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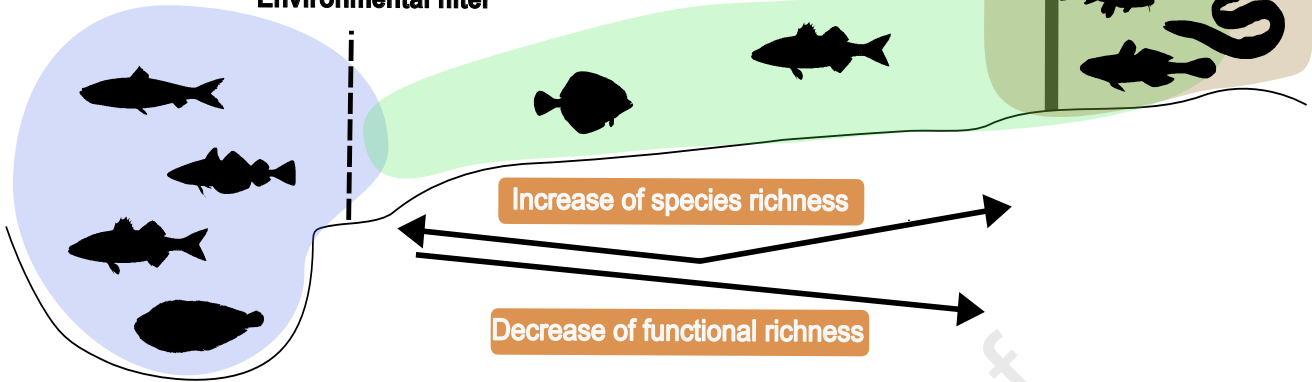


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1 **Estuarine lateral ecotones shape taxonomic and functional structure of**  
2 **fish assemblages. The case of the Seine Estuary, France**

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20 **Abstract**

21 Estuaries are complex ecotones including multiple lateral habitats that play essential functions for fish  
22 assemblages. However, the distribution of fish diversity and community assembly processes remain  
23 poorly documented in these habitats. This paper investigated the taxonomic and functional diversities  
24 of fish assemblages along lateral continuums of three salinity areas over the longitudinal gradient of the  
25 Seine Estuary. We examined fish diversity at a local scale ( $\alpha$ -diversity) and between local scales ( $\beta$ -  
26 diversity) across the lateral habitats (estuarine main channel, tidal marsh, and diked marsh). Overall, the  
27 taxonomic diversity follows a typical ecotone distribution, with the highest richness reported at the  
28 system margins and high species dissimilarity between communities. The decrease of functional  
29 diversity in upper part of the lateral ecotone probably reflects the homogenisation of ecological niches.  
30 Changes in assembly processes between the three salinity conditions suggests that several lateral  
31 ecotones occur in estuaries with complementary functions for fish assemblages.

32 **Keywords:** ecotone concept, transitional waters, fish ecology, taxonomic diversity, functional diversity,  
33 English Channel

34

35

## 36 1 Introduction

37 Transitional areas between contrasted ecological regions or ecosystems can be characterised as  
38 ecotones. These areas, which can occur at large or local spatial scales, are often associated with strong  
39 environmental shifts along ecological gradients (Kark, 2013). They represent locations of strong  
40 interactions between contrasted communities (Kent et al., 1997) with a high rate of changes in structure  
41 or ecological functions (Di Castri et al., 1988). Such processes can be highlighted by investigating the  $\beta$ -  
42 diversity, which attempts to measure the extent of compositional differences between ecological  
43 assemblages. Beta diversity can be partitioned in two different components, i.e., turnover and  
44 nestedness (Baselga, 2010; Legendre 2014). Turnover denotes dissimilarity pattern where some species  
45 replace others as a consequence of environmental sorting and/or spatial and historical constraints  
46 (Leprieur et al., 2009). Turnover can be distinguished from nestedness, which reflects a non-random  
47 process of species loss along gradients where the poorest assemblage is a subset of the richest  
48 assemblage (Ulrich et al., 2009). This pattern is expected to result from various mechanisms such as  
49 selective colonisation, habitat nestedness, or differential species loss related to their environmental  
50 tolerance (Leprieur et al., 2009).

51 Several studies highlighted trends in biodiversity patterns along ecotones, but conflicting conclusions  
52 emerged (see the review of Kark, 2013). At a local scale, some authors showed that biological richness  
53 tends to peak in ecotones, whereas others argued that these areas are poorer in species (Odum, 1953;  
54 Kemp, 2000; Kark et al., 2007; Kark, 2013). At a large scale, a high dissimilarity between assemblages  
55 explained by species turnover is expected because community shifts result from replacement that rely  
56 on species-specific distribution along environmental gradients (Kark, 2013, da Silva Lima et al. 2022). In  
57 this context, estuaries represent interesting study cases as they combine a variety of ecotones (Elliott  
58 and Whitfield, 2011), longitudinal from the sea to the river, and lateral from the estuarine main channel  
59 to lateral habitats.

60 In estuarine ecosystems, abiotic factors (e.g. salinity, oxygen, turbidity, temperature) are major  
61 determinants of the spatial and temporal distributions of species (McLusky et al., 1993; Marshall and  
62 Elliott, 1998; Attril, 2002; Guo and Pennings, 2012). Because estuaries are an interface between the sea  
63 and the river, the estuarine fish assemblages are likely to be composed of marine, freshwater,  
64 diadromous and even resident species (Potter et al., 2015; Whitfield et al. 2022). The pattern of species  
65 diversity ( $\alpha$ -diversity) in estuaries has been described at the local scale by a conceptual model, which  
66 aims at predicting the distribution of fish species along a salinity gradient (Remane, 1934, Whitfield et  
67 al., 2012). This model suggests higher species richness at both poles of the transitional area and a  
68 decrease of richness toward brackish water (Remane, 1934). Concerning  $\beta$ -diversity, the pattern shows  
69 a high dissimilarity in taxonomic structure with a predominance of species turnover (Villéger et al., 2012;  
70 Barros et al., 2014; Henriques et al., 2016; da Silva Lima et al. 2022).

71 The responses of species to environmental gradients are often studied with classical approaches which  
72 aim at describing assemblages through the taxonomic identity of individuals (Jaureguizar et al., 2003;  
73 Barletta et al., 2005; Kolpakov et al., 2010; Nicolas et al., 2010a). However, few studies have addressed  
74 the complementarity of the functional and taxonomic approaches to disentangle the processes  
75 governing community assembly rule (but see Nicolas et al., 2010b; Mouillot et al., 2013; Teichert et al.,  
76 2017; Villéger et al., 2012; Henriques et al., 2016; Maciel et al. 2024). Functional ecology focuses on the  
77 description of species biological traits in communities. These attributes, which can be morphological,  
78 physiological or phenological, are assumed to reflect the influence of species on their environment (i.e.  
79 effect traits) or affect the performances of organisms (i.e. response traits) (Violle et al., 2007). Within  
80 estuaries, the prevailing stressful environmental conditions are expected to decrease functional diversity  
81 ( $\alpha$ -diversity and  $\beta$ -diversity) and promote redundancy in ecological strategies (Villéger et al., 2012;  
82 Baptista et al., 2015; Dolbeth et al., 2016; Teichert et al., 2017).

83 Fish communities are a major biological compartment in estuarine nekton (McLusky and Elliott, 2004).  
84 As a transitional area between contrasted aquatic ecosystems, estuaries play several functional roles for

85 numerous fish species notably thanks to the heterogeneity of environmental conditions and a diversity  
86 of habitats, including subtidal channels, mudflats or tidal marshes (Nagelkerken et al. 2015, Teichert et  
87 al. 2017; Pessanha et al. 2021). They provide migration routes for diadromous species, nursery areas for  
88 marine fishes and permanent habitat for a few resident species (McHugh, 1967; Haedrich, 1983; Elliott  
89 and Hemingway, 2008). In macrotidal systems, estuarine lateral habitats are mainly intertidal, like  
90 mudflats and marshes. These habitats are known to support essential nursery function for marine  
91 juveniles (e.g. sea bass, common sole, plaice, and mullets) (Kneib, 1997; Laffaille et al., 2001; Cattrijsse  
92 et Hampel, 2006; Day et al., 2020). Despite their important functional value, these habitats have been  
93 highly degraded by human activities during the 20th century because of harbour development or  
94 intensive land reclamation (Cattrijsse et al., 2002; Marley et al. 2020). Therefore, accessibility and  
95 connectivity of these habitats have been altered for fish communities (Bice et al. 2023). Functions of  
96 tidal and diked marshes for fish (Cattrijsse et al., 1994; Kneib, 1997; Mathieson et al., 2000; Laffaille et  
97 al., 2000; Laffaille et al., 2001; Hampel et al., 2004; Green et al., 2009) and effects of habitat restoration  
98 on fish and associated functionalities are increasingly studied (Lechêne et al., 2018; Debue et al., 2022).  
99 If the structure of fish assemblages has been widely examined longitudinally in estuaries (Jaureguizar et  
100 al., 2003; Barletta et al., 2005; Selleslagh et al., 2009; Kolpakov et al., 2010; Villéger et al., 2012;  
101 Henriques et al., 2016), the biodiversity patterns along estuarine lateral continuum has not been studied  
102 yet.

103 In this context, we examined community assembly rule shaping fish assemblages, more specifically  
104 diversity patterns, in three distinct habitats (estuarine main channel, tidal marsh and upper-diked marsh)  
105 of a set of lateral continuums of the Seine Estuary (NW France). The consequences of different salinity  
106 conditions on habitat-specific diversity patterns were addressed through the positions of continuums  
107 along the longitudinal estuarine gradient (polyhaline, mesohaline and meso-oligohaline area).  
108 Taxonomic and functional structures of fish assemblages were investigated at two different spatial scales,  
109 i.e.  $\alpha$ - and  $\beta$ -diversity. The aims of this paper are thus to (1) describe the variation of the species and  
110 ecological traits richness between habitats along lateral and longitudinal gradients, (2) investigate the

111 levels of dissimilarity between assemblages and determine the predominant structural processes (i.e.  
112 turnover or nestedness) and (3) test the contributions of environmental and spatial factors to the  
113 variation in fish diversity.

114 We expected high species richness ( $\alpha$ -diversity) in permanently flooded habitats (the estuarine main  
115 channel and diked marsh) due to their greater hydrological stability. The functional traits diversity was  
116 expected to increase in response to habitat connectivity with the marine environment and the diversity  
117 of environmental features (hydrological, trophic and structural factors). We therefore reckon on a high  
118 assemblage dissimilarity between the three habitats, with a predominance of loss of species and  
119 functional traits (nestedness process) in the case of selective colonisation by species originating from  
120 the main channel.

121

## 122 2 Materials and Methods

### 123 2.1 Study site

124 The study was conducted in the Seine Estuary on the northwest coast of France (Figure 1). This system  
125 is one of the three largest French estuaries (160 km long) and is featured by a large semidiurnal  
126 macrotidal range (average amplitude of 8.5 m). Sampling was performed close to the estuary mouth, in  
127 three areas, each area being characterized by a lateral succession from the main estuarine channel to  
128 tidal and then diked marshes. These three areas, hereafter called “sampling areas” (SA#1, SA#2, SA#3;  
129 Figure 1), were located along a longitudinal gradient covering three salinity conditions, i.e. SA#1 was  
130 located in polyhaline waters ( $28,83 \pm 1,12$ ), SA#2 in mesohaline waters ( $17,01 \pm 2,78$ ), and SA#3 in meso-  
131 oligohaline waters ( $15,77 \pm 2,92$ ) (Figure 1). The main channel sampling stations (i.e. two sampling  
132 stations for SA#1 and SA#2, one sampling station for SA#3) were subtidal (Figure 1). The tidal marsh  
133 sampling stations (i.e. three sampling stations for SA#1 and SA#3, two stations for SA#2; Figure 1) were  
134 located in temporally flooded creeks, characterised by cyclic changes in hydrological and physico-  
135 chemical parameters. Tidal marshes connected the main channel and the diked marsh. The diked marsh  
136 sampling stations (i.e. five sampling stations for SA#1 and SA#2, four sampling stations for SA#3) were  
137 featured by the presence of unsinkable dikes and hydraulic valves, which intend to regulate water fluxes  
138 within the web of man-made creeks from the diked marsh. The hydraulic network of the diked marsh is  
139 made up of canals which are supplied by rainwater and a groundwater resurgence from the alluvial plain.  
140 To retain sediment and facilitate navigation in the estuary, a sinkable dike submerged at each tide was  
141 built between the river and the tidal marsh.

### 142 2.2 Fish sampling and associated environmental parameters

143 Fish sampling was conducted during spring (end of May-early June) and autumn (October) during two  
144 years in the main channel and tidal marsh (2020 and 2021; sampling design is detailed in Table A.1).  
145 During autumn, one supplementary sampling station was located in the top of the tidal marsh, near the  
146 unsinkable dyke (SA#1 and SA#3; Table A.1). The diked marshes were sampled during spring during two  
147 years (2020 and 2021; Table A.1) and autumn for one year (2020; Table A.1) in five stations for SA#1 and

148 SA#2. For technical reasons, the sampling could not be conducted during the same period in the diked  
149 marsh of SA#3. Accordingly, historical data from a fishing inventory conducted in spring 2016 in 4 stations  
150 were used as surrogates to complete the dataset. Different sampling methods were used to describe the  
151 fish assemblages of the three habitats because of the heterogeneity of hydro-morphologic conditions,  
152 preventing the use of similar sampling gears. Due to this sampling design, the occurrences of species  
153 were used to minimize the potential bias induced by the use of different sampling gears. Furthermore,  
154 the consistency between sampling sites was assessed by comparing the species accumulation curves  
155 made with the iNEXT package (Hsieh et al.,2016) (Figure A.2). The results demonstrated an acceptable  
156 sampling completeness (>80% of species detection) for each of the three habitats (Figure A.2).

157 The stations located in the main channel were sampled following the standardised monitoring protocol  
158 conducted for evaluating the French transitional waters throughout EU Water Framework Directive  
159 (AFNOR, 2011). The protocol consists of several hauls across the estuary channel using a beam trawl (3  
160 m large, 10 mm mesh size; AFNOR, 2011). Fishes from tidal marshes were sampled using a fyke net (5  
161 mm mesh size, 20 m long and 1.60 m height) set across the main creek. The net was deployed at high  
162 water and sampling conducted during the ebb in order to catch fish leaving the creek. To cover a  
163 maximum range of marsh characteristics, stations were sampled simultaneously in each sampling area  
164 (Figure 1, Table A.1). Nets were verified every 30 min during the sampling and emptied if necessary.  
165 Sampling stopped when the water level was not high enough to cover the net inlet. Diked marshes  
166 stations were sampled using double fyke nets (5 mm mesh size). Fishing gears were positioned in a water  
167 creek for 24 h and 4 replicates were made at each sampling station for each period (Figure 1). All fish  
168 were identified at the species level, measured to the nearest mm (fork length: FL) and released into the  
169 creeks or the main channel following measurement. The list of all identified species is mentioned in the  
170 appendix (Table E.4).

171 During each sampling session, the hydrological parameters (salinity, temperature -°C, and dissolved  
172 oxygen concentration – mg/L) were recorded. Moreover, spatial attributes of stations (i.e. distance from

173 the main channel and bathymetry) were determined using a geographic information system (GIS). The  
174 distance of sampling sites from the main channel (*DistChen*, in m) was recorded by measuring the  
175 distance of the site from the nearest subtidal location. Elevation of sampling sites (*elevation*, in m) was  
176 recorded using Lidar data maps (© Shom-ROL, V20190831) in QGis© software.

### 177 2.3 Fish taxonomic and functional diversity

178 We described changes in fish assemblages along the lateral continuum using the taxonomic and  
179 functional facets of biodiversity. While the taxonomic facet considers all species as equally distinct, the  
180 functional facet accounts for information on species traits to determine their proximity in a  
181 multidimensional functional space (Villéger, 2008). Here the functional facet was examined by assigning  
182 species into three functional guilds, i.e. ecological traits, trophic traits and position of species in the  
183 water column, which are commonly used to describe ecological niches of fish in estuaries (e.g. Henriques  
184 et al., 2017, Teichert et al., 2017; Table E.4). Ecological guilds reflect the way the species use the estuary:  
185 1) the diadromous species that use estuarine habitat as a migration corridor, 2) the estuarine species  
186 that can successfully achieve their entire life cycle in the estuary, 3) the freshwater species that  
187 sporadically use estuarine areas, 4) the marine juveniles that use the estuary as a nursery ground, and  
188 5) the marine species that occasionally use the lower part of the estuary (Elliott et al., 2007; Table E.4).  
189 The trophic guilds reflected the main food resources consumed by species and gathered six categories:  
190 1) suprabenthic invertivorous, 2) benthic invertivorous, 3) planktivorous, 4) omnivorous, 5) herbivorous,  
191 and 6) piscivorous (Power, 1990). The distribution of fish in the water column gathered three categories:  
192 1) benthic, 2) demersal, and 3) pelagic species (Vander Zanden and Vadeboncoeur, 2002; Table E.4).

193 In order to estimate the range of functional traits values of the communities (functional space), we  
194 measured first the pairwise functional distances between each species using Gower's distance (Gower,  
195 1971). Then, the outcomes were synthesised into multidimensional functional space by applying PCoa  
196 (Principal Co-ordinate analysis) on the distance matrix. The first three axes of the PCoa were selected  
197 using the highest *mSD* value from *quality\_funct\_space* function, which provides quantitative metrics for  
198 the quality of the functional space (Maire et al., 2015).

199 Diversity was investigated at both local scale ( $\alpha$ -diversity) and sampling area scale (i.e., between  
200 sampling stations, that corresponds to pairwise  $\beta$ -diversity) to disentangle processes shaping fish  
201 assemblages along the lateral estuarine continuum. For each diversity facet, we used species  
202 presence/absence data (Table E.4). Accordingly,  $\alpha$ -diversity was examined for each sampling station  
203 using taxonomic and functional richness, which did not account for species abundance. The taxonomic  
204 richness was defined as the total number of species observed in a station during a given sampling  
205 session. The functional richness reflects the diversity of ecological guilds in the assemblage and was  
206 assessed by calculating the volume of the functional space filled by the species (Villéger, 2008) with the  
207 *dbFD* function of the FD package (Laliberté and Legendre, 2010). The  $\beta$ -diversity was assessed by the  
208 Sørensen index calculated on presence/absence data. This total dissimilarity ( $\beta$ -diversity) was then  
209 partitioned into two components according to the framework proposed by Baselga (2010). The turnover  
210 of species/traits between two communities was measured using the Simpson dissimilarity index, while  
211 the nestedness component (species loss/gain) was measured with the Sørensen nestedness component  
212 index (Baselga et al., 2012). For each sampling area, the  $\beta$ -diversity value was calculated between each  
213 pair of sampling stations within season (spring and autumn) and year using the *beta.pair* (for taxonomic  
214 dissimilarity) and *functional.beta.pair* (for functional dissimilarity) functions, as implemented in the  
215 *betapart* package (Baselga et al., 2012).

## 216 2.4 Statistical analysis

### 217 2.4.1 Lateral patterns of fish diversity

218 First, we investigated changes in taxonomic and functional richness along the lateral continuum using  
219 General Linear Models (GLMs). For each diversity facet, a model was adjusted to examine the effects of  
220 pairs of habitat-sampling area, their interaction (habitat\*sampling area) and season (spring and  
221 autumn). GLM models were built using *glm* function and the significance levels of parameters were  
222 assessed using an ANOVA test based on a *Chi-square* statistic. Finally, a post-hoc test was performed  
223 between each pair of significant descriptor levels using the *TuckeyHSD* function. In a second step, we

224 used Linear Mixed Models (LMMs) to test for the effects of lateral habitats on the taxonomic and  
225 functional  $\beta$ -diversity values between pairs of habitat stations (main channel – tidal marsh and tidal  
226 marsh – dyked marsh). For each diversity facet and  $\beta$ -diversity component, we adjusted a LMM model  
227 with the pair of habitat-sampling area, interaction of habitat\*sampling area and season as fixed effects.  
228 To prevent non-independency of data when comparing paired stations, models were implemented with  
229 the station as a random effect (Row et al., 2017). The LMMs were built using the *lme* function of the  
230 'lme4' package (Bates et al., 2015). When the data did not meet the assumptions of normality and  
231 variance homogeneity, non-parametric framework based on permutation tests were used on the mixed  
232 linear model to study the significance of differences between groups. Permutation tests were made on  
233 *lme* object with the *PermTest* function of the 'pgrimes' package (Giraudoux et al., 2023).

#### 234 2.4.2 Environmental and spatial drivers of fish diversity

235 Collinearity between environmental descriptors is a common feature of ecotone ecosystems.  
236 Accordingly, we firstly assessed the correlation between variables using the Spearman tests to measure  
237 the degree of information redundancy. The correlation tests revealed some correlations between  
238 descriptors along the main channel-marsh continuum (Figure A.3). Accordingly, we used a variation  
239 partitioning procedure to determine the unique and shared contributions of environmental and spatial  
240 sets of predictors to explain variation in  $\beta$ -diversity values (Borcard et al., 1992). For each diversity  
241 metric, we conducted a partial redundancy analysis with the *varpart* function of the *vegan* package  
242 (Oksanen et al., 2015) to determine the relative influence of environmental (i.e. salinity, oxygen,  
243 temperature), spatial (DistChen and elevation) and temporal (season- spring and autumn) processes.  
244 The proportion of explained variance was assessed through the  $\text{ajdR}^2$  statistic. The significance levels  
245 were assessed using permutation tests on the RDA model built with *dbRDA* function. The effect sizes of  
246 environmental, spatial and seasonal descriptors were represented by the coefficient of each descriptor  
247 to the dbRDA axes (Tables D.3 and D.4).

### 248 2.4.3 Lateral distribution of functional guilds

249 To support our findings on fish functional structure, we used GLM models to examine the fluctuations  
250 in occurrence of the three functional guilds along the lateral continuum for the three sampling areas.  
251 For each functional group, a logistic GLM model was built to test for the effect of habitat type, sampling  
252 area, interaction habitat\*sampling area and season on the group occurrence (i.e. presence/absence).  
253 The significance levels were assessed using ANOVA tests based on the Chi-square statistic. Finally, we  
254 predicted occurrence probabilities of fish functional groups along the lateral gradients for the three  
255 sampling areas by applying *predict.glm* function. The occurrence probabilities between habitats were  
256 illustrated by heatmaps drawn with the 'ggplot' package.

257 All analyses were implemented in R (R Core Team, 2021) within the integrated development  
258 environment (IDE) R-studio.

## 259 3 Results

### 260 3.1 Taxonomic and functional alpha diversities

261 Overall, the taxonomic richness exhibited a concave shape curve in SA#1 and SA#2, where higher  
262 richness values were recorded at the margin of the lateral continuum (i.e. main channel and diked  
263 marshes; Figure 2). In contrast, the taxonomic richness appeared more balanced in SA#3. The species  
264 richness was on average higher in the diked marshes (i.e. until 30 species) in comparison to the two  
265 other habitats (ANOVA,  $P < 0.001$ ; Figure 2; Table B.1). The interactive effect between habitat type and  
266 sampling area on the taxonomic richness was significant (ANOVA,  $P < 0.001$ ), which suggests different  
267 species repartition patterns depending on the sampling area. In SA#2, the minimum species richness  
268 was observed in the tidal marsh, while the maximum values were reported for the diked marsh  
269 (TukeyHSD,  $P < 0.001$ ; Figure 2; Table B.2). In the diked marshes, the taxonomic richness increased in  
270 SA#2 (TukeyHSD,  $P < 0.001$ ; Figure 2).

271 In contrast to the taxonomic richness, the functional richness decreased toward the high part of the  
272 lateral continuum (Figure 2), being significantly lower in the diked marshes in comparison to the tidal

273 marshes and main channel (ANOVA,  $P < 0.001$ ; Table B.1). Within the sampling areas, the functional  
274 richness was lower in the diked marsh of SA#1 (TukeyHSD,  $P < 0.01$ ; Table B.2) and in the tidal marsh of  
275 SA#2 (TukeyHSD,  $P < 0.03$ ; Table B.2) in comparison to the other habitats of the lateral continuum (Figure  
276 2).

277

### 278 3.2 Taxonomic and functional beta diversities

279 The total taxonomic dissimilarity ranged between low (0.13) and high (1.00) values, with the highest  
280 pairwise values reported between main channel and tidal marsh habitats (LMM,  $P < 0.001$ ; Figure 3;  
281 Table C.1). The dissimilarity partitioning revealed that species turnover was lower between the tidal  
282 marshes and the diked marshes than between the tidal marshes and the main channel (LMM,  $P < 0.001$ ;  
283 Figure 3; Table C.3). In contrast, the contribution of turnover and nestedness between tidal marshes and  
284 diked marshes differed between the sampling areas (turnover: LMM,  $P < 0.001$ ; nestedness: LMM,  $P <$   
285  $0.012$ ; Table C.2). In SA#2, the nestedness (Nest) component was the main driver of taxonomic  $\beta$ -  
286 diversity (LMM,  $P < 0.03$ ; Table C.3), whereas the contribution of turnover was dominant in the two  
287 other areas. The nestedness component of taxonomic  $\beta$ -diversity fluctuated seasonally (LMM,  $P < 0.001$ ;  
288 Table C.2), with higher species nestedness in autumn.

289 The total functional  $\beta$ -diversity revealed high dissimilarity in functional traits along the lateral continuum  
290 (total  $\beta$ -diversity  $> 0.60$ ), but values did not differ between the two pairs of habitats (LMM,  $P < 0.08$ ;  
291 Figure 3; Table C.1). The turnover and nestedness processes were equivalent between the two pairs of  
292 habitats (Turnover: LMM,  $P = 0.8$ ; Nestedness:  $P = 0.4$ ; Table C.2). On the contrary, comparison among  
293 sampling areas revealed that the turnover component was lower between tidal and diked marshes in  
294 SA#2 and SA#3 (LMM,  $P = 0.04$ ; LMM,  $P = 0.002$ ; Table C.3).

### 295 3.3 Environmental and spatial drivers of fish diversity

296 The percentages of variance in taxonomic and functional diversity explained by the partial RDAs ranged  
297 from 7 % to 64 % depending on the diversity metric and sampling area (Figure 4). For most of the

298 diversity metrics, the results emphasized that a large proportion of variation was explained by the shared  
299 effect of environmental and spatial descriptors (Environmental  $\cap$  Spatial; Figure 4). For the taxonomic  
300 richness, the variance explained by the model remained low (between 7 and 18 %) and the effects of  
301 descriptors was not significant (Figure 4; Table D.1). For the functional richness, the greatest proportion  
302 of explained variation (between 12 and 46 %) was attributable to the shared contribution of the  
303 environmental and spatial descriptors, especially in SA#1 (SA#1: 46 %; Figure 4). The functional richness  
304 was significantly affected by salinity changes in SA#1 and SA#2 (Figure 4; Table 1; Table D.1).

305 For the taxonomic dissimilarity, the explained deviance ranged from 60 to 65 % (Figure 4), with a large  
306 fraction attributable to the shared contribution of the environmental and spatial descriptors (SA#1 = 54  
307 %, SA#2 = 51 % and SA#3 = 52 % of explained variance). Significant effects of salinity and oxygen were  
308 highlighted for the three sampling areas (Table 1; Table D.2). In addition, a significant effect of the  
309 elevation was identified for SA#1 and SA#2, whereas the distance from the main channel was only  
310 significant for SA#1 (Table 1; Table D.2). Lastly, the results illustrated the significant seasonal effect on  
311 the variation of taxonomic dissimilarity for SA#1 and SA#2 (Table 1; Table D.2).

312 For the functional dissimilarity, the partial RDAs explained a greater proportion of statistical deviance in  
313 SA#1 (43 % of explained deviance; Figure 4). The largest fraction of functional dissimilarity was explained  
314 by the shared part of environmental and spatial descriptors for the three sampling areas (SA#1: 29 %,  
315 SA#2: 10%, SA#3: 17% explained variation). The functional dissimilarity was significantly affected by  
316 salinity for the three sampling areas, and by oxygen and temperature for SA#1 and SA#2 (Table 1; Table  
317 D.2). The results illustrated significant effects of elevation, distance from main channel and season for  
318 SA#1 only (Table 1; Table D.2).

### 319 3.4 Guilds distribution along the lateral continuum

320 The lateral distribution of ecological guilds revealed a similar occurrence pattern regardless of the  
321 sampling area considered (Figure 5, Table E.1). Overall, the occurrence of diadromous species remained  
322 stable between habitats (ANOVA,  $P = 0.3$ ). In contrast, the occurrence of the estuarine species (ANOVA,

323  $P < 0.001$ ) and freshwater species (ANOVA,  $P < 0.001$ ) increased along the lateral continuum, whereas  
324 the occurrence of marine juveniles decreased (ANOVA,  $P < 0.001$ ).

325 The occurrences of benthic (ANOVA,  $P = 0.09$ ) and suprabenthic invertivorous (ANOVA,  $P = 0.07$ ) were  
326 comparable between habitats (Figure 5, Table E.2). Planktivorous fish (ANOVA,  $P < 0.001$ ) declined along  
327 the lateral continuum, while the occurrences of herbivorous (ANOVA,  $P < 0.001$ ) and omnivorous  
328 (ANOVA,  $P < 0.001$ ) increased (Figure 5, Table E.2). The piscivorous fish appeared mainly associated with  
329 the diked marshes (ANOVA,  $P = 0.01$ ; Table E.2). In the main channel and tidal marshes, the occurrence  
330 of omnivorous fish surged toward SA#3 (ANOVA,  $P = 0.001$ ; Table E.2). In the diked marshes, the  
331 occurrence of herbivorous fish increased toward SA#3 (ANOVA,  $P = 0.02$ ; Table E.2).

332 For the water column occupancy, the occurrences of benthic species were stable along the lateral  
333 continuum (ANOVA,  $P = 0.09$ ; Table E.3). On the contrary, demersal species increased along the lateral  
334 habitats (tidal and diked marsh) (ANOVA,  $P = 0.02$ ; Table E.3). Finally, the occurrence of pelagic species  
335 increased in the three habitats towards SA#3 (ANOVA,  $P = 0.001$ ; Table E.3).

#### 336 4 Discussion

337 Species diversity patterns along estuarine ecotones are described by several conceptual models, which  
338 illustrate species distribution along the multiple environmental gradients that shape these ecosystems,  
339 including salinity (Whitfield et al., 2012; Basset et al., 2013; Maciel et al. 2024). Although previous studies  
340 investigated the effects of estuarine ecotones on fish assemblages from the sea to upstream main  
341 channel waters (Jaureguizar et al., 2003; Barletta et al., 2005; Selleslagh et al., 2009; Kolpakov et al.,  
342 2010; Villéger et al., 2012; Henriques et al., 2016), diversity patterns along lateral gradients were never  
343 addressed before. In this context, our study describes how the taxonomic and functional structures of  
344 fish assemblages are structured from the main channel to the upper part of the lateral habitats. In this  
345 purpose, we had to combine datasets produced from different protocols because of the heterogeneity  
346 of hydro-morphologic conditions and associated diverse sampling conditions along the lateral estuarine  
347 ecotones. While the main channel was sampled by an active method (beam trawl), the tidal and diked

348 marshes were sampled using passive fishing gears (fyke nets). Species occurrences were thus used  
349 instead of species abundance in statistical analyses in order to minimize the potential biases. However,  
350 the use of different sampling gears may influence the species observed due to the selectivity of some  
351 methods. For example, the species richness in the main channel is probably underestimated because  
352 beam trawl mainly focuses on benthic and demersal species, while pelagic species are irregularly caught  
353 when raising the trawl. Nevertheless, the species accumulation curves demonstrated an acceptable  
354 sampling completeness (>80% of species detection) for each of the three habitats and for the two  
355 sampling methods (Figure A.2). These limitations should, however, be kept in mind when interpreting  
356 the results. Our findings demonstrate that the succession of lateral habitats strongly structures the  
357 taxonomic and functional fish assemblages. Interestingly, the concave shape of taxonomic richness in  
358 lateral ecotones was comparable to the longitudinal fish diversity shape occurring between marine and  
359 freshwater areas at the estuarine scale (Whitfield et al., 2012). This diversity pattern was characterized  
360 by high species richness in the habitats located on the poles of the ecotone (main channel and diked  
361 marshes) and globally low species number in the transitional areas (tidal marshes). The high taxonomic  
362  $\beta$ -dissimilarity between the main channel and tidal marsh, driven by the turnover component, revealed  
363 the important changes in species composition between subtidal and intertidal habitats (Leprieur et al.,  
364 2009). Despite a high hydrological connectivity, the constraints of environmental factors probably act as  
365 ecological boundaries for several fish species inhabiting the main channel (e.g. brill, tub gurnard, lesser  
366 weever, bib) and lead to the replacement of strict marine species by freshwater species. Such a process  
367 is expected to occur in ecotonal areas where shifts in abiotic factors determine species distribution  
368 (Walker et al., 2003; Villéger et al., 2012; Kark, 2013; Barros et al., 2014; Teichert et al., 2017). In contrast,  
369 turnover was lower between tidal marsh and diked marsh assemblages. These habitats shared more  
370 species (bream, carp, rudd, sand smelt) and nested assemblages seem to occur on lateral habitats.  
371 Nestedness is expected to reflect several ecological mechanisms such as local extinction, selective  
372 colonisation, and species loss related to their environmental tolerance (Ulrich et al., 2009; Leprieur et  
373 al., 2009). On the lateral areas, nestedness illustrates the decline of local species richness from diked

374 marshes to tidal marshes, which can be explained by the constraint of several environmental factors,  
375 including recurrent emersion and huge variability of local conditions (e.g. salinity, oxygen or  
376 temperature).

377 The functional facets ( $\alpha$ - and  $\beta$ -diversity) of the fish assemblages showed a contrasting pattern. The  
378 decline of local richness and the high dissimilarity of ecological traits between habitats suggested that  
379 niche filtering processes occur along the lateral ecotones (Bernard-Verdier et al., 2012; Villéger et al.,  
380 2012; Kraft et al., 2015; Teichert et al., 2017). Indeed, our results highlighted important changes in the  
381 occurrence of functional guilds. Marine juveniles and planktivorous species decreased along the lateral  
382 continuum, whereas freshwater and herbivorous species were promoted by the decline of salinity.  
383 Moreover, only a few diadromous, estuarine and marine juvenile species with omnivorous species from  
384 the main channel seem to be able to colonize the lateral habitats. These observations might be explained  
385 by the homogenisation of environmental conditions (e.g. salinity, turbidity, elevation, substrate type)  
386 and the decreasing prey diversity, which results in a reduction of available ecological niches toward diked  
387 marshes (Macarthur et Levins 1967; Kraft et al., 2015; Dolbeth et al., 2016, Moreno-Valcárcel et al.,  
388 2016; Day et al., 2020).

389 The diversity patterns of fish assemblages differed according to the sampling areas, for each habitat,  
390 probably in response to changes in salinity conditions. Similar findings were already reported in tropical  
391 estuaries, where differences in species and trait composition between habitats are influenced by water  
392 salinity and transparency (Maciel et al. 2024). In the main channel stations, the taxonomic and functional  
393 richness increased toward the estuary mouth, which was consistent with the rising proportion of marine  
394 species in assemblages within polyhaline areas (Whitfield et al., 2012). In contrast, fish assemblages of  
395 lateral habitats showed an opposite trend, which could be explained by the coexistence of several  
396 functional guilds (i.e. freshwater, marine juvenile, diadromous, estuarine). In the meso-oligohaline area  
397 (SA#2 and SA#3), the lateral habitats provide foraging and refuge areas for marine juvenile, estuarine  
398 and diadromous species (e.g. sea bass, sprat, sand goby, thinlip mullet or flounder) and also constitute

399 important shelter from the high salinity and current velocity at high tide for the freshwater species. In  
400 addition, community assembly rules between tidal and diked marshes were mainly explained by  
401 nestedness processes. It is likely that the ubiquitous species (marine juvenile, estuarine and freshwater  
402 species) that use the tidal marshes were able to colonise the diked marshes, where assemblages are  
403 composed of a high proportion of resident freshwater and diadromous species with omnivorous trophic  
404 strategies. Elsewhere, freshwater and diadromous species from diked marshes may also disperse in the  
405 tidal marshes where and when the hydraulic connectivity between the two habitats is made possible.  
406 The hydraulic connectivity and dispersal possibility are known to influence fish diversity (Villéger, 2008;  
407 Peláez and Pavanelli, 2019). In the present case, the diked marshes could play the role of favourable  
408 habitats in estuaries for freshwater and diadromous species, like European eel, by impounding low  
409 salinity water. As a transitional habitat, the tidal marshes can be considered as steppingstones by  
410 temporarily connecting functional patches in estuarine landscape during the estuarine migration of  
411 diadromous, marine and freshwater juveniles (Saura et al., 2014). Furthermore, a seasonal pattern in  
412 community assembly was revealed for lateral habitats (SA#2 and SA#3). In these habitats, the results  
413 illustrated lower taxonomic and functional nestedness during the spring period. This trend probably  
414 reflects the seasonal behaviour of some fish species, such as European flounder, three-spined  
415 stickleback or topmouth gudgeon, that mainly use the tidal marsh during spring as a foraging ground  
416 (Hampel et al., 2004; Green et al., 2009).

417 Our results highlighted contrasting community assembly rules between sampling areas, which can be  
418 linked to different environmental filters and potential connectivity alteration across lateral habitats  
419 (Villéger, 2008). Indeed, the high functional turnover between tidal and diked marshes in the polyhaline  
420 area (SA#1) could reflect different ecological functioning or dispersal limitations for fish (Leprieur et al.,  
421 2009; Villéger et al., 2010). This can result from poor lateral connectivity of the diked marsh in this area  
422 (Leprieur et al., 2009; Villéger et al., 2010; Liu and Wang 2018; Peláez and Pavanelli, 2019). The  
423 intensification of human activity in the Seine Estuary, associated to harbour extension or land  
424 reclamation, has led to a major fragmentation and loss (over 70 %) of highly valuable habitats for fish in

425 the estuarine floodplain (Lesueur, 1999; Le Pape et al., 2007; Rochette et al., 2010). Consequently, a  
426 great proportion of the estuarine lateral connectivity was impacted. This resulted in the isolation of  
427 subtidal refuges at low tide that became relatively distant from the tidal zone and diked marshes. The  
428 proximity and structure of these areas are known to determine the extent and frequency of lateral  
429 habitat utilization by fish and productivity of intertidal areas (Allen et al., 2007; Kneib, 2003, Le Pichon  
430 et al., 2017; Teichert et al., 2018; Bice et al. 2023). Finally, the presence of several dams and hydraulic  
431 infrastructures between tidal and diked marshes seems to restrain further the lateral connectedness  
432 between tidal and diked marshes.

433 To conclude, the consideration of the lateral ecotones appears as a crucial component for the  
434 understanding of fish diversity and associated ecological functions in estuarine habitats. Our study  
435 investigating three habitats along the longitudinal salinity gradient supports the importance of  
436 connectivity between the main channel and estuarine marshes for sustaining a high level of taxonomic  
437 and functional diversity in fish assemblages. The functional relationships among these habitats appear  
438 essential for freshwater fish survival, but also for euryhaline, diadromous and resident species. Among  
439 the multiple fish species generally found in the main channels of estuaries, some will need to migrate  
440 laterally during their estuarine life cycle (seabass, sand goby, thinlip mullet, flounder, European eel,  
441 bream, etc.). In addition, the consideration of different sampling areas shows that variations in diversity  
442 patterns exist along the longitudinal gradient. There are therefore several lateral ecotones with distinct  
443 but complementary ecological functions for estuarine fish communities, depending on their position  
444 along the salinity gradient. For this reason, the conservation of lateral landscapes and its connectivity  
445 with other estuarine areas (particularly the main channel) should be prioritised in management policies  
446 and restoration plans, especially in meso-oligohaline areas and diked marshes, which constitute a unique  
447 component of the estuarine habitat mosaic.

#### 448 **Author contribution**

449 **Matia Pavkovic:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation,  
450 Writing- Original Draft, Visualization. **Alexandre Carpentier:** Conceptualization, Methodology, Validation,

451 Investigation, Writing- Original Draft, Supervision. **Sylvain Duhamel**: Conceptualization, Methodology,  
452 Validation, Investigation. **Laure Carassou**: Validation, Writing- Original Draft. **Jérémy Lobry**: Validation,  
453 Writing- Original Draft. **Eric Feunteun**: Validation, Writing- Original Draft. **Nils Teichert**: Conceptualization,  
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#### 460 **Conflicts of Interest**

461 The authors declare no conflict of interest.

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736 Table

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738 Table 1: Summary of the p. values of the permutation tests from the dbRDA model output for the alpha and beta

739 diversity metrics. Complementary parameters of anova models are described in Appendix D. DistChen parameter

740 stands for the distance of sampling site from the estuarine main channel. Significant values are highlighted in bold.

	Salinity	Oxygen	Temperature	Elevation	DistChan	Season
<b>Taxonomic richness</b>						
SA#1	0.975	0.802	0.522	0.219	0.389	0.186
SA#2	0.127	0.198	0.171	0.354	0.615	0.208
SA#3	0.099	0.446	0.915	0.273	0.649	-
<b>Functional richness</b>						
SA#1	<b>0.001</b>	0.639	0.336	0.439	0.051	0.146
SA#2	<b>0.014</b>	0.251	0.207	0.241	0.425	0.338
SA#3	0.129	0.380	0.948	0.854	0.479	-
<b>Taxonomic dissimilarity</b>						
SA#1	<b>0.001</b>	<b>0.026</b>	0.644	<b>0.002</b>	<b>0.002</b>	<b>0.001</b>
SA#2	<b>0.001</b>	<b>0.027</b>	0.127	<b>0.005</b>	0.614	<b>0.003</b>
SA#3	<b>0.001</b>	<b>0.011</b>	0.081	0.083	0.445	-
<b>Functional dissimilarity</b>						
SA#1	<b>0.001</b>	<b>0.028</b>	<b>0.045</b>	<b>0.026</b>	<b>0.028</b>	<b>0.048</b>
SA#2	<b>0.001</b>	0.614	0.486	0.111	0.311	0.146
SA#3	<b>0.001</b>	<b>0.024</b>	<b>0.045</b>	0.053	0.515	-

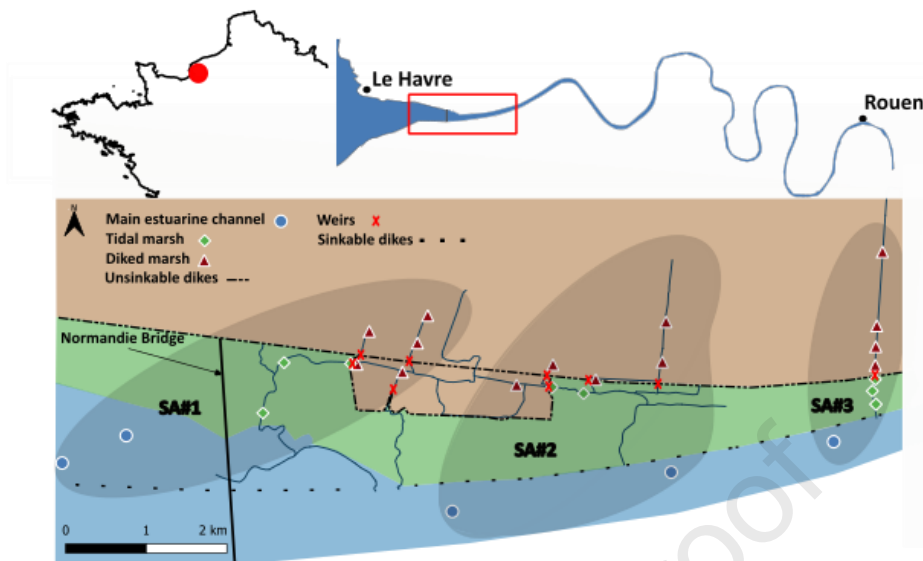
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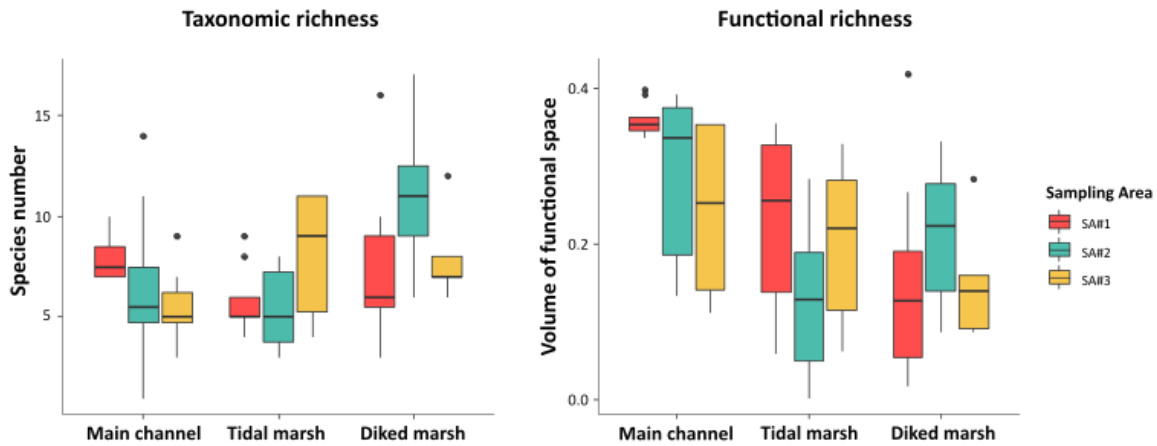
745 Figures



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747 Figure 1: Location of the Seine Estuary (top panel, red dot) and the section of the Seine Estuary where sampling  
 748 was conducted (top panel, red rectangle). The location of the three sampling areas is shown in the bottom panel  
 749 by the grey area on the map (SA#1 polyhaline, SA#2 mesohaline, SA#3 meso-oligohaline). The positions of the  
 750 sampling stations along the lateral continuum in the three habitats and in each sampling area are illustrated by  
 751 blue dots for the main estuarine channel, green diamonds for the tidal marsh and red triangles for the diked marsh.  
 752 Hydrological disruption is represented by the dotted lines indicating the position of sinkable dikes, dashed lines  
 753 indicating the position of unsinkable dikes, and red crosses indicating the positions of weirs.

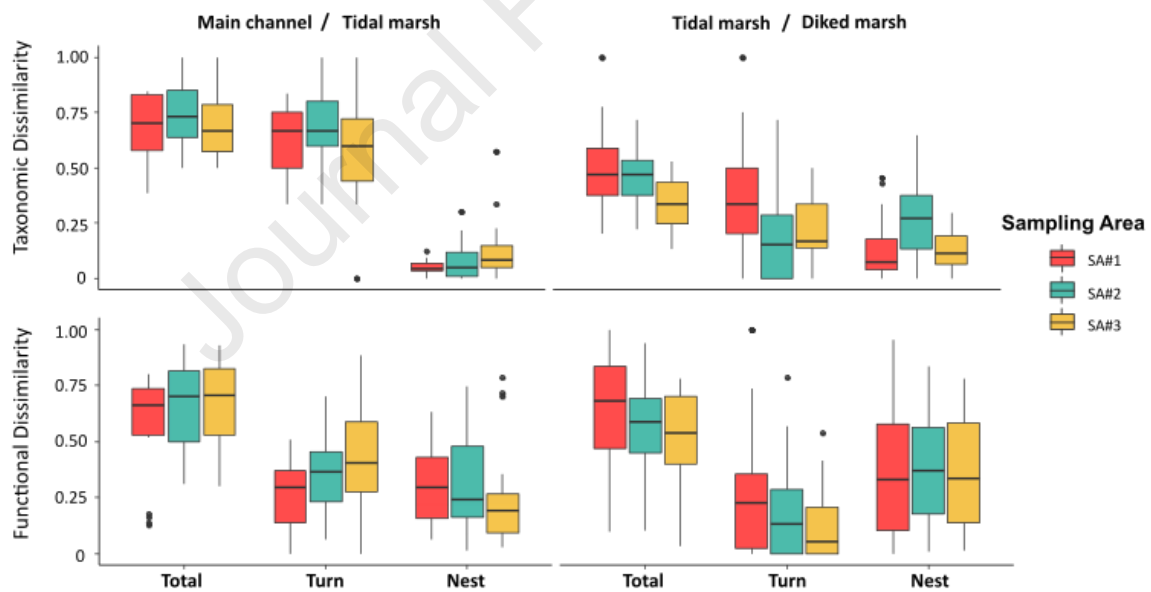
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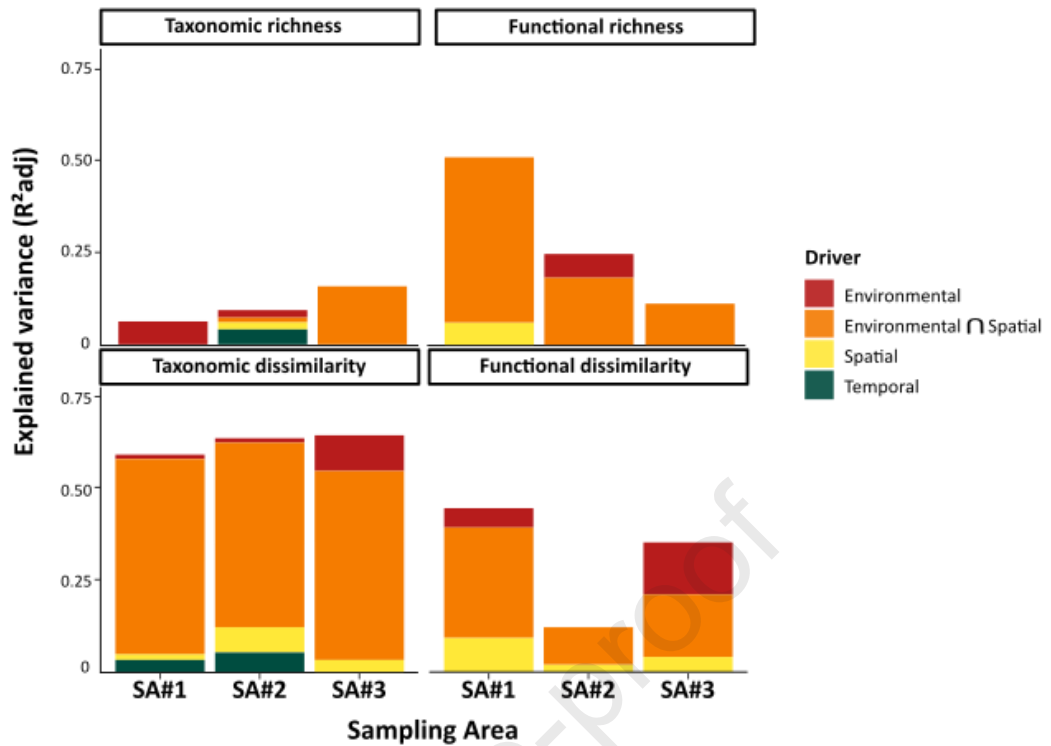
756 Figure 2: Changes in taxonomic richness (left panel) and functional richness (right panel) across the habitats of the  
 757 estuarine lateral continuum. The coloured decomposition of boxplots within habitats represents the different  
 758 sampling areas in the study site (SA#1: polyhaline area; SA#2: mesohaline area; SA#3: meso-oligohaline area).

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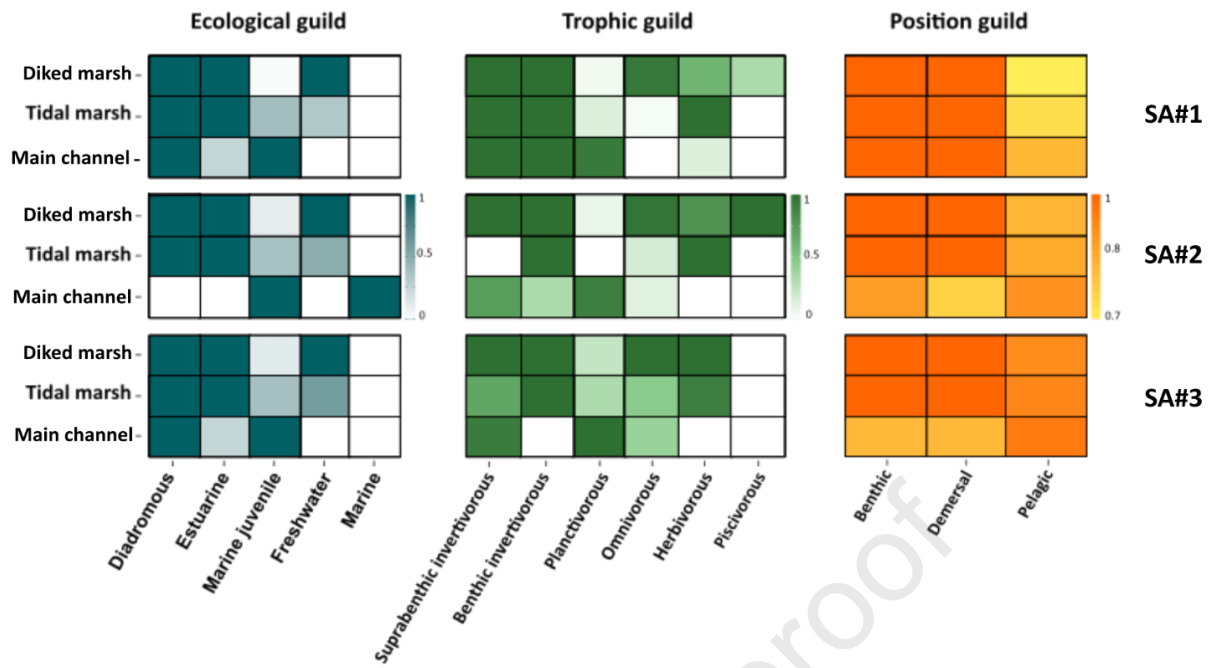
761 Figure 3: Taxonomic (top panel) and functional (bottom panel) dissimilarity in community composition between  
 762 the two pairs of studied habitats along the estuarine lateral continuum (Main channel / Tidal marsh; Tidal marsh /  
 763 Diked marsh). The total dissimilarity (Total) is partitioned into two components: species turnover between  
 764 communities (Turn) and nestedness between communities (Nest). The coloured decomposition of boxplots within  
 765 habitats represents the different sampling areas in the study site (SA#1: polyhaline area; SA#2: mesohaline area;  
 766 SA# 3: meso-oligohaline area).



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768 Figure 4: Effects of environmental, spatial, temporal and shared parts of environmental and spatial descriptors in  
 769 the variation of the diversity facets. The values of bar plots illustrate the proportion of the explained variance  
 770 ( $R^2_{adj}$ ) by each group of descriptors for the taxonomic and functional diversity in the studied area (SA#1:  
 771 polyhaline area; SA#2: mesohaline area; SA#3: meso-oligohaline area).

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774 Figure 5: Lateral distribution of the ecological, trophic and position guilds. The distributions of the functional guilds  
 775 are illustrated by the colour gradients and represent the probability of a guild occurring in each habitat of the  
 776 sampling areas.

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## 779 Appendices

## 780 Appendix A

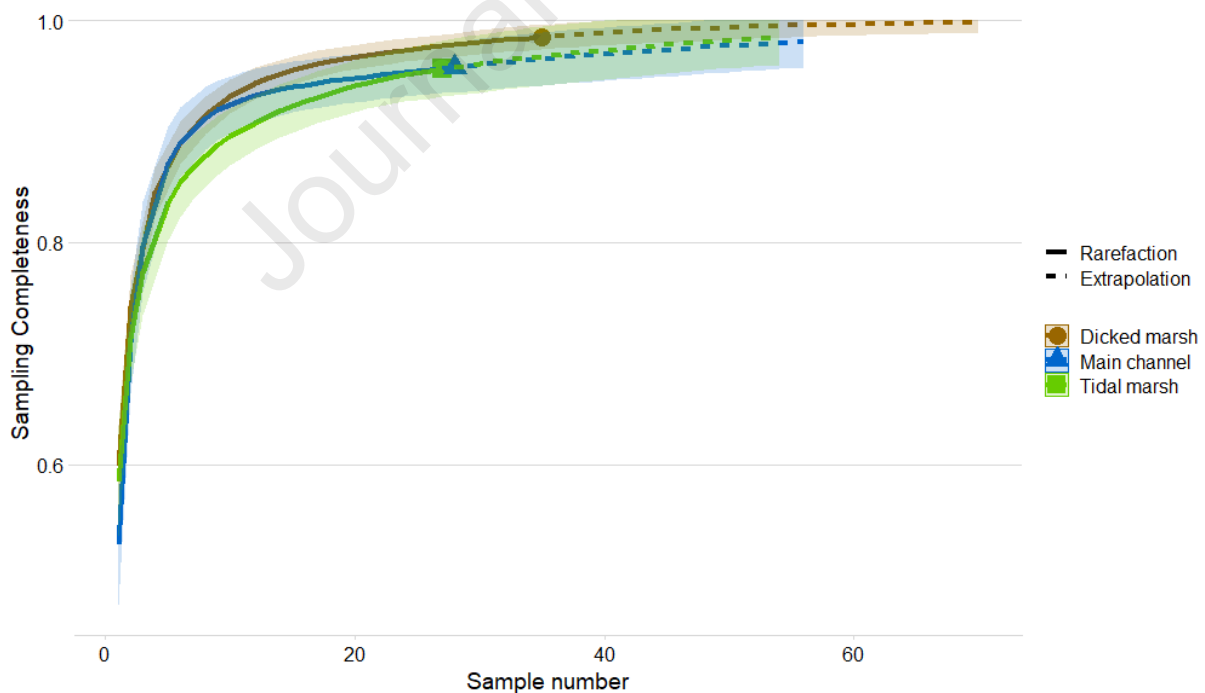
781 Table A.1: Summary of the sampling effort in each habitat of the study site. The number of sampling stations is described for the  
 782 three habitats (main channel, tidal marsh and diked marsh) within each of three sampling areas (SA#1, SA#2, SA#3) for the two  
 783 studied years. The number of replicates per sampling station is mentioned in parentheses. See Figure1 for sampling area  
 784 locations.

Habitat	Sampling Area	Spring			Autumn	
		2016	2020	2021	2020	2021
Main channel	SA#1		2 (1)	2 (1)	2 (1)	2 (1)
	SA#2		2 (2&1)	2 (2&1)	2 (2&1)	2 (2&1)
	SA#3		1 (2)	1 (2)	1 (2)	1 (2)
Tidal marsh	SA#1		2 (4)	3 (4)	2 (4)	3 (4)
	SA#2		2 (4)	2 (4)	2 (4)	2 (4)
	SA#3		2 (4)	3 (4)	2 (4)	3 (4)
Diked marsh	SA#1		5 (4)	5 (4)	5 (4)	
	SA#2		5 (4)	5 (4)	5 (4)	
	SA#3	4 (4)	1 (5)	1 (5)		

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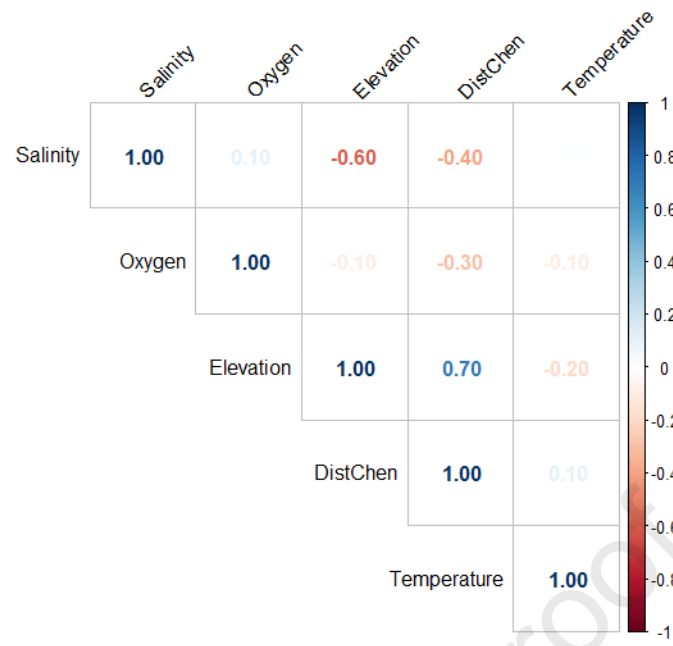
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789 Figure A.2: Species accumulation curves made for the three studied habitats for the two seasons (Main channel = 28, Tidal  
 790 marsh = 27, Diked marsh = 35).

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793 *Figure A.3: Correlation plot between the physico-chemical and spatial descriptors.*

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795 **Appendix B**

796 *Table B.1: Summary of the ANOVA model output for the taxonomic and functional richness. Here, 'sampling areas' (SA#1, SA#2,*  
 797 *SA#3) refer to positions along the longitudinal gradient, while 'habitat' refers to either the main channel, or the tidal and diked*  
 798 *marshes.*

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
<b>Taxonomic richness</b>						
Habitat	2	107.6	53.81	7.692	< 0.001	***
Sampling areas	2	32.4	16.22	2.319	0.104	
Season	2	33.6	16.80	2.402	0.096	
Habitat X Sampling areas	4	154.7	38.67	5.528	< 0.001	***
<b>Functional richness</b>						
Habitat	2	0.290252	96	0.91958	< 0.001	***
Sampling areas	2	0.008231	94	0.91135	0.630	
Season	2	0.010474	92	0.90087	0.555	
Habitat X Sampling areas	4	0.116082	88	0.78479	0.011	*

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800 *Table B.2: Summary of the TuckeyHSD post-test output for the taxonomic and functional richness.*

	diff	lwr	upr	p adj	
<b>Taxonomic richness</b>					
Tidal marsh- Main channel	-0.0515873	-1.7154950	1.612320	0.996	
Diked marsh- Main channel	2.0595238	0.5746657	3.544382	0.003	**
Diked marsh- Tidal marsh	2.1111111	0.6093982	3.612824	0.003	**
Diked marsh X SA#2- Diked marsh X SA#1	3.3011432	0.6980293	5.9042570	0.003	**
Diked marsh X SA#2- Main channel X SA#2	4.0193517	1.0135347	7.0251687	0.001	**
Diked marsh X SA#2- Tidal marsh X SA#2	5.0656414	1.6220454	8.5092374	< 0.001	***
<b>Functional richness</b>					
Tidal marsh- Main channel	-0.0515873	-1.7917263	1.688552	0.997	
Diked marsh- Main channel	2.0595238	0.5066375	3.612410	0.006	**
Diked marsh- Tidal marsh	2.1111111	0.5405979	3.681624	0.005	**
Diked marsh X SA#1- Main channel X SA#1	-0.21900738	-0.34402064	-0.09399411	< 0.001	**
Tidal marsh X SA#2- Main channel X SA#2	-0.14985380	-0.28871232	-0.01099527	0.024	*

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811 **Appendix C**

812 *Table C.1: Summary of the LMM outputs for the taxonomic and functional dissimilarity. "hab" is habitat, "samp.area" is sampling*  
 813 *area.*

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
<b>Taxonomic dissimilarity</b>							
Pairs.hab	0.63967	0.63967	1	46.796	78.007	< 0.001	***
Pairs.samp area	0.02813	0.01406	2	28.582	1.715	0.197	
Pairs.season	0.02584	0.02584	1	29.273	3.151	0.086	
Pairs.hab X Pairs.samp area	0.02877	0.01438	2	47.019	1.754	0.184	
<b>Functional dissimilarity</b>							
Pairs.hab	0.123945	0.123945	1	39.360	3.1806	0.082	
Pairs.samp area	0.018758	0.009379	2	17.430	0.2407	0.788	
Pairs.season	0.008658	0.008658	1	22.311	0.2222	0.641	
Pairs.hab X Pairs.samp area	0.183604	0.091802	2	39.936	2.3557	0.107	

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815 *Table C.2: Summary of the permutation test outputs for the taxonomic and functional dissimilarity. "hab" is habitat, "samp.area"*  
 816 *is sampling area.*

	P value	
<b>Taxonomic turnover</b>		
Pairs.hab	<0,001	***
Pairs.samp area	0,089	
Pairs.season	0,37	
Pairs.hab X Pairs.samp area	0,002	**
<b>Taxonomic nestedness</b>		
Pairs.hab	0,012	*
Pairs.samp area	0,064	
Pairs.season	<0,001	***
Pairs.hab X Pairs.samp area	<0,001	***
<b>Functional turnover</b>		
Pairs.hab	0,8	
Pairs.samp area	0,7	
Pairs.season	0,6	
Pairs.hab X Pairs.samp area	<0,001	***
<b>Functional nestedness</b>		
Pairs.hab	0,4	
Pairs.samp area	0,72	
Pairs.season	0,33	
Pairs.hab X Pairs.samp area	0,35	

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821 *Table C.3: Summary of size effects for the taxonomic and functional facets of dissimilarity.*

	Estimate	Std. Error	df	t value	Pr(> t )	
<b>Taxonomic turnover</b>						
Tidal marsh- Diked marsh	-0.24795	0.07860	51.34882	-3.155	0.002	**
Tidal marsh- Diked marsh X SA#2	-0.24430	0.10256	50.63244	-2.382	0.021	*
<b>Taxonomic nestedness</b>						
Spring	-0.07254	0.03419	42.66584	-2.122	0.039	*
Tidal marsh- Diked marsh X SA#2	0.13698	0.06347	49.74594	2.158	0.035	*
<b>Functional turnover</b>						
Tidal marsh- Diked marsh X SA#2	-0.176567	0.085425	43.479152	-2.067	0.044	*
Tidal marsh- Diked marsh X SA#3	-0.331671	0.103255	41.860364	-3.212	0.002	**

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827 Appendix D

828 Table D.1: Summary of the permutation test from the dbRDA model outputs for the alpha diversity matrix.

	Descriptor	Df	SumOfSqs	F	Pr(>F)	
<b>Taxonomic richness</b>						
SA#1	Salinity	1	0.0003	0.0014	0.975	
	Oxygen	1	0.0115	0.0508	0.802	
	Season	1	0.3865	1.7094	0.186	
	Temperature	1	0.0825	0.3649	0.522	
	Elevation	1	0.3469	1.5344	0.219	
	DistChen	1	0.1693	0.7488	0.389	
SA#2	Salinity	1	1.1486	2.7576	0.127	
	Oxygen	1	0.7716	1.8525	0.198	
	Season	1	0.6515	1.5641	0.208	
	Temperature	1	0.7743	1.8589	0.171	
	Elevation	1	0.4464	1.0717	0.354	
	DistChen	1	0.1035	0.2485	0.615	
SA#3	Salinity	1	1.0755	3.2854	0.099	
	Oxygen	1	0.2087	0.6375	0.446	
	Temperature	1	0.0033	0.0100	0.915	
	Elevation	1	0.4917	1.5020	0.273	
	DistChen	1	0.0785	0.2399	0.649	
<b>Fonctional richness</b>						
SA#1	Salinity	1	0.214074	26.7494	0.001	***
	Oxygen	1	0.002253	0.2815	0.639	
	Season	1	0.009396	1.1740	0.336	
	Temperature	1	0.017807	2.2250	0.146	
	Elevation	1	0.005398	0.6745	0.439	
	DistChen	1	0.035157	4.3930	0.051	.
SA#2	Salinity	1	0.075079	7.7493	0.014	*
	Oxygen	1	0.015926	1.6438	0.251	
	Season	1	0.016907	1.7451	0.207	
	Temperature	1	0.009362	0.9663	0.338	
	Elevation	1	0.013500	1.3934	0.241	
	DistChen	1	0.006318	0.6521	0.425	
SA#3	Salinity	1	0.028633	2.6655	0.129	
	Oxygen	1	0.008897	0.8283	0.380	
	Temperature	1	0.000046	0.0042	0.948	
	Elevation	1	0.000404	0.0377	0.854	
	DistChen	1	0.007649	0.7120	0.479	

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833 Table D.2: Summary of the permutation test from the dbRDA model outputs for the beta diversity matrix.

	Descriptor	Df	SumOfSqs	F	Pr(>F)	
<b>Taxonomic dissimilarity</b>						
SA#1	Salinity	1	2.15048	34.8359	0.001	**
	Oxygen	1	0.22015	3.5663	0.026	*
	Season	1	0.03658	0.5925	0.644	
	Temperature	1	0.64486	10.4462	0.001	**
	Elevation	1	0.42915	6.9519	0.002	**
	DistChen	1	0.30706	4.9741	0.002	**
SA#2	Salinity	1	2.71532	27.2912	0.001	**
	Oxygen	1	0.29918	3.0070	0.027	*
	Season	1	0.64510	6.4838	0.003	**
	Temperature	1	0.17533	1.7622	0.127	
	Elevation	1	0.55799	5.6083	0.005	**
	DistChen	1	0.06703	0.6738	0.614	
SA#3	Salinity	1	2.08549	25.2099	0.001	**
	Oxygen	1	0.38714	4.6798	0.011	*
	Temperature	1	0.20149	2.4357	0.081	.
	Elevation	1	0.19630	2.3730	0.083	.
	DistChen	1	0.07485	0.9048	0.445	
<b>Fonctional dissimilarity</b>						
SA#1	Salinity	1	1.90355	14.1325	0.001	**
	Oxygen	1	0.37043	2.7502	0.028	*
	Season	1	0.35615	2.6441	0.048	*
	Temperature	1	0.32690	2.4270	0.045	*
	Elevation	1	0.46823	3.4763	0.026	*
	DistChen	1	0.42668	3.1678	0.028	*
	SA#2	Salinity	1	0.9447	4.9029	0.001
Oxygen		1	0.1352	0.7017	0.614	
Season		1	0.3102	1.6100	0.146	
Temperature		1	0.1714	0.8895	0.486	
Elevation		1	0.3402	1.7654	0.111	
DistChen		1	0.2241	1.1630	0.311	
SA#3		Salinity	1	1.12613	6.2785	0.001
	Oxygen	1	0.44342	2.4722	0.024	*
	Temperature	1	0.38593	2.1517	0.045	*
	Elevation	1	0.40439	2.2546	0.053	.
	DistChen	1	0.16278	0.9075	0.515	

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839 Table D.3: Summary of size effect of descriptors on the alpha diversity metrics. The size effects are described by the coefficients  
 840 of the descriptor on the dbRda axes.

	Descriptor	dbRDA1
Taxonomic richness		
	Salinity	0.0405
	Oxygen	0.0069
SA#1	Temperature	0.0223
	Season	-0.0237
	Elevation	0.0341
	DistChen	0.0001
	Salinity	-0.0353
SA#2	Oxygen	0.0260
	Temperature	0.0261
	Season	-0.1763
	Elevation	-0.0810
	DistChen	0.0001
SA#3	Salinity	-0.0137
	Oxygen	0.0052
	Temperature	0.0082
	Elevation	-0.0580
	DistChen	0.0001
Functional richness		
	Salinity	0.0010
	Oxygen	0.0106
SA#1	Temperature	0.0098
	Season	-0.0178
	Elevation	-0.0327
	DistChen	0.0001
	Salinity	0.0083
SA#2	Oxygen	-0.0267
	Temperature	-0.0646
	Season	0.0976
	Elevation	0.0081
	DistChen	-0.0001
SA#3	Salinity	-0.0196
	Oxygen	0.0588
	Temperature	0.0197
	Elevation	-0.0164
	DistChen	0.0002

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842 Table D.4: Summary of size effect of descriptors on the beta diversity metrics. The size effects are described by the coefficients  
 843 of the descriptor on the dbRda axes.

	Descriptor	dbRDA1	dbRDA2
Taxonomic dissimilarity			
SA#1	Salinity	0.0054	-0.0055
	Oxygen	0.0018	-0.0011
	Temperature	-0.0006	-0.0056
	Season	0.0705	0.1298
	Elevation	-0.0185	-0.1719
	DistChen	-0.00004	0.0002
SA#2	Salinity	-0.0011	0.0090
	Oxygen	-0.0024	-0.0065
	Temperature	-0.0059	0.0045
	Season	0.0497	0.3175
	Elevation	-0.0177	-0.0046
	DistChen	-0.00007	0.00008
SA#3	Salinity	0.0091	0.0511
	Oxygen	-0.0291	0.2020
	Temperature	-0.0054	0.0251
	Elevation	-0.0219	0.0316
	DistChen	-0.00004	-0.00003
Functional dissimilarity			
SA#1	Salinity	-0.0059	-0.0307
	Oxygen	0.0188	0.0255
	Temperature	0.0047	-0.01042078
	Season	0.0134	0.0696
	Elevation	-0.0482	-0.1371
	DistChen	0.0001	0.00002
SA#2	Salinity	-0.0024	-0.0619
	Oxygen	-0.0137	0.0158
	Temperature	-0.0276	0.0608
	Season	-0.0616	-0.0806
	Elevation	-0.0024	-0.1709
	DistChen	-0.0001	0.0005
SA#3	Salinity	0.0019	0.1038
	Oxygen	-0.0842	0.1243
	Temperature	-0.0449	-0.0708
	Elevation	-0.0227	0.0823
	DistChen	-0.00009	0.00005

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849 *Appendix E*850 *Table E.1: Summary of general linear model outputs for the ecological guilds.*

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
Diadromous	Habitat	2	2.3602	87	8.6283	0.3072	
	Sampling area	2	1.7442	85	6.8841	0.4181	
	Season	1	1.4773	84	5.4067	0.2242	
	Habitat:Sampling area	4	0.0000	80	5.4067	1.0000	
Estuarine	Habitat	2	20.4896	87	33.503	3.554e-05	***
	Sampling area	2	0.2320	85	33.271	0.8905	
	Season	1	0.7117	84	32.559	0.3989	
	Habitat:Sampling area	4	0.0000	80	32.559	1.0000	
Marine juvenile	Habitat	2	17.9926	87	74.784	0.0001239	***
	Sampling area	2	0.0634	85	74.721	0.9688037	
	Season	1	1.5564	84	73.164	0.2121929	
	Habitat:Sampling area	4	2.9062	80	70.258	0.5736479	
Freshwater	Habitat	2	86.973	87	37.393	< 2.2e-16	***
	Sampling area	2	1.385	85	36.008	0.5003089	
	Season	1	13.168	84	22.840	0.0002848	***
	Habitat:Sampling area	4	0.000	80	22.840	1.0000000	
Marine	Habitat	2	4.7720	87	14.410	0.0920	
	Sampling area	2	3.5964	85	10.813	0.1656	
	Season	1	0.0000	84	10.813	1.0000	
	Habitat:Sampling area	4	0.0000	80	10.813	1.0000	

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853 Table E.2: Summary of general linear model outputs for the trophic guilds.

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
Benthic invertivorous	Habitat	2	4.7720	87	14.4098	0.09200
	Sampling area	2	1.4975	85	12.9124	0.47297
	Season	1	3.0070	84	9.9054	0.08291
	Habitat:Sampling area	4	0.0000	80	9.9054	1.00000
Suprabenthic invertivorous	Habitat	2	5.2625	87	27.465	0.07199
	Sampling area	2	4.7076	85	22.758	0.09501
	Season	1	6.1415	84	16.616	0.01320 *
	Habitat:Sampling area	4	0.2575	80	16.359	0.99239
Planctivorous	Habitat	2	17.4801	87	104.427	0.00016 ***
	Sampling area	2	0.4969	85	103.930	0.78002
	Season	1	1.3615	84	102.568	0.24327
	Habitat:Sampling area	4	8.9991	80	93.569	0.06112
Piscivorous	Habitat	2	7.8508	87	24.877	0.01973 *
	Sampling area	2	2.5168	85	22.360	0.28410
	Season	1	3.6410	84	18.719	0.05637
	Habitat:Sampling area	4	0.0000	80	18.719	1.00000
Omnivorous	Habitat	2	38.206	87	82.079	5.055e-09 ***
	Sampling area	2	3.647	85	78.431	0.161423
	Season	1	0.003	84	78.428	0.955393
	Habitat:Sampling area	4	17.139	80	61.289	0.001816 **
Herbivorous	Habitat	2	63.519	87	59.061	1.611e-14 ***
	Sampling area	2	3.404	85	55.657	0.18230
	Season	1	0.001	84	55.656	0.97513
	Habitat:Sampling area	4	10.732	80	44.924	0.02974 *

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855 Table E.3: Summary of general linear model outputs for the position guilds.

Guild	Descriptor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
Benthic	Habitat	2	4.7720	87	14.410	0.092
	Sampling area	2	1.4975	85	12.912	0.473
	Habitat:Sampling area	4	0.0000	81	12.912	1.000
Demersal	Habitat	2	7.2381	87	19.068	0.02681 *
	Sampling area	2	2.2262	85	16.842	0.32854
	Habitat:Sampling area	4	0.0000	81	16.842	1.00000
Pelagic	Habitat	2	2.4065	87	68.275	0.300223
	Sampling area	2	3.1473	85	65.128	0.207284
	Habitat:Sampling area	4	18.0874	81	47.040	0.001186 **

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861 Table E.4: Occurrences per habitat of identified species. The functional guild are shown for ecological (ER : Estuarine, MA : Marine,  
 862 MJ : Marine juvenile, DIA : Diadromous, FW : Freshwater), position (B : Benthic, D : Demersal, P : Pelagic) and trophic guild (SI :  
 863 Suprabenthic invertivorous , BI : Benthic invertivorous, PL : Planktivorous, O : Omnivorous, H : Herbivorous, P : Piscivorous).

Species	Functional guild			Habitat			Habitat distribution
	Ecological	Position	Trophic	Main channel	Tidal marsh	Diked marsh	
<i>Agonus cataphractus</i>	ER	B	BI	1	0	0	Main channel only
<i>Buglossidium luteum</i>	MA	B	BI	1	0	0	
<i>Chelidonichthys lucernus</i>	MJ	B	SI	1	0	0	
<i>Ciliata mustela</i>	ER	B	O	1	0	0	
<i>Echiichthys vipera</i>	MA	B	SI	1	0	0	
<i>Limanda limanda</i>	MJ	B	BI	1	0	0	
<i>Liparis liparis</i>	ER	B	BI	1	0	0	
<i>Pleuronectes platessa</i>	MJ	B	BI	1	0	0	
<i>Scophthalmus rhombus</i>	MJ	B	BI	1	0	0	
<i>Syngnathus sp</i>	ER	D	PL	1	0	0	
<i>Trisopterus luscus</i>	MJ	D	SI	1	0	0	
<i>Aphia minuta</i>	ER	P	PL	1	1	0	Main channel and tidal marsh
<i>Merlangius merlangus</i>	MJ	D	SI	1	1	0	
<i>Anguilla anguilla</i>	DIA	D	O	1	1	1	Common on the three habitats
<i>Clupea harengus</i>	MJ	P	PL	1	1	1	
<i>Dicentrarchus labrax</i>	MJ	D	SI	1	1	1	
<i>Gasterosteus aculeatus</i>	ER	D	BI	1	1	1	
<i>Liza ramada</i>	DIA	D	H	1	1	1	
<i>Osmerus eperlanus</i>	DIA	P	SI	1	1	1	
<i>Platichthys flesus</i>	DIA	B	BI	1	1	1	
<i>Pomatoschistus microps</i>	ER	B	BI	1	1	1	
<i>Pomatoschistus minutus</i>	ER	B	BI	1	1	1	
<i>Solea solea</i>	MJ	B	BI	1	1	1	
<i>Sprattus sprattus</i>	MJ	P	PL	1	1	1	
<i>Ammodytes tobianus</i>	ER	B	PL	0	1	0	Tidal marsh only
<i>Abramis brama</i>	FW	D	BI	0	1	1	Tidal marsh and diked marsh
<i>Atherina boyeri</i>	ER	P	PL	0	1	1	
<i>Blicca bjoerkna</i>	FW	D	BI	0	1	1	
<i>Carassius gibelio</i>	FW	D	O	0	1	1	
<i>Cyprinus carpio</i>	FW	D	O	0	1	1	
<i>Pseudorasbora parva</i>	FW	P	O	0	1	1	
<i>Pungitius pungitius</i>	FW	D	SI	0	1	1	
<i>Rhodeus amarus</i>	FW	D	O	0	1	1	
<i>Rutilus rutilus</i>	FW	P	O	0	1	1	
<i>Scardinius erythrophthalmus</i>	FW	P	O	0	1	1	
<i>Alburnus alburnus</i>	FW	P	PL	0	0	1	Diked marsh only
<i>Carassius carassius</i>	FW	D	O	0	0	1	
<i>Esox lucius</i>	FW	B	F	0	0	1	
<i>Perca fluviatilis</i>	FW	P	SI	0	0	1	
<i>Sander lucioperca</i>	FW	D	F	0	0	1	
<i>Tinca tinca</i>	FW	D	BI	0	0	1	

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1 **Highlights**

- 2       • Lateral ecotones are important functional habitats for estuarine fish communities
- 3       • Numerous lateral ecotones were studied along the estuarine longitudinal gradient
- 4       • Species richness increases at the margins of the lateral ecotones
- 5       • Functional diversity decreases towards upper part of the lateral ecotone
- 6       • Assembly rules differ between habitats in response to environmental constraints
- 7       • Tidal marshes are stepping stones connecting functional patches in estuary

**Declaration of interests**

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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