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

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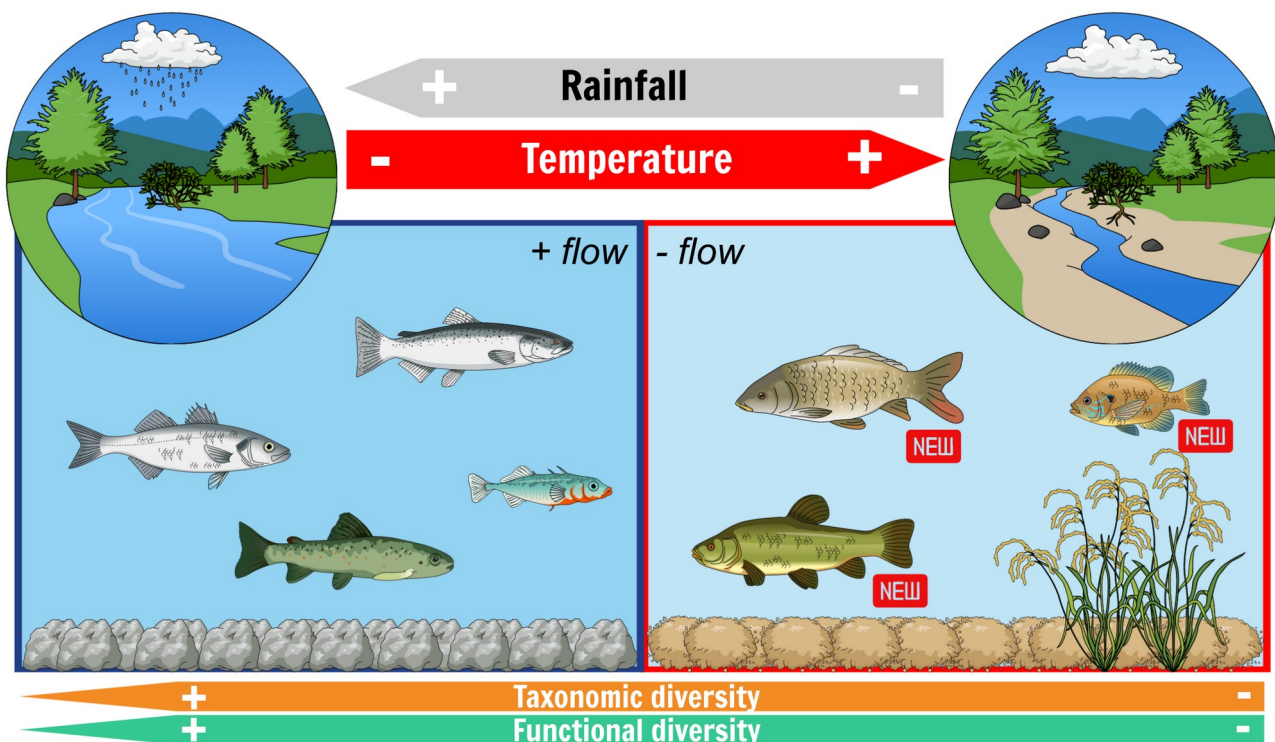
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13 Abstract

14
15 As the effects of climate change continue to intensify, non-native species are becoming more
16 prevalent in estuarine ecosystems. This has implications for the taxonomic and functional diversity
17 of fish communities. Historically, biodiversity has been a synonym of taxonomic diversity, however
18 this approach often fails to provide accurate insights on ecosystem functioning and resilience. To
19 better understand how climate change is impacting fishes and their traits composition, a long-term
20 dataset from Minho Estuary (NW Iberian Peninsula) fish assemblage was analyzed. The results

suggest that climate change and extreme weather events are altering 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 to 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 functional 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 taxonomic diverse than previously.

Keywords

Biological invasions, native species, climatic events, functional traits, biodiversity, ecosystem functioning

Introduction

Historically, biodiversity has been associated to taxonomic diversity (Cardoso et al. 2014). However, taxonomic diversity many times failed to fully provide insights into ecosystem functioning, so the use of functional traits and functional diversity indices can complement the information provided by taxonomic diversity and provide a more holistic understanding of biodiversity (Hulme and Bernard-Verdier 2018). In fact, 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 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. 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). In fact, due to the importance of functional diversity to biodiversity assessments, the number of scientific manuscripts integrating functional diversity in the ecological assessments has been increasing exponentially in the recent years (Palacio et al. 2022), highlighting the increasing relevance of functional diversity in recent ecological assessments.

Climate change is one of the biggest threats to biodiversity currently (IPBES 2019, Reid et al. 2019) and is already affecting many taxonomic groups and ecosystems around the world (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 a warmer climate, while other species may be negatively impacted by shifts in temperature (Sorte 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). Climate change also disrupts species phenologies, alters wildlife behavior (Hauser et al. 2018), and affects migration patterns (Robinson et al. 2009, Howard et al. 2020). 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.

Biological invasions are currently one of the most relevant topics in ecology (Anderson et al. 2021). The effects 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 (Mollet 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, Goedknecht 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

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

99 Among the species groups particularly vulnerable to climate change and biological
 100 invasions are estuarine fishes (Gillanders et al. 2011, Souza et al. 2018, Lauchlan and Nagelkerken
 101 2020, Ilarri et al. 2022). Despite their adaptability to a broad range of environmental conditions,
 102 these animals still exhibit sensitivity to changes in their surroundings (Passos et al. 2016, Souza et
 103 al. 2018). Estuarine assemblages, in fact, often exhibit significant spatial and temporal variability
 104 (Sheaves 2009, Nagelkerken et al. 2015), emphasizing the importance of long-term datasets to
 105 facilitate a comprehensive assessment of fish assemblage dynamics and the influence of
 106 environmental drivers on them.

107 A long-term fish assemblage monitoring has been carrying out in the Minho Estuary
 108 (northwest Iberian Peninsula) from 2010 to 2019. In a recent study it was possible to observe that
 109 the Minho Estuary fish assemblage has been impacted by climatic changes and extreme weather
 110 events, which resulted in a less taxonomic diverse fish community dominated by a few invasive
 111 species (Ilarri et al. 2022). However, the temporal changes in the species trait composition of the
 112 Minho Estuary fish assemblage is still not known. To address this knowledge gap, a decade's worth
 113 of data on fish trait composition and climate (temperature and precipitation) from Minho Estuary
 114 were compiled from weekly *in-situ* fish sampling and satellite data.

115 We hypothesized that I) climate change and extreme weather events have altered the fish
 116 assemblage trait composition of the Minho estuary; II) the success of invasive species in the Minho
 117 Estuary has led to an increase in the functional diversity of the fish assemblage due to the
 118 introduction of novel traits in the fish community.

119

120 **Methods**

121

122 *Study area*

123

124 Sampling took place in Lenta Marina, a small, semi-enclosed bay with approximately 52800 m² of
 125 surface area, located 14.5 kilometers upstream in the Minho Estuary (41°57'18.7"N; 8°44'42.9"W).
 126 Among the estuaries of Portugal, the Minho Estuary has relatively low levels of pollution, but has a
 127 significant history of biological invasions (Sousa et al. 2008, 2013, Reis et al. 2009, Ilarri et al.
 128 2014). The Minho Estuary is described as mesotidal, with an average depth of 2.6 meters and a
 129 maximum depth of 26 meters (Alves 1997). It is partially mixed, except during flood periods when
 130 it tends to exhibit salt wedge conditions (Sousa et al. 2005). During summer or drought events,
 131 marine water enters the Lenta Marina as rainfall and water flow decrease (Ferreira et al. 2003).
 132 However, despite the occurrence of marine water intrusion, the influence of salinity in the Lenta
 133 Marina is relatively small. Salinity values typically range between 0 and 2.0, with higher values
 134 observed in the late summer months or during dry periods (Sousa et al. 2013).

135

136 *Fish data*

137

138 From January 2010 to November 2019, fish samples were collected on a weekly basis. The
 139 collection sites were fixed and had even habitat conditions. Double entry fyke nets with a mesh size
 140 of 10 mm, measuring 7 meters in length, 0.7 meters in mouth diameter, and equipped with a 3.5
 141 meter central wing, were used for the collection. These nets were always deployed in the morning
 142 and remained submerged for an average of 5.7 ± 3.5 days (mean \pm SD). Once the fyke nets were
 143 retrieved, all captured fish were identified to the lowest taxonomic level and counted. In total, 3029
 144 samples were collected throughout the study period. The average catch per unit effort (CPUE) per
 145 sampling date was determined by dividing the number of individuals caught by the number of days
 146 each fyke net remained in the water, taking into account the number of replicates per date. On
 147 average, 4.9 ± 0.4 fyke nets were used per sampling date, although this number varied due to
 148 technical limitations. A more detailed description of the sampling procedure can be found in a
 149 previous study by Ilarri et al. (2022).

150

151 *Trait composition*

152

153 All fish species sampled in the Minho Estuary from January 2010 to November 2019 (more
 154 details in Ilarri et al. 2022) were analyzed according to 20 traits containing 67 modalities (Appendix
 155 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 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). In this study, we have compiled the trait composition data from 23 fish species (17 native and 6 non-native) (Table 1).

Functional diversity indices

Six different functional diversity indices were calculated using the information on fish abundances and their functional 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), the 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 index) was calculated using the *diversity* function 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 functional traits (van der Linden et al. 2016, Maure et al. 2018). FEve measures the evenness of the distribution of the traits abundance. It is 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

190

191 Climate data used in this study included daily mean air temperature (measured 2 meters
192 above ground level) in °C and precipitation in mm.m⁻². These data were scaled down to 1x1° grids
193 and covered the entire duration of the sampling campaign, which ranged from January 2010 to
194 November 2019. Data for the sampled site were obtained from NASA via their application
195 programming interface (API) available through the NASA Langley Research Center (LaRC)
196 POWER Project website. The *jsonlite* package in R developed by Ooms et al. (2022) was used to
197 process the data.

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

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

210

211 *Data analysis*

212 Generalised additive models (GAM) with Gaussian distributions were used to assess the
213 effects of temperature, precipitation and time on the fish trait modalities and diversity indices. Prior
214 to analysis, temperature and precipitation data were scaled using the *scale* function from the *base*
215 package in R (R Core Team 2022). CPUE values, diversity indices and precipitation data were
216 appropriately transformed to account for the characteristics of their respective data distributions.
217 Square root or log(X + 1) transformations were applied using the *sqr* and *log1p* functions from the
218 *base* package in R (R Core Team 2022).

219 For the temperature and precipitation data, cubic regression splines were used to smooth the
220 variables for each season (winter, spring, summer and autumn). This smoothing process was carried
221 out using the function *s* from the package *mgcv* (Wood 2022). The decision to apply smoothing by
222 season was made in view of the different temperature patterns and precipitation profiles observed in
223 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 (ρ) was determined by running a GAM model without the autocorrelation structure. The *start_value_rho* function from the *itsadug* package (Rij et al. 2022) was used to calculate the initial value of ρ . Autocorrelation and partial autocorrelation were evaluated using the *acf* and *pacf* functions from the *stats* package in R package (R Core Team 2022). The GAM models were run with the *bam* function from the *mgcv* package (Wood 2022).

All data analyses were performed using the R (R Core Team 2022).

Results

Fish assemblage trait composition all over the years

Of the 67 fish traits modalities observed, 65.67% have varied through time. Temperature had a greater influence on trait modalities than precipitation, 76.12% of the traits modalities significantly responded to temperature, whereas 38.51% significantly responded to precipitation. Also, temperature influenced the traits modalities mostly during winter (59.70%) and autumn (46.27%). Precipitation influenced the trait modalities in a similar pattern, with winter (23.88%) and autumn (16.42%) having greater influences than summer (7.46%) and spring (0%). Of the 67 GAM models for each trait modality, 19 had a percentage of explanation higher than 50% (Table 2; Fig. 1).

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, Lithophilic and Other, Freshwater-brackish-marine, ≥ 39 , Sh3 (4.78-5.6) and Winter time (Fig. 2). On the other hand, it was also observed that other traits modalities were more frequently associated with invasive species such as Potamodromous, Benthopelagic, Phytophilic and Phyto-litophilic, Freshwater and Freshwater-brackish, >15 , Sh1 (≤ 4.35), Sw3 (>0.43), 3-4, Summer time, ≤ 7 , 55k-60k, 57-200, <1.35 and $1.35-2$, ≤ 4.2 and $4.2-6.3$, Nop (No protection) and <12 (Fig. 2).

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 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 influenced positively and negatively some traits 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%) (Table 3).

Regarding the strong heatwave events, 32.8% of the traits had a decrease during these events (e.g., Egg diameter: >2, decrease of 100%; Habitat: Pelagic, decrease of 100%), and 4% 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 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 4.8% of the trait modalities had a strong increase during these extreme events (Migration: Oceanodromous, increase of 449%; Shape factor: 4.35-4.78, increase of 449%) (Table 3).

During the extreme dry events recorded in the Minho Estuary between 2010 and 2019, there was no trait negatively affected by more than $\geq 70.01\%$ of their mean value (Table 3). Only 4.5% of the trait modalities experienced a large increase in their mean value (e.g., Incubation period: 7-14, increase of 138%; Salinity: Brackish-marine, increase of 96%) during dry events (Table 3).

On the other hand, the wet extreme precipitation events contributed to strong decreases, 10.5% of the trait modalities were negatively influenced (e.g. Incubation period: 7-14, decrease of 100%; Salinity: Freshwater-marine, decrease of 91%) (Table 3). On the other hand, there was no trait positively affected by more than $\geq 70.01\%$ of their mean value during the wet events (Table 3).

280

281 *Taxonomic composition and functional metrics of the fish assemblage*

282

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, with the exception of FEve, which did not increase nor decrease throughout the time, but still responded to changes in temperature. FDis, FRic, and FRAO decreased significantly through time, while FDiv and FRed have increased over the years (Fig. 3, Table 4).

290

291 Discussion

292 We have been monitoring the fish populations in the Minho Estuary to better understand the effects
 293 of changing environmental conditions on biodiversity, for over a decade. Over this period, we have
 294 observed signs of decline in both taxonomic and functional diversities, which seems to correspond
 295 with a decreasing number of native species and an increasing prevalence of invasive species. This
 296 phenomenon seems to be further influenced by changes in environmental factors such as
 297 temperature and precipitation, which appear to impact several key trait characteristics of these
 298 fishes. Overall, there has been a significant shift in fish assemblage occurring in this estuary over
 299 the past decade, which now has an almost equal contribution of native and invasive species in terms
 300 of species richness, whereas the latter dominate in terms of abundance (Ilarri et al. 2022).

301 Over the past few years, the Minho Estuary has witnessed a significant increase in
 302 populations of invasive species (Sousa et al. 2013, Ilarri et al. 2022). The pumpkinseed, in
 303 particular, common carp, and tench are three species that have flourished in the estuary since 2015-
 304 2016 (Ilarri et al. 2022), and their increase is likely due to changes in the prevalent environmental
 305 conditions. These fishes prefer slow currents (Benito et al. 2015, Avlijaš et al. 2018, Lages et al.
 306 2021) and highly vegetated zones (Penne and Pierce 2008, Top et al. 2016, Avlijaš et al. 2018),
 307 which are likely to become more prevalent with changes in temperature (increase) and rainfall
 308 regime (decrease) over time. These three species are also potamodromous, meaning that they
 309 perform migrations in the river. They are also either phytophilic or phyto-litophilic species,
 310 reproducing in areas rich in submerged vegetation and rocks. These species are also either eurytopic
 311 (common carp) or limnophilic (pumpkinseed and tench), which means that the common carp
 312 tolerates a wide range of environmental conditions, while pumpkinseed and tench are associated
 313 with slowly moving waters. Interestingly, these three species also have the shape 1 classification in
 314 body shape (more rounded and compacted body) and are either average (common carp) or slow
 315 swimmers (pumpkinseed and tench) (Schmidt-Kloiber and Hering 2015). The traits characteristics
 316 of these three invasive species seem to be benefited in Minho Estuary, as the decrease in
 317 precipitation and drought events have contributed to reduced river inflow and water currents in the
 318 system. Haubrock et al. (2021) also observed a significant increase over time in short-bodied
 319 species with high body depth (shape factor 1) on the Arno River. According to Vila-Gispert et al.
 320 (2005), this trait modality can be advantageous when competing with native species in slow-flow
 321 waters. On the other hand, the lower river inflow and water currents are not good for many native
 322 species with elongated body shapes that are more associated with fast-flowing waters (rheophilic)
 323 and oceanodromous or diadromous migration modalities, such as eel, shad, three-spined

324 stickleback, European seabass and sea trout. These species have declined sharply over time (Ilarri et
325 al. 2022), and the functional traits associated with them are also disappearing from the system.

326 Interestingly, there was a decline in FRic, and an increase in FRed. This suggests that the
327 fish assemblage is losing some functional traits and that the invasive species are not able to replace
328 the losses of functional traits. This is somewhat expected, as invasive species usually differ from
329 native species in their life-history and ecological traits (Vila-Gispert et al. 2005). However, for the
330 vast majority of functional traits analyzed in the present study, invasive species had very similar
331 modalities to native species, with an important exception of a few traits. One of the most striking
332 differences is probably observed in migration, where the native species have a good amount of
333 diadromous species and almost all invasive species are potamodromous. This result highlights that
334 climate change is indeed seriously threatening diadromous species (Limburg and Waldman 2009,
335 Mota et al. 2016, Braga et al. 2022, de Eyto et al. 2022), putting additional pressure on this group,
336 which is already heavily impacted (Barbarossa et al. 2020, Duarte et al. 2021, Podda et al. 2022).
337 The decline of diadromous species is also reflected in the substantial difference in the distribution
338 of trait modalities regarding salinity preferences. Our results have revealed a decline in species with
339 an affinity for marine and brackish water, and a replacement for species with an affinity for
340 freshwater. It is widely reported that climate change may favor marine and brackish water species in
341 this estuary, at least in the near-term (Souza et al. 2018, 2022a). However, this may not be true for
342 all species, as observed in this study. The sampled area is in the upper part of the estuary, where the
343 saline intrusion is historically not so strong, but despite the decrease in the river inflow and the
344 precipitation regime, it looks like that the saline intrusion is not affecting much the upper estuary,
345 with the exception of European seabass, which in some years can reach the upper parts of the river
346 in summer due to higher saline intrusion (Ilarri et al. 2022). On the contrary, the change in
347 hydrologic conditions seems to favor freshwater species that prefer slow currents or standing waters
348 (limnophilic or eurytopic), which are also invasive (common carp, goldfish, largemouth bass,
349 pumpkinseed, and tench). This might be explained by the decreased hydrodynamics in the area,
350 which started to attract species with affinity to slow moving freshwater.

351 Another important divergence in trait modality composition between native and invasive
352 species is in the reproduction habitat. Redundancy in this trait is low, with native species preferring
353 to spawn in rocky areas (litophilic species), whereas invasive species are more associated to densely
354 vegetated areas (phytophilic species) with some rocky bottoms (phyto-litophilic) or in sandy areas
355 (psammophilic species). The decreased rainfall and river inflow probably contributed to the growth
356 of submerged vegetation and the accumulation of finer substrate (sand) in the area. These conditions
357 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. 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.

Life history 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. In our study, heatwaves had the greatest impact on functional 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-

392 bodied species. Our results are in part corroborated by Fujiwara et al. (2022), that suggested that
 393 fish species sensitive to changes in temperature, generally have functional traits associated with
 394 longer generation time, maximum length and length at maturity. In our study, traits associated with
 395 these aspects were negatively influenced by the extreme temperature events. Interestingly, these
 396 trait modalities were also negatively influenced by the long-term effects of temperature. Therefore,
 397 the heatwave events (especially the strong ones) are possibly accelerating the speed of change in the
 398 fish community in Minho Estuary.

399 Regarding extreme precipitation weather events, both dry and wet events can be critical in
 400 estuarine ecosystems due to the hydrological dynamics of these systems. Although the extreme dry
 401 events influenced a large number of species (Ilarri et al. 2022), these events seem to have a broad
 402 effect on the whole fish community, with fish traits benefiting more than being negatively affected
 403 (mainly considering cases where there was a change in abundance $\geq 70.01\%$). This result differs
 404 from our expectations, as we expected that these conditions have mainly negative impacts on the
 405 fish functional diversity. Normally, extreme dry events are associated with an increase in salinity
 406 and changes in other water biochemical properties (Martinho et al. 2007, Kinard et al. 2021). In this
 407 case, salinity and water quality act as abiotic filters in the fish assemblage and select fishes with
 408 traits better adapted to harsh conditions (Kinard et al. 2021). Overall, drought events were linked to
 409 an increase in the abundance of trait modalities associated with the marine environment (brackish-
 410 marine), which was expected as the decreasing water flow can lead to stronger saltwater intrusion
 411 into the upper parts of the estuary. Drought events also positively influenced some traits modalities
 412 related to reproduction, such as incubation period, egg diameter and larval length. The favored
 413 modalities are not in the extremes of the ranges of the traits, suggesting that they might be
 414 indicative of moderate and stable environments, which also suggested that drought events probably
 415 did not cause severe stress to the fishes in Minho Estuary. On the other hand, the extreme wet
 416 events, despite of affecting a lower number of species than the extreme dry events (see Ilarri et al.
 417 2022), they negatively affected several trait modalities. This result was also different than expected,
 418 as areas with more precipitation are normally expected to create more stable conditions than areas
 419 submitted to dry conditions. In this sense, wet events can be expected to affect the extreme
 420 modalities of traits, and to favor the moderate modalities of traits, which was not the case for
 421 several traits in this study. The extreme wet events were mostly linked to a decline in traits
 422 associated with the marine environment, such as oceanodromous and freshwater-marine modalities,
 423 which makes sense given the lower saline influence under this condition. Other traits modalities that
 424 were negatively influenced were pelagic, psammophilic, shape 2 and incubation period of 7-14
 425 (intermediary modality).

Some studies indicate that changes in functional diversity are easier to detect than changes in taxonomic diversity and serve as an early warning signal for threatened ecosystems. However, in this study it was possible to see the same signal in both metrics, suggesting that in 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 instance the FDiv increase indicates that some of the most abundant species in the system nowadays have highly divergent characteristics from the rest of the fish assemblage, 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 faster 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 functional 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). FEve was the only functional diversity index that did not change through time, which might suggest that it is a less sensitive index to detect disruptions in the ecosystem. Indeed, previous studies have already suggested that FEve may perform poorly to detect assembly patterns (Mouchet et al. 2010, 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.

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472

473 *Author Contribution Statement*

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

478

479 *Data Availability Statement*

480 The dataset used for analysis during the current study is deposited on Zenodo repository (doi:
 481 10.5281/zenodo.8046541).

482

483 *Conflict of interest Statement*

484 The authors declare that they have no known competing financial interests or personal relationships
 485 that could have appeared to influence the work reported in this paper.

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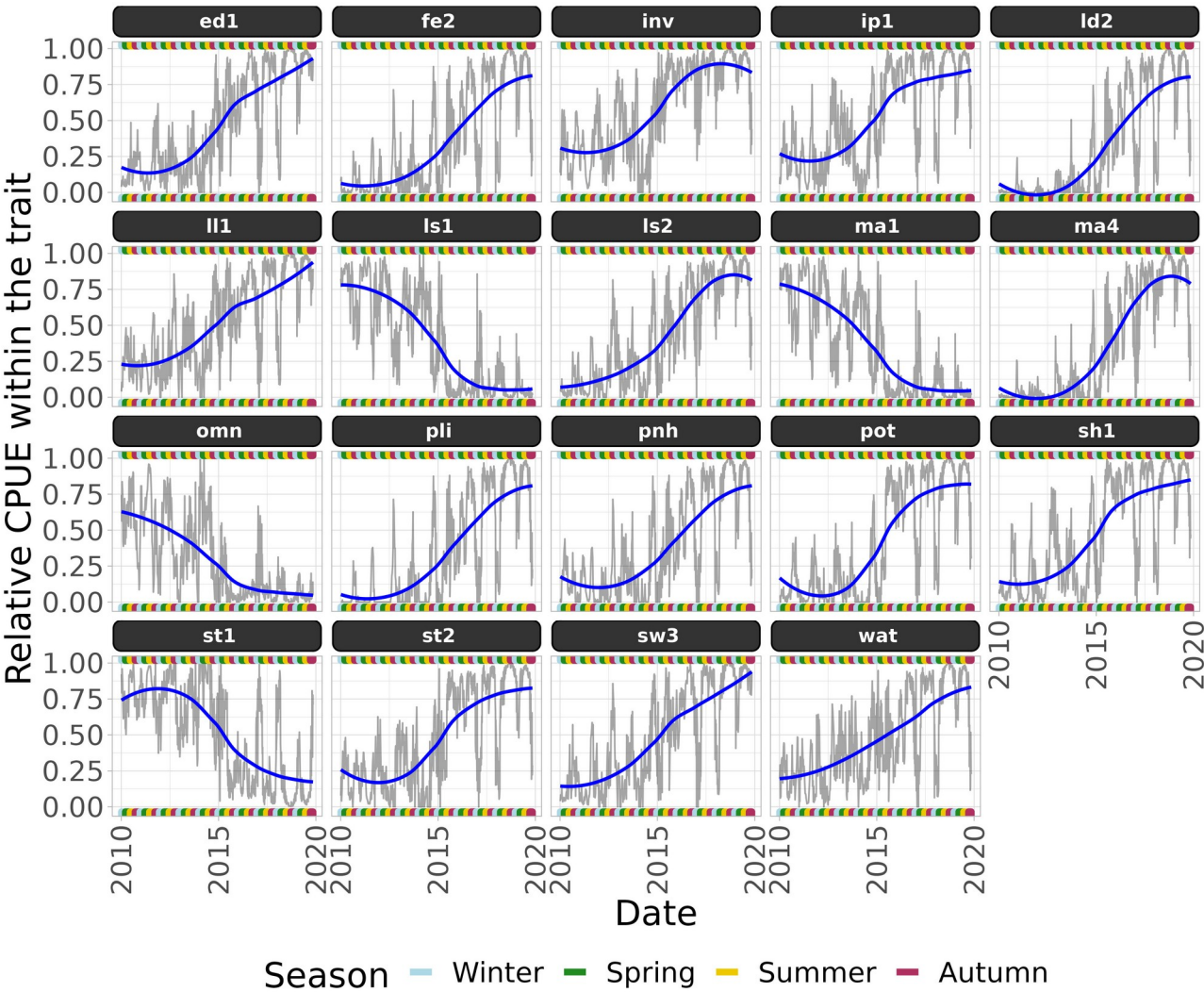
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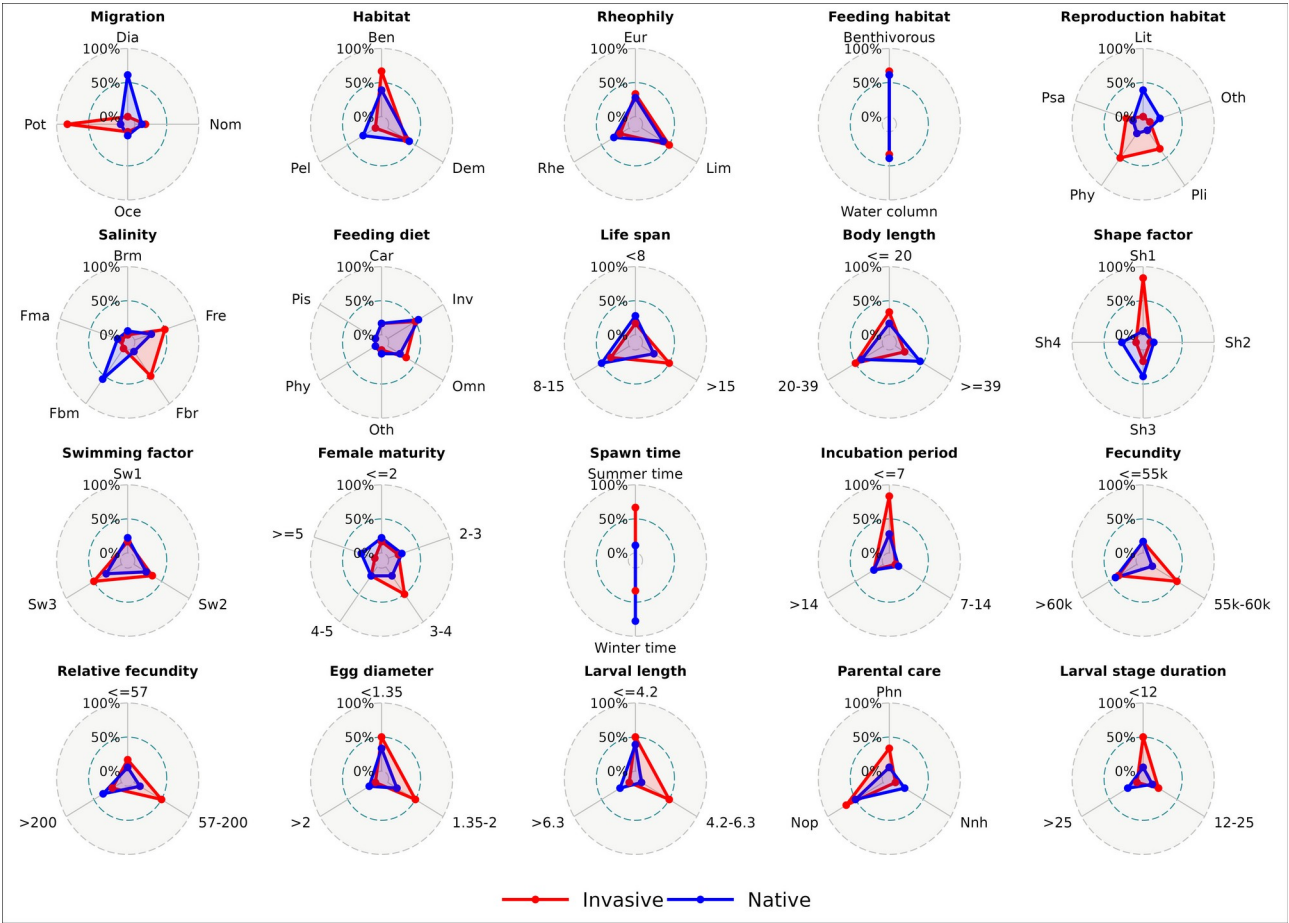
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488 *Figures*
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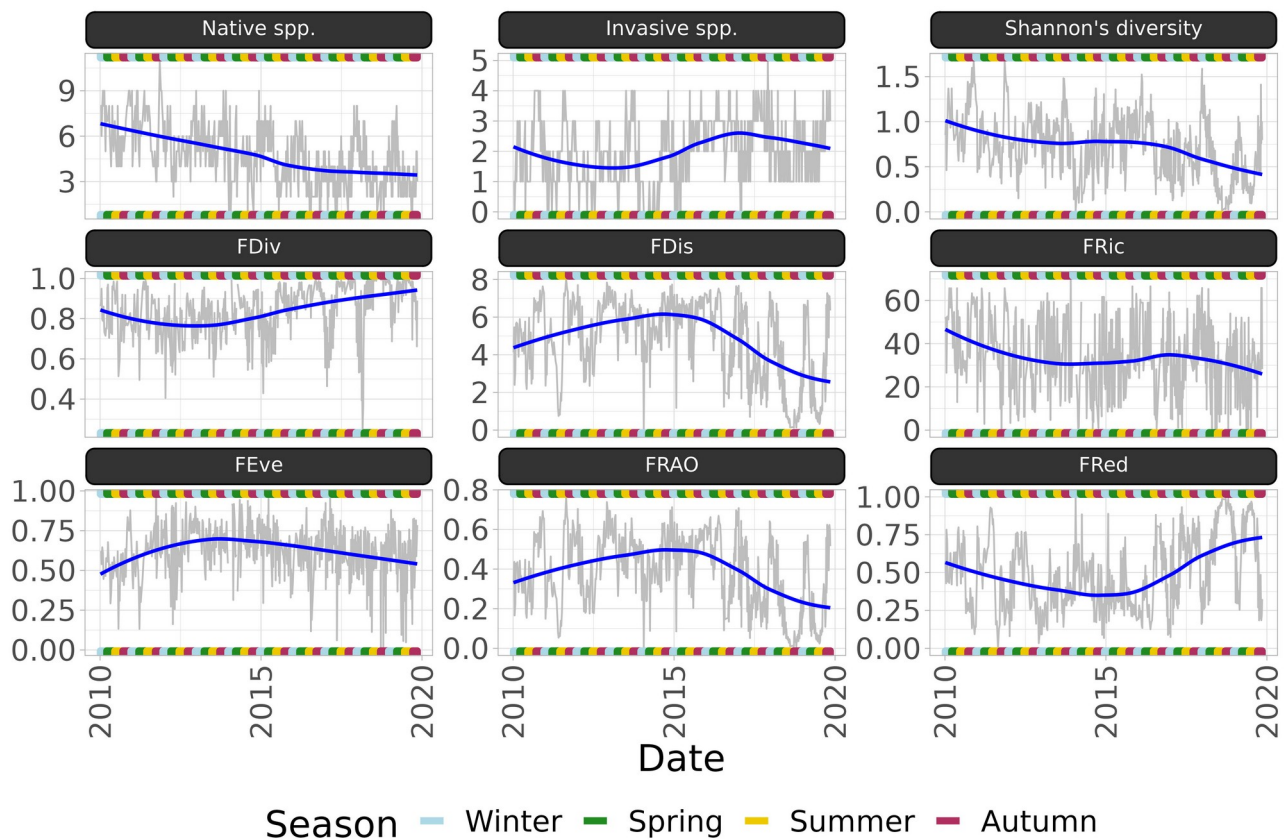


490 Figure 1. Selection of fish trait modalities in the Minho Estuary (Portugal) that had strong temporal
491 changes (selected by the highest % explained by the models). Blue lines refer to a simple moving
492 regression (loess) and are only indicative of the temporal changes. Statistical tests can be found in
493 table 2. ed1 = egg diameter smaller than 1.35mm, fe2 = number of oocytes between 55000 and
494 60000, inv = invertivorous (feed on invertebrates), ip1 = incubation period is less or equal to seven
495 days, ld2 = larval stage duration between 12 and 25 days, ll1 = larval length is smaller or equal to
496 4.2 cm, ls1 = life span is less than eight years, ls2 = life span is between eight and fifteen years, ma1
497 = females are mature before two years, ma4 = females are mature between four and five years, omn
498 = omnivorous (feed on animals and plants), pli = reproduction habitat is phyto-litophilic (associated
499 with plants and rocks), pnh = parental care by protection with nesting or egg hiding, pot =
500 potamodromous migration (between different freshwater bodies), sh1 = shape factor ratio is smaller

501 or equal to 4.35 (compact, rounded body shape), st1 = spawn time is during winter, st2 = spawn
502 time is during summer, sw3 = slow swimmer, wat = feeding habitat is in the water column.
503



504 Figure 2. Comparison between invasive and native fish species at the Minho Estuary (Portugal) on
505 the average score of each trait modality. The description of all modalities can be found in appendix
506 1.
507



508 Figure 3. Dynamics of the number of native and invasive species, taxonomic diversity (Shannon's
509 diversity) and six functional diversity indices (FDiv, FDis, FRic, FEve, FRAO and FRed) computed
510 with weekly data on the fish captured by fike nets in Minho Estuary (Portugal) from 2010 and 2019.
511 Blue lines refer to a simple moving regression (loess) and are only indicative of the temporal
512 changes. Statistical tests that can be found in table 4. FDiv = functional divergence, FDis =
513 functional dispersion, FRic = functional richness, FEve = functional evenness, FRAO = Rao's
514 quadratic entropy and FRed = functional redundancy.
515

516 Tables

517

518 Table 1. Origin, species and common name of the fishes sampled in the Minho Estuary (Portugal)
 519 from January of 2010 to November of 2019. Fish species are ordered by origin and phylogenetic
 520 order (order and family).

Origin	Order	Family	Species	Common name
Native	Petromyzontiformes	Petromyzontidae	<i>Petromyzon marinus</i>	Sea lamprey
Native	Anguilliformes	Anguillidae	<i>Anguilla anguilla</i>	European eel
Native	Clupeiformes	Clupeidae	<i>Alosa</i> spp.	Allis and twaite shads
Native	Cypriniformes	Cobitidae	<i>Cobitis paludica</i>	Iberian loach
Native	Cypriniformes	Leuciscidae	<i>Achondrostoma archasii</i>	Panjorca
Native	Cypriniformes	Leuciscidae	<i>Pseudochondrostoma duriense</i>	Douro nase
Native	Cypriniformes	Leuciscidae	<i>Squalius carolitertii</i>	Iberian chub
Native	Salmoniformes	Salmonidae	<i>Salmo trutta</i> var. <i>fario</i>	Brown trout
Native	Salmoniformes	Salmonidae	<i>Salmo trutta</i> var. <i>trutta</i>	Sea trout
Native	Atheriniformes	Atherinidae	<i>Atherina boyeri</i>	Sand smelt
Native	Mugiliformes	Mugilidae	<i>Chelon auratus</i>	Golden grey mullet
Native	Mugiliformes	Mugilidae	<i>Chelon labrosus</i>	Thicklip grey mullet
Native	Mugiliformes	Mugilidae	<i>Chelon ramada</i>	Thinlip mullet
Native	Mugiliformes	Mugilidae	<i>Mugil cephalus</i>	Flathead grey mullet
Native	Perciformes	Gasterosteidae	<i>Gasterosteus aculeatus</i>	Three-spined stickleback
Native	Eupercaria	Moronidae	<i>Dicentrarchus labrax</i>	European seabass
Native	Pleuronectiformes	Pleuronectidae	<i>Platichthys flesus</i>	European flounder
Non-native	Centrarchiformes	Centrarchidae	<i>Lepomis gibbosus</i>	Pumpkinseed
Non-native	Centrarchiformes	Centrarchidae	<i>Micropterus salmoides</i>	Largemouth bass
Non-native	Cypriniformes	Tincidae	<i>Tinca tinca</i>	Tench
Non-native	Cypriniformes	Gobionidae	<i>Gobio lozanoi</i>	Iberian gudgeon
Non-native	Cypriniformes	Cyprinidae	<i>Carassius auratus</i>	Goldfish
Non-native	Cypriniformes	Cyprinidae	<i>Cyprinus carpio</i>	Common carp

521

522 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.

Trait	Modality	Temperature				Precipitation				Time	%	r ²
		Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	F	exp.	adj.
Migration	Nom (No migration)	0.76	0.05	1.74	0.73	0.60	0.05	3.40**	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*	1.33	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	0.00	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**	0.16	1.37	6.18*	1.64	0.82	0.23	0.64	0.06	12.1	0.097
	Rhe (Rheophilic)	0.49	0.28	1.52	0.63	0.05	0.00	0.17	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	4.62*	13.99***	0.03	1.06	1.47	-1.88	11.1	0.091
	Lit (Lithophilic)	2.63*	0.07	1.53	2.59	0.03	0.24	0.09	0.30	-5.09***	14.5	0.13
	Phy (Phyto-lithophilic)	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
	Fre (Freshwater)	3.64*	0.00	3.11	7.95**	0.02	1.35	0.45	0.23	3.81***	23.8	0.222
Salinity	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)	9.00***	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	3.02	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
	Car (Carnivorous)	0.78	1.22	1.33	2.82	1.17	0.47	0.01	2.96*	-3.75***	10.4	0.09
	Inv (Invertivorous)	1.37	1.26	0.18	0.26	0.40	0.68	0.14	0.00	13.44***	58.5	0.577
Life span	Omn (Omnivorous)	0.06	3.28	1.16	0.22	0.04	1.77	0.11	1.11	-11.76***	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
	<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**	1.39	0.72	3.94*	9.80**	0.08	0.84	0.98	16.63***	70.5	0.699
Body length	>15	0.08	0.05	0.61	5.44*	0.24	0.33	0.32	1.73	-1.06	3.43	0.017
	<=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	0.08	0.28	-3.34**	32.9	0.309
		**										
Swimming factor	Sh4 (>=5.6)	3.44*	1.06	3.18	9.67**	4.17*	0.29	0.06	0.14	-1.82	11.9	0.103
	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
		**										
Female maturity	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
	<=2	4.00**	2.56	3.49*	0.00	5.74*	1.07	2.09*	0.00	-16.68***	66.5	0.655
	2-3	2.69*	0.01	6.84***	0.80	0.26	0.13	7.01***	1.22	-4.17***	18.9	0.162
	3-4	0.16	0.48	0.01	0.94	2.03	0.03	0.64	2.29	-0.63	1.14	-0.01
	4-5	4.12**	1.37	0.00	1.53	9.21**	0.15	0.62	2.34	14.62***	70.7	0.7

Spawn time	>=5	0.60	1.43	3.06	9.03**	0.40	0.41	0.13	0.33	-1.72	6.7	0.051
	Winter time	3.22*	3.61	0.34	2.16	2.85*	1.56	0.01	0.71	-10.24***	51.1	0.5
	Summer time	3.29**	3.53	0.37	1.86	4.01*	1.41	0.03	1.31	10.12***	53.8	0.53
Incubation period	<=7	4.72**	3.41	1.54	5.37*	2.26	0.94	0.18	0.68	10.04***	55.0	0.54
	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	8.43***	0.97	5.59**	6.20*	7.12**	0.18	0.00	0.03	-8.89***	34.1	0.328
	55k-60k	1.31	2.27	0.55	3.87*	0.56	0.00	0.92	0.78	12.18***	60.3	0.60
	>60k	0.02	0.03	0.01	4.09*	0.06	0.44	0.93	0.91	-1.30	3.52	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	1.62	-0.01
	>200	4.69**	0.72	4.85*	4.68*	4.29**	1.36	0.06	0.25	-1.45	18.8	0.165
Egg diameter	<1.35	5.98***	6.34*	0.68	1.37	2.45	0.00	0.24	0.31	17.09***	68.1	0.675
	1.35-2	1.45	0.02	2.43	1.84	5.56**	0.34	0.47	3.11*	-5.97***	20.5	0.188
	>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	0.21
	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*	6.06	0.032
	12-25	2.02	2.66	0.12	2.02	1.50	0.01	0.76	2.05	11.86***	62.9	0.62
	>25	7.26***	0.28	1.25	5.37*	0.77	0.06	0.31	0.02	-5.31***	14.0	0.123

Table 3. Categorically 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 $\pm 10\%$ 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 $\geq 70.01\%$; - 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 $\geq 70.01\%$.

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

	<=2	-	--	-	+	-
	2-3	-	-	+	-	0
Female maturity	3-4	++	-	+	-	+
	4-5	+	++	0	0	0
	>=5	-	--	+	0	++
Spawn time	Winter time	-	-	0	0	-
	Summer time	+	+	0	0	+
	<=7	+	+	0	-	+
Incubation period	7-14	--	---	---	+++	---
	>14	++	---	--	+	--
Fecundity	<=55k	--	---	--	0	-
	55k-60k	+	++	0	0	+
	>60k	+	-	+	-	+
Relative fecundity	>=57	--	---	++	0	+
	57-200	++	-	0	-	+
	>200	-	---	-	0	-
Egg diameter	<1.35	+	++	0	0	+
	1.35-2	-	---	-	-	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
	<12	+	-	+	-	+
Larval stage duration	12-25	+	+++	0	0	+
	>25	+	-	+++	+	-

537

538 Table 4. Summary of the GAM models with the functional diversity indices calculated with the fish
539 abundances from the Minho Estuary (Portugal) and temperature, precipitation and time. Statistical
540 significance at: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Win = winter, Spr = spring, Sum = summer, and
541 Aut = autumn.

Index	Temperature				Precipitation				Time	% exp	r ² 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	7.90***	1.65	0.46	0.09	1.56	0.25	0.54	0.19	6.80***	26.7	0.247
FDis	4.38*	0.19	0.54	0.25	4.58***	0.09	0.90	0.12	-4.80***	20.7	0.191
FRic	1.13	1.59	3.19*	4.64**	0.14	0.52	0.05	0.21	-3.46***	9.8	0.079
FEve	1.46	1.75	0.65	6.21*	0.25	1.32	0.53	1.13	-1.76	6.6	0.045
FRAO	4.67*	0.19	0.90	0.50	5.09***	0.25	0.88	0.11	-4.36***	18.1	0.163
FRED	5.46*	0.00	0.52	0.54	4.71***	0.55	0.88	0.43	3.80***	15.9	0.140

542

543

544 *Appendix*

545

546 Appendix 1. Fish traits and modalities descriptions based on the information contained in the
547 www.freshwaterecology.info database.

Trait	Trait abbreviation	Modality	Modality description
Body length	bod	bl1	Smaller or equal to 20 cm
		bl2	Between 20 and 39 cm
		bl3	Larger or equal to 39 cm
		car	Carnivorous
		inv	Invertivorous
Feeding diet	die	omn	Omnivorous
		oth	Other
		pis	Piscivorous
		phy	Phytophagous
		ed1	Smaller than 1.35 mm
Egg diameter	egg	ed2	Between 1.35 and 2 mm
		ed3	Larger than 2 mm
		fe1	Less or equal to 55000
Fecundity (# of oocytes)	fec	fe2	Between 55000 and 60000
		fe3	More than 60000
Feeding habitat	fee	ben	Benthivorous
		wat	Water column
		ma1	Before 2 years
Female maturity	fem	ma2	Between 2 and 3 years
		ma3	Between 3 and 4 years
		ma4	Between 4 and 5 years
		ma5	After 5 years
		ben	Benthopelagic
Habitat	hab	dem	Demersal
		pel	Pelagic
		ip1	Less or equal to 7 days
Incubation period	inc	ip2	Between 7 and 14 days
		ip3	More than 14 days
		ll1	Smaller or equal to 4.2 cm
Larval length	lar	ll2	Between 4.2 and 6.3 cm
		ll3	Larger than 6.3 cm
		ld1	Less than 12 days
Duration of larval stage	ldu	ld2	Between 12 and 25 days
		ld3	More than 25 days
		ls1	Less than 8 years
Life span	lif	ls2	Between 8 and 15 years
		ls3	More than 15 years
		dia	Diadromous
Migration	mig	nom	No migration
		oce	Oceanodromous
		pot	Potamodromous
Parental care	par	nnh	No protection with nester or egg hiders
		nop	No protection
		pnh	Protection with nester or egg hiders
Relative fecundity ¹	rel	fr1	Less or equal to 57
		fr2	Between 57 and 200
		fr3	More than 200
Reproduction habitat	rep	lit	Lithophilic
		oth	Other
		phy	Phytophilic
		pli	Phyto-litophilic
		psa	Psammophilic

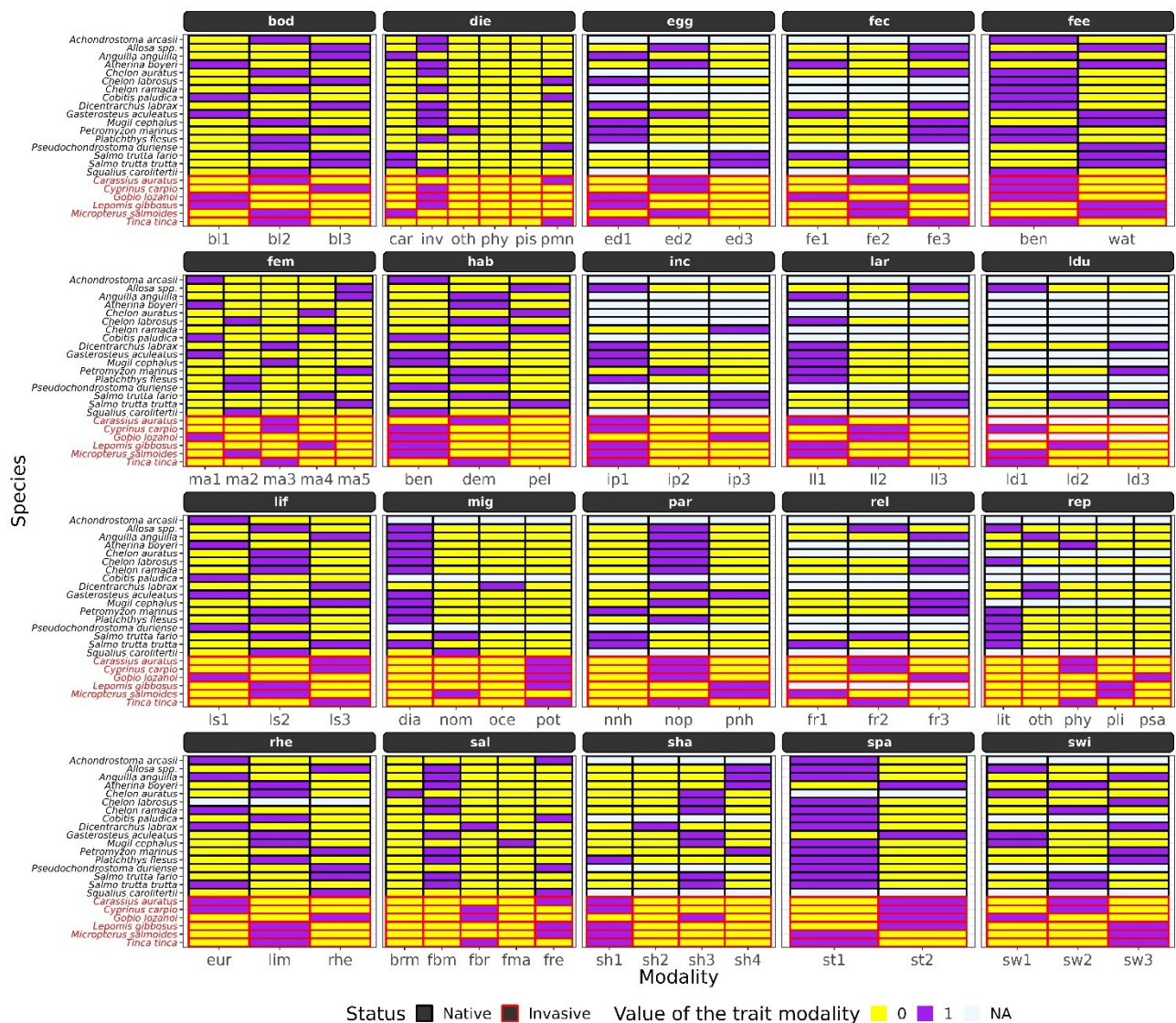
Rheophily	rhe	eur	Eurytopic
		lim	Limnophilic
		rhe	Rheophilic
		brm	Brackish-marine
Salinity	sal	fbm	Freshwater-brackish-marine
		fbr	Freshwater-brackish
		fma	Freshwater-marine
		fre	Freshwater
Shape factor ²	sha	sh1	Ratio smaller or equal to 4.35
		sh2	Ratio between 4.35 and 4.78
		sh3	Ratio between 4.78 and 5.6
		sh4	Ratio larger than 5.6
Spawn time	spa	st1	Winter time
		st2	Summer time
Swimming factor	swi	sw1	Fast swimmer
		sw2	Average swimmer
		sw3	Slow swimmer

548 ¹Maximum number of oocites per 100g

549 ²Total length divided by maximum body depth

550

551



552 Appendix 2. Values of the modalities of each trait from the fish species captured in the Minho
 553 Estuary by fike nets throughout the course of a decade (2010 – 2019). Modality classification was
 554 based on the information contained in www.freshwaterecology.info database.
 555

