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Biogeographical region and environmental conditions drive functional traits of estuarine fish assemblages worldwide

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Abstract

Assessing trait–environment relationships is crucial for predicting effects of natural and human-induced environmental change on biota. We compiled a global database of fish assemblages in estuaries, functional traits of fishes and ecosystem features of estuaries. And we quantified the relative importance of ecosystem features as drivers of patterns of fish functional traits among estuaries worldwide (i.e. drivers of the proportions of fish traits). In addition to biogeographical context, two main environmental gradients regulate traits patterns: firstly temperature, and secondly estuary size and hydrological connectivity of the estuary with the marine ecosystem. Overall, estuaries in colder regions, with larger areas and with higher hydrological connectivity with the marine ecosystem, have higher proportions of marine fish (versus freshwater), macrocarnivores and planktivores (versus omnivores, herbivores and detritivores) and larger fish, with greater maximum depth of distribution and longer lifespan. The observed trait patterns and trait–environment relationships are likely generated by multiple causal processes linked to physiological constraints due to temperature and salinity, size-dependent biotic interactions, as well as habitat availability and connectivity. Biogeographical context and environmental conditions drive species richness and composition, and present results show that they also drive assemblage traits. The observed trait patterns and trait–environment relationships suggest that assemblage composition is determined by the functional role of species within ecosystems. Conservation strategies should be coordinated globally and ensure protection of an array of estuaries that differ in ecosystem features, even if some of those estuaries do not support high species richness.

KEYWORDS

body size, depth, functional group, longevity, salinity, trophic

1 | INTRODUCTION

Continuously increasing human activities and rate of biodiversity loss at a global scale threaten ecosystem functioning and services provided to mankind and pose urgent management and conservation challenges (Worm *et al*., 2006). Whilst taxonomic biodiversity is the most commonly addressed dimension of biodiversity, increasing evidence shows that the functional dimension of biodiversity (i.e. the variety of functions that species perform in ecosystems, regardless of their taxonomy) generally responds more rapidly and consistently to disturbances than taxonomic diversity (Mouillot, Graham, Villeger, Mason, & Bellwood, 2013).

The environmental tolerances of fish species and the way they use resources, together with abiotic (e.g. biogeographical barriers, temperature, salinity, habitat complexity) and biotic factors (e.g. adaptation, competition), delimit species distributions as well as the spatial and temporal homogeneity of biological assemblages (e.g. Rice, 2005), creating species pools which may or not differ in their functional traits. In general, if environmental features and historical-evolutionary factors differ among areas, then we can expect to observe functionally distinct communities (i.e. community divergence) (Heino, Schmera, & Erős, 2013). On the contrary, areas with similar environmental conditions are expected to exhibit functionally similar communities (i.e. community convergence), even in areas with different evolutionary histories (Heino *et al.*, 2013). For instance, in marine ecosystems, fish trait patterns along the Atlantic Ocean are influenced by both biogeography and environmental features, with a convergence of functional diversity observed between several coral habitats but a divergence between coral and rocky reef habitats (Bender, Pie, Rezende, Mouillot, & Floeter, 2013). Furthermore, in freshwater ecosystems, functional divergence is expected among river basins over different spatial scales (biogeographical, ecoregional) as environmental conditions tend to differ (Heino *et al.*, 2013), whilst functional convergence is expected among basins with similar environmental characteristics, even among assemblages with different species (Heino *et al.*, 2013).

Understanding trait–environment relationships is fundamental to the assessment of functional diversity patterns and mapping functional biogeography (Violle, Reich, Pacala, Enquist, & Kattge, 2014). Moreover, sound trait–environment relationships are imperative to the definition of functional niches of species and to the development of the predictive ability of trait-based ecology, namely to forecast how species and communities will respond to environmental changes (Violle *et al.*, 2014), both of which are fundamental to define conservation strategies. Despite the relevance of trait–environment relationships and their prominent development in plants and terrestrial ecosystems (e.g. Reich *et al.*, 2014), they are still poorly known in fish and aquatic ecosystems (e.g. Bender *et al.*, 2013; Brind'Amour, Boisclair, Dray, & Legendre, 2011; Erõs, Heino, Schmera, & Rask, 2009).

Estuaries link marine and freshwater ecosystems, and their biological assemblages are naturally faced with strong environmental variations, particularly from salinity which is the main driver of community structure (Whitfield, Elliott, Basset, Blaber, & West, 2012). Therefore, fish assemblages in estuaries typically include resident estuarine brackish species, marine and freshwater species that enter estuaries as stragglers or migrants, as well as migratory diadromous and amphidromous species (Elliott *et al.*, 2007; Potter, Tweedley, Elliott, & Whitfield, 2015). Global patterns and drivers of fish species richness in marine, estuarine and freshwater ecosystems have been widely studied (Tisseuil *et al.*, 2013; Tittensor *et al.*, 2010; Vasconcelos *et al.*, 2015), similar to many other biological groups. This contrasts with scarce knowledge on patterns and drivers of the functional dimension of biodiversity at large spatial extents. Nevertheless, patterns in functional traits of fish have been investigated at mismatched (and mostly small) spatial extents and ecosystems (e.g. Bender *et al.*, 2013; Floeter, Behrens, Ferreira, Paddack, & Horn, 2005; González-Bergonzoni *et al.*, 2012; Nicolas *et al.*, 2010a), as well as the functional richness and diversity of coral reef fishes at a global scale (e.g. Kulbicki, Parravicini, & Mouillot, 2015; Parravicini *et al.*, 2014).

Estuaries are among the most biologically productive and valuable ecosystems, yet increasing human activities in coastal regions intensify pressures in and around estuaries and affect their ecosystem functioning and services (Barbier *et al.*, 2011). Intense human activities and land reclamation for human use in coastal areas have led to a rapid loss of habitat in many estuarine ecosystems (Rochette *et al.*, 2010). Moreover, intense damming and diversion of rivers and streams significantly alters the size of drainage basins as well as the freshwater flow that arrives in estuaries, consequently affecting the size of estuaries and their physical connectivity with the marine ecosystem (Syvitski, 2008). Severe worldwide changes in primary productivity have been brought upon by fast changes in land cover notably due to agriculture expansion, namely coastal eutrophication induced by riverine runoff of fertilizers (Tilman *et al.*, 2001). Moreover, global greenhouse gas emissions from industrialization, deforestation and pollution forced a rapid and continuing increase in temperature in aquatic ecosystems globally (Sunday *et al.*, 2015). And estuaries are expected to suffer multiple impacts from future climate change, including shifts in habitat availability due to sea level rise, and changes in river flow with consequences in terms of frequency of floods and droughts, and estuarine mixing and salinity regimes (Robins *et al.*, 2016). If fish assemblages in estuaries show strong trait–environment relationships, they may be potentially vulnerable to human-driven environmental changes. Likewise, if functional traits of these fish assemblages show strong geographical patterns, some traits may be potentially vulnerable to unevenly distributed anthropogenic impacts at a global scale (Halpern, Walbridge *et al.*, 2008; Vorosmarty *et al.*, 2010).

Given the unique ecological characteristics of estuarine fish assemblages, it is crucial to investigate: (i) how their individual functional traits vary among estuaries worldwide and (ii) to disentangle the relative effects of biogeographical and environmental drivers on these patterns. We formulated a set of hypotheses to explain variation of fish functional traits among estuaries, derived from prevailing patterns described in the literature for estuaries and other ecosystems (Table 1). The formulated hypotheses concern ecosystem thermal energy and primary productivity, as well ecosystem size, hydrological connectivity and suitability (Table 1). Briefly, and following general ecological theory, the rationale underlying the several proposed hypotheses is that ecosystem thermal energy affects species distributions through physiological constrains (and also affects species richness), whilst primary productivity affects ecosystem carrying capacity (higher primary productivity sustains larger populations and individuals). Moreover, larger ecosystems can support more individuals (and species, sensu species-area relationships), whilst hydrological connectivity between ecosystems affects species dispersal (with higher connectivity favouring migrations), and finally ecosystem suitability influences species occurrence through habitat filtering (in estuaries the main filter is salinity). As species geographical distributions are influenced by functional traits that constrain their ability to colonize and persist in habitats (Bender *et al.*, 2013; Luiz *et al.*, 2012, 2013), we hypothesize that fish functional traits related to salinity preference, diet and body size (as well as traits that scale with body size such as depth of distribution and

TABLE 1 Hypotheses on the drivers of functional traits of fish assemblages among estuaries

Trait	Hypotheses	Driver
Body size	(1) Estuaries in warmer regions of the globe are inhabited by species with smaller body size, as proposed for endotherms by Bergmann's rule, as heat loss is proportional to surface-to-volume ratio, and for ectotherms by the temperature–size rule (Edeline *et al.*, 2013; Fisher *et al.*, 2010)	Thermal energy
	(2) Alternatively, primary productivity generates variation in body size of fishes between estuaries across the globe (as proposed for marine species by Huston & Wolverton, 2011 on the basis of higher primary productivity supporting higher food availability and larger body sizes)	Primary productivity
Diet	(3) Detritivore, herbivore and omnivore fish in estuaries across the globe increase in importance towards the equator [as shown for fishes in marine ecosystems (Floeter *et al.*, 2005) and in estuarine and freshwater ecosystems (González-Bergonzoni *et al.*, 2012)] possibly because they meet their energetic demands more efficiently at higher temperatures	Thermal energy
Salinity preference	(4) Proportions of marine species in estuaries globally are higher in estuaries adjacent to marine ecosystems with high primary productivity, as primary productivity has been associated with fisheries yield in marine and freshwater ecosystems (Friedland et al., 2012). Similarly, proportions of freshwater species in estuaries globally are higher in estuaries in regions with high terrestrial primary productivity	Primary productivity
	(5) Marine species dominate fish assemblages in estuaries worldwide (as reported for many estuaries e.g. in the review by Elliott *et al.*, 2007) and their proportion is higher in estuaries that have a higher hydrological connectivity with the marine ecosystem due to facilitated immigration of marine species (as shown in temporarily open estuaries during periods when estuary mouth is open, e.g. James *et al.*, 2007)	Hydrological connectivity
	(6) Across the globe, larger estuaries host higher proportions of marine species (as shown for estuaries across regional extents by Nicolas *et al.*, 2010a; Harrison & Whitfield, 2008), due to their larger high salinity areas. Moreover, estuaries with wider adjacent marine ecosystems host higher proportions or marine species, whilst estuaries with wider freshwater ecosystems host higher proportions of freshwater and or diadromous species, as estuaries are colonized by species from adjacent ecosystems and species-area relationships have been shown for marine fish in marine ecosystems (Tittensor *et al.*, 2010) and for freshwater and diadromous species in freshwater ecosystems (Lassalle *et al.* 2009; Tisseuil *et al.*, 2013)	Size
	(7) Globally, marine and freshwater species in estuaries are affected by the salinity regimes of estuaries (their proportions decreasing in hyperhaline estuaries), whilst estuarine brackish species are not as affected (their proportions increasing in hyperhaline estuaries) (considering the salinity ranges typically inhabited by these types of species within estuaries, as revisited in Whitfield *et al.*, 2012)	Suitability

lifespan; Woodward *et al.*, 2005; Kulbicki *et al.*, 2015) relate to ecosystem features (Table 1) and thus determine species distributions among estuaries worldwide.

To test the proposed hypotheses on global drivers of functional traits (Table 1), we used a comprehensive database on fish assemblages of estuaries distributed worldwide (based on studies at single estuary scale), as well as on the functional traits of these fishes and features of these estuaries. With this approach, we aimed to improve the understanding of how ecosystem features regulate the functional traits of their communities and ultimately contribute to develop our ability to predict how functional traits respond to environmental changes.

2 | METHODS

We built a database compiled from published data on (i) fish assemblages in estuaries distributed worldwide, (ii) characteristics of those estuaries and (iii) functional traits of those fishes (see details about the construction of the database in Appendix S1 and about data sources in Appendix S2). This database has been previously used to study global patterns and drivers of fish species richness in estuaries (Vasconcelos *et al.*, 2015) and of fish species composition in estuaries, including a proposal of estuarine biogeographical regions based on beta-diversity (Henriques *et al.*, 2016).

2.1 | Fish assemblages database

Each sample in the fish database consisted of the total species list of the sampled assemblage in a given estuary and study, and also, whenever available, species abundances (in number of individuals). The obtained "composition database" included 547 samples in 386 estuaries distributed worldwide (Figure 1), and a subset "abundance database" includes 414 samples in 297 estuaries. To minimize the bias of different sampling methods, the database only included studies that used active fishing gears such as trawls, seines and cast nets (see details about the construction of the database in Appendix S1 and about data sources in Appendix S2).

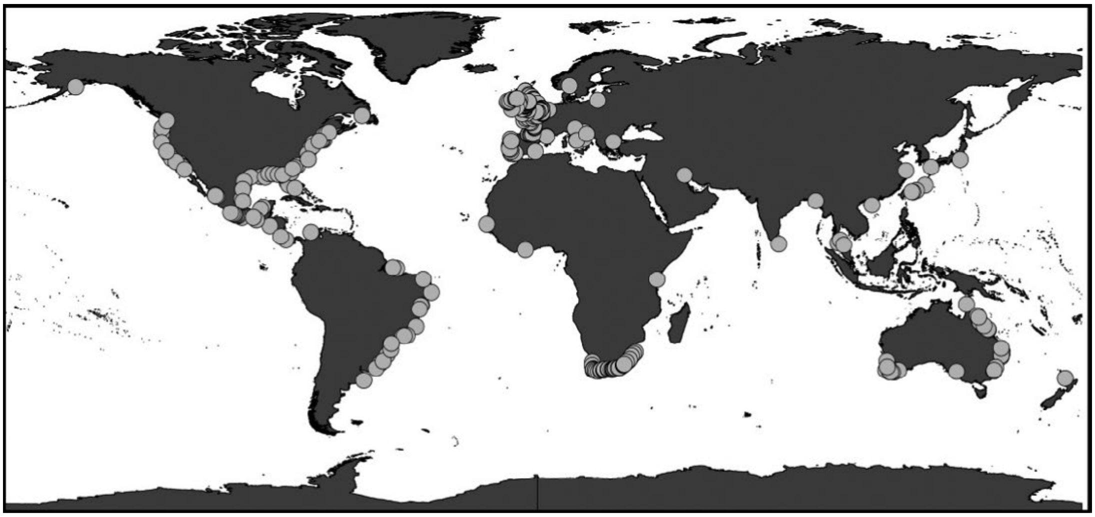

FIGURE 1 Location of estuaries included in fish assemblage databases: the composition database with presence/absence data included 547 samples in 386 estuaries, and the composition database with abundance data included 414 samples in 297 estuaries. Each sample represents the total fish assemblage sampled in a given estuary and study

2.2 | Environmental database

For each estuary in the fish database, we determined a set of biogeographical and environmental variables (Appendix S1 in supporting information). We identified the estuarine biogeographical region (i.e. a region that shares species with similar biogeographical history) to which each estuary belongs (Henriques *et al.*, 2016). We also characterized each estuary regarding latitude (measured at estuary mouth), thermal energy (mean annual water temperature measured outside the estuary mouth—SST) and primary productivity (of the adjoining marine and terrestrial ecosystems, respectively with chlorophyll a concentration measured outside the estuary mouth, and terrestrial net primary productivity measured around the estuary—NPP). Estuarine primary productivity could not be estimated for most sites in our database and therefore was not included as a variable. Ecosystem size was described using the area of the estuarine ecosystem (estuary area) and of its adjacent freshwater ecosystem (measured with drainage basin area) and marine ecosystem (measured with minimum distance from estuary mouth to the continental shelf limit). We characterized hydrological connectivity between the estuary and the adjacent marine ecosystem based on three parameters: tidal range [microtidal [<2 m], mesotidal [2–4 m], macrotidal [>4 m]), estuary type (temporarily open, open) and estuary mouth width. Finally, we described habitat suitability of each estuary in terms of salinity, through the variable estuary salinity type [hyperhaline (estuaries with frequent and recurring hyperhaline conditions, i.e. salinity above 40, in considerable areas), regular to hyperhaline (estuaries with occasional hyperhaline conditions), regular (estuaries with rare hyperhaline conditions)]. A more refined characterization of salinity of each estuary (i.e. extension of areas with distinct salinities—euhaline, polyhaline, mesohaline, oligohaline) was not possible for the full set of estuaries due to data limitation, and thus it was not included in the database.

Our dataset covers estuaries distributed worldwide, from tropical to temperate latitudes (absolute latitude 1°–59°) and cold to warm SST (5–31°C). Sampled estuaries included regions with low-to-high terrestrial NPP (0.001–1.166 gC m^2 day^{-1}; which increased slightly with SST), and coasts with low-to-high marine chlorophyll a (0–57 mg chlorophyll *a*.m^{-3}; which increased with continental shelf width 177–979,234 m, and decreased lightly with SST) (Appendix S4). Estuarine ecosystems differed notably in estuary area (0.01–70,000 km^2), estuary mouth width (3–90,000 m), drainage basin area (1–1,808,500 km^2) and estuary type (82% open), and also in terms of tidal range (62% microtidal; which increased slightly with shelf) and salinity type (89% regular) (Appendix S3). At this global extent, estuaries with larger area had larger estuary mouth/s and drainage basin area (due to higher river flow) and were more often permanently open to the marine ecosystem than smaller ones (many of which were temporarily open), with temporarily open estuaries rare in cooler regions (Appendix S3). Nevertheless, this worldwide trend does not invalidate known variability from estuary to estuary.

2.3 | Functional traits database

For each species in the fish database (2,434 species in the composition database; 2,126 species in the abundance database), we characterized a set of traits (Table 2). Selected traits describe complementary facets of fish ecology that determine fishes' ability to live in estuaries and have been previously used to explore fish community assembly and functional diversity (Table 2). Trait values were obtained for the adult life-stage using information available in FishBase (Froese & Pauly, 2014).

To portray species physiological tolerance and adaptations to habitat (Costello, Claus, & Dekeyzer, 2015), we characterized species regarding their salinity preference using four categories (i.e. marine, freshwater, brackish, diadromous as defined in Table 2 and following Whitfield *et al.*, 2012) and maximum depth of distribution using four

TABLE 2 Description and relevance of fish traits

Trait	Category	Description	Relevance
Salinity preference	Marine	Lives predominantly in marine waters from inshore (intertidal) to offshore	Reflects the physiological ability to deal with osmotic stress in brackish estuarine waters. Is commonly used to distinguish habitat
	Brackish	Lives predominantly in estuarine and brackish waters as well as lagoons	
	Freshwater	Lives predominantly in streams, lakes and caves	
	Diadromous	Migrates between freshwater and marine waters throughout its life cycle	
Diet	Detritivore	Feeds on detritus	Relates to position in the food web, influence on abundance of other species, and adaptations to habitat
	Herbivore	Feeds predominantly on macroalgae, macrophytes, phytoplankton and microphytobenthos	
	Omnivore	Feeds on detritus, filamentous algae, macrophytes, epifauna and infauna	
	Planktonivore	Feeds on planktonic crustaceans, hydroids and fish eggs/larvae	
	Invertivore	Feeds predominantly on non-planktonic invertebrates	
	Macrocarnivore	Feeds on macroinvertebrates and vertebrates (mostly fish)	
Maximum body size	Small	<15 cm	Reflects position in the food web, species abundance, metabolic rates, dispersal ability, mobility and home range
	Medium	15–50 cm	
	Large	50–100 cm	
	Very large	>100 cm	
Maximum depth of distribution	Shallow	Mainly occurs between 0 and 30 m	Reflects the physiological ability to deal with pressure and temperature associated with depth. Is commonly used to distinguish habitat
	Medium	Typically occurs between 30 and 200 m	
	Deep	Typically occurs between 200 and 500 m	
	Very deep	Mainly occurs deeper than 500 m	
Lifespan	Low	<2 years	Describes the longevity of individuals. Relates with stability of populations over time
	Medium	2–7 years	
	High	7–15 years	
	Very high	>15 years	

categories (i.e. shallow, medium, deep and very deep as defined in Table 2 and adapted from Halpern & Floeter, 2008).

We also characterized the diet of each species using six categories (i.e. detritivores, herbivores, omnivores, planktivores, invertivores, macrocarnivores as defined in Table 2 and adapted from Elliott *et al.*, 2007), as it is indicative of species' position in the food web, the way in which they influence the abundance of other species, and reflects adaptations to habitat (Costello *et al.*, 2015).

Species size is a key trait related to many facets of fish ecology, such as metabolism, mobility and trophic interactions (Costello *et al.*, 2015; Kulbicki *et al.*, 2015; Luiz *et al.*, 2012), and was described using four categories (i.e. small, medium, large and very large as defined in Table 2 and adapted from Halpern & Floeter, 2008).

Lifespan (longevity) is a trait that describes the persistence of individuals and populations, and can be indicative of population stability through time and dispersal potential (Costello *et al.*, 2015), and was characterized based on frequency distribution via four categories (i.e. low, medium, high and very high as defined in Table 2).

For each trait, we computed the proportions of the several trait categories per sample in two ways. First, using the composition database, we determined the metric "relative species richness" per sample as the proportion of the species richness in a sample that is represented by fishes from each trait category (for instance, for the trait body size—the proportions of the species richness in a sample that are represented by species with small, medium, large and very large body sizes). Secondly, using the abundance database, we determined the metric "relative abundance" per sample as the proportion of the individuals in a sample that are represented by each trait category (for instance, again for the trait body size—the proportions of the number of individuals in the sample with small, medium, large and very large body sizes)(as in Nicolas *et al.*, 2010a; Henriques *et al.*, 2014b). The two metrics provide complementary information as species richness indicates how many species represent each trait category in assemblages, whereas abundance informs on the dominance of trait categories. We used relative values to control for sampling effects and make the data comparable, and thus the richness (or abundance) of each trait category per sample is estimated in relation to the total richness (or abundance) observed in that sample (Henriques *et al.*, 2014b; Nicolas *et al.*, 2010a; Shipley, Vile, & Garnier, 2006).

2.4 | Data analysis

To identify the ecosystem features that determine the higher or lower importance of fish trait categories in estuaries, and aiming at a robust outcome, we ran a set of statistical analyses, all of which were conducted in parallel with the metrics relative species richness and relative abundance of trait categories (using the composition database and abundance database, respectively).

As a preliminary step, we evaluated pairwise associations between all continuous environmental variables as well as between all fish traits using Pearson correlation (package stats; R). To avoid multicollinearity, several environmental variables were excluded from subsequent statistical analyses, namely latitude ($r = .74$ with temperature), estuary mouth width ($r = .79$ with estuary area) and drainage basin area ($r = .72$ with estuary area) (Appendix S3).

We used linear models (LM) to disentangle the importance of biogeographical and environmental features as predictors of fish traits in estuaries (response variable), namely estuarine biogeographical region (qualitative predictor), sea surface temperature, terrestrial net primary productivity, marine chlorophyll a and estuary area (quantitative predictors), tidal range, estuary type and salinity type (ordinal predictors). Each trait category (see Table 2) was modelled as a response variable separately. And for each of these trait categories, we fitted two alternative models: with and without the biogeographical variable. Aiming at a sound estimate of parameters and of their importance in each fitted model, we implemented two model-average approaches: hierarchical partition of variation (HPV) which quantifies the difference in R^2 of all models with and without each predictor (Carvalho & Cardoso, 2014) (package relaimpo; R); and multi model inference which evaluates the relative importance of model terms by determining the overall support for each variable across all models considering Akaike information criteria (package glmulti; R).

In addition, as each sample in our fish database consisted of the fish assemblage in a given estuary and study, and for some estuaries there was more than one study, we also used linear mixed models (LMM) to explore the importance of biogeographical and environmental features as predictors of fish traits in estuaries. The LMM were formulated in the same way as the linear models previously fitted, but also included estuary as a random factor. We estimated the parameters and their significance in the fitted LMM (packages lme4 and nlme; R).

Finally, to explore multivariate patterns of functional traits, we applied ordination techniques based on permutation tests (packages stats and vegan; R). Specifically, principal coordinates analysis (PCO; Anderson, Gorley, & Clarke, 2008) was used as an unconstrained technique to visualize pairwise dissimilarities (Bray-Curtis) of traits. canonical analysis of principal coordinates (CAP; Anderson *et al.*, 2008) was used as a constrained method to reveal patterns undetected in unconstrained analysis, by fitting axes through the multivariate cloud of pairwise dissimilarities (Bray-Curtis) of traits that have the strongest correlation with the set of environmental variables (canonical correlation).

In all of the analyses above, quantitative environmental predictors were fourth root transformed to reduce right skewness and the effect of extreme observations, whilst keeping variability in the data. Assumptions of linear models (normality and homoscedasticity of residuals) were verified, and variance inflation factor of predictors was below a 3.5 threshold. All statistical analyses were run in R software (R Core Team, 2016), and a significance level of 0.05 was employed. Example R codes for statistical analyses and dataset are provided in Appendix S4.

3 | RESULTS

Several traits were correlated in the sampled estuarine fish assemblages (Appendix S3). Macrocarnivores and planktivores were more common among marine fishes, whilst omnivores, herbivores and detritivores among freshwater and brackish ones. Marine species frequently had larger body size than freshwater and brackish. Larger body size was generally associated with greater maximum depth of distribution of species and longer lifespan.

The spatial variation of fish functional traits among estuaries was largely explained by biogeographical region and environmental gradients, with results consistent between the different metrics (relative species richness and relative abundance) and between the several methods—linear models and linear mixed models (Tables 3 and 4, Figures 2 and 3), principal coordinates analysis and canonical analysis of principal coordinates (Figure 4 and Appendix S5). Overall, and regarding the importance of the predictors, the higher the deviance of a trait explained by a given predictor (as determined in a LM) the more likely that predictor was considered important in that LM and significant in the corresponding LMM, with the threshold generally at around 1%–3% of explained deviance.

Linear models explained 4%–57% of variation in trait patterns (mean ± *SD*: 27 ± 13%), with higher fits for relative species richness than for relative abundance, and highest fits for the traits maximum depth of distribution, salinity preference and diet (Tables 3 and 4). Across all traits, estuarine biogeographical region explained high proportions of variance of functional traits in LM (mean ± *SD*: 19 ± 6% for relative species richness, 13 ± 6% for relative abundance) followed by environmental features, especially sea surface temperature (7 ± 7% for relative species richness, 2 ± 3% for relative abundance) and also tidal range (6 ± 4% for relative species richness, 2 ± 2% for relative abundance) and estuary type (5 ± 5% for relative species richness, 2 ± 3% for relative abundance; Tables 3 and 4). Although less important, the other environmental variables also explained part of the trait variance (terrestrial net primary productivity—NPP, continental shelf width, marine chlorophyll a, estuary area and salinity type; Tables 3 and 4).

Marine species dominated fish assemblages in estuaries (Table 5), and the proportions of marine, freshwater, estuarine and diadromous fishes varied among estuaries and were strongly related to ecosystem features (LM and LMM: tables 3 and 4 and Figures 2 and 3, PCO and CAP: Figure 4 and Appendix S5). Proportions of freshwater and brackish fishes in estuaries generally showed similar responses to environmental features, they both increased greatly with SST (contrarily to the notable decrease of diadromous) and they also

TABLE 3 Effect of ecosystem features (in columns) on relative species richness of fish traits (in rows) among estuaries distributed worldwide, according to the fitted linear models (LM) and linear mixed models (LMM)

Trait	Bio.	Environment																																Total		
		SST				NPP				C. shelf				Mar chla				Tidal regime				Est. type				Est. area				Est. salinity				LM	LMM	
	LM	LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		F	F	F+R
	%	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	R^2	R^2
Marine	**15**	0	0.3			**3**	**1**	*	-	0	0.6			0	0.6			**3**	**0.9**		+	**14**	**1**	*	+	3	0.3			**1**	**0.9**		-	41	0.40	0.68
	na	0	0.3			**4**	**1**	*	-	0	0.4			**0**	**0.9**		-	**4**	**0.9**		+	**17**	**1**	*	+	**4**	**1**	*	+	1	0.8			32	0.31	0.67
Brackish	**20**	**10**	**1**	*	+	1	0.4			2	0.8			1	0.3			3	0.4			1	0.3			1	0.5			**1**	**0.9**		+	38	0.37	0.60
	na	**14**	**1**	*	+	1	0.6			2	0.6			1	0.7			3	0.5			1	0.3			**1**	**1**	*	-	**1**	**1.0**		+	25	0.23	0.61
Freshwater	**9**	2	0.5			1	0.5			1	0.3			1	0.3			**5**	**0.9**		-	**13**	**1**	*	-	2	0.3			**1**	**0.9**		-	33	0.32	0.43
	na	**3**	**1**	*	+	**2**	**0.9**	*	+	1	0.4			1	0.3			**6**	**1**		-	**15**	**1**	*	-	2	0.5			**1**	**0.9**	*	-	31	0.30	0.40
Diadromous	**21**	**8**	**1**	*	-	**2**	**1**	*	+	0	0.3			0	0.4			1	0.1			**4**	**1**	*	-	3	0.3			2	0.6			42	0.43	0.56
	na	**10**	**1**	*	-	**3**	**1**	*	+	0	0.3			**1**	**0.7**	*	+	1	0.3			**6**	**1**	*	-	**6**	**1**	*	-	2	0.6			29	0.31	0.56
Detritivores	**25**	3	0.4			0	0.3			**3**	**0.9**	*	-	**1**	**1**	*	+	**7**	**1**		-	**9**	**1**	*	-	3	0.3			0	0.4			51	0.52	0.82
	na	**4**	**1**	*	+	1	0.8			**4**	**1**	*	-	**1**	**1**	*	+	**11**	**1**	*	-	**13**	**1**	*	-	**5**	**1**	*	-	0	0.2			39	0.38	0.82
Herbivores	**25**	3	0.4			0	0.3			**3**	**0.9**	*	-	**1**	**1**	*	+	**7**	**1**		-	**9**	**1**	*	-	3	0.3			0	0.4			51	0.52	0.82
	na	**4**	**1**	*	+	1	0.8			**4**	**1**	*	-	**1**	**1**	*	+	**11**	**1**	*	-	**13**	**1**	*	-	**5**	**1**	*	-	0	0.2			39	0.38	0.82
Omnivores	**16**	**3**	**1**	*	+	**2**	**1**	*	+	1	0.3			2	0.4			**4**	**0.9**		-	**8**	**1**	*	-	4	0.5			**1**	**0.9**	*	+	41	0.42	0.53
	na	**4**	**1**	*	+	**3**	**1**	*	+	1	0.3			2	0.6			**5**	**1**		-	**11**	**1**	*	-	**7**	**1**	*	-	1	0.7			33	0.34	0.49
Planktonivores	**26**	3	0.3			1	0.6			**6**	**1**	*	+	0	0.3			8	0.3			5	0.8			0	0.3			**2**	**1**		+	51	0.50	0.73
	na	**4**	**1**	*	-	1	0.7			**9**	**1**	*	+	**1**	**1**	*	-	**13**	**1**	*	+	**7**	**1**	*	+	1	0.3			**3**	**1**	*	+	38	0.36	0.73
Invertivores	**6**	0	0.3			0	0.4			**2**	**0.9**	*	-	1	0.3			**4**	**1**	*	-	1	0.5			0	0.3			0	0.1			15	0.15	0.24
	na	1	**1**	*	-	0	0.5			2	0.6			**1**	**0.9**	*	-	**4**	**1**	*	-	**1**	**0.8**	*	+	0	0.3			1	0.5			10	0.10	0.21
Macrocarnivores	**28**	1	**1**	*	-	0	0.4			**2**	**0.6**	*	+	2	0.5			**4**	**1**	*	+	**6**	**1**	*	+	6	0.6			**1**	**0.9**	*	-	51	0.51	0.68
	na	1	0			0	0.3			3	0.4			**3**	**0.9**	*	+	**3**	**0.9**	*	+	**8**	**1**	*	+	**10**	**1**	*	+	**2**	**1**		-	29	0.29	0.66

(Continues)

TABLE 3 (Continued)

Trait	Bio.	Environment																																Total		
		SST				NPP				C. shelf				Mar chla				Tidal regime				Est. type				Est. area				Est. salinity						
	LM	LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM	LMM	
																																		F	F	F+R
	%	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	R^2	R^2
Small size	**21**	**1**	**1**	*	-	0	0.4			1	0.3			1	0.3			**7**	**1**	*	-	3	0.7			1	0.5			1	0.2			36	0.35	0.36
	na	1	0.5			0	0.3			1	0.3			**2**	**0.9**	*	-	**11**	**1**	*	-	**4**	**1**	*	-	1	0.5			**2**	**1**	*	-	22	0.22	0.27
Medium size	**17**	**8**	**1**	*	+	1	0.3			0	0.5			0	0.3			**2**	**1**		+	0	0.6	*	-	1	0.3			**2**	**0.9**		+	31	0.31	0.46
	na	**11**	**1**	*	+	**1**	**1**	*	-	0	0.3			0	0.7			**3**	**1**		+	0	0.3			**1**	**0.9**	*	+	2	0.5			19	0.20	0.46
Large size	**26**	7	0.4			**0**	**1**	*	+	3	0.4			1	0.3			8	0.4			4	0.7			0	0.3			1	0.2			50	0.50	0.63
	na	**11**	**1**	*	-	0	0.6			4	0.4			1	0.3			**12**	**1**	*	+	**6**	**1**	*	+	1	0.3			**1**	**0.9**	*	+	36	0.36	0.62
V. large size	**7**	**3**	**0.9**	*	-	0	0.5			2	0.3			**2**	**0.8**		+	**6**	**1**	*	+	**1**	**0.9**		+	0	0.6			2	0.7			22	0.21	0.34
	na	**3**	**0.9**	*	-	0	0.3			2	0.3			**2**	**1**	*	+	**7**	**1**	*	+	0	0.3			0	0.3			**2**	**1**		-	17	0.17	0.35
Shallow	**28**	**8**	**1**	*	+	**4**	**1**	*	-	2	0.7			**4**	**1**	*	-	**6**	**1**	*	-	1	0.3			0	0.4			3	0.2			55	0.54	0.69
	na	**10**	**1**	*	+	**5**	**1**	*	-	2	0.3			**6**	**1**	*	-	**8**	**1**	*	-	1	0.4			**1**	**0.9**	*	+	**4**	**1**		+	37	0.37	0.70
Medium depth	**20**	**1**	**1**	*	+	0	0.4			2	0.5			**2**	**1**	*	+	1	0.4			**1**	**0.8**		+	**2**	**0.7**	*	-	0	0.6			28	0.28	0.59
	na	**1**	**1**	*	+	1	0.6			**3**	**1**	*	+	**2**	**1**	*	+	1	0.4			**1**	**0.8**		+	**3**	**1**	*	-	0	0.2			11	0.15	0.60
Deep	**18**	**23**	**1**	*	-	**1**	**1**	*	+	**1**	**0.9**		-	1	0.6			**8**	**1**	*	+	**3**	**0.9**	*	+	1	0.5			1	0.1			57	0.53	0.79
	na	**32**	**1**	*	-	0	0.4			**2**	**1**	*	-	1	0.3			**10**	**1**	*	+	**4**	**1**	*	+	**1**	**0.9**	*	+	2	0.7			52	0.47	0.78
V. deep	**14**	**19**	**1**	*	-	**1**	**1**	*	+	**1**	**1**			1	0.3			**12**	**1**	*	+	2	0.3			**1**	**0.9**	*	+	1	0.2			52	0.49	0.71
	na	**25**	**1**	*	-	0	0.4			**2**	**1**	*	-	1	0.3			**16**	**1**	*	+	3	0.4			**1**	**1**	*	+	1	0.3			50	0.47	0.70
Low l. span	**24**	0	0.3			1	0.5			**2**	**1**	*	+	0	0.7			0	0.2			1	0.4			**2**	**1**	*	-	2	0.8			33	0.32	0.48
	na	0	0.3			**2**	**1**	*	-	**3**	**1**	*	+	**0**	**0.8**	*	-	**1**	**1**	*	-	1	0.7			1	0.5			**2**	**0.9**		+	11	0.28	0.78
Medium l. span	**26**	**8**	**1**	*	+	0	0.6			**1**	**0.9**	*	+	1	0.3			3	0.2			0	0.3			1	0.3			3	0.2			42	0.42	0.42
	na	**13**	**1**	*	+	0	0.3			**1**	**1**	*	+	**2**	**1**	*	-	**5**	**1**	*	-	0	0.3			**2**	**1**	*	+	**5**	**1**		-	28	0.13	0.24
High l. span	**16**	**7**	**1**	*	-	0	0.4			0	0.3			2	0.4			1	0.1			**1**	**0.8**	*	-	0	0.3			2	0.3			29	0.29	0.31
	na	**10**	**1**	*	-	0	0.3			**1**	**0.7**	*	-	**3**	**1**	*	+	2	0.6	*	+	**1**	**0.8**	*	-	1	0.8			**3**	**1**		+	21	0.12	0.18
V. high l. span	**21**	6	0.5			0	0.3			**1**	**0.7**	*	-	1	0.5			4	0.4			**2**	**1**	*	+	0	0.5			2	0.2			36	0.35	0.46
	na	**10**	**1**	*	-	0	0.3			**1**	**1**	*	-	1	0.6			**6**	**1**	*	+	**3**	**1**	*	+	0	0.5			**3**	**1**		+	24	0.15	0.50

For each trait category, we built two alternative models (in rows): with and without the biogeographical variable (estuarine biogeographical region). To explore linear models (LM), we used hierarchical partition of variation (HPV) and multimodel inference (MMI): for HPV, the table shows the relative importance of each predictor to trait variation (%, between 0 and 100), and the predictor coefficient (C, represented only as "+" if positive or "−" if negative); for MMI, the table shows the predictor coefficient (C, represented only as "+" if positive or "−" if negative) and the importance of each predictor to trait variation (I, between 0 and 1; values >0.8 are significant and in those cases the models are marked in bold). For linear mixed models (LMM), the table shows the predictor coefficient (C, represented only as "+" if positive or "−" if negative) and the significance of each predictor to trait variation (S, with * meaning significant at $p < .05$ and no value meaning not significant). Trait category–predictor relationships that are consistent across models are marked with light grey (when the predictor coefficient is positive) and dark grey (when the predictor coefficient is negative). The table also shows the total explained deviance of the fitted LM (%), and the Pseudo R^2 of the fitted LMM (pR^2) namely conditional R^2 for fixed effects and marginal R^2 for fixed and random effects. Ecosystem features are estuarine biogeographical region and environmental variables (fourth root transformed)—sea surface temperature (SST), terrestrial net primary productivity (NPP), continental shelf width (C. shelf), marine chlorophyll a concentration (Mar chla), tidal regime (from microtidal, mesotidal to macrotidal), estuary type (from "temporarily open" to "open" to the marine ecosystem), estuary area (Est. area), estuary salinity type (Est. type: from regular, regular-hyperhaline to hyperhaline). Fish traits are salinity preference, diet, maximum body size, maximum depth of distribution and lifespan. (n = 547 samples in a total of 386 estuaries).

TABLE 4 Effect of ecosystem features (in columns) on relative abundance of fish traits (in rows) among estuaries distributed worldwide, according to the fitted linear models (LM) and linear mixed models (LMM)

Trait	Bio.	Environment																																Total		
		SST				NPP				C. shelf				Mar chla				Tidal regime				Est. type				Est. area				Est. salinity				LM	LMM	
	LM	LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		F	F	F+R
	%	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	R^2	R^2
Marine	**24**	1	0.8			**4**	**1**	*	-	1	0.3			1	0.3			**2**	**0.7**	*	+	**9**	**1**	*	+	5	0.5			**1**	**0.9**	*	-	46	0.45	0.56
	na	1	0.5			**5**	**1**	*	-	1	0.3			1	0.3			2	0.3			**12**	**1**	*	+	**8**	**1**	*	+	**1**	**0.8**		-	30	0.28	0.52
Brackish	**11**	0	0.3			0	0.4			0	0.3			0	0.3			**4**	**0.9**		-	**1**	**0.8**	*	+	**2**	**0.8**	*	-	**3**	**1**	*	+	21	0.20	0.58
	na	0	0.6			0	0.3			0	0.3			0	0.3			**5**	**1.0**	*	-	**1**	**0.8**	*	+	**3**	**1**	*	-	**3**	**1**	*	+	13	0.15	0.59
Freshwater	**16**	1	0.3			1	0.3			2	0.3			1	0.5			2	0.4			**6**	**1**	*	-	5	0.5			1	0.2			35	0.34	0.41
	na	1	0.5			**2**	**0.9**	*	+	2	0.6			1	0.3			2	0.6			**9**	**1**	*	-	**8**	**1**	*	-	1	0.3			26	0.25	0.34
Diadromous	**8**	**4**	**1**	*	-	2	0.6			0	0.3			0	0.3			0	0.1			1	0.3			1	0.3			0	0.1			16	0.17	0.45
	na	**3**	**1**	*	-	**3**	**1**	*	+	0	0.3			0	0.3			0	0.2			1	0.8			1	0.7			0	0.1			8	0.09	0.42
Detritivores	**12**	1	0.3			0	0.3			0	0.2			0	0.2			3	0.2			1	0.4			2	0.3			1	0.5			20	0.23	0.70
	na	**2**	**1**		+	0	0.3			1	0.3			0	0.6			**4**	**1**		-	2	0.3			**3**	**1**	*	-	**2**	**0.9**		-	14	0.14	0.69
Herbivores	**12**	1	0.3			0	0.3			0	0.2			0	0.2			3	0.2			1	0.4			2	0.3			1	0.5			20	0.23	0.70
	na	**2**	**1**		+	0	0.3			1	0.3			0	0.6			**4**	**1**		-	2	0.3			**3**	**1**	*	-	**2**	**0.9**		-	14	0.14	0.69
Omnivores	**11**	**1**	**0.8**	*	+	**5**	**1**	*	+	0	0.4			0	0.3			**3**	**0.8**		-	3	0.7			2	0.3			**3**	**1**	*	+	29	0.28	0.31
	na	1	0.5			**6**	**1**	*	+	0	0.3			0	0.3			**4**	**1**		-	**4**	**0.9**	*	-	**3**	**1**	*	-	**3**	**1**	*	+	22	0.22	0.23
Planktonivores	**16**	0	0.3			**5**	**1**	*	-	1	0.4			1	0.4			1	0.7			1	0.5			1	0.3			**4**	**0.9**		-	30	0.29	0.37
	na	0	0.5			**5**	**1**	*	-	1	0.7			**2**	**1.0**	*	-	1	0.4			1	0.4			**2**	**1**	*	+	**6**	**1**		-	19	0.19	0.34
Invertivores	**4**	**2**	**1**	*	-	0	0.3			0	0.3			0	0.3			**4**	**1**		-	0	0.3			**1**	**0.8**		-	1	0.3		-	12	0.12	0.17
	na	**3**	**1**	*	-	0	0.3			0	0.3			0	0.3			**5**	**1**		-	0	0.3			**1**	**0.9**	*	-	1	0.3		-	10	0.10	0.17
Macrocarnivores	**24**	0	0.3			0	0.5			0	0.3			1	0.3			0	0.4			3	0.7			**8**	**1**	*	+	1	0.3		+	38	0.39	0.57
	na	0	0.3			0	0.3			0	0.4			**2**	**0.8**	*	+	0	0.1			**4**	**0.8**	*	+	**13**	**1**	*	+	**2**	**1**		+	22	0.25	0.56

(Continues)

TABLE 4 (Continued)

Trait	Bio.	Environment																																Total		
		SST				NPP				C. shelf				Mar chla				Tidal regime				Est. type				Est. area				Est. salinity						
	LM	LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM		LMM		LM	LMM	
																																		F	F	F+R
	%	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	I	S	C	%	R^2	R^2
Small size	**10**	**1**	**1**	*	-	0	0.6			1	0.4			0	0.3			1	0.3			**2**	**0.8**		-	**2**	**0.9**	*	-	1	0.1			18	0.18	0.27
	na	**1**	**0.8**	*	-	0	0.3			**1**	**0.9**	*	+	**1**	**0.8**	*	-	**1**	**0.7**	*	-	**2**	**0.9**	*	-	**2**	**0.8**		-	**2**	**0.9**		-	10	0.10	0.21
Medium size	**11**	**4**	**1**	*	+	0	0.3			1	0.5			0	0.3			0	0.1			0	0.3			**4**	**1**	*	+	0	0.2			22	0.21	0.29
	na	**4**	**1**	*	+	1	0.6			**1**	**1.0**	*	-	**1**	**0.8**	*	+	0	0.3			0	0.3			**4**	**1**	*	+	0	0.2			12	0.12	0.24
Large size	**9**	1	0.4			**1**	**0.9**	*	+	**1**	**0.9**		+	1	0.5			1	0.3			1	0.3			1	0.3			0	0.1			16	0.16	0.34
	na	**1**	**0.9**		-	0	0.6			**1**	**0.8**		+	1	0.3			1	0.5			1	0.5			**1**	**0.8**	*	+	1	0.3			8	0.09	0.33
V. large size	**3**	0	0.2			1	0.8			0	0.2			0	0.3			0	0.1			0	0.4			1	0.5			1	0.4			7	0.07	0.31
	na	0	0.2			1	0.7			0	0.3			0	0.2			1	0.2			0	0.3			**1**	**0.8**		-	1	0.8			5	0.05	0.29
Shallow	**8**	**1**	**0.9**	*	+	1	0.5			0	0.3			1	0.3			0	0.1			0	0.3			1	0.5			0	0.1			12	0.12	0.29
	na	0	0.3			**1**	**0.9**		-	0	0.3			**1**	**0.9**	*	-	0	0.1			0	0.3			1	0.6			1	0.2			4	0.03	0.25
Medium depth	**13**	1	0.3			0	0.2			1	0.3			1	0.5			**2**	**0.9**		-	0	0.2			0	0.3			0	0.1			19	0.18	0.40
	na	**2**	**1**	*	+	1	0.7			1	0.7			**2**	**1**	*	+	**2**	**1**		-	0	0.3			0	0.4			0	0.1			9	0.08	0.38
Deep	**17**	**8**	**1**	*	-	1	0.5			**2**	**0.8**		-	0	0.4			**3**	**1**	*	+	1	0.3			**2**	**1**	*	+	0	0.2			35	0.35	0.43
	na	**13**	**1**	*	-	**2**	**0.9**		-	**4**	**1**	*	-	1	0.3			**4**	**1**	*	+	1	0.3			**2**	**1**	*	+	0	0.2			26	0.26	0.42
V. deep	**9**	**8**	**1**	*	-	**1**	**1**	*	+	0	0.3		+	0	0.4			**5**	**1**		-	1	0.3			0	0.5			0	0.2			25	0.22	0.41
	na	**11**	**1**	*	-	0	0.3			0	0.5		-	0	0.3			**5**	**1**		+	1	0.3			0	0.3			0	0.2			19	0.16	0.39
Low l. span	**25**	1	0.6			1	0.4			2	0.4			0	0.5			4	0.8			1	0.3			**1**	**1**	*	-	**5**	**1**		+	40	0.39	0.76
	na	**1**	**0.7**	*	+	1	0.6			**4**	**1**	*	+	0	0.7			**6**	**1**		-	2	0.4			0	0.3			**8**	**1**		-	22	0.28	0.78
Medium l. span	**19**	1	0.7			0	0.7			**1**	**0.9**	*	+	0	0.3			3	0.2			0	0.4			1	0.3			1	0.1			27	0.26	0.32
	na	1	0.5			0	0.5			**2**	**1**	*	+	**0**	**0.8**	*	-	**5**	**1**	*	-	1	0.5			**2**	**1**	*	+	**2**	**1**	*	-	13	0.13	0.24
High l. span	**11**	1	0.5			**1**	**0.9**	*	+	**2**	**0.9**	*	-	**1**	**0.8**	*	+	1	0.7			1	0.5			1	0.3			1	0.2			20	0.20	0.25
	na	**2**	**0.9**	*	-	**1**	**0.9**	*	+	**3**	**1**	*	-	**2**	**1**	*	+	**1**	**0.9**	*	+	1	0.6			1	0.7			1	0.5			13	0.12	0.18
V. high l. span	**19**	0	0.3			0	0.3			0	0.3			**1**	**0.8**	*	-	1	0.8			1	0.8			**1**	**0.9**	*	+	**8**	**1**	*	+	31	0.31	0.53
	na	0	0.3			0	0.3			0	0.5			1	0.6			1	0.5			1	0.7			1	0.7			**11**	**1**	*	+	15	0.15	0.50

For each trait category, we built two alternative models (in rows): with and without the biogeographical variable (estuarine biogeographical region). To explore linear models (LM), we used hierarchical partition of variation (HPV) and multifcmodel inference (MMI): for HPV, the table shows the relative importance of each predictor to trait variation (%, between 0 and 100), and the predictor coefficient (C, represented only as "+" if positive or "−" if negative); for MMI, the table shows the predictor coefficient (C, represented only as "+" if positive or "−" if negative) and the importance of each predictor to trait variation (I, between 0 and 1; values >0.8 are significant and in those cases the models are marked in bold). For linear mixed models (LMM), the table shows the predictor coefficient (C, represented only as "+" if positive or "−" if negative) and the significance of each predictor to trait variation (S, with * meaning significant at $p < .05$ and no value meaning not significant). Trait category-predictor relationships that are consistent across models are marked with light grey (when the predictor coefficient is positive) and dark grey (when the predictor coefficient is negative). The table also shows the total explained deviance of the fitted LM (%), and the Pseudo R^2 of the fitted LMM (pR^2) namely conditional R^2 for fixed effects and marginal R^2 for fixed and random effects. Ecosystem features are estuarine biogeographical region and environmental variables (fourth root transformed)—sea surface temperature (SST), terrestrial net primary productivity (NPP), continental shelf width (C. shelf), marine chlorophyll a concentration (Mar chla), tidal regime (from microtidal, mesotidal to macrotidal), estuary type (from "temporarily open" to "open" to the marine ecosystem), estuary area (Est. area), estuary salinity type (Est. type: from regular, regular-hyperhaline to hyperhaline). (n = 414 samples in a total of 297 estuaries).

(Continues)

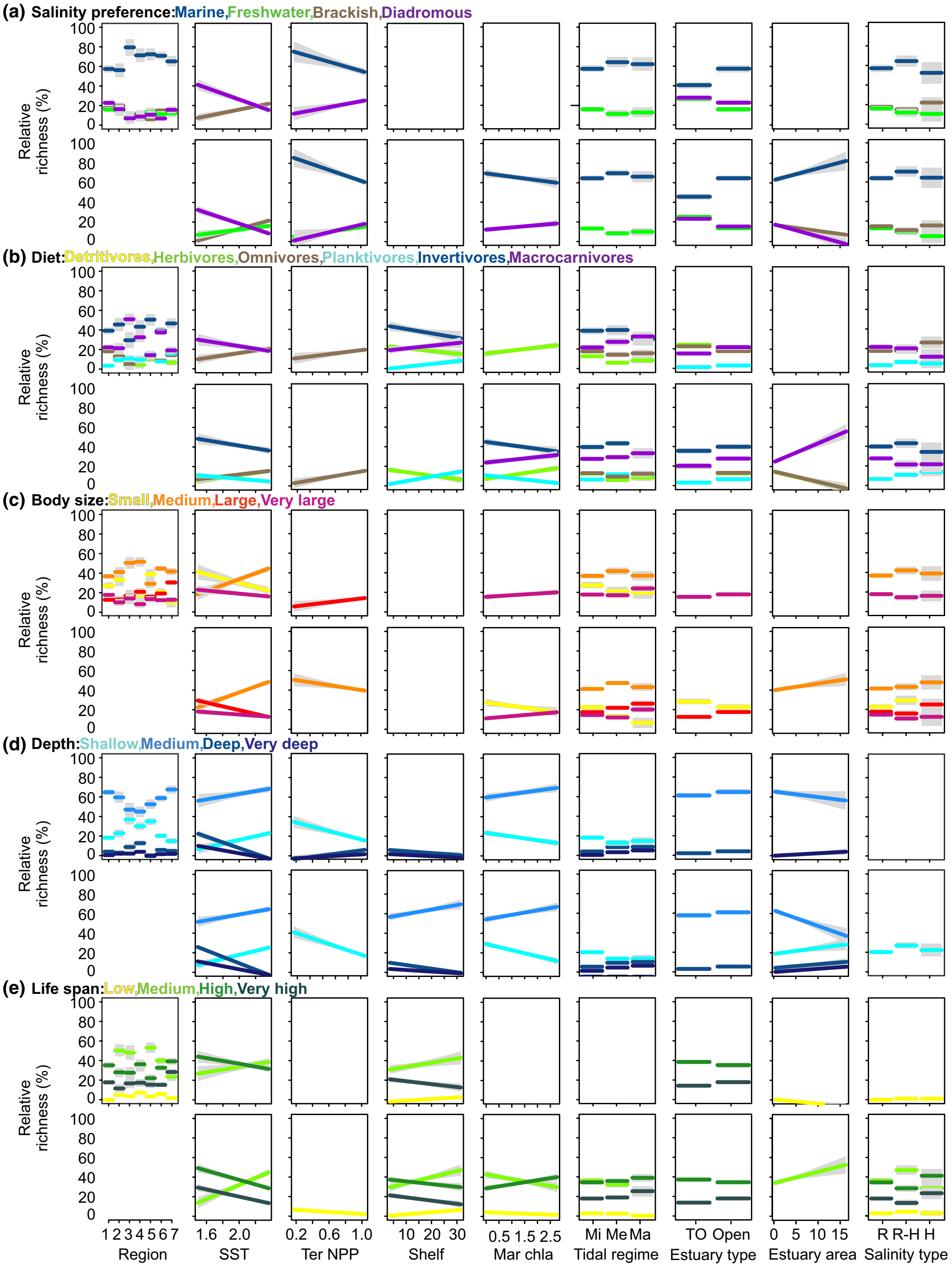

FIGURE 2 Effect of ecosystem features on relative species richness of fish trait categories in estuaries worldwide according to the fitted linear models. Ecosystem features are estuarine biogeographical region (1—Temperate Southern Africa, 2—Indo-Pacific, 3—Tropical Eastern Pacific, 4—Cold temperate North America, 5—Temperate Australasia, 6—Warm and Warm temperate Western Atlantic, 7—Eastern temperate North Atlantic) and environmental variables (fourth root transformed)—sea surface temperature (SST), terrestrial net primary productivity (Ter NPP), continental shelf width (Shelf), marine chlorophyll a concentration (Mar chla), tidal regime (Mi—microtidal, Me—mesotidal, Ma - macrotidal), estuary type (TO—temporarily open, Open), estuary area, salinity type (R—regular, R-H—regular-hyperhaline, H—hyperhaline). Fish traits are (a) salinity preference (marine, brackish, freshwater, diadromous), (b) diet (detritivores, herbivores, omnivores, planktivores, invertivores, macrocarnivores), (c) maximum body size (small, medium, large, very large), (d) maximum depth of distribution (shallow, medium, deep, very deep), (e) lifespan (low, medium, high, very high). Two alternative models were built for each trait category: with (upper row of each trait category) and without the biogeographical variable (lower row of each trait category). (n = 547 samples in a total of 386 estuaries). The figure only includes the trait category-predictor relationships that were significant in linear models or linear mixed models

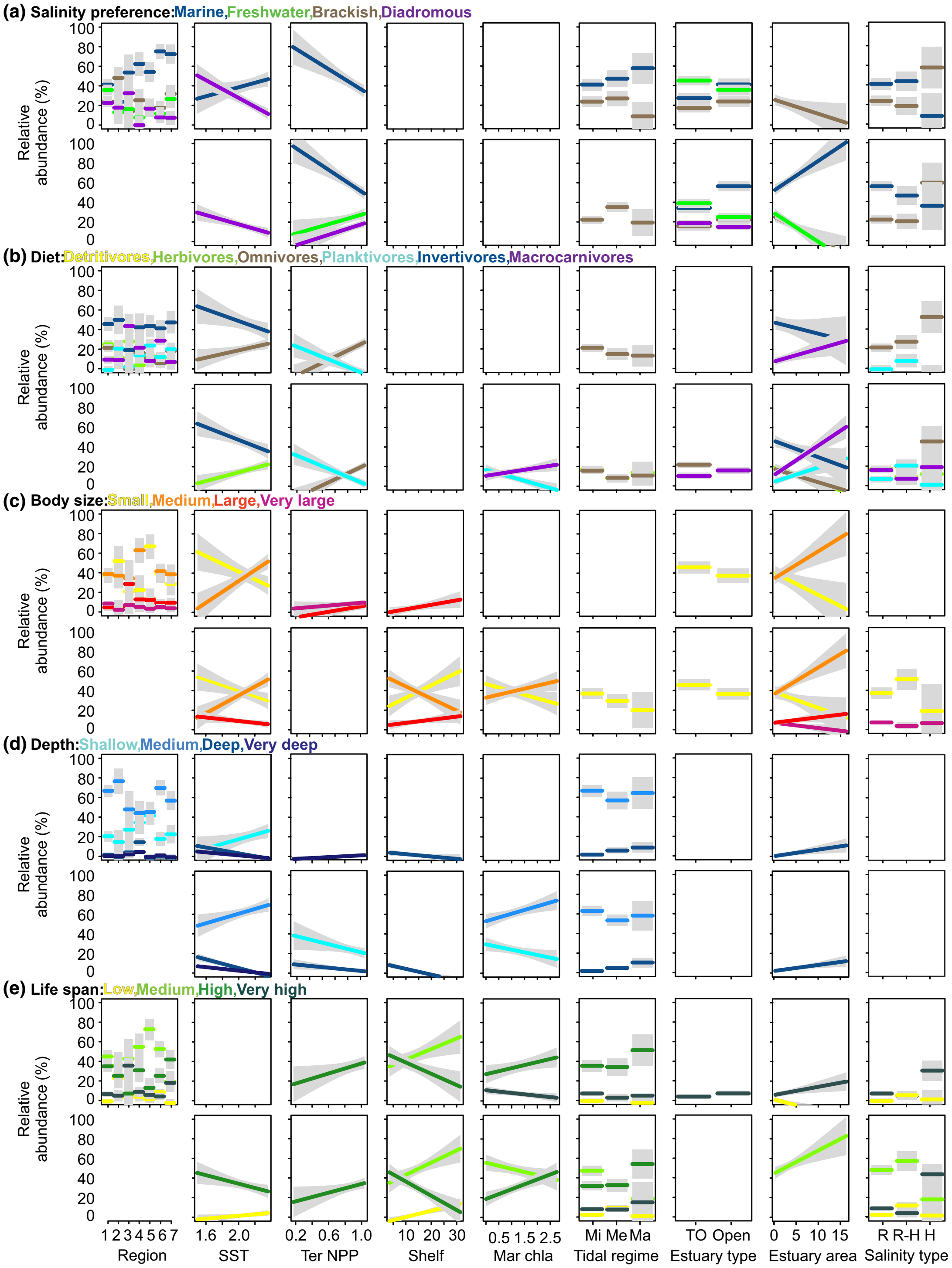

FIGURE 3 Effect of ecosystem features on relative abundance of fish trait categories in estuaries worldwide according to the fitted linear models. Ecosystem features are: estuarine biogeographical region (1—Temperate Southern Africa, 2 – Indo-Pacific, 3—Tropical Eastern Pacific, 4—Cold temperate North America, 5—Temperate Australasia, 6—Warm and Warm temperate Western Atlantic, 7—Eastern temperate North Atlantic) and environmental variables (fourth root transformed) —sea surface temperature (SST), terrestrial net primary productivity (Ter NPP), continental shelf width (Shelf), marine chlorophyll a concentration (Mar chla), tidal regime (Mi—microtidal, Me—mesotidal, Ma—macrotidal), estuary type (TO—temporarily open, Open), estuary area, salinity type (R—regular, R-H—regular-hyperhaline, H—hyperhaline). Fish traits are (a) salinity preference (marine, brackish, freshwater, diadromous), (b) diet (detritivores, herbivores, omnivores, planktivores, invertivores, macrocarnivores), (c) maximum body size (small, medium, large, very large), (d) maximum depth of distribution (shallow, medium, deep, very deep), (e) lifespan (low, medium, high, very high). Two alternative models were built for each trait category: with (upper row of each trait category) and without the biogeographical variable (lower row of each trait category). (*n* = 414 samples in a total of 297 estuaries). The figure only includes the trait category-predictor relationships that were significant in linear models or linear mixed models

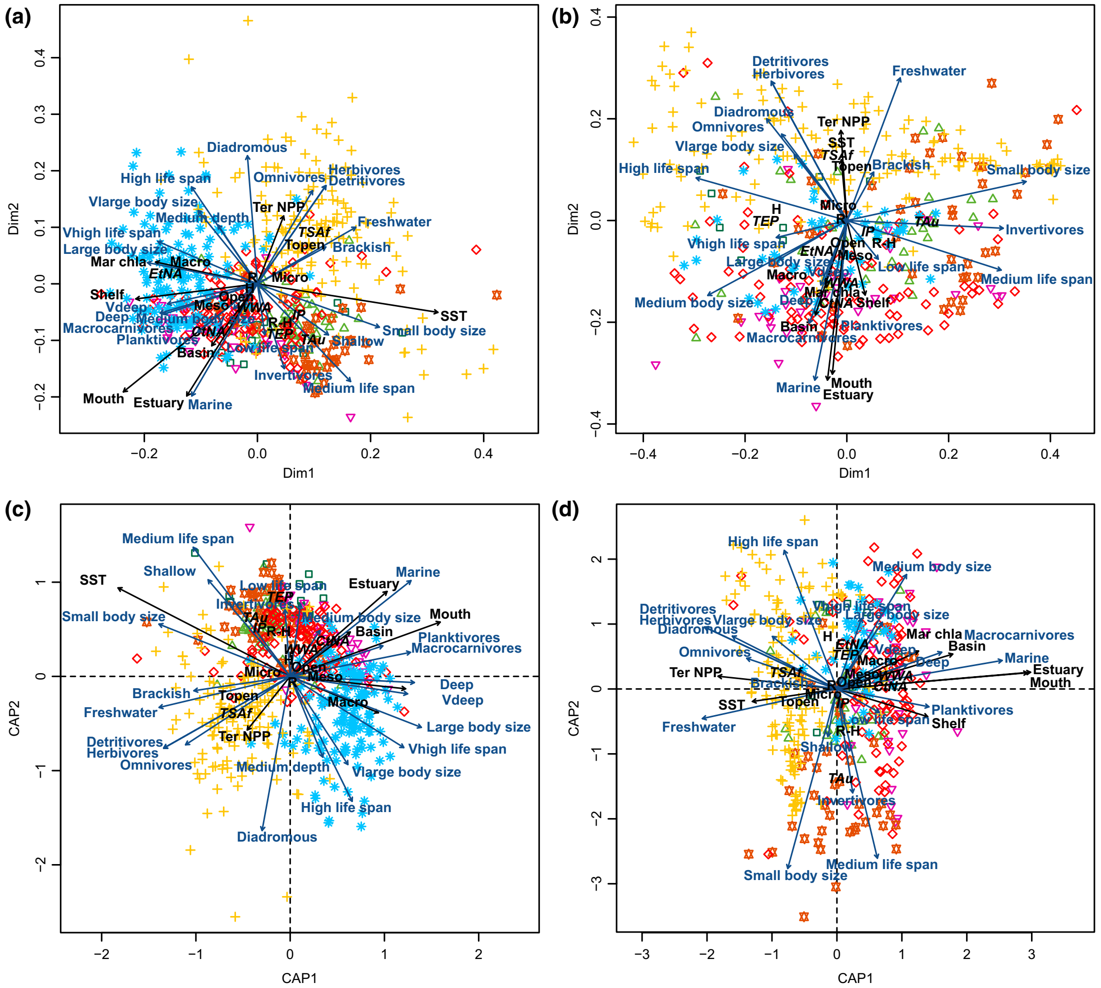

FIGURE 4 Ordination plots of fish traits in estuaries distributed worldwide and ecosystem features: principal coordinates analysis of (a) relative species richness of traits and (b) relative abundance of traits, as well as canonical analysis of rincipal coordinates of (c) relative species richness of traits and (d) relative abundance of traits. Fish traits are salinity preference (marine, brackish, freshwater, diadromous), diet (detritivores, herbivores, omnivores, planktivores, invertivores, macrocarnivores), maximum body size (small, medium, large, very large), maximum depth of distribution (shallow, medium, deep, very deep) and lifespan (low, medium, high, very high. Ecosystem features are estuarine biogeographical region (△ IP—Indo-Pacific, □ TEP—Tropical Eastern Pacific, ▽ CtNA—Cold temperate North America, ✡ TAu—Temperate Australasia, ◇ WWA—Warm and Warm temperate Western Atlantic, ✳ EtNA—Eastern temperate North Atlantic, + TSAf—Temperate Southern Africa) and environmental variables (fourth root transformed) —sea surface temperature (SST), terrestrial net primary productivity (NPP), continental shelf width (Shelf), marine chlorophyll a concentration (Mar chla), tidal regime (microtidal, mesotidal, macrotidal), estuary mouth width (Mouth), estuary type (from "temporarily open" to "open" to the marine ecosystem), estuary area (Estuary), drainage basin area (Basin), salinity type (regular, regular-hyperhaline, hyperhaline). (for relative species richness n = 547 samples in a total of 386 estuaries; for relative abundance n = 414 samples in a total of 297 estuaries)

increased with terrestrial primary productivity (together with diadromous fishes but contrarily to marine). Also, the proportion of marine species in estuaries increased greatly with the degree of connectivity of the estuary with the marine ecosystem (higher in open estuaries) and increased with estuary area, whilst the inverse was observed for freshwater and diadromous species. Hyperhaline estuaries had a higher proportion of brackish fishes.

Invertivores dominated estuarine fish assemblages (Table 5), and these assemblages showed relevant spatial patterns of different diets (LM and LMM: Tables 3 and 4 and Figures 2 and 3, PCO and CAP: Figure 4 and Appendix S5). Overall, detritivores, herbivores and omnivores showed similar responses to several environmental features, which was also observed between responses of macrocarnivores and planktivores. Proportions of detritivores, herbivores and omnivores in estuaries decreased notably with tidal range, in permanently open estuaries (also estuary mouth width; Figure 4) and with estuary area, whilst they slightly increased with SST and NPP, and slightly decreased with continental shelf width and marine chlorophyll *a*. Results for macrocarnivores and planktivores in estuaries showed the opposite trend, whilst the proportion of omnivores also increased in hyperhaline estuaries.

Estuarine assemblages were dominated by fishes with small and medium body sizes, fishes with shallow and medium maximum depths of distribution (i.e. down to the continental shelf limit at around

TABLE 5 Relative abundance (%) and relative species richness (%) of fish traits among estuaries distributed worldwide

		Relative abundance		Relative species richness	
Trait	Category	Mean	*SD*	Mean	*SD*
Salinity preference	Marine	53	33	63	19
	Brackish	21	24	12	9
	Freshwater	24	28	13	13
	Diadromous	15	20	17	13
Diet	Detritivores	12	20	10	12
	Herbivores	12	20	10	12
	Omnivores	14	20	13	10
	Planktivores	12	20	10	9
	Invertivores	47	30	40	16
	Macrocarnivores	15	20	28	5
Body size	Small	40	33	20	16
	Medium	41	28	42	12
	Large	9	14	19	11
	Very large	5	10	14	9
Maximum depth	Shallow	24	24	19	13
	Medium	61	27	59	14
	Deep	3	10	7	9
	Very deep	1	4	3	5
Lifespan	Low	5	13	3	4
	Medium	49	31	36	17
	High	30	27	35	12
	Very high	8	13	17	10

200 m) and medium and high lifespan fishes (Table 5). And these traits showed comparable relationships with environmental variables (LM and LMM: Tables 3 and 4 and Figures 2 and 3, PCO and CAP: Figure 4 and Appendix S5). Body size, maximum depth of distribution and lifespan of fishes in estuaries notably decreased with SST (especially maximum depth of distribution). Moreover these three traits increased largely with tidal range and increased in permanently open estuaries (also estuary mouth width; Figure 4) and larger estuaries. Moreover, hyperhaline estuaries had high proportions of very high lifespan fishes.

4 | DISCUSSION

Results of the present study provide new insights into how biogeography and environmental gradients drive functional traits of fish assemblages in estuaries worldwide. Here, we used data for a large set of sites across a global geographical extent to advance knowledge on trait–environment relationships (see summary in Figure 5). Briefly, in addition to biogeographical region (that drives patterns of the five analysed traits; first box in Figure 5), the observed trait patterns seem to be driven by two major environmental gradients: a first gradient linked to ecosystem temperature (second box in Figure 5), and a second gradient associated with habitat size of the estuary and its hydrological connectivity with the marine ecosystem (third box in Figure 5). In particular, fishes with macrocarnivore diets and fishes with larger body size (and also maximum depth of distribution and lifespan) tended to increase in importance in estuaries of cooler regions (second box in Figure 5) and, together with fishes with marine salinity preference, increased importance in estuaries with higher hydrological connectivity with the marine ecosystem (permanently open estuaries and with high tidal range) and with larger area (third box in Figure 5). Opposite patterns were observed for fishes with freshwater salinity preference, fishes with detritivore, herbivore or omnivore diets and fishes with smaller body size—and also smaller maximum depth and shorter lifespan)(second box in Figure 5). In addition, diadromous fishes increased importance in cooler estuaries whilst brackish decreased (second box in Figure 5). Finally, hyperhaline estuaries tended to have more brackish and omnivore fishes (third box of Figure 5).

Biogeography strongly influenced functional traits of fish assemblages in estuaries, similarly to its described influence on other aspects of these fish assemblages, namely species richness (Vasconcelos *et al.*, 2015) and species composition (Henriques *et al.*, 2016). The

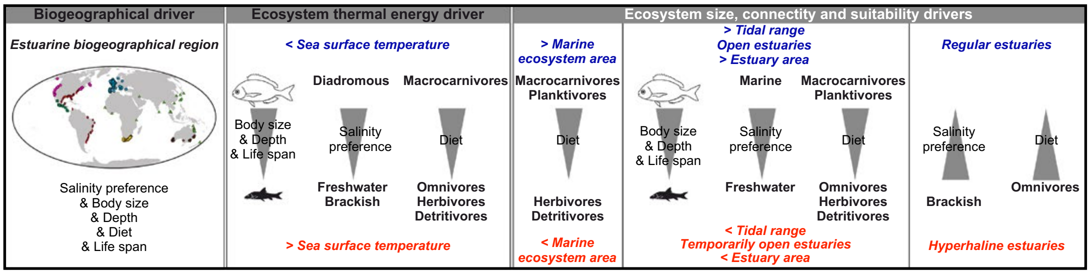

FIGURE 5 Summary of ecosystem drivers of fish traits among estuarine assemblages worldwide. Drivers considered were estuarine biogeographical region (Henriques *et al.*, 2016) and environmental features—sea surface temperature (SST), terrestrial net primary productivity, continental shelf width, marine chlorophyll a concentration, tidal regime (from microtidal, mesotidal to macrotidal), estuary mouth width, estuary type (from “temporarily open” to “open” to the marine ecosystem), estuary area, drainage basin area, estuary salinity type (from regular, regular-hyperhaline to hyperhaline). Functional traits considered were salinity preference, diet, maximum body size, maximum depth of distribution and lifespan. Trends highlighted here are the ones consistently identified in the data analyses, considering both relative abundance and relative species richness of traits [Colour figure can be viewed at wileyonlinelibrary.com]

apparent higher influence of biogeographical region on global trait patterns than on species richness (Vasconcelos *et al.*, 2015) or taxonomic beta-diversity (Henriques *et al.*, 2016) deserves further research. The suggested explanatory mechanism for an uneven global distribution of fish functional traits is that evolutionary history and historical contingencies [i.e. appearance of geographical barriers such as land barriers, mid-ocean ridges, glaciation and desiccation events; see Henriques *et al.* (2016)] limit the dispersal and persistence of species which are defined by species traits (e.g. body size, longevity, schooling behaviour, fecundity, egg size, mode of larval development) (Bender *et al.*, 2013; Luiz *et al.*, 2012, 2013; Mims, Olden, Shattuck, & Poff, 2010). For instance, large-bodied species (which tend to have greater lifespan and maximum depth of distribution) are expected to have higher dispersal ability due to their mobility, as well as higher persistence in the assemblages due to their intrinsic ecological plasticity (e.g. more diverse diets and environmental tolerance) and longevity (Bender *et al.*, 2013; Luiz *et al.*, 2013). Biogeographical patterns have been reported for traits such as body size and maximum depth of distribution in marine reef fish assemblages (Bender *et al.*, 2013; Fisher, Frank, & Leggett, 2010; Kulbicki *et al.*, 2015). For instance, proportion of smaller species tends to be larger in Atlantic and Tropical Eastern Pacific than in Indo-Pacific, with species maximum depth of distribution also higher in the Atlantic and overall increasing with body size (on the shelf) (Kulbicki *et al.*, 2015). Furthermore, the environmental features of biogeographical regions could also contribute to strengthen trait–biogeography relationships, as several environmental features of estuaries and adjacent ecosystems are more alike within than between biogeographical regions (temperature, productivity of the adjacent ecosystems, continental shelf width and tidal range).

Prominent trait–environment relationships were evident in estuarine fish assemblages worldwide. The relationship of environmental features with traits observed in this study may be more relevant than the relationships of environmental features with species richness (previously reported in Vasconcelos *et al.*, 2015) or taxonomic beta-diversity (previously reported in Henriques *et al.*, 2016), which calls for further investigation. Temperature acted as an important driver of these three aspects of fish assemblages in estuaries, whereas other environmental features (especially tidal range, estuary type, estuary area) seem to act as strong drivers of assemblages' traits despite their smaller influence on species richness or composition. This suggests that the composition of fish assemblages in estuaries worldwide is possibly determined by their functional features and role in ecosystems.

Regarding the thermal energy and primary productivity gradient, the observed increase in body size with the decrease in temperature supports our ***hypothesis 1*** and agrees with Bergmann′s rule for endotherms and the corresponding temperature-size rule for ectotherms that larger body sizes are favoured in cooler climates (Table 1; third box in Figure 5). However, no consistent trend was observed for the small fish category, which was mostly driven by local estuary-related features (Tables 2 and 3). This can be due to the rate of change of small species versus large species. For marine fishes, it has been reported that body size decreases with the increase in species richness globally, but the proportion of large marine fish species changes faster than that of small species and is more easily detected; although the slope of change depends on biogeographical region (Kulbicki *et al.*, 2015) and is steeper in the Atlantic (which hosts larger species and less diversity) than in the Indo-Pacific (with higher diversity and mostly composed by small species) (Fisher *et al.*, 2010; Kulbicki *et al.*, 2015). Gradients of increasing fish body size with decreasing temperature have also been shown for marine fish assemblages at smaller spatial extents (e.g. Daufresne, Lengfellner, & Sommer, 2009; Fisher *et al.*, 2010; Kulbicki *et al.*, 2015), even if the widespread applicability of Bergman's rule/temperature-size rule has been questioned (e.g. Belk & Houston, 2002; Edeline, Lacroix, Delire, Poulet, & Legendre, 2013; Fisher *et al.*, 2010; Kulbicki *et al.*, 2015). Body size patterns probably have multiple causal processes operating at different scales. For instance, at higher temperatures, oxygen concentrations are lower and smaller species have a physiological advantage over larger species in these conditions due to the former's shorter oxygen diffusion path (Edeline *et al.*, 2013; Ohlberger, 2013) and lower energy requirements (lower oxygen concentration implies higher respiration rate, movement, energy loss and less energy available for growth) (Huston & Wolverton, 2011). At higher temperatures, there is also a competitive asymmetry of small and large fish, with small fish favoured by size-dependent selection due to intra- and interspecific competition and predation (Edeline *et al.*, 2013). In addition, Bergman's rule/temperature-size rule does not fully account for the global patterns of body size observed here, as this trait was also driven by other environmental gradients (especially hydrological connectivity of the estuary and the marine ecosystem) and temperature also accounted for the observed patterns of most functional traits.

Diet is related to body size due to metabolic, physiological and ecological reasons (Kulbicki *et al.*, 2015; Woodward *et al.*, 2005). In our study, fish species with macrocarnivore diets tended to have larger body size, whereas planktivores and omnivores tended to have smaller body size. Similar relationships between body size and diet were established in coral reef fish globally (Kulbicki *et al.*, 2015). And the covariation of body size–diet traits in our study may partially justify some of similarity in their spatial patterns (i.e. of macrocarnivore species and larger body sizes, and of omnivore species and smaller body sizes). However, results did not clearly corroborate ***hypothesis 2*** about an effect of productivity on body size via food availability (Table 1; Huston & Wolverton, 2011), even if terrestrial net primary productivity was weakly related to some diet traits (i.e. directly for omnivores and inversely for planktivores) and marine chlorophyll a was weakly related to macrocarnivores and very large body size. Nevertheless, further research is needed to test this hypothesis, particularly as we used primary productivity data for marine and terrestrial ecosystems and not directly for estuaries which is harder to estimate remotely and was not available for most estuaries in our database. Still, phytoplankton biomass in estuaries is influenced by nutrients and organic carbon inputs from both marine and terrestrial ecosystems (Cloern, Foster, & Kleckner, 2014). However, estuarine food webs are typically sustained by two main sources of organic matter—primary productivity (e.g. from phytoplankton, mangrove, salt marsh, seagrass, macroalgae but especially resuspended microphytobenthos) and detritus (mainly indirectly from freshwater runoff and directly from intertidal saltmarsh and subtidal macrophytes) (Elliott *et al.*, 2002). To better understand trophic trait–productivity relationships at global extent, knowledge of estuarine productivity is needed at matching extents, and thus encompassing important seasonal and within estuary dynamics (Elliott *et al.*, 2002).

Dietary traits were mostly driven by hydrological connectivity of the estuary with the marine ecosystem, ecosystem size and ecosystem suitability, but our ***hypothesis 3*** (Table 1) seems to be supported by the association of detritivores, herbivores and omnivores with warmer waters and the association of macrocarnivores and planktivores with cooler waters. The first trend is probably related with higher efficacy in digestion of plants and detritus in warmer than in cooler conditions (i.e. better enzymatic performance) as well as higher digestibility of dominant filamentous green and red algal assemblages, which are important in tropical environments (Behrens & Lafferty, 2007; Floeter *et al.*, 2005; Kulbicki *et al.*, 2015). This means that it could be more difficult for detritivore, herbivore and omnivore fish to meet their metabolic demands at cooler temperatures (Floeter *et al.*, 2005). Moreover, metabolic rates of fish decrease with the decrease in temperature, and carnivores have a higher ecological advantage in cooler waters than herbivores, as carnivores have higher assimilation efficiency (consume food with higher energetic content) and consequently need lower feeding rates. Furthermore, carnivores also have improved chances of finding suitable feeding or shelter habitat as they tend to be larger and therefore have higher dispersal ability (Floeter *et al.*, 2005; Gillooly, Brown, West, Savage, & Charnov, 2001; Kulbicki *et al.*, 2015; Luiz *et al.*, 2012, 2013; Sunday *et al.*, 2015). In agreement, a latitudinal/temperature trend in the distribution of carnivores and herbivores/omnivores has been shown for marine, brackish and freshwater ecosystems (e.g. Behrens & Lafferty, 2007; Clements, Raubenheimer, & Choat, 2009; Edeline *et al.*, 2013; Floeter *et al.*, 2005; Kulbicki *et al.*, 2015).

Estuary size and its hydrological connectivity with the marine ecosystem strongly drive functional traits of estuarine assemblages. These environmental features of estuaries have also been reported to drive total species richness, which increases with estuary size (Nicolas, Lobry, & Lepage, 2010b; Vasconcelos *et al.*, 2015) and with the connectivity of the estuary with the marine ecosystem (Harrison & Whitfield, 2008; James, Cowley, Whitfield, & Lamberth, 2007; Vasconcelos *et al.*, 2015). Permanently open estuaries allow unrestricted emigration and immigration of marine species (Harrison & Whitfield, 2008; James *et al.*, 2007). Accordingly, assemblages were dominated by fishes with marine salinity preference. Moreover, the importance of these fishes increased in permanently open estuaries and with estuary area (which is positively correlated with estuary mouth width). Thus confirming the hypotheses that hydrological connectivity of the estuary with the marine ecosystem (***hypothesis 5***) and larger estuaries (***hypothesis 6***) enhance the importance of marine species in estuaries globally (Table 1). Results also demonstrated the effect of ecosystem size and hydrological connectivity with the marine ecosystem on species assembly, via effects on habitat suitability within estuaries (in terms of salinity).

However, results did not support an increase in importance of marine fishes in estuaries adjacent to large marine ecosystems, or of an increase in the relative importance of freshwater and diadromous fishes in estuaries with larger river basins (***hypothesis 6***, Table 1). In fact, at this extent, the latter relationship was inverse, as freshwater fishes decreased their importance in estuaries with large river basin (which at this extent have large estuary area) and with high connectivity with the marine ecosystem (wide tidal range and permanently open), likely due to the larger size of high salinity areas in those estuaries. In addition, the lack of relationship between marine fishes and chlorophyll a, and the weak-positive relationship between freshwater fishes and terrestrial net primary productivity (in parallel with an inverse relationship between marine fishes and terrestrial net primary productivity) did not allow us to incontestably corroborate ***hypothesis 4*** (Table 1). Still, diadromous fishes increased with terrestrial net primary productivity possibly because they migrate to feed on regions with high productivity (Gross, Coleman, & McDowall, 1988). Together, these results suggest that despite the transitional nature of estuaries, their features are more important in determining fish species assembly than features of the adjacent ecosystems.

The increased importance of brackish fishes in hyperhaline estuaries supports ***hypothesis 7*** (Table 1) and is justified by the higher physiological tolerance of these fishes to high salinity conditions (high osmoregulatory capacity), their generalist behaviour and dietary flexibility (Elliott & Whitfield, 2011; Whitfield *et al.*, 2012). Here, brackish fishes were more frequently detritivores, herbivores and omnivores. Likely taking advantage from lower inter-specific competition and predation, brackish and omnivores increased in hyperhaline estuaries. However, for freshwater and marine fish, no relationship with hyperhaline conditions was found. Their importance is expected to be influenced by the salinity gradient within estuaries and the extent of different salinity areas (Whitfield *et al.*, 2012), but this could not be analysed here in further detail due to data limitation.

The natural covariation among several environmental features of estuaries and among several fish traits might help explain some of the observed trait–environment relationships, namely (i) the decreased importance of brackish and freshwater fishes in colder temperatures, and (ii) the higher importance of macrocarnivore and planktivore fishes (and decreased importance of detritivore, herbivore and omnivore fishes) in estuaries with larger area and hydrological connectivity with the marine ecosystem. The first relationship likely arises as freshwater species have higher relative importance in smaller and temporarily open estuaries globally [in agreement with Harrison and Whitfield (2008) at smaller spatial extent] which are rare in colder regions with lower terrestrial primary productivity. Moreover, in our study, brackish and freshwater species are more often detritivores, herbivores and omnivores (which seem to benefit physiologically from higher temperatures further justifying the first relationship) whilst marine species have higher relative importance in large and open estuaries [in agreement with Nicolas *et al.* (2010a)] and are more often macrocarnivore and planktivore, justifying the second relationship.

In the examined estuaries, fishes with marine salinity preference tended to have larger body size and greater maximum depth of distribution, and our results showed a higher importance of fishes with these traits in colder estuaries, estuaries with larger area (which tend to be deeper) and with higher connectivity with marine ecosystems (which is also promoted by larger tidal ranges and enhanced flood/ebb currents). Firstly, the link between larger body size and greater maximum depth of distribution in estuarine fish assemblages supports a within-fauna "bigger-deeper" trend which has been advocated for marine teleost fishes (Cheung, Watson, Morato, Pitcher, & Pauly, 2007; Kulbicki *et al.*, 2015; Macpherson, 1994; Stefanescu, Rucabado, & Lloris, 1992). These authors suggest that the bigger-deeper trend may arise from higher resource limitation and predation risk and lower temperature in deeper marine areas, which favour marine fish species with high mobility and lower habitat dependence. However, the ubiquity of this trend has been widely challenged by reports of opposite trends and of possible methodological insufficiencies (Collins, Bailey, Ruxton, & Priede, 2005; Stefanescu *et al.*, 1992). Furthermore, present results indicate a remarkable barrier imposed by higher temperature on the occurrence of deeper water fishes in estuaries. In deeper water, fishes are typically exposed to colder temperatures, and our results show that warmer estuaries have a much lower importance of deeper water species than colder estuaries. This is relevant in the context of climate change, as distribution shifts in both latitude and depth of demersal marine fishes have been shown to be linked to changes in temperature (Dulvy *et al.*, 2008; Perry, Low, Ellis, & Reynolds, 2005). Secondly, the similar trait–environment relationships observed for lifespan and body size are justified by the scaling of body size with longevity (Kulbicki *et al.*, 2015; Woodward *et al.*, 2005). Body size scales with several traits, such as longevity, age at maturity, length at maturity and generation time (Cheung, Pitcher, & Pauly, 2005; Cheung *et al.*, 2007). Long-lived species are more persistent in marine biological communities (Costello *et al.*, 2015) and tend to have periodic and equilibrium life-history strategies, contrarily to short-lived species which tend to be associated with opportunistic strategies (Winemiller, 2005). In our study, colder estuaries and with higher connectivity with the sea seem to favour equilibrium and periodic life-history strategies (i.e. these estuaries have increased importance of fishes with larger maximum body sizes and lifespan), whilst warmer estuaries and with lower connectivity with the sea seem to benefit opportunistic species (i.e. these estuaries have increased importance of fishes with smaller body size and shorter lifespan). Accordingly, in North America, freshwater fishes with opportunistic strategies capitalize on basins that are historically less stable (south and south-east), whilst equilibrium and periodic strategies are favoured in more stable basins (west and north; Mims *et al.*, 2010).

Trait-based approaches can clarify processes leading to species distributions and adaptation via species' fitness and performance (e.g. metabolism, energy requirement, physiological limitations) (Violle *et al.*, 2014). Moreover, comparatively to species identities, traits can improve knowledge about community assembly processes (Mlambo, 2014; Violle *et al.*, 2014) and provide a mechanistic understanding of community ecology (McGill, Enquist, Weiher, & Westoby, 2006). The present study indicates that traits of estuarine fish assemblages are not homogeneous worldwide, rather they are driven by biogeographical and environmental features—which also drive species richness and species composition (previously reported in Vasconcelos *et al.*, 2015; Henriques *et al.*, 2016). The species richness (Vasconcelos *et al.*, 2015), species composition (Henriques *et al.*, 2016) as well as species traits (present study) that can occur in an estuary are firstly constrained by biogeographical region. Secondly, they are regulated by temperature with species segregated along a latitudinal temperature gradient (Henriques *et al.*, 2016), with higher species richness in the tropics (Vasconcelos *et al.*, 2015) where estuarine assemblages tend to have relatively more fishes with freshwater and brackish salinity preference, herbivore/detritivore/omnivore diets, smaller body size, smaller maximum depths of distribution and reduced lifespan (versus larger body size, greater maximum depth of distribution and lifespan)(present study). Thirdly, a higher connectivity of estuaries with the marine ecosystem (and larger estuary area) positively influences species richness (Vasconcelos *et al.*, 2015) and species turnover (Henriques *et al.*, 2016), promoting the colonization of estuaries by fishes with marine salinity preference and simultaneously favouring macrocarnivore and planktivore diets, larger body size, greater maximum depth of distribution and lifespan (versus fishes with freshwater salinity preferences, with herbivore, detritivore and omnivore diets, smaller body size, smaller maximum depth of distribution and lifespan)(present study). Finally, extreme hyperhaline conditions of estuaries favour species with brackish salinity preference and omnivore diet (present study). Further research should dedicate to investigating these proposed community assembly mechanisms. Progress in the field of functional biodiversity and trait–environment relationships has been hampered by the lack of trait data for many species (especially for some biological groups), lack of agreement on which fundamental traits to be used, as well as potential intraspecific trait variation (Violle *et al.*, 2014). Research should focus on overcoming these limitations as trait-based approaches seem fundamental to predict communities' responses to environmental change (McGill *et al.*, 2006; Violle *et al.*, 2014).

The global extent of the present study and the use of published data in the construction of the database imposed some limitations. As anthropogenic pressures induce changes in taxonomic and functional aspects of fish assemblages (Henriques *et al.*, 2014a; Mouillot *et al.*, 2013), it would be relevant to evaluate, in the future, the link between functional diversity of these estuarine fish assemblages and the intensity of human activities and human-driven impacts in these ecosystems. In addition, intraspecific trait variability was not quantified in our study (especially as most published studies did not include information on individual size) and may have hindered the identification of some of the trait–environment relationships, especially for the traits diet and body size. Many fish species have dietary ontogenetic shifts (e.g. changing from planktivores to generalists consuming larger prey; Elliott *et al.*, 2002) and many estuaries act as nursery grounds; thus, estuarine fish assemblages may include large proportions of young fish (Able, 2005). A refined classification of traits should improve the identification of trait–environment relationships. Furthermore, estuaries are dynamic ecosystems subject to notable variability of environmental conditions and their fish assemblages show within-estuary seasonal and spatial variations, and encompassing for this variability should further clarify trait patterns and drivers. For instance, large seasonal changes in assemblage composition and abundance (Shimadzu, Dornelas, Henderson, & Magurran, 2013) can occur due to migrations of juveniles and spawning adults (Vasconcelos, Reis-Santos, Costa, & Cabral, 2011) and to changes in river flow which largely affect habitat suitability for marine versus freshwater species (Whitfield & Harrison, 2003). Moreover, estuarine fish assemblages are typically structured along a longitudinal salinity gradient (Whitfield *et al.*, 2012) and among a mosaic of habitats with differing degrees of complexity (Minello, Able, Weinstein, & Hays, 2003; Pihl *et al.*, 2002). As the present study aimed to cover a wide spatial extent, it was not feasible to include spatially (within estuary) or seasonally resolved fish assemblage data, especially as this information was lacking in the vast majority of studies included in the database. Nevertheless, the validity of the present study is further supported by the agreement of the observed global patterns and drivers with other ecosystems and with estuarine ecosystems at smaller spatial extents. Still, understanding smaller-scale processes that affect functional diversity and trait–environment relationships should benefit from further studies taking into consideration factors such as anthropogenic impacts, seasonality and within-estuary variability.

The stability and resilience of ecosystems' functional diversity can increase with the number of species, individuals and biomass presenting a given functional trait, although the differential response of individual species to stress and biotic interactions also play a role (Mouillot *et al.*, 2013). Therefore, understanding patterns of ecosystems' functional structure at global scales seems crucial for prioritization of conservation and management efforts which progressively tend to incorporate relationships between biodiversity—ecosystem functioning—services (Bender *et al.*, 2013; Hattam *et al.*, 2015; Strong *et al.*, 2015; Violle *et al.*, 2014). Previous studies showed that estuarine ecosystems distributed worldwide support different species richness (Vasconcelos *et al.*, 2015) and species composition (Henriques *et al.*, 2016), and present results show that they also support different functional traits. Moreover, results show that biogeography and ecosystem features notably drive functional traits of estuarine assemblages. In all, knowledge of global taxonomic and functional patterns of fish assemblages in estuaries and of their environmental driverssuggests that global conservation efforts should take into consideration biogeography and estuary features. Conservation strategies should embrace a tiered approach including estuaries representative of the several biogeographical regions and with different features (e.g. different estuary types and area, tidal range) to include the highest heterogeneity possible, even if some of those estuaries do not support high species richness (e.g. temperate). However, further research is still needed to develop adequate conservation strategies that effectively protect and recover biodiversity in estuaries. In addition, functional traits of estuarine fish assemblages are driven by biogeography and by environmental characteristics that are vulnerable to rapid changes (i.e. temperature and primary productivity, size of estuarine ecosystems and their hydrological connectivity with marine ecosystems). Anthropogenic pressures are unevenly distributed globally (Halpern *et al.*, 2008; Vorosmarty *et al.*, 2010) and can also vary spatially within estuaries (Borja *et al.*, 2006), as well as seasonally due to variation in environmental conditions and coastal population density. In this context, estuarine fish assemblages worldwide may be differentially affected by human-induced impacts, thus reinforcing the need for global conservation efforts (as referred above) that also take into account anthropogenic pressures and that are managed to maximize efficiency. Overall, these conservation guidelines are important to support heterogeneity of biological assemblages and their habitats (from benthic to pelagic), essential to properly safeguard global biodiversity and contribute to ecosystems resilience (Barton *et al.*, 2013).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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