WILEY **Global Ecology and Biogeography** A Journal of Macroecology

Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread

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Abstract

Aim: The aim was to analyse the morphological diversity of the world freshwater fish fauna. We tested to which extent the distributions of morphological traits are supported by extreme morphologies and how those extreme morphologies are distributed among realms and affect the functional vulnerability. We also analysed the contribution of between- and within-order morphological variability to the morphological differences between realms.

Major taxa studied: Freshwater fish.

Location: Global.

Time period: 1960s–2010s.

Methods: We used a global database of freshwater fishes from the six realms. Ten morphological traits were measured on 9,150 species, that is, 75% of the *ca.* 13,000 freshwater fish species. A principal components analysis was conducted to combine the 10 traits into a multidimensional space. We used Kolmogorov–Smirnov tests to compare the difference in morphological diversity between the six realms and between and within the major fish orders. We then identified the morphologically extreme species and quantified their contributions to the morphological range to assess the functional vulnerability and redundancy of fish faunas in the six biogeographical realms for freshwater ecosystems.

Results: We report a strong morphological variability among freshwater fishes of the world, with significant morphological differences among realm fish faunas, caused by an interplay between taxonomic composition of the realm faunas and morphological differences within orders among the realms. Morphologically extreme species accounted for a large percentage of the filling of the global morphological space and are distributed throughout the world.

Main conclusions: Fish morphological diversity is largely supported by a few species with extreme trait combinations, indicating that functional vulnerability exists throughout the world. Our results suggest that more attention should be paid to these morphologically extreme species and that they should be protected to ensure the sustainability of functions they support.

KEYWORDS
biogeographical realms, freshwater fish, functional redundancy, functional vulnerability, morphologically extreme species, morphological traits, rivers

1 | INTRODUCTION

Biodiversity is as a multifaceted concept, encompassing several dimensions, including the number and identity of species (taxonomic facet), their evolutionary breadth (phylogenetic facet) and their variability in functional traits (functional facet) (Garnier, Navas, & Grigulis, 2016; Gaston & Spicer, 2004). Most global and regional scale studies have focused on the taxonomic facet, but the recent development of functional databases encompassing large numbers of species for plants (e.g., Díaz et al., 2016; Kattge et al., 2011) and animals (e.g., Mouillot et al., 2014; Ricklefs, 2012; Toussaint, Charpin, Brosse, & Villéger, 2016) allows the consideration of the functional dimensions of biodiversity at macroecological scales. Most of the previous studies have revealed a mismatch between taxonomic and functional dimensions of diversity (Kuczynski et al., 2018; Parravicini et al., 2014; Toussaint et al., 2016) because of a difference in trait distributions between realm faunas. For instance, Toussaint et al. (2016) reported that the Nearctic realm hosts a functional diversity similar to that of the Australian realm, although it hosts almost twice the number of species.

Freshwater fishes account for more than one-quarter of all vertebrates species, with *ca.* 13,000 species described to date (Nelson, Grande, & Wilson, 2016; Tedesco et al., 2017). In addition, because of their weak ability to disperse both between and within continents, fish faunas from the six biogeographical realms share only a few species (Levêque, Oberdorff, Paugy, Stiassny, & Tedesco, 2008; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). Freshwater fishes show a huge diversity of ecological strategies (e.g., diet, mobility) and contribute to key ecosystem processes, such as the regulation of food webs and biogeochemical cycles (Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017). Fish morphology, although not accounting for the entire range of fish functional roles, is a proxy of some key functions performed by fish and is more informative of fish roles than a taxonomy-based approach (Leitão et al., 2018; Villéger, Miranda, Hernandez, & Mouillot, 2010). For instance, morphological traits provide information on locomotion (Watson & Balon, 1984; Winemiller, 1991) and food acquisition (Albouy et al., 2011; Hugueny & Pouilly, 1999), which are biological features related to the contribution of the fish to the regulation of food webs and nutrient cycles (Villéger et al., 2017). However, the distribution of key fish morphological traits within and among realms and orders remains largely unknown except for body size (Blanchet et al., 2010; Olden, Hogan, & Zanden, 2007; Villéger et al., 2017). Freshwater fish size ranges from <3 cm [e.g., tiny killifish (genus *Rivulus*) and mosquitofish (*Gambusia affinis*)] to >2 m [e.g., sturgeon (*Acipenser sturio*), wels catfish (*Silurus glanis*)] (Blanchet et al., 2010; Stone, 2007). The variability of other morphological traits has been investigated far less, although they can provide complementary information, because fishes of similar body size can have contrasting locomotion and nutrition characteristics (Cucherousset, Blanchet, & Olden, 2012). Using multivariate approaches is a way to consider those traits altogether and to deal with correlations among traits (e.g., Schleuter, Daufresne, Massol, & Argillier, 2010; Villéger et al., 2010). This has been proved an efficient method to reveal overall variations of fish morphology across the globe, and Toussaint et al.

(2016) reported large differences in freshwater fish morphological richness among realms. Indeed, fish faunas have different percentages of their species richness in the main fish orders (Levêque et al., 2008), and orders have marked morphological differences (Toussaint et al., 2016). Moreover, differences in environmental constraints and/or evolutionary legacies among realms should also promote differences in trait values between species from a given order, but the magnitude of this variability is still unknown.

Furthermore, trait distribution can also discriminate ecological strategies. For instance, Díaz et al. (2016) demonstrated that trait distribution is bimodal in plants, corresponding to distinct strategies between trees (long life, late maturity, large size) and herbs (short life, early maturity, small size). In contrast, trait distribution is often unimodal in animals, with a core of generalist species and distribution tails indicating specialist species [see Ricklefs (2012) for birds, Mouillot et al. (2014) for coral reef fish and Toussaint et al. (2016) for freshwater fish]. Nevertheless, the identity of morphologically extreme species (i.e., species with values in tails of trait distribution) and their spatial and taxonomic distributions remains to be quantified, because those extreme species probably play unique functions in ecosystems (Leitão et al., 2018; Mouillot et al., 2014). Therefore, the percentage of the morphological space filled by the extreme species can be considered as a measure of the functional vulnerability of each realm. For instance, Mouillot et al. (2014) reported that coral reef fish across the world pack disproportionately into a few particular functions, while leaving many functions highly vulnerable.

Here, we assess the distribution of 10 morphological traits for 9,150 freshwater fish species. We compare the morphological differences between the six biogeographical realms for the entire fish faunas and for the five most species-rich orders to test whether the high distinctiveness of taxonomic diversity of fishes translates into morphological distinctiveness or convergence across realms. We then quantify the proportion of the morphological space filled by the morphologically extreme species and assess the fish functional vulnerability in each realm.

2 | MATERIALS AND METHODS

2.1 | Datasets

We considered the six terrestrial biogeographical realms [Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palaearctic] commonly used for freshwater fishes (Levêque et al., 2008; Nelson et al., 2016). The identity of the fish species occurring in each realm was obtained using the occurrences database from Brosse et al. (2013) and Tedesco et al. (2017), in >3,000 river basins. Nine thousand one hundred and fifty of these species (i.e., 75% of the species described; Supporting Information Table S1) were described morphologically using 10 traits describing size and shape of body parts involved in food acquisition and locomotion (Supporting Information Figure S1b). More precisely, fish size was described using the maximum body length (Max. Body Length) taken from FishBase (Froese & Pauly, 2018). Those maximum body lengths were carefully

reviewed, and irrelevant measures have been corrected according to the appropriate literature. In addition to size, 11 morphological measures were assessed on side-view pictures (Supporting Information Figure S1a) collected during an extensive literature review from >200 scientific literature sources, including peer-reviewed articles, books and scientific Websites. We collected at least one picture (validated photograph or scientific drawing) per species. Only good-quality pictures and scientific side-view drawings of entire adult animals were kept. For species with marked sexual dimorphism, we considered male morphology, because female pictures are scarce for most species (especially for Perciformes and Cyprinodontiformes). Morphological measures were achieved using ImageJ software (https://rsb.info.nih.gov/ij/index.html). As a check, we compared those measures with a set of measures taken from 10 individuals per species of 55 preserved fish specimens belonging to the Palaearctic and Neotropical realms (Cilleros, Allard, Grenouillet, & Brosse, 2016), and all our measures fell within the trait range measured on preserved specimens. The 11 morphological measures were used to compute nine unitless traits describing the morphology of the fish head (including mouth and eye), body, pectoral and caudal fins (Supporting Information Figure S1b). For 35% of the species, one or more morphological trait remains unmeasured because the fish position or picture quality did not permit us to achieve one or several relevant measures. Traits were therefore measured on different numbers of species, ranging from 6,891 species for relative maxillary size to 8,531 species for maximum body length (Supporting Information Table S2).

Some species have unusual morphologies (species without tails, flatfishes) that prevented us from measuring some morphological traits. We thus defined rules for these few exceptions as in Villéger et al. (2010) and Toussaint et al. (2016): (a) for species with no visible caudal fin (e.g., Sternopygidae, Anguillidae), caudal peduncle throttling (CFd/CPd) was set to zero (Supporting Information Figure S1b); (b) for species with the mouth positioned under the body (e.g., Loricariidae, some Balitoridae, such as *Gastromyzon*) mouth vertical position (Mo) was set to zero; (c) for the species having a specialized sucker mouth for grazing algae (e.g., Loricariidae, *Chiloglanis*, *Gastromyzon*), relative maxillary length (Jl/Hd) was set to zero; (d) for the species without pectoral fins (e.g., Synbranchiformes and some Anguiliformes), pectoral fin vertical position (Pec. Fin Vert. Pos., PFi/Bd) was set to zero; and (e) for flatfishes, body depth (Bd) was the body width as the fish lies on one side of its body. We thus assumed that Pleuronectiformes are morphologically closer to dorsoventrally flattened fishes (e.g., *Gastromyzon*) than to laterally compressed fishes (e.g., *Symphysodon*). All these conventions are relevant from a biological point of view and contribute to the quality of the data because, for instance, a fish without a caudal fin has nil propulsion effect of its caudal fin, and therefore setting caudal peduncle throttling to zero accounts for the absence of caudal propulsion in this species. Likewise, setting mouth position to zero in the Loricariids accounts for the ventral position of the mouth. All traits apart from size are ratios of morphological measurements (length or area); therefore, all values are positive and unitless. Three traits, namely relative maxillary length (Rel. Maxil. Length), body elongation (Body Elong.) and caudal peduncle throttling (Cau. Ped. Throt.), could potentially reach high values and are hereafter called non-rightbounded traits. Six traits, namely relative eye size (Rel. Eye Size), oral gape position (Oral Gape Pos.), eye vertical position (Eye Vert. Pos.), body lateral shape (Body Lat. Shape), pectoral fin vertical position (Pec. Fin Vert. Pos.) and pectoral fin size (Pec. Fin size), range from zero to one and are hereafter called bounded traits.

Owing to the deficiency of phylogenetic information on the global freshwater fishes, phylogenetic independent contrasts (PICs) analyses were applied to only a subset of 493 species from phylogeny by Betancur-R et al. (2017) matching our morphological traits dataset. We first computed the value of Pagel's λ (Pagel, 1999) to test the phylogenetic signal of each trait and then compared the correlation between traits before and after accounting for phylogeny (Felsenstein, 1985).

2.2 | Statistical analyses

Missing values among the morphological traits dataset were filled using a random forest algorithm, which takes the taxonomic information into account (Penone et al., 2014). Then, after standardizing and centralizing values for the 10 traits, all species from the global pool were ordered in a multidimensional morphological space using a principal components analysis (PCA). The first five principal component (PC) axes, which account for 78.6% of the total variance (each selected axis had an eigenvalue ≥1; Supporting Information Figure S2a) were selected to conduct the following analyses. We assessed the robustness of our findings given traits accounted for, using a sensitivity procedure. We tested the effect of trait identity on the morphological distance between species by rerunning PCA based on all combinations of nine morphological traits out of 10. The distance between species was hardly affected by morphological traits accounted for (Mantel tests, $r > 0.900$, $p < 0.001$).

We compared the distribution of species coordinates on the first five PC axes among realms using the Kolmogorov–Smirnov test (hereafter K–S test). We then tested, for each of the five orders represented by >15 species in at least two realms, whether distribution of species in the morphological space differed between realms using the K–S test.

In order to determine the contribution of extreme morphologies to the filling of the morphological space, we identified the 2.5% of species with the lowest values and the 2.5% of species with the highest values on each of the five PC axes as morphologically extreme species (MES). We then considered the 0.5% of species with the lowest values and the 0.5% of species with the highest values on each of the five PC axes as the most morphologically extreme species (MMES). The remaining species with trait values among the 95% closest to that of the average among all species from the world were considered to be part of the morphological core species (MCS). Furthermore, in order to assess the distribution of morphologically extreme species among biogeographical realms, we subsequently computed the number of morphologically extreme species in each realm and their contribution to the species richness of the realm. We then computed the contributions of these extreme species to

the value ranges of the five PC axes and to the five-dimensional space volume in the global and realm fish faunas. In addition, we calculated the functional originality (FOri) and specialization (FSpe) values for the entire fish faunas and for only the extreme species assemblages according to Mouillot, Graham, Villéger, Mason, and Bellwood (2013). The FOri measures the distance between each species and its nearest neighbour in a multidimensional space and indicates the functional redundancy between species, with a lower FOri value indicating higher functional redundancy. The FSpe measures the dominance of specialist species (species having extreme trait combinations) in a given assemblage, with a higher FSpe value indicating a higher proportion of specialist species (Mouillot et al., 2013; Rodrigues-Filho, Leitão, Zuanon, Sánchez-Botero & Baccaro, 2018).

We used scripts from Mouillot et al (2013) to compute FSpe and FOri metrics. We used the "convhulln" function from the "geometry" R package to compute the five-dimensional space volume and the "ks.test" function from the "stats" R package to conduct the K–S tests. The PICs analyses were done using the "phylosig" function from the "phytools" R package and the "pic" function from the "ape" R package. All statistical analyses were performed with R software version 3.3 (R Core Team, 2017).

3 | RESULTS

The 10 morphological traits all showed unimodal continuous distributions (Supporting Information Figure S3). Among the six bounded traits, none filled the entire range of possible values (i.e., zero to one). The proportion of potential range filled varied from 51% (pectoral fin size) to 94% (oral gape position). The four remaining non-right-bounded traits exhibited a skewed to the right distribution (Supporting Information Figure S3), with skewness values higher than three (Supporting Information Table S2). See Supporting Information Figure S4 for an illustration of the morphological diversity in freshwater fishes. The 10 traits were

significantly although weakly correlated between each other among the 9,150 species considered (Spearman test, |rho| ≤ 0.46). Analysis on the subset of 493 species present in the phylogeny from Betancur-R et al. (2017) showed that all the traits had strong phylogenetic signals (Pagel's λ > 0.5, $p < 0.001$; Supporting Information Table S3). Nevertheless, the effect of phylogeny on the correlation between traits remained weak (Supporting Information Figure S5).

3.1 | Differences in morphological diversity between realm fish faunas

The distribution of fish species along the five axes of the morphological space was significantly different between most realm pairs (K–S tests, $p < 0.05$; Figure 1). Distributions on PC1 significantly differed between all the six realm faunas. Only one or two pairwise comparisons of the distributions on PC2–PC5 showed no significant differences, which were pairs of Nearctic versus Neotropical on PC2, Australian versus Oriental on PC3, Australian versus Palaearctic and Nearctic versus Oriental on PC4, Australian versus Nearctic and Neotropical versus Palaearctic on PC5. Those differences paired with differences in the distribution of the 10 morphological traits between biogeographical realms (K–S tests, $p < 0.05$; Supporting Information Figure S6).

Comparison of species position along morphological axes between the five most species-rich orders (Siluriformes, Cypriniformes, Perciformes, Characiformes and Cyprinodontiformes) revealed significant differences between all the orders (K–S tests, $p < 0.05$; Supporting Information Figure S7). Within those five orders, the distribution of the species on the morphological axes between realms also differed significantly (K–S tests, $p < 0.05$; Table 1; Figure 2). For all the 220 pairwise comparisons within the five orders between realms, 70% (154 pairs) were significantly different (Table 1). Differences among realms were the most marked for Siluriformes and Perciformes, which are the most species-rich orders while being present in all the six realms (Table 1).
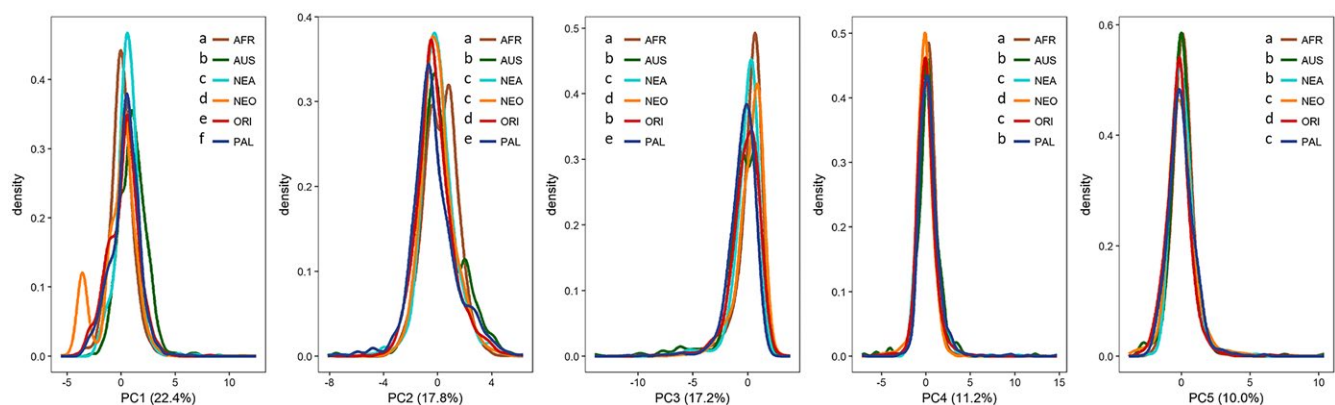

FIGURE 1 Kernel density estimation for the distributions of fish species from the six realms along five morphological axes (PCs). Letters in front of keys indicate the difference in trait distributions between realms; different letters indicate a significant difference between realms (Kolmogorov–Smirnov tests, $p < 0.05$). AFR = Afrotropical; AUS = Australian; NEA = Nearctic; NEO = Neotropical; ORI = Oriental; PAL = Palaearctic [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Difference between realms in distribution of fish species from the five most species-rich fish orders along five morphological axes (PCs)

	Realm number	PC1	PC2	PC3	PC4	PC5
Siluriformes	6	13/15	13/15	12/15	10/15	6/15
Perciformes	6	14/15	13/15	14/15	10/15	8/15
Cypriniformes	5	6/10	5/10	9/10	4/10	8/10
Cyprinodontiformes	3	1/3	0/3	0/3	2/3	3/3
Characiformes	2	0/1	1/1	0/1	1/1	1/1

Note. Values are the number of significantly different pairs (Kolmogorov–Smirnov tests, $p < 0.05$) out of all realm pairs considered. Only realms with >15 species in each taxonomic order were considered. PC = principal component.

3.2 | Morphologically extreme species among the global and realm fish faunas

Of the 9,150 species considered in this study, 1,663 species (18.2% of the total species number) identified as morphologically extreme species filled >50% of the range of each morphological axis (Figure 3), and even up to 80% for the fourth PC axis, which is driven by maximum body length, body elongation and relative eye size (Supporting Information Figure S2b). Overall, the extreme species filled a large percentage of the five-dimensional morphological volume (97.8%), whereas the other species were packed into the remaining 2.2% of the space (Figure 3). Restricting the most morphologically extreme species to the 0.5% tails of the distribution on each morphological axis limited their contribution to 356 species, which filled 89.7% of the morphological volume (Figure 3).

Even though the number of morphologically extreme species varied markedly among biogeographical realms, these species were widespread. Indeed, fish fauna in the Neotropical realm accounted for most of the species with extreme trait combinations (791 species, 21.6% of the Neotropical fauna), followed by the Oriental (338 species, 22.5%), the Afrotropical (267 species, 11.5%) and the Palaearctic (176 species, 20.0%) realm. In contrast, Australian and Nearctic fish faunas host only 106 (28.2%) and 93 (13.8%) species with extreme trait combinations, respectively (Table 2).

The contributions of extreme species to the range filled by each realm fauna for each morphological axis exceeded 40% (Figure 4). Likewise, extreme species filled >90% of the morphological volume filled by species from each realm (Figure 4). The values of FSpe and FOri for the entire faunas of the globe and in the six realms remained low (*ca*. 10%), but the extreme species had higher FSpe and FOri levels than the core species, with values *ca*. 20% for MES and *ca*. 30% for MMES (Table 2).

4 | DISCUSSION

The morphological diversity of freshwater fish across the globe is packed around one core combination of trait values, with a few extreme species remaining outside this core (Figure 3). More precisely,

the distribution of trait values among the global freshwater fish fauna was continuous (i.e., no marked gaps) and unimodal, with distributions of trait values peaking around median values for all traits (Supporting Information Figure S3). Hence, most of the world freshwater fishes have a similar morphology characterized by average trait values (e.g., maximum body length *ca*. 15 cm, body elongation ratio *ca*. 4, terminal and medium-sized mouth), which fits with the most commonly represented morphology in freshwater fishes, such as roaches and chubs (e.g., *Gila brevicauda* in the Nearctic realm or *Rutilus rutilus* in the Palaearctic realm). Trait distributions of freshwater fishes thus differ markedly from that of world plant flora (Díaz et al., 2016), which is clustered between woody and non-woody plants, with few intermediate species, illustrating two distinct ecological strategies (long-lived and tall ligneous species with a late sexual maturity versus short-lived and small non-ligneous species with an early sexual maturity). In contrast to plants, we did not detect any clustering between opposite strategies in freshwater fish, but a continuum between extreme strategies, as in coral reef fishes (Mouillot et al., 2014) or passerine birds (Ricklefs, 2012).

Nevertheless, morphological characteristics of the fish varied significantly among realms, and these differences were driven partly by the differences in the taxonomic order membership of the fish inhabiting each realm (Supporting Information Table S4). For instance, a substantial proportion of the Siluriformes has a ventral mouth (oral gape position = 0) and a pectoral fin at the bottom of the body (pectoral fin position = 0). Given that Siluriformes are the most species-rich order in Neotropical fish fauna (Levêque et al., 2008; Nelson et al., 2016), they contribute disproportionally to the morphological distinctiveness of the Neotropical compared with other realm fish faunas (Toussaint et al., 2016). Therefore, the evolutionary processes that have promoted order composition distinctiveness (Supporting Information Table S4) between realms partly explain the current morphological differences between realms. Thus, the difference of trait distributions is attributable, at least in part, to distinct evolutionary histories between realm fish faunas, as pointed out by Lamouroux, Poff, and Angermeier (2002) and Heino, Schmera, and Erős (2013) for European fish faunas.

In addition, differences in the distribution of morphologies between realm faunas were also driven by morphological differences among species belonging to the same order. Given that freshwater
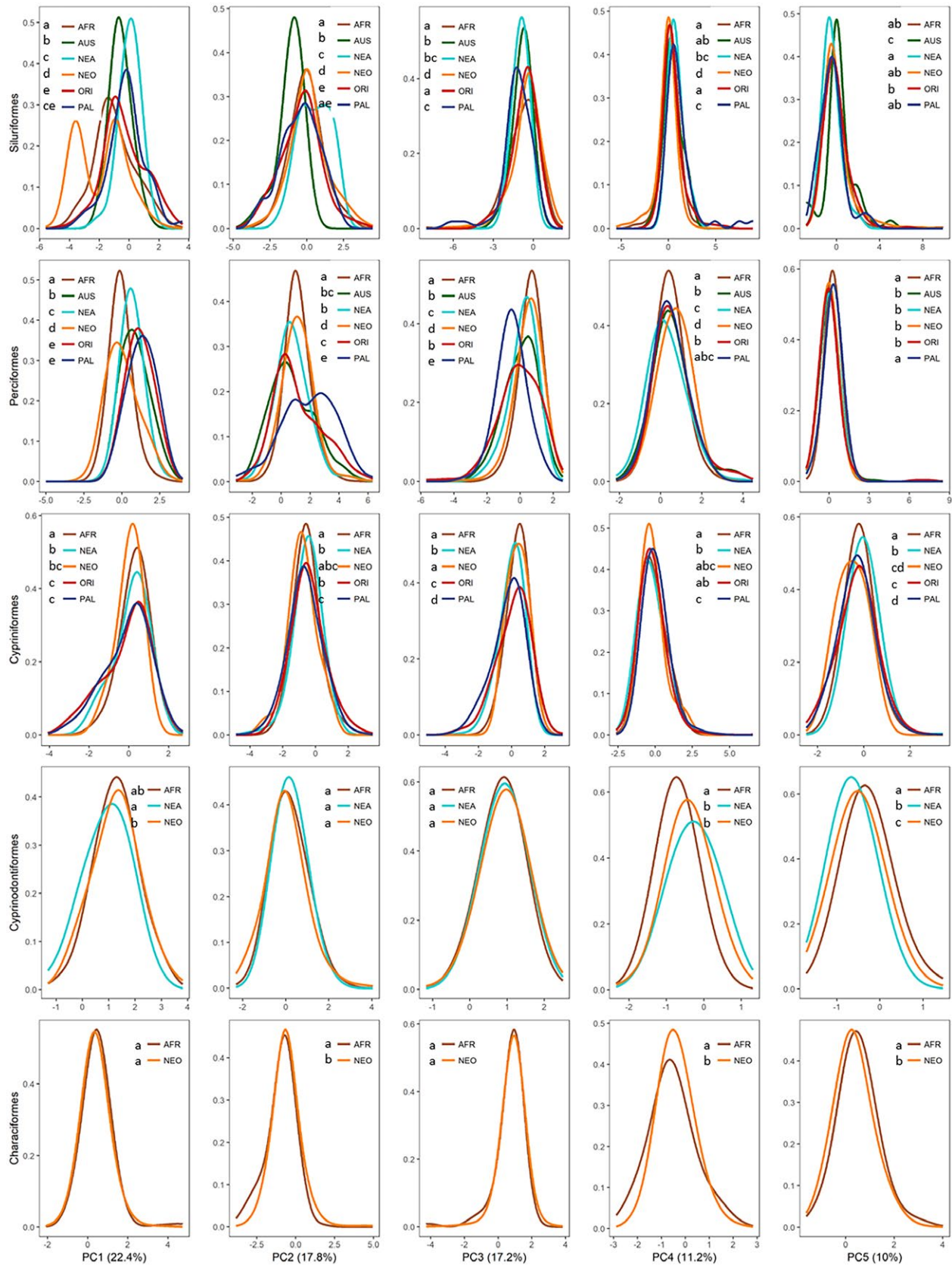
FIGURE 2 Kernel density estimation for the distributions of fish species between realms from the five most species-rich fish orders along five morphological axes (PCs). Letters in front of keys depict the difference in trait distributions between realms; different letters indicate a significant difference between realms (Kolmogorov–Smirnov tests, $p < 0.05$). AFR = Afrotropical; AUS = Australian; NEA = Nearctic; NEO = Neotropical; ORI = Oriental; PAL = Palaearctic [Colour figure can be viewed at wileyonlinelibrary.com]

fish cannot easily disperse between realms (Hugueny, 1989), realm faunas have evolved independently for millions of years, leading to distinct fish species inhabiting each realm (Leprieur et al., 2011; Villéger et al., 2011). Fish species from the same order occurring in distinct realms have thus evolved in independent and probably distinct environments (e.g., tropical rivers have a different flow regime and diversity of prey from arctic ones (Dudgeon, 2008)), which could ultimately have affected their morphological diversity. This was the case for oral gape position, relative maxillary length and pectoral fin position (represented by PC1) of the Siluriformes, which differed significantly between the Neotropical species and those belonging to the five other realms (Figure 2). Such distinctiveness of the Siluriformes in the Neotropical realm can be attributed, in part, to the Loricariidae family, which has a modified suckermouth adapted to graze on algae and biofilms, with small jaws in the ventral position and with ventral pectoral fins (Covain & Fisch-Muller, 2007). Our results therefore confirm the prediction that the fauna having the same deep evolutionary history (i.e., fish belonging to the same taxonomic order) evolved under distinct environmental constraints, leading to different morphological trait distributions among realms.

This also means that fish from a taxonomic order exhibit a distinct range of ecological strategies among realms.

Considering the distribution of traits, we show that the 1,663 morphologically extreme species, which account for 18.2% of the world freshwater fish fauna, fill 97.8% of the morphological space. The limited functional specialization and originality measured for the world fish fauna (Table 2) hence translate into a core of 81.8% of the species with trait values close to the average (i.e., centre of functional space defined by the world species pool). This contrasts with the remaining 18.2% of species with extreme morphologies. In addition, there is a diversity of morphologies among these extreme species, with no marked gap in the filling of morphological axes (Figure 3). This pattern is even more marked when considering the most extreme species (0.5% tails of the distribution), which account for only 3.9% of the global fish fauna but support 89.7% of the morphological space. These results parallel those of Mouillot et al. (2014), who found, using ecological–behavioural traits, that a substantial proportion of functional diversity is supported by a few coral reef fish species. In the same way, we extend the findings of Rodrigues-Filho et al. (2018) demonstrating that extreme species at
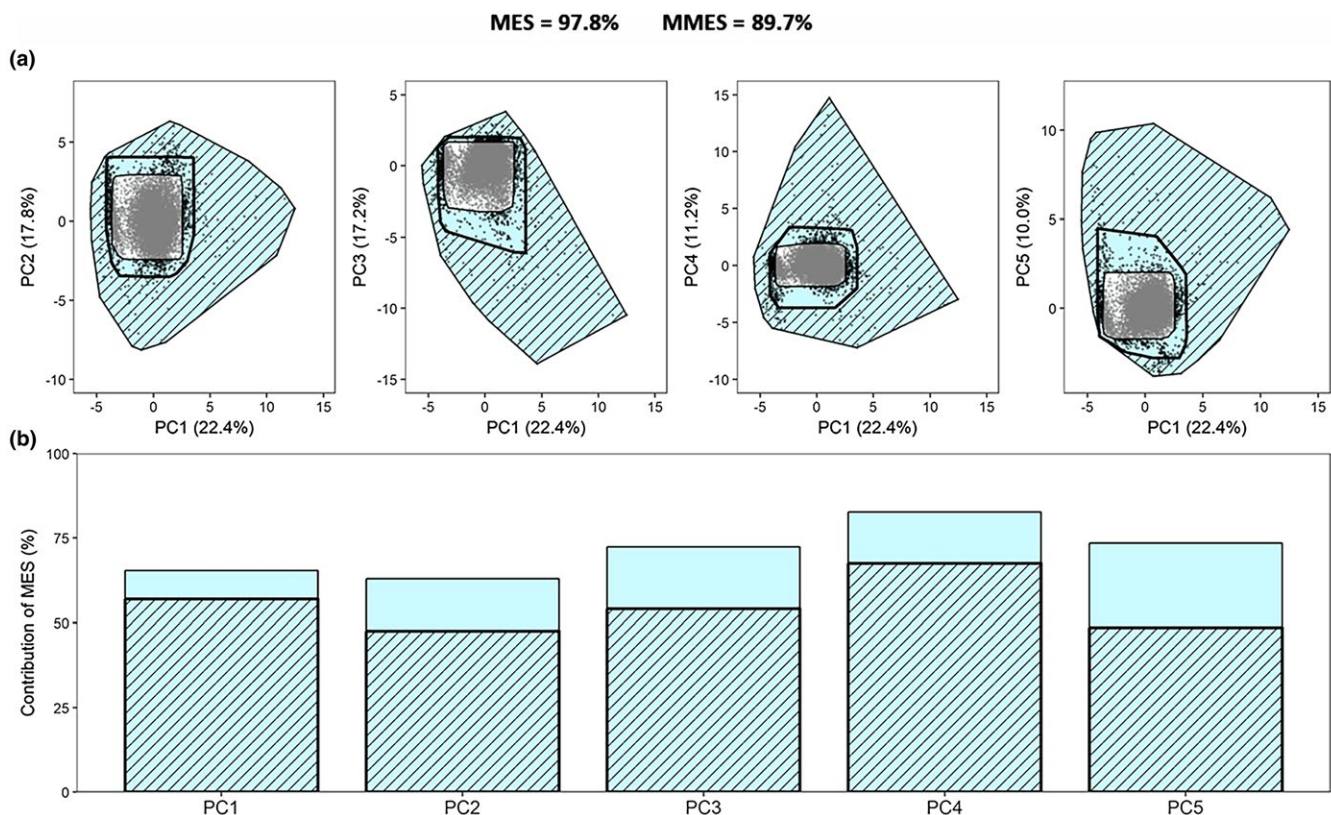

FIGURE 3 Contribution of morphologically extreme species to morphological diversity of the world freshwater fish fauna. Values of MES and MMES above the convex hulls represent the contributions of the morphologically extreme species [MES; i.e., the 2.5% of species with the lowest or highest values on each of the five principal component (PC) axes] and the most morphologically extreme species (MMES; i.e., the 0.5% of species with the lowest or highest values on each of the five PC axes) to the five-dimensional space volume. (a) The global convex hull, including 9,150 species, is delimited by the external black line. Blue-filled areas show the morphological volume filled by MES, and hatched parts represent MMES. The white-filled areas show the morphological volume filled by the morphological core species (MCS; i.e., species among the 95% closest to the average position of all species). Black dots represent the 9,150 species. (b) Bars represent the contributions of MES (blue) and of MMES (hatched) to PC1–PC5 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Functional specialization (FSpe) and functional originality (FOri) of fish, and number and percentage of morphologically extreme species [MES; i.e., the 2.5% of species with the lowest or highest values on each of the five principal component (PC) axes] and most morphologically extreme species (MMES; i.e., the 0.5% of species with the lowest or highest values on each of the five PC axes) in the six realms and in the global freshwater fish faunas

	FSpe (%)	FOri (%)	MES (2.5%)				MMES (0.5%)			
			Number of species	Percentage of fauna	FSpe (%)	FOri (%)	Number of species	Percentage of fauna	FSpe (%)	FOri (%)
Afrotropical	10.2	8.6	267	11.5	19.7	18.0	27	1.2	33.7	29.9
Australian	13.9	11.8	106	28.2	23.4	19.5	28	7.4	36.7	35.2
Nearctic	10.7	9.5	93	13.8	23.0	21.5	23	3.4	37.2	36.5
Neotropical	12.6	9.1	791	21.6	23.2	16.0	191	5.2	34.9	24.2
Oriental	12.3	10.4	338	22.5	21.4	18.9	74	4.9	32.4	30.7
Palaearctic	12.7	10.7	176	20.0	23.2	20.3	46	5.2	37.2	31.4
Global	11.7	9.3	1,663	18.2	22.2	17.5	356	3.9	34.6	27.3

the margins of morphological space tend to be more original than the other species of Neotropical stream fishes, indicating that extinction of a single extreme species could have marked consequences for the functional diversity of the fish fauna at local and regional scales. Given that functionally extreme species are also often threatened, as shown for fish body size by Olden et al. (2007) and, more recently, by Ripple et al. (2017) for large vertebrates, it is likely that other extreme morphological traits indicate particular habitat or life strategies that make the extreme species more vulnerable to anthropogenic disturbances. For instance, the species having extremely elongated bodies and large mouths represent predators specialized in the capture of small fishes (e.g., some Beloniformes and some Cyprinodontiformes) with a strict range of prey sizes (Nelson et al., 2016), or eyeless fishes that live only in caves (Borowsky, 2018).

Our assessment of the number of morphologically extreme species per realm reveals strong variations that are in large part attributable to the species richness in each realm, with the exception of the Australian fauna, which contains the fewest species but hosts the highest proportion of morphologically extreme species among the six realm faunas (Table 2). Regardless of how the extreme species were distributed among realms, functional specialization and originality remained low in all the realms. Nevertheless, these two metrics doubled for the extreme species assemblages (Table 2), which indicates a consistent pattern of high functional specialization and low functional redundancy among extreme species. Considering the huge proportion of functional space occupied by these extreme species (Figure 4), a remarkable functional vulnerability is supported by MES and MMES among all the realms, therefore paralleling the results of Mouillot et al. (2014) on ecological–behavioural traits of coral reef fishes. This finding contrasts with the discrepancy of functional vulnerability among realms revealed by Toussaint et al. (2016). This last measure was based on the morphological diversity supported by endangered species, but as underlined by Vitule et al. (2017), this measure only accounts for the species currently known to be endangered. Indeed, only 7% of the MES (and 10% of the MMES) are currently listed as threatened (IUCN, 2018; see Supporting Information Table S5), meaning that most of the MES and MMES species are currently not considered to be endangered. Nevertheless, given that climate change is affecting most of the species and ecosystems (Pörtner & Knust, 2007; Thomas et al., 2004), and thousands of dams are planned on most of the world's rivers, although they are known potentially to be detrimental to aquatic biodiversity (Anderson et al., 2018; Winemiller et al., 2016), a substantial proportion of those species will be pushed to risk of extinction in the next decades. Given that the most morphologically extreme species account for almost 90% of the morphological diversity of the world's freshwater fish, we suggest that their vulnerability to increasing anthropogenic pressures should be monitored accurately to ensure the sustainability of the unique functions they support in all the six realms (see Supporting Information Table S5). We therefore suggest that the current functional vulnerability of fish faunas (as in Toussaint et al., 2016) and the potential vulnerability supported by the morphologically
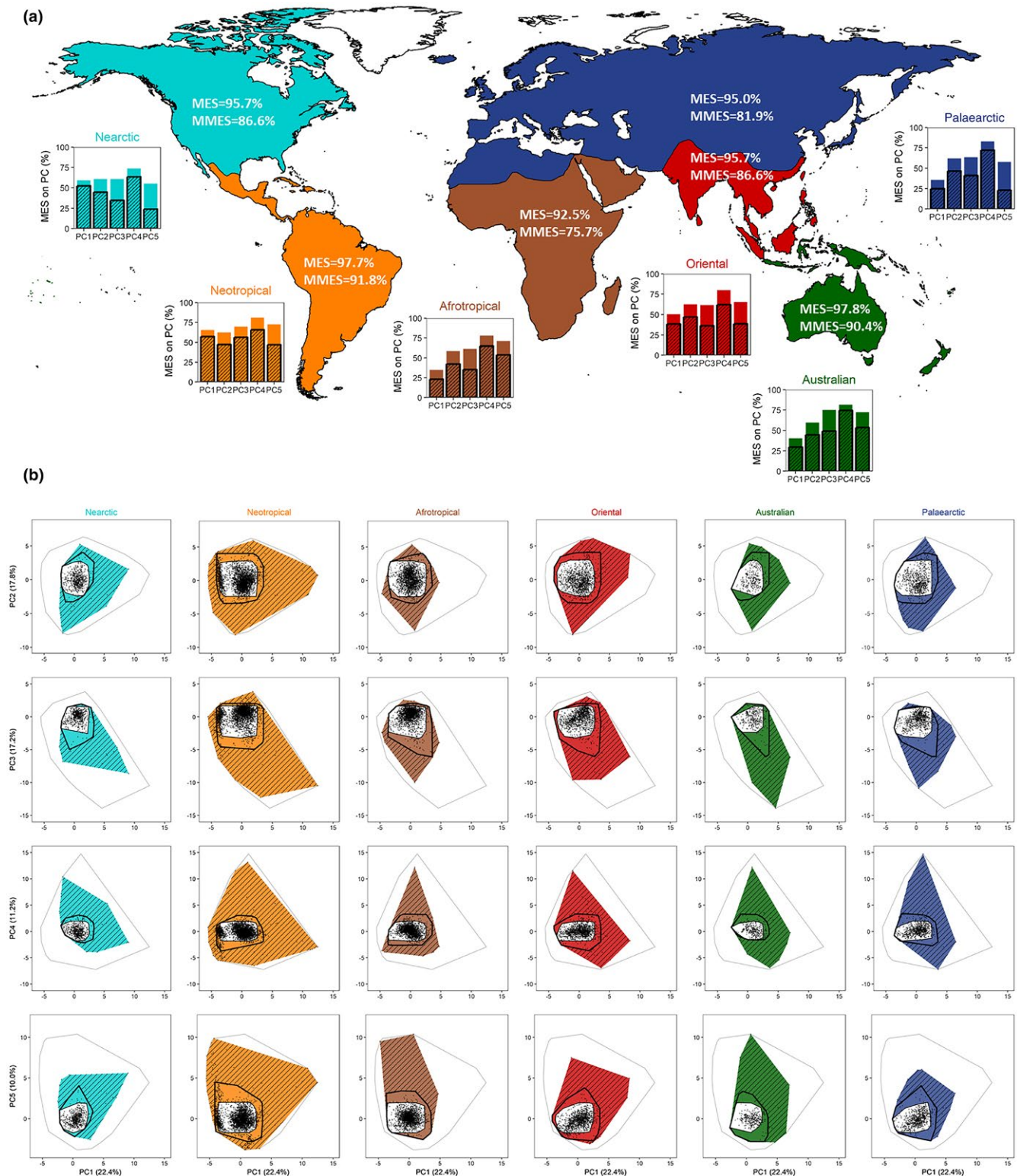
FIGURE 4 Contribution of morphologically extreme species to morphological diversity of the six realm fish faunas. (a) Values of MES and MMES on the map represent the contributions of the morphologically extreme species [MES; i.e., the 2.5% of species with the lowest or highest values on each of the five principal component (PC) axes] and the most morphologically extreme species (MMES; i.e., the 0.5% of species with the lowest or highest values on each of the five PC axes) to the five-dimensional space volume in each realm. Bars represent the contributions of MES to PC1–PC5. The hatched part of the bars represents MMES. (b) The global convex hull, including 9,150 species, is in grey. Colour-filled areas show the morphological volume filled by MES (hatched parts represent MMES) in each realm fauna. The white-filled areas show the morphological volume filled by the morphological core species (MCS; i.e., species among the 95% closest to the average position of all species). Black dots represent species belonging to each realm fauna [Colour figure can be viewed at wileyonlinelibrary.com]

extreme species in each realm should be considered together to develop biodiversity conservation guidelines.

In conclusion, our findings suggest that the difference in morphological distributions between the fish faunas of the six biogeographic realms is driven not only by the evolutionary divergence between realm fish faunas (Heino et al., 2013; Hugueny, 1989; Tedesco et al., 2017), but also by the distinct environmental constraints acting in each realm. Moreover, such morphological differences among realms translates into a shared strong contribution of morphologically extreme species among realms. Therefore, in all the six realms, >90% of the morphological diversity is supported by a few morphologically extreme species, accounting for <20% of the fish fauna (i.e., MES) that deserve to be conserved. Among those species, the <5% MMES are of paramount importance to maintain the morphological diversity of the fish faunas, because they support *ca.* 90% of the morphological diversity of the realms and therefore also support a wide range of associated functions.

DATA ACCESSIBILITY

Fish occurrence data can be retrieved freely from https://doi.org/10.6084/m9.figshare.c.3739145, and metadata are available in Tedesco et al. (2017). Information about the 9,150 species with combined trait values (PC1–PC5) used in this study is provided as a supplementary (Table S5), which also indicates the morphologically extreme and most morphologically extreme species and the IUCN Red List status for each species.

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