RESEARCH ARTICLE

Disruptions caused by invasive species and climate change on the functional diversity of a fish community

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Abstract

As the effects of climate change continue to intensify, non-native species are becoming more prevalent in estuarine ecosystems. This has implications for the taxonomic and functional diversity of fish communities. Historically, biodiversity has been a synonym of taxonomic diversity, however this approach often fails to provide accurate insights on ecosystem functioning and resilience. To better understand how climate change is impacting fishes and their traits' composition, a long-term dataset from Minho Estuary (NW Iberian Peninsula) fish assemblage was analyzed. The results suggest that climate change and extreme weather events altered the prevailing trait modalities of fishes, which led to the overall decrease in functional diversity of the fish assemblage over the course of a decade. This decrease is associated to the loss of some trait modalities that are exclusively found in native species. On the other hand, the invasive species added novel traits associated with the conditions of high temperatures and low precipitation regime currently observed in the studied area. Our results highlight that the shift in the presence and dominance of some traits is directly influenced by climatic changes. Also, despite the addition of novel modalities by the invasive species, the fish assemblage is now less functional and taxonomically diverse than previously.

Graphical abstract
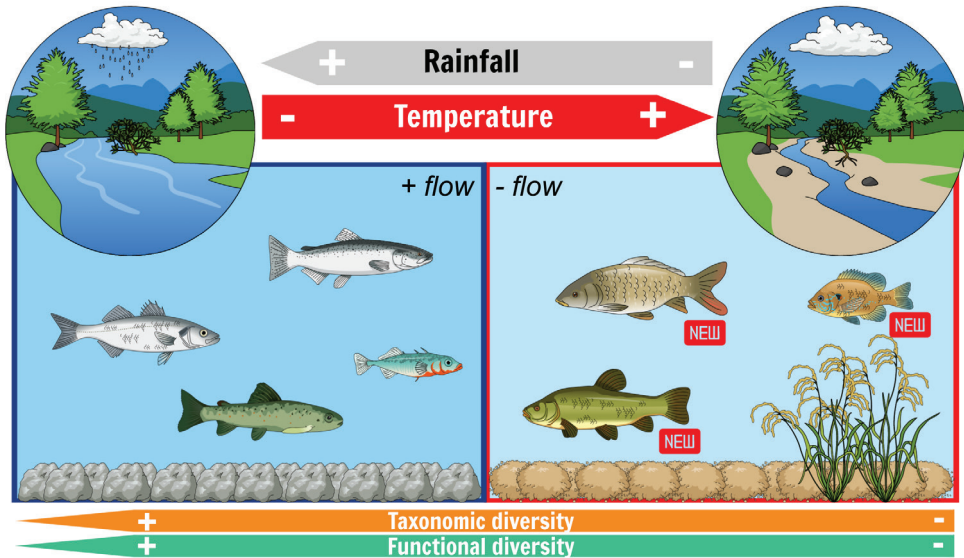
Keywords

biodiversity, biological invasions, climatic events, ecosystem functioning, native species, traits

Introduction

Climate change is one of the biggest threats to biodiversity currently (IPBES 2019; Reid et al. 2019), and nowadays many taxonomic groups and ecosystems around the world have already been affected (Alan Pounds et al. 2006; Moritz et al. 2008; Jarić et al. 2019). As global temperatures rise and weather patterns shift, ecosystems across the globe are undergoing drastic changes in their stability and functioning (Markham 1996; Walther et al. 2002; Parmesan and Yohe 2003). This can have a significant impact on the functional diversity of an ecosystem, as climate change can either favor certain species or cause the local extinction of others (Thuiller et al. 2006). The effects of climate change on functional diversity vary depending on the types of species present in a particular ecosystem. For example, species that are heat-tolerant may spread and flourish during periods of warmer climate; this is expected, for example, for the largemouth bass (*Micropterus salmoides*) in Iberian Peninsula (Bae et al. 2018). Other species, however, may be negatively impacted by shifts in temperature, which may translate into changes in species physiology, phenology, behavior, and geographic range (Robinson et al. 2009; Sorte et al. 2010; Hauser et al. 2018; Howard et al. 2020); this is the case for several tropical and subtropical fish species that have reach the northern Gulf of Mexico (Fodrie et al. 2010). Additionally, some species may require certain

conditions for foraging or nesting, and climate change may limit their access to these resources, thus preventing them from obtaining enough food and reproducing normally (Segev et al. 2014; Descamps et al. 2017). These factors collectively contribute to changes in functional diversity within ecosystems, leading to disruptions in populations and communities that vary depending on the compatibility between a species' ecological traits and the prevailing climatic conditions.

Historically, biodiversity has been associated to taxonomic diversity (Cardoso et al. 2014). However, this approach many times failed to provide insights into ecosystem functioning. Therefore, the use of traits and functional diversity indices alongside with taxonomic diversity provide a more holistic understanding about biodiversity (Hulme and Bernard-Verdier 2018). Both types of diversity metrics are important when evaluating the biodiversity of a given ecosystem (Villéger et al. 2010; Moore 2013; Teittinen and Virta 2021). In fact, due to the importance of functional diversity to biodiversity assessments, the number of scientific manuscripts integrating functional diversity into the ecological assessments has been increasing exponentially in recent years (Palacio et al. 2022). In general, ecosystems with high levels of both taxonomic and functional diversity are more stable and resilient to disturbances than ecosystems with low levels of diversity (Walker et al. 1999; Cadotte et al. 2011). By looking at the range of functions that different species perform in the ecosystem, the functional diversity indices provide a more in depth assessment of the ecosystem's overall condition. This is because a greater variety of functions creates greater redundancy within the system, meaning that if one species is lost, there are others that can perform its role in the ecosystem (Biggs et al. 2020).

On the other hand, climate change plays an important role in the establishment and spread of invasive species, a phenomenon that is widely recognized (Stachowicz et al. 2002). Currently, biological invasions are one of the most important topics in ecology (Anderson et al. 2021). The impacts of biological invasions can be extensive and often detrimental to native ecosystems (Pyšek et al. 2020). Invasive species can disrupt food webs (Wainright et al. 2021), alter habitats (Crooks 2002; Guy-Haim et al. 2018), displace native species (Catford et al. 2018), cause biodiversity loss (Pyšek et al. 2020), alter ecosystem functioning (Haubrock et al. 2021), and lead to significant social and economic impacts (Simberloff et al. 2013; Diagne et al. 2020). Invasive species can also out-compete native species for resources (Catford et al. 2018; Ferreira-Rodríguez et al. 2018), leading to a decline in diversity (Mollot et al. 2017; Williams-Subiza and Epele 2021) that can affect the entire ecosystem and affect various taxonomic groups that are directly or indirectly linked to them (Crooks 2002; Guy-Haim et al. 2018; Goedknegt et al. 2020; Vivó-Pons et al. 2020). Additionally, climate change is likely to exacerbate the impacts of biological invasions (Rahel and Olden 2008; Diez et al. 2012; Bellard et al. 2013), as rising temperatures and changes in precipitation regimes create new opportunities for the establishment of non-native species in new areas (Stachowicz et al. 2002; McKnight et al. 2021; Souza et al. 2022b).

While it is well documented that biological invasions usually have a negative impact on taxonomic diversity (Pyšek et al. 2020; Ilarri et al. 2022), few studies have

addressed the effects of this phenomenon on functional diversity (but see Sîrbu et al. 2022; Renault et al. 2022). Invasive species can fill empty trait gaps in the invaded ecosystems or replace the ones occupied by native species (Loiola et al. 2018), thereby disrupting functional diversity in these ecosystems (Hatfield et al. 2022; Linares et al. 2022). While the decline in taxonomic diversity can be accompanied by the loss of certain traits, it is crucial to understand how the decline in taxonomic diversity translates into changes in functional diversity, particularly in the context of simultaneous biological invasions and climate change. Hence, it is imperative to monitor ecosystem function and functional diversity as a means to address the threats posed by biological invasions and climate change. Through a continuous tracking of these indices, ecologists can identify areas at risk of species or functional loss (Santini et al. 2017) and pinpoint regions where appropriate management or conservation efforts are required.

Among the species groups particularly vulnerable to climate change and biological invasions are estuarine fishes (Gillanders et al. 2011; Souza et al. 2018; Lauchlan and Nagelkerken 2020; Ilarri et al. 2022). Despite their adaptability to a broad range of environmental conditions, these animals still exhibit sensitivity to the abiotic changes (e.g. in salinity and temperature) (Passos et al. 2016; Souza et al. 2018). Estuarine assemblages, in fact, often exhibit significant spatial and temporal variability (Sheaves 2009; Nagelkerken et al. 2015), emphasizing the importance of long-term datasets to facilitate a comprehensive assessment of fish assemblage dynamics and the influence of environmental drivers on them. Long-term monitoring data may also contribute to advances in invasion biology. In fact, there are few studies on the temporal aspects of invasive species impacts, and most of these studies are of short duration (less than 1 year), making it difficult to develop effective invasive management strategies and implement effective conservation measures (Matsuzaki et al. 2011). In addition, the use of traits can be useful in understanding invasion patterns and predicting which native species are most likely to be vulnerable to invasive species (Matsuzaki et al. 2011).

In this way, a long-term fish assemblage monitoring was conducted in the Minho Estuary (northwestern Iberian Peninsula) from 2010 to 2019. A recent study found that the Minho Estuary fish assemblage has been impacted by climatic changes and extreme temperature (heatwaves and cold-spells) and precipitation (dry and wet) events, which resulted in a less taxonomically diverse fish community dominated by a few invasive species (Ilarri et al. 2022). However, the temporal changes in the species trait composition of the Minho Estuary fish assemblage are still not known. To address this knowledge gap, a decade's worth of data on fish trait composition and climate (temperature and precipitation) from Minho Estuary were compiled from weekly *in-situ* fish sampling and satellite data. We hypothesize that climate change and extreme weather events alter the trait and functional diversity of estuarine fish communities, with most indices of functional diversity (e.g. functional divergence, dispersion, richness, evenness and RAO's quadratic entropy) being expected to decrease, while the functional redundancy is expected to increase. This is due to the increased prevalence of invasive species, which might introduce different traits compared to those originally found in the fish community, but also contribute to the loss or decline of some traits in the fish community.

Methods

Study area

Sampling took place in Lenta Marina, a small, semi enclosed bay (660 m × 80 m), located 14.5 kilometers upstream in the Minho Estuary (41°57'18.7"N, 8°44'42.9"W) (Fig. 1). Among the estuaries of Portugal, the Minho Estuary has relatively low levels of pollution (Reis et al. 2009), being used as a reference site in toxicology studies (Moreira et al. 2006; Guimarães et al. 2012). The Minho Estuary has also a significant history of biological invasions (Sousa et al. 2008, 2013; Ilarri et al. 2014), nevertheless, the number of invasive species in this area is comparatively lower than in other areas of the Iberian Peninsula (Muñoz-Mas et al. 2021). The Minho Estuary is described as mesotidal, with an average depth of 2.6 meters and a maximum depth of 26 meters (Alves 1997). It is partially mixed, except during flood periods when it tends to exhibit salt wedge conditions (Sousa et al. 2005). During summer or drought events, marine water enters the Lenta Marina as rainfall and water flow decrease (Ferreira et al. 2003). However, despite the occurrence of marine water intrusion, the influence of salinity in the Lenta Marina is relatively small. Salinity values typically range between 0 and 2.0 psu, with higher values observed in the late summer months or during dry periods (Sousa et al. 2013).

Fish data

Fish samples were collected from January 2010 to November 2019, even though the samples were generally collected on a weekly basis, the actual intervals between samples varied slightly (Souza et al. 2023). The fyke nets were placed in fixed locations near the entrance of the peninsula where the Lenta Marina is harbored (Fig. 1). Double entry
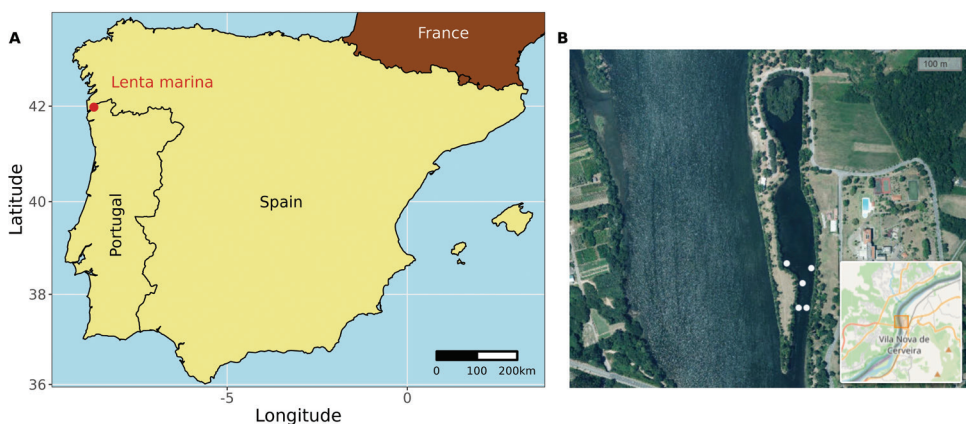

Figure 1. Representation of the study area (Lenta Marina) and sampling locations (Fyke nets) in the Minho estuary **A** map of the Iberian Peninsula showing the sampling site in the Minho estuary **B** an enlarged view of the study area highlighting the precise locations of the fyke nets (white circles) within the Lenta Marina.

fyke nets with a mesh size of 10 mm, measuring 7 meters in length, 0.7 meters in mouth diameter, and equipped with a 3.5 meter central wing, were used for the collection. These nets were always deployed in the morning and remained submerged for an average of 5.7 ± 3.5 days (mean ± SD). Once the fyke nets were retrieved, all captured fish were identified to the lowest taxonomic level and counted. In total, 3029 samples were collected throughout the study period. The average catch per unit effort (CPUE) per sampling date was determined by dividing the number of individuals caught by the number of days each fyke net remained in the water, taking into account the number of replicates per date. On average, 4.9 ± 0.4 fyke nets were used per sampling date, although this number varied due to technical limitations. A more detailed description of the sampling procedure can be found in a previous study by Ilarri et al. (2022).

Trait composition

All fish species sampled in the Minho Estuary from January 2010 to November 2019 (more details in Ilarri et al. 2022) were analyzed according to 20 traits (14 biological and 6 ecological) containing 69 modalities (Appendix 1). The specific trait for each species and/or genera was classified following the information presented in the www.freshwaterecology.info database (see Appendix 2) (Schmidt-Kloiber and Hering 2015), that follows a single category assignment approach for fishes. When the value of any given species and trait was missing, the trait classification was complemented, if possible, with the information present in Cano-Barbacil et al. (2020). When the information of a particular trait modality was missing, NA (not available) was attributed to it, otherwise the values were either zeroes (0) or ones (1). The value used for each trait modality per sample was obtained by the computation of the community-weighted mean (CWM) using the function *dbFD* from the *FD* package in R (Laliberté et al. 2022). The CWM uses the classification of each species into a trait category as previously described and the abundance of species (in our case, CPUE) to compute the values of each modality per sample, which were used for further statistical analysis. In this study, we have compiled the trait composition data from 23 taxa (17 native and 6 non-native) (Table 1).

Functional diversity indices

Six different functional diversity indices that were often used in previous studies (Villéger et al. 2008, van der Linden et al. 2016) to investigate the effects of environmental disturbances were selected. Functional diversity indices were calculated using the information on fish abundances and their traits classification, namely the functional divergence index (FDiv), the functional dispersion index (FDis), the functional richness index (FRic), the functional evenness index (FEve) (Villéger et al. 2008), Rao's quadratic entropy index (FRAO) (Lepš et al. 2006), and the functional redundancy index (FRed) (de Bello et al. 2007). The first five indices (FDiv, FDis, FRic, FEve and FRAO) were computed using the *dbFD* function from the *FD* package in R (Laliberté et al. 2022), while FRed was interpreted as a normed version of the mean functional similarity (Ricotta et al. 2016). The taxonomic index of diversity (Shannon's diversity

Table 1. Origin, family, species, vernacular name, total number of individuals captured (N), first record in the study area (only for the invasive species), and native range (only for the invasive species) of the fishes sampled from January 2010 to November 2019 in the Minho Estuary (Portugal). Fish species are ordered by origin and phylogenetic order (family).

Origin	Family	Species	Vernacular name	N	1st record	Native range
Native	Petromyzontidae	*Petromyzon marinus*	Sea lamprey	12	–	
Native	Anguillidae	*Anguilla anguilla*	European eel	2971	–	
Native	Clupeidae	*Alosa* spp.	Allis and twaite shads	1	–	
Native	Cobitidae	*Cobitis paludica*	Iberian loach	9031	–	
Native	Leuciscidae	*Achondrostoma arcasii*	Panjorca	413	–	
Native	Leuciscidae	*Pseudochondrostoma duriense*	Douro nase	684	–	
Native	Leuciscidae	*Squalius carolitertii*	Iberian chub	20	–	
Native	Salmonidae	*Salmo trutta* subsp. *fario*	Brown trout	162	–	
Native	Salmonidae	*Salmo trutta* subsp. *trutta*	Sea trout	259	–	
Native	Atherinidae	*Atherina boyeri*	Sand smelt	1079	–	
Native	Mugilidae	*Chelon auratus*	Golden grey mullet	51	–	
Native	Mugilidae	*Chelon labrosus*	Thicklip grey mullet	28	–	
Native	Mugilidae	*Chelon ramada*	Thinlip mullet	1581	–	
Native	Mugilidae	*Mugil cephalus*	Flathead grey mullet	167	–	
Native	Gasterosteidae	*Gasterosteus aculeatus*	Three-spined stickleback	1221	–	
Native	Moronidae	*Dicentrarchus labrax*	European seabass	100	–	
Native	Pleuronectidae	*Platichthys flesus*	European flounder	1207	–	
Invasive	Centrarchidae	*Lepomis gibbosus*	Pumpkinseed	47302	2000s (Sousa et al. 2008)	ENA
Invasive	Centrarchidae	*Micropterus salmoides*	Largemouth bass	570	1950s (Antunes 1990)	ENA
Invasive	Tincidae	*Tinca tinca*	Tench	577	1990s (Antunes and Rodrigues 2004)	EUR
Invasive	Gobionidae	*Gobio lozanoi*	Iberian gudgeon	255	1990s (Hervella and Caballero 1999)	IBE
Invasive	Cyprinidae	*Carassius auratus*	Goldfish	20	1950s (Antunes 1990)	ASIA
Invasive	Cyprinidae	*Cyprinus carpio*	Common carp	3146	1990s (Antunes and Rodrigues 2004)	ASIA, EU

ENA = Eastern North America; EUR = Europe; IBE = Iberian Peninsula; ASIA = Eastern Asia

index) was calculated using the function diversity from the vegan package in R (Oksanen et al. 2022).

FDiv refers to how trait categories are distributed among individuals (Mason et al. 2005; Villéger et al. 2008). FDiv is low when the most abundant species have trait categories that are near the center of the trait space and high when the most abundant species have extreme trait categories (Mason et al. 2005). FDis measures the mean distance of the individual species from the center of the trait space occupied by the species, it computes the distance of the species from the mean dissimilarity (Villéger et al. 2008, van der Linden et al. 2016). FRic measures the amount of trait space filled by the species in the community. Typically, lower FRic values are associated with communities with similar traits (van der Linden et al. 2016; Maure et al. 2018). FEve measures the evenness of the distribution of the traits' abundance. It is the highest when there is an even distribution of species and abundance of traits (van der Linden et al. 2016). FRAO is an index that measures the trait dissimilarities in the community (Botta-Dukát 2005) and it is conceptually similar to FDis (Laliberté and Legendre 2010). FRed defines the extent

to which a community is saturated with species that have similar traits, with higher values indicating that the community is functionally redundant, while low values indicate that the functional redundancy in the community is low (de Bello et al. 2007).

Climate data

Climate data used in this study included daily mean air temperature (measured 2 meters above ground level) in °C and precipitation in mm.m^{-2}. These data were scaled down to 1×1° grids and covered the entire duration of the sampling campaign, which ranged from January 2010 to November 2019. Data for the sampled site were obtained from NASA via their application programming interface (API) available through the NASA Langley Research Center (LaRC) POWER Project website. The jsonlite package in R developed by Ooms et al. (2022) was used to process the data.

Two different categories were used for the identification of extreme temperature events: cold spells and heat waves. The daily averages of air temperature were used to detect and determine the duration and strengthen of these extreme weather events. For this purpose, the *detect_event* function from the *heatwaveR* package in R, introduced by Schlegel and Smit (2021), was used. To assign a specific category to each climate extreme event, the category function from the same package was used, following the methodology described by Hobday et al. (2018).

To analyze precipitation patterns, the standard precipitation index (SPI) was calculated. The SPI quantifies the number of standard deviations by which the observed cumulative precipitation deviates from the climatological mean, as described by McKee et al. (1993). The daily precipitation data were processed using the *spi* function from the *precintcon* package (Povoa and Nery 2016). Based on the SPI values, each date was assigned to one of three precipitation state groups: normal (SPI greater than -1 and less than 1), dry (SPI less than -1) or wet (SPI greater than 1).

Data analysis

Generalized additive models (GAM) with Gaussian distributions were used to assess the effects of temperature, precipitation and time on the fish trait means and diversity indices. Prior to analysis, the temperature and precipitation data were scaled (i.e. standardized with a mean of zero and a standard deviation of one) using the *scale* function from the *base* package in R (R Core Team 2023). CPUE values, diversity indices and precipitation data were appropriately transformed when necessary. Square root or log(X + 1) transformations were applied using the *sqrt* and *log1p* functions from the *base* package in R (R Core Team 2023).

For the temperature and precipitation data, cubic regression splines were used to smooth the variables for each season (winter, spring, summer and autumn). This smoothing process was carried out using the function *s* from the package *mcgv* (Wood 2022). The decision to apply smoothing by season was made in view of the different temperature patterns and precipitation profiles observed in each season, which are better captured when the penalty is applied on a seasonal basis.

As the dataset was a time series, the models from GAM included an autocorrelation structure with a lag effect. The initial value for the autocorrelation parameter (rho) was determined by running a GAM model without the autocorrelation structure. The *start_value_rho* function from the *itsadug* package (van Rij et al. 2022) was used to calculate the initial value of rho. Autocorrelation and partial autocorrelation were evaluated using the *acf* and *pacf* functions from the *stats* package in R package (R Core Team 2023). The GAM models were run with the *bam* function from the *mgcv* package (Wood 2022). All data analyses were performed using the R software, version 4.3.1 (R Core Team 2023).

Data availability statement

Data used in this study are available for validation and further investigation. The fish occurrences dataset is archived on Zenodo (doi: 10.5281/zenodo.8279744), and detailed trait classification information can be found in Appendix 2. Climate data were sourced from the NASA using an API and a copy of the raw data and its description can be found in Suppl. material 1.

Results

Fish assemblage trait composition all over the years

Of the 67 fish traits modalities observed, 65.7% have varied significantly over time (Table 2). Temperature had correlated more strongly with trait modalities than precipitation, 59.7% of the traits modalities responded significantly to temperature, while 23.9% responded significantly to precipitation (Table 2). In addition, temperature correlated to the traits' modalities mostly during winter (59.7%) and autumn (46.3%). Precipitation influenced the trait modalities in a similar pattern, with winter (23.9%) and autumn (16.4%) having greater correlations than summer (7.5%) and spring (0%) (Table 2). Of the 67 GAM models for each trait modality, 19 had a percentage of explanation higher than 50% (Table 2, Fig. 2).

Traits' composition associated with the invasive and native species

There were some traits' modalities that were more frequently associated with the native species, such as Diadromous (Migration), Litophilic and Other (Reproduction habitat), Freshwater-brackish-marine (Salinity), >=39 (Body length), Sh3 (Shape factor) and Winter time (Spawn time) (Fig. 3). On the other hand, it was also observed that other traits modalities were more frequently associated with invasive species such as Potamodromous (Migration), Benthopelagic (Habitat), Phytophilic and Phyto-litophilic (Reproduction habitat), Freshwater and Freshwater-brackish (Salinity), >15 (Life span), Sh1 (Shape factor), Sw3 (Swimming factor), 3–4 (Female maturity), Summer time (Spawn time), <=7 (Incubation period), 55k–60k

Table 2. Results of GAM models made to evaluate the effects of temperature, precipitation, and time on the fish assemblage trait composition of the Minho Estuary (Portugal). Statistical significance at: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Win = winter, Spr = spring, Sum = summer, and Aut = autumn. The description of all modalities and their units can be found in Appendix 1.

Trait	Modality	Temperature				Precipitation				Time	% exp.	r² adj.
		Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	F		
Migration	Nom (No migration)	0.76	0.05	1.74	0.73	0.60	0.05	3.41**	5.80***	-4.39***	15	0.124
	Oce (Oceanodromous)	2.25	3.69*	1.79	0.97	0.00	1.66	1.41	0.01	-1.55	4.6	0.028
	Pot (Potamodromous)	3.57**	0.42	1.63	2.59	1.79	0.00	0.03	4.06*	10.64***	58.3	0.572
	Dia (Diadromous)	4.09**	0.12	2.43	8.93**	0.75	0.52	0.06	1.41	-4.07***	28.7	0.27
Habitat	Ben (Benthopelagic)	6.97***	0.26	1.07	10.86***	0.38	0.62	0.13	0.43	1.64	22.6	0.211
	Dem (Demersal)	3.54*	1.34	0.31	6.67**	1.23	0.18	0.08	0.08	-2.7**	12.9	0.112
	Pel (Pelagic)	12.15***	1.54	1.06	4.20*	6.10***	0.42	0.01	0.23	2.48*	24.5	0.223
Rheophily	Lim (Limnophilic)	9.53**	0.16	1.17	2.74*	1.04	0.84	0.28	0.55	1.81	11.8	0.104
	Eur (Eurytopic)	4.42**	0.17	1.37	6.18*	1.64	0.82	0.23	0.64	0.06	12.1	0.097
	Rhe (Rheophilic)	0.50	0.28	1.52	0.63	0.05	0.00	0.18	0.26	-6.95***	15.9	0.144
Feeding habitat	Benthivorous	3.21*	3.68	0.40	1.34	1.73	0.71	0.83	1.37	-10.93***	49.3	0.48
	Water column	3.01*	4.39*	0.26	1.24	1.39	0.61	0.80	1.26	10.81***	50.8	0.496
Reproduction habitat	Phy (Phytophilic)	3.23*	0.44	0.95	4.63*	13.99***	0.03	1.06	1.47	-1.88	11.1	0.091
	Lit (Litophilic)	2.64	0.07	1.53	2.59	0.03	0.24	0.09	0.30	-5.09***	14.5	0.13
	Phy (Phyto-litophilic)	2.23	2.62	0.61	5.18*	1.10	0.00	0.91	0.69	12.31***	61.8	0.61
	Psa (Psammophilic)	0.27	0.07	1.33	1.12	0.02	1.18	0.05	0.29	-4.64***	10.8	0.091
	Oth (Other)	1.72	1.53	2.68	5.03*	2.42	0.13	0.21	0.12	-4.81***	12.9	0.114
Salinity	Fre (Freshwater)	3.64*	0.00	3.11	7.95**	0.02	1.35	0.46	0.23	3.81***	23.8	0.222
	Frb (Freshwater-brackish)	0.32	0.59	0.06	0.63	3.44	0.08	1.39	3.62*	-1.53	2.4	0.004
	Fbm (Freshwater-brackish-marine)	9.01***	0.01	3.18*	12.22**	2.18*	0.18	0.01	0.29	-3.51***	29.9	0.28
	Fma (Freshwater-marine)	1.31	1.23	0.97	0.03	0.01	1.63	0.05	1.17	-0.40	3.0	0.014
	Brm (Brackish-marine)	0.00	0.07	1.30	7.23***	2.04	0.00	0.00	3.81***	-1.72	14.3	0.117
Feeding diet	Car (Carnivorous)	0.78	1.23	1.33	2.82	1.17	0.47	0.01	2.96*	-3.75***	10.4	0.088
	Inv (Invertivorous)	1.37	1.26	0.18	0.26	0.40	0.68	0.15	0.00	13.44***	58.5	0.577
	Omn (Omnivorous)	0.06	3.28	1.16	0.22	0.04	1.77	0.11	1.11	-11.77***	51.5	0.506
	Oth (Other)	3.42**	0.09	0.01	0.00	1.67	0.04	0.02	0.00	-1.73	4.4	0.023
Life span	<8	2.75*	2.04	1.18	0.00	5.34*	0.51	0.17	0.38	-15.91***	66.7	0.658
	8–15	4.01**	1.40	0.72	3.94*	9.80**	0.08	0.84	0.98	16.63***	70.5	0.699
	>15	0.08	0.05	0.61	5.44*	0.24	0.33	0.32	1.73	-1.06	3.40	0.017
Body length	<=20	3.37	0.13	0.05	1.59	0.84	1.42	0.49	0.99	2.74**	10.6	0.09
	20–39	6.66***	0.96	1.74	0.90	2.20*	1.45	3.84***	4.71*	-2.61**	12.2	0.088
	>=39	1.07	0.23	0.71	7.70**	0.24	0.12	0.30	2.02	-1.31	5.3	0.037
Body shape	Sh1 (<= 4.35)	4.21**	0.63	2.44	7.19**	0.94	0.03	0.77	1.03	11.29***	58.8	0.577
	Sh2 (4.35–4.78)	2.25	3.69*	1.79	0.97	0.00	1.66	1.41	0.01	-1.55	4.6	0.028
	Sh3 (4.78–5.6)	14.07***	2.32	4.61**	4.38	3.32**	1.40	0.09	0.28	-3.34***	32.9	0.309
	Sh4 (>=5.6)	3.44*	1.06	3.18	9.67**	4.18*	0.29	0.06	0.14	-1.82	11.9	0.103

Trait	Modality	Temperature				Precipitation				Time	% exp.	r² adj.
		Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	F		
Swimming factor	Sw1 (Fast swimmer)	0.20	4.06***	5.07**	0.41	0.08	2.02	0.02	0.86	-8.97***	30.0	0.283
	Sw2 (Average swimmer)	13.89***	0.96	3.71	8.69**	0.94	0.15	0.15	0.86	-0.26	26.6	0.251
	Sw3 (Slow swimmer)	9.05***	3.48*	1.69	3.03	3.29	0.02	0.03	0.33	17.84***	69.7	0.69
Female maturity	<=2	4.00**	2.57	3.49*	0.00	5.75*	1.07	2.09*	0.00	-16.68***	66.5	0.655
	2–3	2.69*	0.01	6.84***	0.80	0.27	0.13	7.01***	1.22	-4.17***	19.0	0.162
	3–4	0.16	0.48	0.01	0.94	2.03	0.03	0.64	2.29	-0.63	1.1	-0.006
	4–5	4.12**	1.37	0.00	1.53	9.21**	0.15	0.62	2.34	14.62***	70.7	0.7
	>=5	0.60	1.43	3.06	9.03**	0.40	0.41	0.13	0.33	-1.72	6.7	0.051
Spawn time	Winter time	3.23*	3.61	0.35	2.16	2.85*	1.56	0.01	0.71	-10.24***	51.1	0.499
	Summer time	3.30**	3.53	0.37	1.86	4.01*	1.41	0.03	1.31	10.12***	53.8	0.528
Incubation period	<=7	4.72***	3.41	1.54	5.37*	2.26	0.94	0.18	0.68	10.04***	55.0	0.538
	7–14	3.42**	0.09	0.01	0.00	1.67	0.04	0.02	0.00	-1.73	4.4	0.023
	>14	10.69***	1.68	2.01	1.87	5.35***	0.75	0.03	0.01	0.72	24.1	0.219
Fecundity	<=55k	2.70*	1.98	1.35	0.01	4.57*	0.52	0.27	0.36	-16.74***	67.7	0.668
	55k-60k	1.31	2.27	0.55	3.87	0.56	0.00	0.92	0.78	12.18***	60.3	0.595
	>60k	0.02	0.03	0.01	4.09*	0.06	0.44	0.93	0.91	-1.30	3.5	0.018
Relative fecundity	>=57	0.44	0.03	1.32	0.20	0.13	0.02	1.82	4.80**	-4.71***	14.0	0.12
	57–200	0.14	0.90	0.27	0.38	1.83	0.06	1.43	3.67**	-0.99	1.6	-0.008
	>200	4.70***	0.72	4.85*	4.68*	4.29***	1.36	0.06	0.25	-1.45	18.8	0.165
Egg diameter	<1.35	7.35***	0.80	3.21	4.54*	1.98	0.12	0.30	0.60	6.05***	29.5	0.282
	1.35–2	2.03	0.05	3.47	1.39	11.80***	0.15	0.50	2.79*	-6.98***	25.9	0.244
	>2	6.37***	0.16	3.49	9.91**	0.26	0.06	0.21	0.06	-5.23***	21.4	0.199
Larval length	<=4.2	9.93***	8.81**	0.29	2.23	3.68	0.38	0.45	1.47	15.6***	64.3	0.636
	4.2–6.3	0.30	1.04	0.04	0.22	3.10	0.00	2.03	3.78**	-1.46	2.1	0.001
	>6.3	6.31***	0.16	3.51	9.94**	0.26	0.06	0.21	0.18	-5.26***	21.5	0.199
Parental care	Phn (Protection with nester or eggs hiders)	3.44*	4.61*	0.20	4.44*	1.92	0.99	0.98	0.60	10.65***	57.0	0.561
	Nnh (No protection with nester or eggs riders)	6.99***	0.13	3.88*	10.26**	0.26	0.08	0.18	0.06	-5.42***	22.0	0.205
	Nop (No protection)	9.37**	0.01	0.64	6.35*	0.42	1.15	1.01	0.59	-0.93	11.7	0.099
Larval stage duration	<12	0.17	0.50	2.14	0.02	2.60	0.14	2.29*	5.78***	-2.09*	6.1	0.032
	12–25	2.02	2.66	0.12	2.02	1.50	0.01	0.76	2.05	11.86***	63.0	0.62
	>25	7.27***	0.28	1.25	5.37*	0.78	0.06	0.31	0.02	-5.31***	14.0	0.123

(Fecundidty), 57–200 (Relative fecundity), <1.35 and 1.35–2 (Egg diameter), <=4.2 and 4.2–6.3 (Larval length), Nop (No protection) (Parental care) and <12 (Larval stage duration) (Fig. 3).

Extreme weather events

Over the study period, there were 52 extreme temperature events (19 heatwaves: 9 moderate and 10 strong; 33 cold-spells: 32 moderate and 1 strong), and 44 extreme
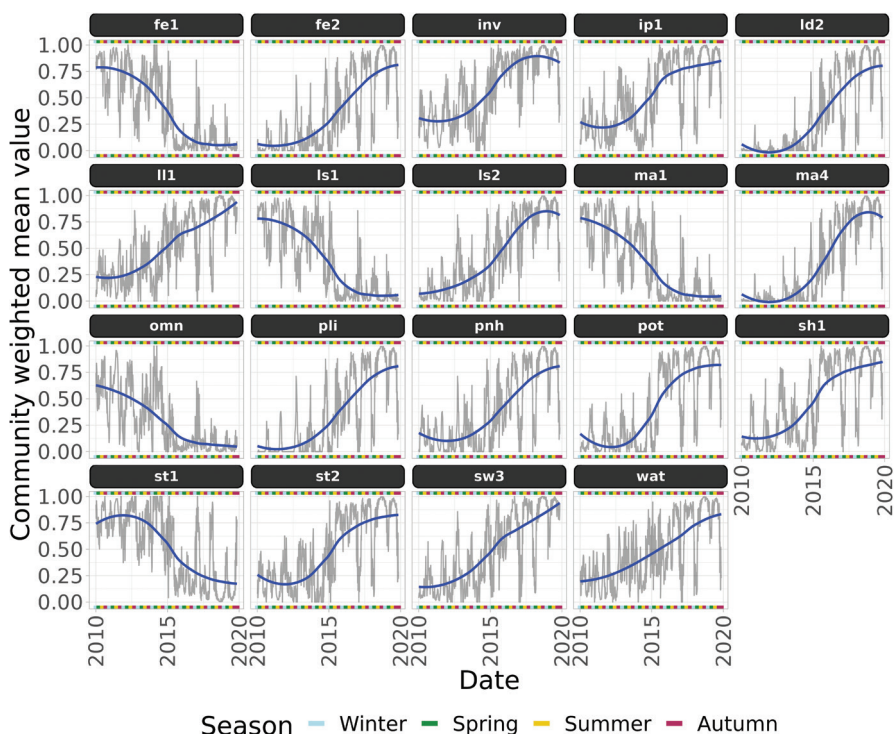
Figure 2. Selection of fish trait modalities in the Minho Estuary (Portugal) that had strong temporal changes (selected by the highest % of variation). Blue lines refer to a simple moving regression (loess) and are only indicative of the temporal changes. Statistical tests can be found in Table 2. fe1 = number of oocites less or equal to 55000, fe2 = number of oocites between 55000 and 60000, inv = invertivorous (feed on invertebrates), ip1 = incubation period is less or equal to seven days, ld2 = larval stage duration between 12 and 25 days, ll1 = larval length is smaller or equal to 4.2 cm, ls1 = life span is less than eight years, ls2 = life span is between eight and fifteen years, ma1 = females are mature before two years, ma4 = females are mature between four and five years, omn = omnivorous (feed on animals and plants), pli = reproduction habitat is phyto-litophilic (associated with plants and rocks), pnh = parental care by protection with nesting or egg hiding, pot = potamodromous migration (between different freshwater bodies), sh1 = shape factor ratio is smaller or equal to 4.35 (compact, rounded body shape), st1 = spawn time is during winter, st2 = spawn time is during summer, sw3 = slow swimmer, wat = feeding habitat is in the water column. The description of all modalities and their units can be found in Appendix 1.

precipitation events (21 dry and 23 wet) in the area of the Minho Estuary sampled. For more details see Ilarri et al. (2022).

The moderate heatwave events correlated positively and negatively with some trait modalities, and of these, only 1.5% of the traits had a strong decrease in their mean value during these kind of extreme events (e.g., Salinity: Brackish-marine, decrease of 100%), and about 4.5% had a strong increase (Migration: Oceanodromous, increase of 316%; Shape factor: 4.35–4.78, increase of 316%; Reproduction habitat: Psammophilic, increase of 117%) (Table 3).
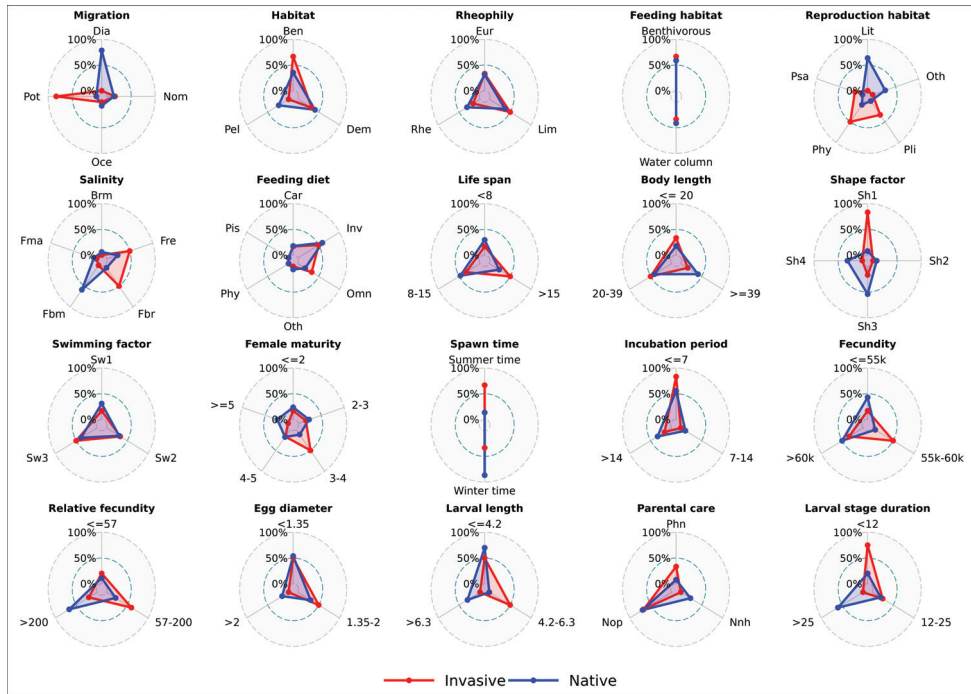
Figure 3. Comparison between invasive and native fish species at the Minho Estuary (Portugal) on the average score of each trait modality. The description of all modalities and their units can be found in Appendix 1.

Regarding the strong heatwave events, 31.3% of the traits had a strong decrease during these events (e.g., Egg diameter: >2, decrease of 100%; Habitat: Pelagic, decrease of 100%), and 4.5% had a strong increase (e.g., Migration: Oceanodromous, increase of 291%; Shape factor: 4.35–4.78, increase of 291%) (Table 3).

Over 6% of the traits had a strong decrease in their values during moderate cold-spells' events (e.g., Incubation period: 7–14, decrease of 100%; Salinity: Brackish-marine, decrease of 100%), while about 4.5% of the trait modalities had a strong increase during these extreme events (Migration: Oceanodromous, increase of 450%; Shape factor: 4.35–4.78, increase of 450%) (Table 3).

During the dry events recorded in the Minho Estuary between 2010 and 2019, there was no trait negatively affected by more than >=70.01% of their mean value (Table 3). Only 4.5% of the trait modalities experienced a strong increase in their mean value (e.g., Incubation period: 7–14, increase of 139%; Feeding diet: Other, increase of 139%; Salinity: Brackish-marine, increase of 96%) during dry events (Table 3).

On the other hand, the wet events contributed to strong decreases, 10.4% of the trait modalities were negatively influenced (e.g. Incubation period: 7–14, decrease of 100%; Feeding diet: Other, decrease of 100%) (Table 3). On the other hand, there was no trait positively affected by more than >=70.01% of their mean value during the wet events (Table 3).

Table 3. Categorical representation of the influence of the extreme climatic events (temperature heatwaves: moderate and strong, and temperature cold-spells: moderate; precipitation: dry and wet) on the traits modalities of the fish assemblage of the Minho Estuary (Portugal). The traits classification was made considering the traits mean values per event. Classification as: 0 refers to change of ±10% in the traits mean values during the event compared to the mean values during the normal conditions; + refers to an increase in the traits mean values from 10.01 to 40%; ++ refers to an increase in the traits mean values from 40.01 to 70% , +++ refers to an increase in the traits mean values abundance >= 70.01%; - refers to a decrease in the traits mean values from 10.01 to 40%; -- refers to a decrease in the traits mean values from 40.01 to 70% , --- refers to a decrease in the traits mean values >= 70.01%. The description of all modalities can be found in Appendix 1.

Trait	Modality	Temperature			Precipitation	
		Heatwave		Cold-spells	Dry	Wet
		Moderate	Strong	Moderate		
Migration	Nom (No migration)	--	---	+	-	++
	Oce (Oceanodromous)	+++	+++	+++	--	---
	Pot (Potamodromous)	+	++	0	0	+
	Dia (Diadromous)	-	---	-	0	-
Habitat	Ben (Benthopelagic)	0	+	0	0	0
	Dem (Demersal)	-	--	0	0	0
	Pel (Pelagic)	++	---	--	+	---
Rheophily	Lim (Limnophilic)	0	+	0	0	0
	Eur (Eurytopic)	+	--	0	-	0
	Rhe (Rheophilic)	0	-	-	0	0
Feeding habitat	Benthivorous	0	-	0	0	-
	Water column	0	+	0	0	0
Reproduction habitat	Phy (Phytophilic)	+	--	-	-	0
	Lit (Litophilic)	-	-	+	0	0
	Phy (Phyto-litophilic)	+	++	0	0	+
	Psa (Psammophilic)	+++	---	---	++	---
	Oth (Other)	-	--	0	-	+
Salinity	Fre (Freshwater)	0	+	0	0	0
	Frb (Freshwater-brackish)	++	-	+	-	+
	Fbm (Freshwater-brackish-marine)	-	---	-	0	-
	Fma (Freshwater-marine)	-	---	0	+	---
	Brm (Brackish-marine)	---	---	---	+++	+
Feeding diet	Car (Carnivorous)	-	---	+	0	++
	Inv (Invertivorous)	+	+	0	0	0
	Omn (Omnivorous)	-	0	0	+	-
	Oth (Other)	--	---	---	+++	---
Life span	<8	-	-	-	0	-
	8–15	+	++	0	0	0
	>15	+	--	+	0	+
Body length	<=20	0	+	0	0	0
	20–39	0	--	0	0	-
	>=39	+	--	+	0	++
Body shape	Sh1 (<= 4.35)	+	++	+	0	+
	Sh2 (4.35–4.78)	+++	+++	+++	--	---
	Sh3 (4.78–5.6)	0	---	--	0	--
	Sh4 (>=5.6)	-	---	0	0	+
Swimming factor	Sw1 (Fast swimmer)	-	---	--	-	--
	Sw2 (Average swimmer)	+	---	-	-	-
	Sw3 (Slow swimmer)	+	++	+	0	+

Trait	Modality	Temperature			Precipitation	
		Heatwave		Cold-spells	Dry	Wet
		Moderate	Strong	Moderate		
Female maturity	<=2	-	--	-	+	-
	2–3	-	-	+	-	0
	3–4	++	-	+	-	+
	4–5	+	++	0	0	0
	>=5	-	--	+	0	++
Spawn time	Winter time	-	-	0	0	-
	Summer time	+	+	0	0	+
Incubation period	<=7	+	+	0	-	+
	7–14	--	---	---	+++	---
	>14	++	---	--	+	--
Fecundity	<=55k	-	-	-	0	-
	55k–60k	+	++	0	0	+
	>60k	+	-	+	-	+
Relative fecundity	>=57	--	---	++	0	+
	57–200	++	-	0	-	+
	>200	0	---	-	0	-
Egg diameter	<1.35	0	+	0	0	0
	1.35–2	-	---	0	-	0
	>2	-	---	-	+	+
Larval length	<=4.2	0	+	0	0	+
	4.2–6.3	++	-	0	-	+
	>6.3	-	---	-	+	+
Parental care	Phn (Protection with nester or eggs hiders)	0	++	0	0	+
	Nnh (No protection with nester or eggs hiders)	-	---	-	+	+
	Nop (No protection)	+	--	0	0	0
Larval stage duration	<12	+	-	+	-	+
	12–25	+	+++	0	0	+
	>25	+	-	+++	+	-

Taxonomic composition and functional metrics of the fish assemblage

Over the years, there was a significant reduction in the number of native species, a significant increase in the number of invasive species, and a significant decrease in the taxonomic diversity of the fish community of the Minho Estuary. Significant changes in the functional diversity indices were also recorded for all indices calculated. FDiv, FDis, FEve, FRic, and FRAO decreased significantly through time, while FRed have increased over the years (Fig. 4, Table 4).

Discussion

We have been monitoring the fish populations in the Minho Estuary for over a decade to better understand the effects of changing environmental conditions on biodiversity. During this period, we have observed signs of decline in both taxonomic and functional diversities, which seems to correspond to a decreasing number of native species and an increasing prevalence of invasive species. This phenomenon seems to be further influenced by changes in environmental factors such as temperature and precipitation,
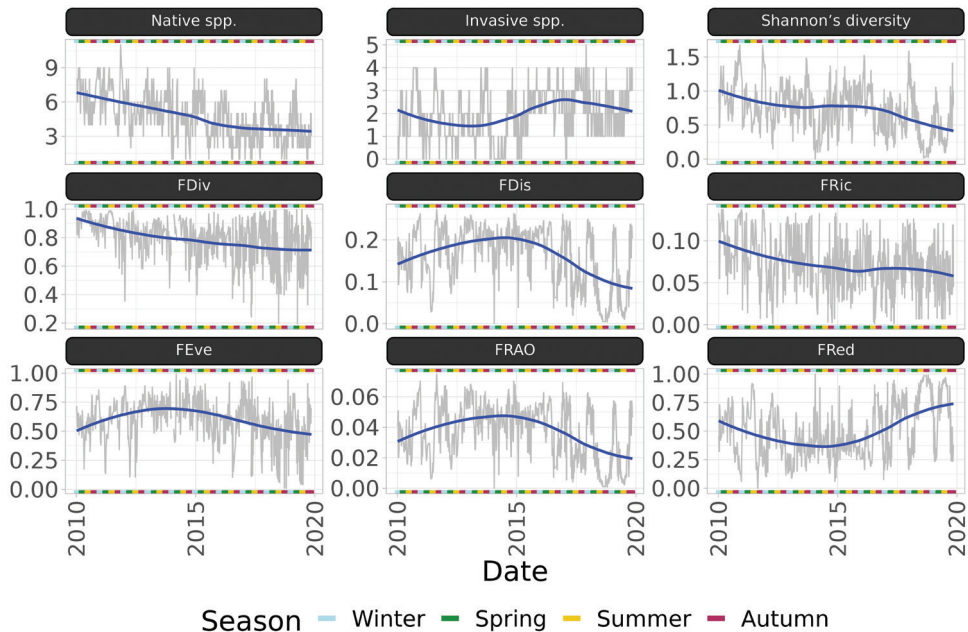
Figure 4. Dynamics of the number of native and invasive species, taxonomic diversity (Shannon's diversity) and six functional diversity indices (FDiv, FDis, FRic, FEve, FRAO and FRed) computed with weekly data on the fish captured by fyke nets in Minho Estuary (Portugal) from 2010 and 2019. Blue lines refer to a simple moving regression (loess) and are only indicative of the temporal changes. Statistical tests can be found in Table 4. FDiv = functional divergence, FDis = functional dispersion, FRic = functional richness, FEve = functional evenness, FRAO = Rao's quadratic entropy and FRed = functional redundancy.

which appear to impact several key trait characteristics of these fishes. Overall, there has been a significant shift in fish assemblage occurring in this estuary over the past decade, which now has an almost equal contribution of native and invasive species in terms of species richness, whereas the latter dominate in terms of abundance (Ilarri et al. 2022).

Over the past few years, the Minho Estuary has witnessed a significant increase in populations of invasive species (Sousa et al. 2013; Ilarri et al. 2022). The pumpkinseed, in particular, common carp, and tench are three species that have flourished in the estuary since 2015–2016 (Ilarri et al. 2022), and their increase is likely due to changes in the prevalent environmental conditions. Cano-Barbacil et al. (2022) and Bae et al. (2018) propose temperature as a central factor in explaining the spread of invasive species in the Iberian Peninsula. They emphasize this proposition by pointing out the strong correlation between temperature and thermophilic characteristics of most invasive species, as those from the aforementioned species. Additionally, the pumpkinseed, common carp, and tench prefer slow currents (Benito et al. 2015; Avlijaš et al. 2018; Lages et al. 2021) and highly vegetated zones (Penne and Pierce 2008; Top et al. 2016; Avlijaš et al. 2018), which are likely to become more prevalent with changes in temperature (increase) and rainfall regime (decrease) over time. These three species are also potamodromous, meaning that they perform migrations in the river. In addition,

Table 4. Summary of the GAM models with the functional diversity indices calculated with the fish abundances from the Minho Estuary (Portugal) and temperature, precipitation and time. Statistical significance at: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. FDiv = functional divergence index, FDis = functional dispersion index, FRic = functional richness index, FEve = functional evenness index, FRAO = Rao's quadratic entropy index, FRed = functional redundancy index, Win = winter, Spr = spring, Sum = summer, and Aut = autumn.

Index	Temperature				Precipitation				Time	% exp	r² adj
	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	F		
# of native species	10.32***	1.64	2.46	20.80***	3.01*	2.28	6.14*	1.87	-11.23***	38.8	0.374
# of invasive species	1.02	1.65	4.24*	0.70	2.76*	0.89	0.04	2.16	4.44***	13.1	0.113
Shannon diversity	2.55	0.70	0.13	0.98	2.38*	0.01	1.60	0.81	-4.25***	18.0	0.170
FDiv	1.28	1.41	3.19	0.81	1.08	0.06	0.03	0.32	-8.10***	16.3	0.147
FDis	2.89*	0.63	0.54	0.33	5.84***	0.67	0.70	0.00	-5.08***	23.9	0.221
FRic	1.29	1.09	0.52	11.85**	0.02	0.03	0.52	0.93	-5.26***	11.8	0.102
FEve	2.55	1.67	0.15	6.05*	0.51	1.52	3.04	0.03	-3.85***	10.8	0.093
FRAO	3.56*	0.87	0.98	0.83	6.52***	0.94	0.52	0.00	-4.99***	22.5	0.206
FRed	3.96**	0.14	0.48	0.68	5.65***	0.52	0.47	0.05	4.37***	20.2	0.183

they are either phytophilic or phyto-litophilic species, reproducing in areas rich in submerged vegetation and rocks. These species are also either eurytopic (common carp) or limnophilic (pumpkinseed and tench), which means that the common carp tolerates a wide range of environmental conditions, while pumpkinseed and tench are associated with slow moving waters. Interestingly, these three species also have the shape 1 classification in terms of body shape (more rounded and compacted body) and are either average (common carp) or slow swimmers (pumpkinseed and tench) (Schmidt-Kloiber and Hering 2015). The traits' characteristics of these three invasive species seem to have been benefited in the Minho Estuary, as the decrease in precipitation and drought events have contributed to reduced river inflow and water currents in the system. Haubrock et al. (2021) also observed a significant increase over time in short-bodied species with high body depth (shape factor 1) on the Arno River (Italy). According to Vila-Gispert et al. (2005), this trait modality can be advantageous when competing with native species in slow-flow waters. On the other hand, the lower river inflow and water currents are not good for many native species with elongated body shapes that are more associated with fast-flowing waters (rheophilic) and oceanodromous or diadromous migration modalities, such as eel, shad, three-spinned stickleback, European seabass and sea trout. These species have declined sharply over time (Ilarri et al. 2022), and the traits associated with them are also disappearing from the system.

Interestingly, there was a decline in FRic, and an increase in FRed. This suggests that the fish assemblage is losing some traits and that the invasive species are not able to replace the losses of these traits. This is somewhat expected, as invasive species usually differ from native species in their life-history and ecological traits (Vila-Gispert et al. 2005). However, for the vast majority of traits analyzed in the present study, invasive species had very similar modalities to native species, with an important exception of a few traits. One of the most striking differences is probably observed in migration, where the native species have a good amount of diadromous species and almost all

invasive species are potamodromous. This result highlights that climate change is indeed seriously threatening diadromous species (Limburg and Waldman 2009; Mota et al. 2016; Braga et al. 2022; de Eyto et al. 2022), putting additional pressure on this group, which is already heavily impacted (Barbarossa et al. 2020; Duarte et al. 2021; Podda et al. 2022). For diadromous species in the Minho River, in addition to climate change, additional factors such as an increasing number of dams have exacerbated their decline. The work of Azeiteiro et al. (2021) highlights a notable reduction in Allis shad populations due to the increased dam count in the river. The decline of these species is further evident in the significant shift in trait modalities related to salinity preference. In particular, our results show a decline in species that prefer marine and brackish waters, accompanied by a replacement by species that prefer freshwater environments. It is widely reported that climate change may favor marine and brackish water species in this estuary, at least in the near-term (Souza et al. 2018, 2022a). However, this may not be true for all species, as observed in this study. The sampled area is in the upper part of the estuary, where the saline intrusion is historically not so strong, ranging from 0–2.0 psu during late summer month or droughts period (Souza et al. 2013). Despite the decrease in the river inflow and the precipitation regime, it looks like that the saline intrusion is not affecting much the upper estuary, with the exception of European seabass, which in some years can reach the upper parts of the river in summer due to higher saline intrusion (Ilarri et al. 2022). On the contrary, the change in hydrologic conditions seems to favor freshwater species that prefer slow currents or standing waters (limnophilic or eurytopic), which are also invasive (common carp, goldfish, largemouth bass, pumpkinseed, and tench). This might be explained by the decreased hydrodynamics in the area, which started to attract species with affinity to slow moving freshwater.

Another important divergence in trait modality composition between native and invasive species is in the reproduction habitat. Redundancy in this trait is low, with native species preferring to spawn in rocky areas (litophilic species), while invasive species are more associated to densely vegetated areas (phytophilic species) with some rocky bottoms (phyto-litophilic) or in sandy areas (psammophilic species). The decreased rainfall and river inflow probably contributed to the growth of submerged vegetation and the accumulation of finer substrate (sand) in the area. These conditions are also likely behind the invasion success of the aquatic plant *Egeria densa* in the Minho Estuary, which became very abundant after 2015 (authors' personal observation). A change in the phenology of fish species was also observed. Previously, most species had a spawning season associated with the winter season, but with the increase of invasive species in the area, there has been a change in this trait with an increase in the occurrence of species that have a summer spawning season. Fujiwara et al. (2022) also observed an increasing pattern in non-winter spawners and a decreasing trend in winter spawners when analyzing the temporal patterns of estuarine fish communities from the northwestern Gulf of Mexico. Along with the increase in summer spawning species, a reduction in the incubation period (increase in modality less or equal to seven days) was also a feature introduced by the invasive species now present in the area.

Another trait that showed important divergence between native and invasive species is the life span, with native species having a shorter life span than invasive species. This result is interesting as it is largely recognized that successful invasive species have short life spans (e.g. Jaspers et al. 2018), but this may be different for freshwater fish species in the Iberian Peninsula (e. g. Vila-Gispert et al. 2005). In this region, many of the invasive aquatic organisms arrived several centuries ago and were influenced in the past by the wishes of the rulers of society (monarchs), who deliberately introduced species from Central Europe (Clavero 2022). This important remark is necessary because the characteristics of the traits of the invasive species currently found in the studied system may not be initially selected by the environment, but by men attempting to create an ecosystem similar to that observed in Central Europe. Of the invasive fish species recorded in our study, two originate from North America (largemouth bass and pumpkinseed), while the common carp, goldfish, and tench originate from Eurasia, and the Iberian gudgeon is native to other areas of the Iberian Peninsula but not to the Minho Estuary. Another noteworthy aspect regarding invasive species in the Minho Estuary is that a significant proportion of them consists of species targeted by recreational fisheries, which, usually have different traits when compared with their native counterparts. The introduction of these species follows a meticulous selection by humans aimed at propagating certain desirable traits for angling activities, notably larger body size and a wide ecological tolerance (Alcaraz et al. 2005; Grabowska and Przybylski 2015). Unfortunately, the illegal introduction of species targeted by recreational fishermen in the Iberian Peninsula is still a problem (Clavero and Hermoso 2011).

The traits of fish species are influenced by environmental conditions and are therefore good predictors of how fish species will respond to different climate change events (Winemiller and Rose 1992; Dahlke et al. 2020). The effects of extreme weather events on fish species varies from species to species, probably related to the sensitivity of each species to the type and intensity of the event. Overall, extreme weather events had mostly strong negative effects on fish traits modalities than positive ones (i.e. decreases on the values of trait modalities were more frequent than increases). In our study, heatwaves had the greatest impact on traits compared to the other extreme events. Indeed, Barbarossa et al. (2021) suggest that increases in water temperature constitute a larger threat to freshwater fishes than changes in high and low flow conditions. The heatwaves caused a decline in trait modalities associated with higher salinity preference, reproduction in sandy habitats (Psammophilic), longer body (species with higher shape factors), average and fast swimmers, longer incubation period, low fecundity, high egg diameter, and longer larval length. On the other hand, it was observed a total benefit for short-bodied species. Our results are in part corroborated by Fujiwara et al. (2022), that suggested that fish species sensitive to changes in temperature, generally have traits associated with longer generation time, maximum length and length at maturity. In our study, traits associated with these aspects negatively responded to extreme temperature events. Interestingly, these trait modalities were also negatively correlated with the long-term effects of temperature. Therefore, the heatwave events (especially the strong ones) are possibly accelerating the speed of change in the fish community in Minho Estuary.

Regarding extreme precipitation weather events, both dry and wet events can be critical in estuarine ecosystems due to the hydrological dynamics of these systems. Although the extreme dry events correlated with a large number of species (Ilarri et al. 2022), these events seem to have a broad effect on the whole fish community, with fish traits benefiting more than being negatively affected (mainly considering cases where there was a change in abundance ≥ 70.01%). This result differs from our expectations, as we expected that these conditions have mainly negative impacts on the fish functional diversity. Normally, extreme dry events are associated with an increase in salinity and changes in other water biochemical properties (Martinho et al. 2007; Kinard et al. 2021). In this case, salinity and water quality act as abiotic filters in the fish assemblage and select fishes with traits better adapted to harsh conditions (Kinard et al. 2021). Overall, drought events were linked to an increase in the abundance of trait modalities associated with the marine environment (brackish-marine), which was expected as the decreasing water flow can lead to stronger saltwater intrusion into the upper parts of the estuary. Drought events also positively correlated with some traits modalities related to reproduction, such as incubation period, egg diameter and larval length. The favored modalities are not in the extremes of the ranges of the traits, suggesting that they might be indicative of moderate and stable environments, which also suggested that drought events probably did not cause severe stress to the fishes in Minho Estuary. On the other hand, the extreme wet events, despite of affecting a lower number of species than the extreme dry events (see Ilarri et al. 2022), they affect negatively several trait modalities. This result was also different than expected, as areas with more precipitation are normally expected to create more stable conditions than areas submitted to dry conditions. In this sense, wet events can be expected to affect the extreme modalities of traits, and to favor the moderate modalities of traits, which was not the case for several traits in this study. The extreme wet events were mostly linked to a decline in traits associated with the marine environment, such as oceanodromous and freshwater-marine modalities, which makes sense given the lower saline influence under this condition. Other traits' modalities that were negatively correlated were pelagic, psammophilic, shape 2 and incubation period of 7–14 (intermediary modality).

Some studies indicate that changes in functional diversity are easier to detect than changes in taxonomic diversity and serve as early warning signals for threatened ecosystems. However, in this study it was possible to see the same signal in both metrics, suggesting that in the Minho Estuary the deterioration of taxonomic and functional diversity occurred simultaneously. Each functional diversity index provided a different perspective on the functional change that is occurring in the system. For example, the decrease in the FDiv index indicates that some of the most abundant species in the system nowadays have highly convergent characteristics, while FDis, FRic and FRAO tell more or less the same story, namely that the fish assemblage is losing trait richness and diversity, and particularly rapidly after 2015, a period when the dominance of a few invasive species increased significantly. The FRed index, which is a potential early warning indicator of increasing disturbances in the system (van der Linden et al. 2016), shows that the fish assemblage is becoming more functionally redundant. This

result may indicate two different things: first, that some traits that were present, but not dominant are being lost; and second, that the remaining traits are more similar to each other, which may provide some resilience to the assemblage in terms of functional stability (van der Linden et al. 2016).

Conclusion

The findings of this study demonstrate the negative impacts of climate change and extreme weather on fish communities in estuarine ecosystems. The decline in both taxonomic and functional diversity suggests a threat to the overall balance and health of the ecosystem. These changes show no signs of slowing down, highlighting the need for immediate and effective action to mitigate environmental damage caused by climate change. Furthermore, this loss in fish diversity has implications for local cultures and economies that rely on fish as a source of food and income. It is therefore crucial to address climate change before further harm is inflicted on fish communities and the humans they support.

Author contributions statement

Conceptualization: ATS, MI. Data curation: ATS, MI. Formal analysis: ATS, MI. Investigation: ATS, CA, ED, MI. Methodology: ATS, CA, MI. Project administration: CA. Resources: CA. Software: ATS, MI. Validation: ATS, CA, ED, MI. Visualization: ATS, MI. Writing original draft: ATS, MI. Writing, review and editing: CA, ED.

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References

Alan Pounds J, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL, Foster PN, La Marca E, Masters KL, Merino-Viteri A, Puschendorf R, Ron SR, Sánchez-Azofeifa GA, Still CJ, Young BE (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439(7073): 161–167. https://doi.org/10.1038/nature04246

Alcaraz C, Vila-Gispert A, García-Berthou E (2005) Profiling invasive fish species: The importance of phylogeny and human use. Diversity & Distributions 11(4): 289–298. https://doi.org/10.1111/j.1366-9516.2005.00170.x

Alves AMC (1997) Causas e processos da dinâmica sedimentar na evolução actual do Litoral do Alto Minho. doctoral Thesis. http://repositorium.sdum.uminho.pt/

Anderson SC, Elsen PR, Hughes BB, Tonietto RK, Bletz MC, Gill DA, Holgerson MA, Kuebbing SE, McDonough MacKenzie C, Meek MH, Veríssimo D (2021) Trends in ecology and conservation over eight decades. Frontiers in Ecology and the Environment 19(5): 274–282. https://doi.org/10.1002/fee.2320

Antunes C (1990) Abundância, distribuição e diversidade da fauna ictiológica do estuário do rio Minho. ICBAS, Porto. Bolsa de Investigação BIC-22/88. Junta Nacional de Investigação Científica e Tecnológica., 80 pp.

Antunes C, Rodrigues H (2004) Guia Natural do Rio Minho – os peixes. Aquamuseu do Rio Minho, 88 pp.

Avlijaš S, Ricciardi A, Mandrak NE (2018) Eurasian tench (*Tinca tinca*): The next Great Lakes invader. Canadian Journal of Fisheries and Aquatic Sciences 75(2): 169–179. https://doi.org/10.1139/cjfas-2017-0171

Azeiteiro UM, Pereira MJ, Soares AMVM, Braga HO, Morgado F, Sousa MC, Dias JM, Antunes C (2021) Dynamics of two anadromous species in a dam intersected river: analysis of two 100-year datasets. Fishes 6(2): 21. https://doi.org/10.3390/fishes6020021

Bae M-J, Murphy CA, García-Berthou E (2018) Temperature and hydrologic alteration predict the spread of invasive Largemouth Bass (*Micropterus salmoides*). The Science of the Total Environment 639: 58–66. https://doi.org/10.1016/j.scitotenv.2018.05.001

Barbarossa V, Schmitt RJP, Huijbregts MAJ, Zarfl C, King H, Schipper AM (2020) Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. Proceedings of the National Academy of Sciences of the United States of America 117(7): 3648–3655. https://doi.org/10.1073/pnas.1912776117

Barbarossa V, Bosmans J, Wanders N, King H, Bierkens MFP, Huijbregts MAJ, Schipper AM (2021) Threats of global warming to the world's freshwater fishes. Nature Communications 12(1): 1701. https://doi.org/10.1038/s41467-021-21655-w

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Global Change Biology 19(12): 3740–3748. https://doi.org/10.1111/gcb.12344

Benito J, Benejam L, Zamora L, García-Berthou E (2015) Diel cycle and effects of water flow on activity and use of depth by common carp. Transactions of the American Fisheries Society 144(3): 491–501. https://doi.org/10.1080/00028487.2015.1017656

Biggs CR, Yeager LA, Bolser DG, Bonsell C, Dichiera AM, Hou Z, Keyser SR, Khursigara AJ, Lu K, Muth AF, Negrete Jr B, Erisman BE (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11(7): e03184. https://doi.org/10.1002/ecs2.3184

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16(5): 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Braga HO, Bender MG, Oliveira HMF, Pereira MJ, Azeiteiro UM (2022) Fishers' knowledge on historical changes and conservation of Allis shad – *Alosa alosa* (Linnaeus, 1758) in Minho River, Iberian Peninsula. Regional Studies in Marine Science 49: 102094. https://doi.org/10.1016/j.rsma.2021.102094

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48(5): 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cano-Barbacil C, Radinger J, García-Berthou E (2020) Reliability analysis of fish traits reveals discrepancies among databases. Freshwater Biology 65(5): 863–877. https://doi.org/10.1111/fwb.13469

Cano-Barbacil C, Radinger J, García-Berthou E (2022) The importance of seawater tolerance and native status in mediating the distribution of inland fishes. Journal of Biogeography 49(11): 2037–2049. https://doi.org/10.1111/jbi.14493

Cardoso P, Rigal F, Borges PAV, Carvalho JC (2014) A new frontier in biodiversity inventory: A proposal for estimators of phylogenetic and functional diversity. Methods in Ecology and Evolution 5(5): 452–461. https://doi.org/10.1111/2041-210X.12173

Catford JA, Bode M, Tilman D (2018) Introduced species that overcome life history tradeoffs can cause native extinctions. Nature Communications 9(1): 2131. https://doi.org/10.1038/s41467-018-04491-3

Clavero M (2022) The King's aquatic desires: 16th-century fish and crayfish introductions into Spain. Fish and Fisheries 23(6): 1251–1263. https://doi.org/10.1111/faf.12680

Clavero M, Hermoso V (2011) Reservoirs promote the taxonomic homogenization of fish communities within river basins. Biodiversity and Conservation 20(1): 41–57. https://doi.org/10.1007/s10531-010-9945-3

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97(2): 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Dahlke FT, Wohlrab S, Butzin M, Pörtner H-O (2020) Thermal bottlenecks in the life cycle define climate vulnerability of fish. Science 369(6499): 65–70. https://doi.org/10.1126/science.aaz3658

de Bello F, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment of trait composition: An example based on pollinator communities. Community Ecology 8(2): 163–170. https://doi.org/10.1556/ComEc.8.2007.2.3

de Eyto E, Kelly S, Rogan G, French A, Cooney J, Murphy M, Nixon P, Hughes P, Sweeney D, McGinnity P, Dillane M, Poole R (2022) Decadal Trends in the Migration Phenology of Diadromous Fishes Native to the Burrishoole Catchment, Ireland. Frontiers in Ecology and Evolution 10: 915854. https://doi.org/10.3389/fevo.2022.915854

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H (2017) Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. Global Change Biology 23(2): 490–502. https://doi.org/10.1111/gcb.13381

Diagne C, Leroy B, Gozlan RE, Vaissière A-C, Assailly C, Nuninger L, Roiz D, Jourdain F, Jarić I, Courchamp F (2020) InvaCost, a public database of the economic costs of biological invasions worldwide. Scientific Data 7(1): 277. https://doi.org/10.1038/s41597-020-00586-z

Diez JM, D'Antonio CM, Dukes JS, Grosholz ED, Olden JD, Sorte CJ, Blumenthal DM, Bradley BA, Early R, Ibáñez I, Jones SJ, Lawler JJ, Miller LP (2012) Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment 10(5): 249–257. https://doi.org/10.1890/110137

Duarte G, Segurado P, Haidvogl G, Pont D, Ferreira MT, Branco P (2021) Damn those damn dams: Fluvial longitudinal connectivity impairment for European diadromous fish throughout the 20th century. The Science of the Total Environment 761: 143293. https://doi.org/10.1016/j.scitotenv.2020.143293

Ferreira JG, Simas T, Nobre A, Silva M, Shifferegger K, Lencart e Silva J (2003) Application of the United States National Estuarine Eutrophication Assessment to the Minho Identification of sensitive areas and vulnerable zones in transitional and coastal Portuguese systems. Instituto da Água e Instituto do Mar, Lisbon, 151 pp.

Ferreira-Rodríguez N, Sousa R, Pardo I (2018) Negative effects of *Corbicula fluminea* over native freshwater mussels. Hydrobiologia 810(1): 85–95. https://doi.org/10.1007/s10750-016-3059-1

Fodrie FJ, Heck Jr KL, Powers SP, Graham WM, Robinson KL (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. Global Change Biology 16(1): 48–59. https://doi.org/10.1111/j.1365-2486.2009.01889.x

Fujiwara M, Simpson A, Torres-Ceron M, Martinez-Andrade F (2022) Life-history traits and temporal patterns in the incidence of coastal fishes experiencing tropicalization. Ecosphere 13(8): e4188. https://doi.org/10.1002/ecs2.4188

Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ, Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ (2011) Potential effects of climate change on Australian estuaries and fish utilising estuaries: A review. Marine and Freshwater Research 62(9): 1115–1131. https://doi.org/10.1071/MF11047

Goedknegt MA, Buschbaum C, van der Meer J, Wegner KM, Thieltges DW (2020) Introduced marine ecosystem engineer indirectly affects parasitism in native mussel hosts. Biological Invasions 22(11): 3223–3237. https://doi.org/10.1007/s10530-020-02318-1

Grabowska J, Przybylski M (2015) Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. Reviews in Fish Biology and Fisheries 25(1): 165–178. https://doi.org/10.1007/s11160-014-9375-5

Guimarães L, Medina MH, Guilhermino L (2012) Health status of *Pomatoschistus microps* populations in relation to pollution and natural stressors: Implications for ecological risk assessment. Biomarkers 17(1): 62–77. https://doi.org/10.3109/1354750X.2011.638442

Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queirós AM, Chatzinikolaou E, Arvanitidis C, Como S, Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G (2018) Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem func-

tions: A global review and meta-analysis. Global Change Biology 24(3): 906–924. https://doi.org/10.1111/gcb.14007

Hatfield JH, Davis KE, Thomas CD (2022) Lost, gained, and regained functional and phylogenetic diversity of European mammals since 8000 years ago. Global Change Biology 28(17): 5283–5293. https://doi.org/10.1111/gcb.16316

Haubrock PJ, Pilotto F, Innocenti G, Cianfanelli S, Haase P (2021) Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. Global Change Biology 27(3): 606–623. https://doi.org/10.1111/gcb.15442

Hauser DDW, Laidre KL, Stern HL, Suydam RS, Richard PR (2018) Indirect effects of sea ice loss on summer-fall habitat and behaviour for sympatric populations of an Arctic marine predator. Diversity & Distributions 24(6): 791–799. https://doi.org/10.1111/ddi.12722

Hervella F, Caballero PJ (1999) Inventariación piscícola de los ríos gallegos. Junta de Galicia = Xunta de Galicia. https://dialnet.unirioja.es/servlet/libro?codigo=48749

Hobday A, Oliver E, Sen Gupta A, Benthuysen J, Burrows M, Donat M, Holbrook N, Moore P, Thomsen M, Wernberg T, Smale D (2018) Categorizing and Naming Marine Heatwaves. Oceanography (Washington, D.C.) 31(2): 162–173. https://doi.org/10.5670/oceanog.2018.205

Howard C, Stephens PA, Pearce-Higgins JW, Gregory RD, Butchart SHM, Willis SG (2020) Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds. Diversity & Distributions 26(11): 1442–1455. https://doi.org/10.1111/ddi.13144

Hulme PE, Bernard-Verdier M (2018) Evaluating differences in the shape of native and alien plant trait distributions will bring new insights into invasions of plant communities. Journal of Vegetation Science 29(2): 348–355. https://doi.org/10.1111/jvs.12625

Ilarri MI, Souza AT, Antunes C, Guilhermino L, Sousa R (2014) Influence of the invasive Asian clam *Corbicula fluminea* (Bivalvia: Corbiculidae) on estuarine epibenthic assemblages. Estuarine, Coastal and Shelf Science 143: 12–19. https://doi.org/10.1016/j.ecss.2014.03.017

Ilarri M, Souza AT, Dias E, Antunes C (2022) Influence of climate change and extreme weather events on an estuarine fish community. The Science of the Total Environment 827: 154190. https://doi.org/10.1016/j.scitotenv.2022.154190

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo, 60 pp. https://doi.org/10.5281/zenodo.3553579

Jarić I, Lennox RJ, Kalinkat G, Cvijanović G, Radinger J (2019) Susceptibility of European freshwater fish to climate change: Species profiling based on life-history and environmental characteristics. Global Change Biology 25(2): 448–458. https://doi.org/10.1111/gcb.14518

Jaspers C, Marty L, Kiørboe T (2018) Selection for life-history traits to maximize population growth in an invasive marine species. Global Change Biology 24(3): 1164–1174. https://doi.org/10.1111/gcb.13955

Kinard S, Patrick CJ, Carvallo F (2021) Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages in coastal streams. PeerJ 9: e12137. https://doi.org/10.7717/peerj.12137

Lages A, Costa D de A, Gomes N, Antunes C (2021) Exotic Pumpkinseed Sunfish *Lepomis gibbosus* (Linnaeus, 1758) in the International Minho River (Iberian Peninsula), and Parasitic

Association with *Myzobdella lugubris* Leidy, 1851 (Annelida, Hirudinea) 13: 555872. https://doi.org/10.19080/OFOAJ.2021.13.555872

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91(1): 299–305. https://doi.org/10.1890/08-2244.1

Laliberté E, Legendre P, Shipley B (2022) FD: Measuring Functional Diversity (FD) from Multiple Traits, and Other Tools for Functional Ecology. https://CRAN.R-project.org/package=FD

Lauchlan SS, Nagelkerken I (2020) Species range shifts along multistressor mosaics in estuarine environments under future climate. Fish and Fisheries 21(1): 32–46. https://doi.org/10.1111/faf.12412

Lepš J, Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. Preslia 78: 481–501.

Limburg KE, Waldman JR (2009) Dramatic Declines in North Atlantic Diadromous Fishes. Bioscience 59(11): 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Linares MS, Amaral PHM, Callisto M (2022) *Corbicula fluminea* (Corbiculidae, Bivalvia) alters the taxonomic and functional structure of benthic assemblages in neotropical hydropower reservoirs. Ecological Indicators 141: 109115. https://doi.org/10.1016/j.ecolind.2022.109115

Loiola PP, de Bello F, Chytrý M, Götzenberger L, Carmona CP, Pyšek P, Lososová Z (2018) Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. Journal of Ecology 106(6): 2230–2241. https://doi.org/10.1111/1365-2745.12986

Markham A (1996) Potential impacts of climate change on ecosystems: A review of implications for policymakers and conservation biologists. Climate Research 6: 179–191. https://doi.org/10.3354/cr006179

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuarine, Coastal and Shelf Science 75(4): 537–546. https://doi.org/10.1016/j.ecss.2007.05.040

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. Oikos 111(1): 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Matsuzaki S-IS, Takamura N, Arayama K, Tominaga A, Iwasaki J, Washitani I (2011) Potential impacts of non-native channel catfish on commercially important species in a Japanese lake, as inferred from long-term monitoring data. Aquatic Conservation 21(4): 348–357. https://doi.org/10.1002/aqc.1198

Maure LA, Rodrigues RC, Alcântara ÂV, Adorno BFCB, Santos DL, Abreu EL, Tanaka RM, Gonçalves RM, Hasui E (2018) Functional Redundancy in bird community decreases with riparian forest width reduction. Ecology and Evolution 8(21): 10395–10408. https://doi.org/10.1002/ece3.4448

McKee TB, Doesken NJ, Kleist J (1993) The relationship of drought frequency and duration to time scales. Eighth Conference on Applied Climatology.

McKnight E, Spake R, Bates A, Smale DA, Rius M (2021) Non-native species outperform natives in coastal marine ecosystems subjected to warming and freshening events. Global Ecology and Biogeography 30(8): 1698–1712. https://doi.org/10.1111/geb.13318

Mollot G, Pantel JH, Romanuk TN (2017) Chapter Two – The Effects of Invasive Species on the Decline in Species Richness: A Global Meta-Analysis. In: Bohan DA, Dumbrell AJ, Massol F (Eds) Advances in Ecological Research. Networks of Invasion: A Synthesis of Concepts. Academic Press, 61–83. https://doi.org/10.1016/bs.aecr.2016.10.002

Moore JC (2013) Diversity, Taxonomic versus Functional. In: Levin SA (Ed.) Encyclopedia of Biodiversity (2nd edn.). Academic Press, Waltham, 648–656. https://doi.org/10.1016/B978-0-12-384719-5.00036-8

Moreira SM, Moreira-Santos M, Guilhermino L, Ribeiro R (2006) An in situ postexposure feeding assay with *Carcinus maenas* for estuarine sediment-overlying water toxicity evaluations. Environmental Pollution 139(2): 318–329. https://doi.org/10.1016/j.envpol.2005.05.004

Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. Science 322(5899): 261–264. https://doi.org/10.1126/science.1163428

Mota M, Rochard E, Antunes C (2016) Status of the Diadromous Fish of the Iberian Peninsula: Past, Present and Trends. Limnetica, 1–18. https://doi.org/10.23818/limn.35.01

Muñoz-Mas R, Carrete M, Castro-Díez P, Delibes-Mateos M, Jaques JA, López-Darias M, Nogales M, Pino J, Traveset A, Turon X, Vilà M, García-Berthou E (2021) Management of invasive alien species in Spain: A bibliometric review. NeoBiota 70: 123–150. https://doi.org/10.3897/neobiota.70.68202

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries 16(2): 362–371. https://doi.org/10.1111/faf.12057

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, Caceres MD, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J (2022) vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan

Ooms J, Lang DT, Hilaiel L (2022) jsonlite: A Simple and Robust JSON Parser and Generator for R. https://CRAN.R-project.org/package=jsonlite

Palacio FX, Callaghan CT, Cardoso P, Hudgins EJ, Jarzyna MA, Ottaviani G, Riva F, Graco-Roza C, Shirey V, Mammola S (2022) A protocol for reproducible functional diversity analyses. Ecography 2022(11): e06287. https://doi.org/10.1111/ecog.06287

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918): 37–42. https://doi.org/10.1038/nature01286

Passos CVB, Fabré NN, Malhado ACM, Batista VS, Ladle RJ (2016) Estuarization increases functional diversity of demersal fish assemblages in tropical coastal ecosystems. Journal of Fish Biology 89(1): 847–862. https://doi.org/10.1111/jfb.13029

Penne CR, Pierce CL (2008) Seasonal distribution, aggregation, and habitat selection of common carp in Clear Lake, Iowa. Transactions of the American Fisheries Society 137(4): 1050–1062. https://doi.org/10.1577/T07-112.1

Podda C, Palmas F, Pusceddu A, Sabatini A (2022) When the eel meets dams: larger dams' long-term impacts on *Anguilla anguilla* (L., 1758). Frontiers in Environmental Science 10: 1–11. https://doi.org/10.3389/fenvs.2022.876369

Povoa LV, Nery JT (2016) precintcon: Precipitation Intensity, Concentration and Anomaly Analysis. https://CRAN.R-project.org/package=precintcon

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2023) R: A language and environment for statistical computing. https://www.R-project.org/

Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22(3): 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews of the Cambridge Philosophical Society 94(3): 849–873. https://doi.org/10.1111/brv.12480

Reis PA, Antunes JC, Almeida CMR (2009) Metal levels in sediments from the Minho estuary salt marsh: A metal clean area? Environmental Monitoring and Assessment 159(1–4): 191–205. https://doi.org/10.1007/s10661-008-0622-x

Renault D, Hess MCM, Braschi J, Cuthbert RN, Sperandii MG, Bazzichetto M, Chabrerie O, Thiébaut G, Buisson E, Grandjean F, Bittebiere A-K, Mouchet M, Massol F (2022) Advancing biological invasion hypothesis testing using functional diversity indices. The Science of the Total Environment 834: 155102. https://doi.org/10.1016/j.scitotenv.2022.155102

Ricotta C, de Bello F, Moretti M, Caccianiga M, Cerabolini BEL, Pavoine S (2016) Measuring the functional redundancy of biological communities: A quantitative guide. Methods in Ecology and Evolution 7(11): 1386–1395. https://doi.org/10.1111/2041-210X.12604

Robinson R, Crick H, Learmonth J, Maclean I, Thomas C, Bairlein F, Forchhammer M, Francis C, Gill J, Godley B, Harwood J, Hays GC, Huntley B, Hutson AM, Pierce GJ, Rehfisch MM, Sims DW, Santos BM, Sparks TH, Stroud DA, Visser ME (2009) Travelling through a warming world: Climate change and migratory species. Endangered Species Research 7: 87–99. https://doi.org/10.3354/esr00095

Santini L, Belmaker J, Costello MJ, Pereira HM, Rossberg AG, Schipper AM, Ceauşu S, Dornelas M, Hilbers JP, Hortal J, Huijbregts MAJ, Navarro LM, Schiffers KH, Visconti P, Rondinini C (2017) Assessing the suitability of diversity metrics to detect biodiversity change. Biological Conservation 213: 341–350. https://doi.org/10.1016/j.biocon.2016.08.024

Schlegel RW, Smit AJ (2021) heatwaveR: Detect Heatwaves and Cold-Spells. https://CRAN.R-project.org/package=heatwaveR

Schmidt-Kloiber A, Hering D (2015) An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators 53: 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007

Segev U, Tielbörger K, Lubin Y, Kigel J (2014) Consequences of climate and body size on the foraging performance of seed-eating ants. Ecological Entomology 39(4): 427–435. https://doi.org/10.1111/een.12115

Sheaves M (2009) Consequences of ecological connectivity: The coastal ecosystem mosaic. Marine Ecology Progress Series 391: 107–115. https://doi.org/10.3354/meps08121

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: What's what and the way forward. Trends in Ecology & Evolution 28(1): 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Sîrbu I, Benedek A-M, Brown BL, Sîrbu M (2022) Disentangling structural and functional responses of native versus alien communities by canonical ordination analyses and variation partitioning with multiple matrices. Scientific Reports 12(1): 12813. https://doi.org/10.1038/s41598-022-16860-6

Sorte CJB, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91(8): 2198–2204. https://doi.org/10.1890/10-0238.1

Sousa R, Guilhermino L, Antunes C (2005) Molluscan fauna in the freshwater tidal area of the River Minho estuary, NW of Iberian Peninsula. Annales de Limnologie – International. Annales de Limnologie 41(2): 141–147. https://doi.org/10.1051/limn/2005009

Sousa R, Dias S, Guilhermino L, Antunes C (2008) Minho River tidal freshwater wetlands: Threats to faunal biodiversity. Aquatic Biology 3: 237–250. https://doi.org/10.3354/ab00077

Sousa R, Freitas FEP, Mota M, Nogueira AJA, Antunes C (2013) Invasive dynamics of the crayfish *Procambarus clarkii* (Girard, 1852) in the international section of the River Minho (NW of the Iberian Peninsula). Aquatic Conservation 23(5): 656–666. https://doi.org/10.1002/aqc.2323

Souza AT, Dias E, Nogueira A, Campos J, Marques JC, Martins I (2013) Population ecology and habitat preferences of juvenile flounder *Platichthys flesus* (Actinopterygii: Pleuronectidae) in a temperate estuary. Journal of Sea Research 79: 60–69. https://doi.org/10.1016/j.seares.2013.01.005

Souza AT, Ilarri MI, Timóteo S, Marques JC, Martins I (2018) Assessing the effects of temperature and salinity oscillations on a key mesopredator fish from European coastal systems. The Science of the Total Environment 640–641: 1332–1345. https://doi.org/10.1016/j.scitotenv.2018.05.348

Souza AT, Ilarri M, Campos J, Ribas FO, Marques JC, Martins I (2022a) Boom and bust: Simulating the effects of climate change on the population dynamics of a global invader near the edge of its native range. The Science of the Total Environment 851: 158294. https://doi.org/10.1016/j.scitotenv.2022.158294

Souza AT, Argillier C, Blabolil P, Děd V, Jarić I, Monteoliva AP, Reynaud N, Ribeiro F, Ritterbusch D, Sala P, Šmejkal M, Volta P, Kubečka J (2022b) Empirical evidence on the effects of climate on the viability of common carp (*Cyprinus carpio*) populations in European lakes. Biological Invasions 24(4): 1213–1227. https://doi.org/10.1007/s10530-021-02710-5

Souza A, Ilarri M, Dias E, Araújo M, Roleira A, Braga AC, Carvalho AR, Mota M, Correia MH, Lages A, Moura A, Antunes C (2023) Long-term monitoring of the fish community in the Minho Estuary (NW Iberian Peninsula). ARPHA Preprints 4: e112222. https://doi.org/10.3897/arphapreprints.e112222

Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America 99(24): 15497–15500. https://doi.org/10.1073/pnas.242437499

Teittinen A, Virta L (2021) Exploring Multiple Aspects of Taxonomic and Functional Diversity in Microphytobenthic Communities: Effects of Environmental Gradients and Temporal Changes. Frontiers in Microbiology 12: 668993. https://doi.org/10.3389/fmicb.2021.668993

Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity & Distributions 12(1): 49–60. https://doi.org/10.1111/j.1366-9516.2006.00216.x

Top N, Tarkan AS, Vilizzi L, Karakuş U (2016) Microhabitat interactions of non-native pumpkinseed *Lepomis gibbosus* in a Mediterranean-type stream suggest no evidence for impact on endemic fishes. Knowledge and Management of Aquatic Ecosystems 36(417): 36. https://doi.org/10.1051/kmae/2016023

van der Linden P, Borja A, Rodríquez JG, Muxika I, Galparsoro I, Patrício J, Veríssimo H, Marques JC (2016) Spatial and temporal response of multiple trait-based indices to natural- and anthropogenic seafloor disturbance (effluents). Ecological Indicators 69: 617–628. https://doi.org/10.1016/j.ecolind.2016.05.020

van Rij J, Wieling M, Baayen RH, van Rijn H (2022) itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs. https://CRAN.R-project.org/package=itsadug

Vila-Gispert A, Alcaraz C, García-Berthou E (2005) Life-history traits of invasive fish in small Mediterranean streams. Biological Invasions 7(1): 107–116. https://doi.org/10.1007/s10530-004-9640-y

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89(8): 2290–2301. https://doi.org/10.1890/07-1206.1

Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecological Applications 20(6): 1512–1522. https://doi.org/10.1890/09-1310.1

Vivó-Pons A, Alós J, Tomas F (2020) Invasion by an ecosystem engineer shifts the abundance and distribution of fish but does not decrease diversity. Marine Pollution Bulletin 160: 111586. https://doi.org/10.1016/j.marpolbul.2020.111586

Wainright CA, Muhlfeld CC, Elser JJ, Bourret SL, Devlin SP (2021) Species invasion progressively disrupts the trophic structure of native food webs. Proceedings of the National Academy of Sciences of the United States of America 118(45): e2102179118. https://doi.org/10.1073/pnas.2102179118

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems (New York, N.Y.) 2(2): 95–113. https://doi.org/10.1007/s100219900062

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879): 389–395. https://doi.org/10.1038/416389a

Williams-Subiza EA, Epele LB (2021) Drivers of biodiversity loss in freshwater environments: A bibliometric analysis of the recent literature. Aquatic Conservation 31(9): 2469–2480. https://doi.org/10.1002/aqc.3627

Winemiller KO, Rose KA (1992) Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation. Canadian Journal of Fisheries and Aquatic Sciences 49(10): 2196–2218. https://doi.org/10.1139/f92-242

Wood S (2022) mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. https://CRAN.R-project.org/package=mgcv

Appendix 1

Table A1. Fish traits and modalities descriptions based on the information contained in the www.freshwaterecology.info database.

Trait category	Trait	Trait abbreviation	Modality	Modality description
Biological	Body length	bod	bl1	Smaller or equal to 20 cm
			bl2	Between 20 and 39 cm
			bl3	Larger or equal to 39 cm
Biological	Egg diameter	egg	ed1	Smaller than 1.35 mm
			ed2	Between 1.35 and 2 mm
			ed3	Larger than 2 mm
Biological	Fecundity (# of oocites)	fec	fe1	Less or equal to 55000
			fe2	Between 55000 and 60000
			fe3	More than 60000
Biological	Feeding diet	die	car	Carnivorous
			inv	Invertivorous
			omn	Omnivorous
			oth	Other
			pis	Piscivorous
			phy	Phytophagous
Biological	Female maturity	fem	ma1	Before 2 years
			ma2	Between 2 and 3 years
			ma3	Between 3 and 4 years
			ma4	Between 4 and 5 years
			ma5	After 5 years
Biological	Incubation period	inc	ip1	Less or equal to 7 days
			ip2	Between 7 and 14 days
			ip3	More than 14 days
Biological	Larval length	lar	ll1	Smaller or equal to 4.2 cm
			ll2	Between 4.2 and 6.3 cm
			ll3	Larger than 6.3 cm
Biological	Duration of larval stage	ldu	ld1	Less than 12 days
			ld2	Between 12 and 25 days
			ld3	More than 25 days

Trait category	Trait	Trait abbreviation	Modality	Modality description
Biological	Life span	lif	ls1	Less than 8 years
			ls2	Between 8 and 15 years
			ls3	More than 15 years
Biological	Parental care	par	nnh	No protection with nester or egg hiders
			nop	No protection
			pnh	Protection with nester or egg hiders
Biological	Relative fecundity[1]	rel	fr1	Less or equal to 57
			fr2	Between 57 and 200
			fr3	More than 200
Biological	Shape factor[2]	sha	sh1	Ratio smaller or equal to 4.35
			sh2	Ratio between 4.35 and 4.78
			sh3	Ratio between 4.78 and 5.6
			sh4	Ratio larger than 5.6
Biological	Spawn time	spa	st1	Winter time
			st2	Summer time
Biological	Swimming factor	swi	sw1	Fast swimmer
			sw2	Average swimmer
			sw3	Slow swimmer
Ecological	Feeding habitat	fee	ben	Benthivorous
			wat	Water column
Ecological	Habitat	hab	ben	Benthopelagic
			dem	Demersal
			pel	Pelagic
Ecological	Migration	mig	dia	Diadromous
			nom	No migration
			oce	Oceanodromous
			pot	Potamodromous
Ecological	Reproduction habitat	rep	lit	Lithophilic
			oth	Other
			phy	Phytophilic
			pli	Phyto-litophilic
			psa	Psammophilic
Ecological	Rheophily	rhe	eur	Eurytopic
			lim	Limnophilic
			rhe	Rheophilic
Ecological	Salinity	sal	brm	Brackish-marine
			fbm	Freshwater-brackish-marine
			fbr	Freshwater-brackish
			fma	Freshwater-marine
			fre	Freshwater

[1]Maximum number of oocites per 100g [2]Total length divided by maximum body depth.
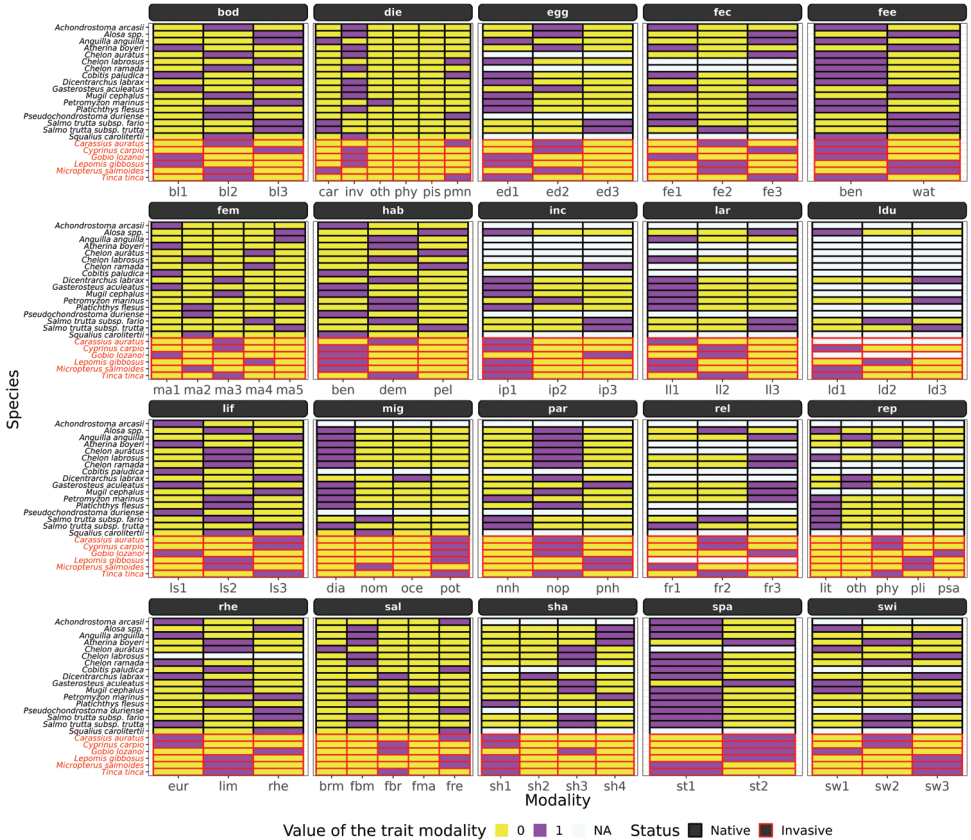
Appendix 2

Figure A1. Values of the modalities of each trait from the fish species captured in the Minho Estuary by fyke nets throughout the course of a decade (2010–2019). Modality classification was based on the information contained in www.freshwaterecology.info database and complemented by the information present on Cano-Barbacil et al. (2020). For the description of traits and modalities see Appendix 1.

Supplementary material 1

Daily air temperature and precipitation data, extracted from the NASA Langley Research Center (LaRC) POWER Project website

Authors: Allan T. Souza, Ester Dias, Carlos Antunes, Martina Ilarri

Data type: csv

Explanation note: The data ranges from 2010-01-01 to 2019-12-31 (yyyy-mm-dd).

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