritisation is to secure the functional insurance of biota⁶⁵. In practical terms, our results suggest that functional metrics could be directly incorporated into management frameworks. For instance, fisheries institutions such as the Food and Agriculture Organisation (FAO) could promote the exploitation of functionally redundant species while imposing stricter quotas on functionally unique ones, thereby reducing the functional vulnerability of targeted assemblages to enhance ecosystem stability⁶⁶. At the international level, trade regulations such as CITES could also integrate trait-based indicators—particularly functional distinctiveness—to better safeguard ecological functions^{21,52}. This is consistent with recent studies on reptile trade revealing strong functional biases favouring large-bodied, long-lived taxa, underscoring that extinction risk alone is insufficient to preserve key functional roles⁶⁷. Expanding such frameworks to include functionally irreplaceable but non-threatened species could prevent pre-emptive functional loss in vulnerable ecosystems. Together, these perspectives advocate for a shift from purely taxonomic conservation paradigms toward approaches explicitly incorporating functional indicators as a core dimension of biodiversity value.

While our analysis provides new insights into the functional consequences of human uses on the global diversity of freshwater fishes, our results remain limited by the global extent of the study. Such a global approach captures trends that are essential to provide a broad understanding of how human uses filter functional diversity by preferentially targeting morphologically distinctive species and, consequently, how their disappearance would erode the global freshwater fish morphospace. Yet, the results we report will hold at finer scales because species designed as functionally distinct over the globe would remain in that category when considering ecoregions, basins or sites. Yet such a global-scale approach overlooks regional contrasts and thus omits functionally unique species within a region or a river basin, making it necessary for further studies to disentangle how the intensity

and nature of human uses shape functional diversity across different regions²⁹. Furthermore, our analysis is restricted to the morphological consequences of direct exploitation by humans, while indirect threats (e.g., river damming, habitat destruction, pollution, and invasive species) remain one of the primary drivers of freshwater biodiversity loss globally⁶⁸. Quantifying the morphological consequences of such indirect pressures remains an important avenue for future research.

Our findings reveal a global, non-random pattern in the morphological traits of freshwater fish species used by humans, with strong implications for ecosystem functioning and conservation. Human activities selectively target functionally distinctive species, intensifying the risk of losing irreplaceable ecological strategies. Yet, use can also confer protection, especially when tied to cultural or economic value. This duality highlights the need to move beyond taxonomic conservation toward frameworks that integrate functional diversity metrics. By identifying which traits and ecological strategies are most vulnerable, trait-based approaches offer actionable insights for reconciling sustainable use with biodiversity protection. These results underscore the urgency of integrating functional indicators into international policy, management, and trade regulation to safeguard the resilience of freshwater ecosystems and, more broadly, the global biota.

Methods

Data collection

Morphological traits and phylogenies. We used morphological traits from the FishMORPH database²⁵, the most complete database of morphological traits for freshwater fishes. This database included eleven morphological traits related to the locomotion and feeding strategies of fishes¹². These traits have been measured on 8970 species (see Brosse et al. (2021)²⁵ for details on database completion). Briefly, nine morphological traits were obtained from measures on side-view photographs of a single adult specimen. Intraspecific morphological trait variability was not considered in this study, as it hardly affects

functional diversity at the large spatial resolution considered⁶⁹. The morphological traits considered were body elongation (BEI), body lateral shape (BLs), Relative eye size (REs) and vertical eye position (VEp), relative maxillary length (RMI) and oral gape position (OGp), pectoral fin size (PFs) and pectoral fin vertical position (PFv), and caudal peduncle throttling (Cpt). In addition, fish maximum standard body length (SBI) and maximum body mass (Bm) have been retrieved from FishBase²⁶. Information on morphological measures and trait calculation is provided in Brosse et al. (2021)²⁵.

Due to the loss of body parts or the quality of fish pictures, some traits have not been measured for some species. Overall, 26.57% of the values were missing in the raw morphological trait dataset. We imputed those missing values using a machine learning trait imputation procedure (i.e., ‘missForest’ v1.5 package available in R⁷⁰), commonly used in macroecology^{71,72}. Before imputation, traits have been log₁₀-transformed, centred, and scaled. As suggested by Penone et al. (2014)⁷², we considered evolutionary relationships in the imputation process by including phylogenetic eigenvectors as additional predictors, such that missing values for each morphological trait were imputed from all informed morphological traits plus the first ten phylogenetic eigenvectors derived from the square-root-transformed cophenetic distance matrix of the fish phylogeny⁷³. To evaluate the accuracy of trait imputation in a phylogenetically informed framework, we used a simulation-based procedure following Toussaint et al. (2021)²⁸. We evaluated imputation uncertainty using the procedure used by Carmona et al. 2021²⁷. For that, we artificially masked a subset of species with fully informed trait values (10% per iteration, 100 iterations) following the structure of missing values in the original dataset (see details Supplementary Table 3). We then compared the position of those species in the morphological space between the observed position (i.e., with all informed trait values) and the imputed position (i.e., with informed plus artificial missing trait values) using normalised root mean squared error (NRMSE, see details in Supplementary Table 3). Across 100 bootstraps, the mean RMSE of species' positions in morphological space was $5.47\% \pm 1.52\%$ of axis ranges (Supplementary Table 3), indicating minimal distortion from imputation. To test the robustness of a single imputation, we compared single imputation values to a mean imputation value obtained with multiple imputations (Supplementary Table 4). Multiple imputations were performed based on 100 independent missForest imputations using the same parameters but randomised seeds. For each species $\times$ trait combination with missing data, we quantified (i) variability across imputations, (ii) deviation of the multiple-imputation mean from our reference single-imputation values, and (iii) impacts on the multidimensional functional space. Differences ranged from 0.68% to 3.70%, which were comparable to the multiple imputation variability (ranging from 0.737% to 3.43%). This suggests the choice between single and multiple imputation exerts only a minor influence relative to inherent stochasticity in the procedure. Procrustes analyses of all pairwise comparisons among the 100 imputed datasets further confirmed high geometric stability of the functional space (mean $r = 0.9952$; range: 0.9907–0.9999), with minimal residual deviation (mean sum of squares = 0.0095). These results indicate our principal findings are robust to imputation uncertainty. We thus conclude that single and multiple imputation are functionally equivalent here, with imputation uncertainty exerting negligible effects on species positions within functional trait space.

Taxonomy was standardised using the R package ‘taxize’ (v0.10.0)⁷⁴. All names were resolved with the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy^{75,76}. The species names that were not standardised using ‘taxize’ were checked based on the taxonomic classifications provided by Fricke et al. (2025)⁷⁵. After taxonomy homogenisation, our analyses are based on 8,970 fish species with informed morphological traits.

Human uses. Data on human uses were retrieved from the FishBase database²⁶, which considers the fisheries, aquarium trade, aquaculture and game fish as the four main categories of fish use. We used two complementary approaches to extract this information from FishBase. First, we extracted all available information on species uses through the R package ‘rfishbase’ (v5.0.1)⁷⁷. Yet, we noticed that not all fields were systematically filled for all species, leading to potential gaps in usage assignment. To address this limitation and complete the dataset, we developed a web scraping protocol using the R package ‘rvest’ (v1.0.4)⁷⁸ to directly retrieve usage information from the website (www.fishbase.se). We used automated scripts to extract the “Human uses” section of each species. To assess the potential bias introduced by the web scraping method, we conducted additional analyses comparing the results derived from each data source independently and the merged dataset. We tested whether the inclusion of species identified through data scraping altered the structure of trait-based morphological spaces for each usage category. Scraped data contributed an additional 1.7% of usage records (see Supplementary Table 5), with the most notable increase observed in the game fish category with a 14.65% usage records from web scraping. To assess the impact of these additions, we recalculated morphological spaces and visually compared them with and without scraped species (Supplementary Fig. 4). Morphological structure remained globally unchanged, indicating limited influence of the added data.

Fisheries' interest referred to the species captured in the wild and used as a protein supply for humans. Freshwater fisheries provide essential protein for over 150 million people, particularly in low-income countries⁷⁹, and account for ~12 million tons of annual harvest²⁴. Fisheries interest was determined from FAO data²⁴, which classifies species from “highly commercial” to “no interest.” To restrict the analysis to intensively exploited taxa, only species labelled as “highly commercial” or “commercial” were retained ($n = 1688$; 75.52% of all fish used in fisheries), hereafter referred to as species of fishery interest.

Aquaculture interest relied on the species cultured in ponds, lakes, and cages, excluding ornamental trade. Aquaculture has surpassed capture fisheries in volume, reaching 130.9 million tonnes in 2022²⁴. Aquaculture interest was derived from FAO data, which categorises species as “never/rarely,” “experimental,” “likely future use,” or “commercial.” Only species labelled as “commercial” were considered of aquaculture interest ($n = 237$; 89.77% of aquaculture-used species).

Ornament referred to the species used in ornamental trade in ponds or aquaria. Species kept only in public aquariums were not considered in this category. Aquarium trade use was classified into “never/rarely,” “potential,” “show aquarium,” and “commercial.” We retained only species categorised as “commercial” ($n = 1505$), which account for most aquarium-traded species (97.66%) and were commonly sold in aquarium shops worldwide. Categories such as “potential” or “show aquarium” were excluded due to their limited or non-commercial exploitation.

Game use referred to the fish targeted by anglers. It was identified based on FishBase records, which report 389 species targeted in game fishing. This information primarily stems from the annual World Record Game Fishes list published by the International Game Fish Association (IGFA)⁸⁰.

Each category of human use was not mutually exclusive: a given species can be assigned to multiple human uses. For instance, the common carp, *Cyprinus carpio*, is used in all categories, i.e., fisheries, aquaculture, aquarium trade and game fish.

Morphospace

We built a morphological trait space (hereafter called morphospace) of freshwater fish using a principal component analysis (PCA) on the 11 log-transformed and scaled morphological traits, summarising the main axes of morphological trait variation. We kept the first four PC

axes, which summarise 74.02% of the morphological trait variability in agreement with the Horn's parallel analysis available in the 'paran' package⁸¹. We assessed the contribution of each morphological trait along each of the four PC axes by calculating the mean and standard deviation of the PC scores for each axis (1–4). We evaluated the probabilistic distribution of the species within the morphospace by performing multivariate kernel density using the 'TPD' and 'ks' packages^{82,83}. We divided the four-dimensional space into 810,000 cells, 30 per dimension, as the best compromise between data visualisation and computation time²⁷.

Biodiversity indices

Taxonomic diversity was calculated as the number of species for each usage (species richness), and morphological diversity was calculated as the volume of morphospace occupied by those species (morphological richness, hereafter called FRic⁸⁴), measured using the 'TPD' package⁸². We expressed the amount of morphospace of each usage as a percentage of the volume occupied by all freshwater fish species (Supplementary Table 6). To quantify the morphological redundancy between the species belonging to the four usages for which we have morphological traits, we measured their overlap in the morphospace using the 'TPD' package⁸². The overlap index varies between 0 and 1, where a value of 1 indicates no overlap (complete dissimilarity in trait space) and a value of 0 indicates full overlap (no dissimilarity in trait space) (Table 1).

Null models

Null models were used to assess whether the volume occupied by the species associated with a usage was different from what would be expected if traits of the species were randomly sorted within the global pool. We generated 999 simulations where morphological traits were randomly sorted within the global pool of freshwater fish species. In each simulation, we kept the number of species per usage constant. For each simulation, we calculated the morphological richness along with the corresponding standardised effect sizes (SES). The SES provides a standardised measure of how much the observed value differs from the mean of the simulated distribution, expressed in units of standard deviation, as follows:

$$SES = \frac{\text{Observed value} - \text{Simulated values}}{\sigma \text{Simulated values}} \quad (1)$$

To determine the statistical significance of the ranking, we calculated associated *P* values. A *P* value lower than 0.025 implies that the observed value is significantly lower than expected by chance, while a *P* value higher than 0.975 indicates that the observed value is significantly higher than expected²⁸ (Supplementary Tables 2 and 6).

Morphological distinctiveness of species used by humans

To quantify how morphologically distinct a species is within the global species pool, we calculated its morphological distinctiveness as the average distance from that species to all other species, using the 'funrar' package⁸⁵. By doing this, we captured how unique an organism is in terms of its morphological traits, and quantified it by measuring its morphological distance relative to all other species¹⁸.

To test whether morphologically distinctive species are more likely to be used by humans, we fitted a binomial generalised additive model (GAM) with a logit link, using species use (as a binary response) as a function of their distinctiveness score. The effect of morphological distinctiveness was evaluated using the approximate significance test of the smooth term provided by the 'mgcv' package⁸⁶ (χ^2 statistic and associated *P* value, Supplementary Table 7), and model fit was summarised using the percentage of deviance explained.

As a complementary analysis, we also calculated species uniqueness, defined as the distance to the nearest neighbour in the trait space. These two metrics were positively correlated (Pearson's

$r = 0.69$, $t = 8,968$, $p < 2 \times 10^{-16}$, 95% CI = [0.68, 0.70], two-sided; Supplementary Fig. 5), indicating that morphologically distinct species in the global pool also tend to be isolated from their closest neighbours in morphospace.

Simulating threatened species extinction

We considered the extinction risk of the 2334 freshwater fish species used in our study using the IUCN Red List categories. Among them, 65 species are classified as Critically Endangered (CR), 117 as Endangered (EN), 121 as Vulnerable (VU), and 93 as Near Threatened (NT), totalling 396 species (17.0%) that we considered as "threatened" in our study. We also identified 139 as Data Deficient species. The proportion of threatened and used species (i.e., 396/2,334) is lower than the global estimate of threatened freshwater fish species¹⁹ (26.3%, 4064 out of 15,433 assessed species).

To assess whether the species both used by humans and threatened to extinction depict disproportionately unique morphological traits, we quantified the loss of morphological diversity due to the loss of species both used and threatened compared to the loss of species threatened but not used by humans. For that, we used scenarios where threatened species were sequentially removed according to their extinction risk, starting with the most threatened species (i.e., Critically Endangered species, noted -CR), followed by scenarios removing species with less threatened status (Toussaint et al. 2021)²⁸. Scenarios were named by the least threatened category considered: -EN: CR + EN removed; -VU: CR + EN + VU removed; -NT: CR + EN + VU + NT removed. These scenarios mimic a temporal gradient from the loss of the most threatened species (i.e., Critically Endangered) which are more likely to disappear first, to the extinction of species with lower extinction risks²⁸. For each scenario and usage category, morphological richness (FRic) was recalculated using the trait probability density (TPD) framework.

Reporting summary

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

Data availability

All analyses were based on publicly available datasets: species conservation status from the IUCN Red List (<https://www.iucnredlist.org>), phylogenetic data from Rabosky et al. (2018) (<https://doi.org/10.5061/dryad.fc71cp4>), human uses from FishBase (<https://www.fishbase.org>) and morphological traits from the FishMORPH database (Brosse et al. 2021; <https://doi.org/10.6084/m9.figshare.14891412>). Each of these datasets can be accessed directly from the original providers under their respective licences and terms of use. The full datasets required to reproduce these analyses are freely available in the Data folder of the associated GitHub repository (<https://github.com/pierrolaloune/FishUsage>) and archived on Zenodo (<https://doi.org/10.5281/zenodo.21873314>).

Code availability

All R scripts used for data processing, statistical analysis, and generation of the figures in this study are available in the GitHub repository (<https://github.com/pierrolaloune/FishUsage>) and archived on Zenodo (<https://doi.org/10.5281/zenodo.21873314>).

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Acknowledgements

We are grateful to the genotoul bioinformatics platform Toulouse Occitanie (Bioinfo Genotoul, <https://doi.org/10.15454/1.5572369328961167E12>) for providing help and/or computing and/or storage resources.

Author contributions

P.B., A.T., and S.B. conceived the study. A.T. and S.B. contributed data. P.B. and A.T. designed and performed analyses. P.B. designed and coded all the figures and wrote a first draft of the manuscript, and all authors contributed to analyse and interpret results and contributed to writing the manuscript.

Funding

P.B., A.T., and S.B. were supported by French Laboratory of Excellence projects ANR-10-LABX-41, ANR-10-LABX-25-01. A.T. was supported by ANR-10-LABX-25-01 (INTRAIT project) and University of Toulouse (TREMLIN, INTRAIT project).

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-026-78568-9>.

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Peer review information *Nature Communications* thanks Emili García-Berthou, and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. A peer review file is available.

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