

## **Predicting fish community responses to environmental policy targets**

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## **Abstract**

The European Union adopted the Water Framework Directive (WFD) in the year 2000 to tackle the rapid degradation of freshwater systems. However, biological, hydromorphological, and physico-chemical water quality targets are currently not met, and identifying successful policy implementation and management actions is of key importance. We built a joint species distribution model for riverine fish in Flanders (Belgium) to better understand the response of fish communities to current environmental policy goals. Environmental covariates included physico-chemical variables and hydromorphological quality indices, while waterway distances accounted for spatial effects. We detected strong effects of physico-chemistry on fish species' distributions. Evaluation of fish community responses to simulated policy scenarios revealed that targeting a 'good' status, following the WFD, increases average species richness with a fraction of species (0.13 to 0.69 change in accumulated occurrence probabilities). Targeting a 'very good' status, however, predicted an increase of 0.17 to 1.38 in average species richness. These simulations indicated that riverbed quality, nitrogen, and conductivity levels should be the focal point of policy. However, the weak response of species to a 'good' quality together with the complexity of nutrient-associated problems, suggest a challenging future for river restoration in Flanders.

## **Key words**

Environmental quality; fish community structure; hydromorphology; joint species distribution modelling; physico-chemistry; species richness

## 1 **Introduction**

2 Freshwater biodiversity is facing a worldwide crisis, with an increasing number of species becoming  
3 critically endangered as a result of direct (e.g. pollution) and indirect (e.g. climate change) anthropogenic  
4 changes (Strayer and Dudgeon 2010). Freshwater species are subject to extinction rates estimated to be five  
5 times higher than those for terrestrial species (Ricciardi and Rasmussen 1999). This rapid loss of freshwater  
6 biodiversity makes it clear that more effective management and successful implementation of policy actions  
7 are imperative to mitigate the degradation of freshwater ecosystems.

8         In order to protect and enhance freshwater systems in Europe, the European Union (EU) adopted  
9 the Water Framework Directive 2000/60/EC (WFD; EC 2000). This directive aimed at achieving a good  
10 ecological status for each EU waterbody by the end of 2015. The assessment of a waterbody's ecological  
11 status is based on a combination of five biological quality elements (i.e. phytoplankton, phytobenthos,  
12 macroinvertebrates, macrophytes, and fish) and supporting hydromorphological and physico-chemical  
13 parameters. Methods to describe biological quality differ between member states, but generally include  
14 taxonomy-based (i.e. species richness, abundance, diversity, community composition) and autoecology-  
15 based (i.e. sensitivity, traits, individual condition) indices for each of the five groups (Birk et al. 2012).  
16 Implementing WFD objectives has been challenging and only 53% of all surface waters achieved a good  
17 ecological status (EEA 2018). Furthermore, improvements in ecological quality during the first  
18 management cycle (2009-2015) were limited as only an additional 10% of all waterbodies reached a good  
19 ecological status (van Rijswick and Backes 2015). Therefore, WFD environmental objectives have been  
20 extended to a second (2015-2021) and third (2021-2027) management cycle (EEA 2018). During these  
21 cycles, identifying successful restoration measures is of key importance (Carvalho et al. 2019). However,  
22 the responses of biological variables, and more specifically fish communities, to restoration have been  
23 highly unpredictable, making it difficult to prioritize and successfully plan restoration projects (Kail et al.  
24 2015; Stoll et al. 2013; Thomas et al. 2015).

25         Several factors have been suggested to explain the variable outcome of restoration measures. First,  
26 the desired environmental change may not have been achieved. Therefore, a significant increase is observed

27 neither in abundance nor in diversity (Frissell and Nawa 1992). Second, restoration may fail to address the  
28 limiting stressor at the appropriate spatial scale, or may meet habitat requirements of only one specific  
29 species or life stage (Briers and Gee 2004). For example, local restoration efforts may fail to address  
30 stressors acting at the catchment scale, such as persistent land use change, inadequate sediment quality, or  
31 other large-scale hydromorphological features such as extensive river straightening and dredging (Lake et  
32 al. 2007; Sundermann et al. 2011). Third, long term effects at catchment scale, such as wide-spread  
33 historical chronic pollution and fragmentation, reduce the number of species present in the regional species  
34 pool by eliminating populations of fragile species. Consequently, local source populations for re-  
35 colonisation are absent (Lake et al. 2007; Sundermann et al. 2011). Fourth, source populations might be  
36 available but new populations might be unable to establish in a suitable environment as migration barriers  
37 or long distances may interfere with dispersal (Stoll et al. 2014). Fifth, biotic interactions, such as  
38 competition, predation, and the presence of food sources potentially play a key role in determining fish  
39 community structure. Although some restoration projects focus on the control of invasive species, these  
40 interactions are generally not taken into account in the planning of river restoration (Jackson et al. 2001;  
41 Wisz et al. 2013). Finally, many freshwater systems are subjected to multiple types of pollution and  
42 degradation. Therefore, tackling one specific stressor may have unexpected or even negative outcomes due  
43 to complex interactions with other stressors (Jackson et al. 2001; Nöges et al. 2016; Teichert et al. 2016).

44 A modelling approach, focusing on responses of fish communities to environmental pollution and  
45 degradation, may provide important insights needed to efficiently restore, protect, and enhance fish  
46 communities. An effective fish community model should consider the following issues in conservation  
47 planning. First, dispersal is important and cannot be neglected (Altermatt 2013). This requires a spatially  
48 explicit model considering the impacts of dispersal and colonization, more specifically the effect of nearby  
49 source populations. Second, the model should explicitly account for species co-occurrence patterns, either  
50 by setting constraints to the number of species that co-occur in a patch (Guisan and Rahbek 2011), or by  
51 estimating species associations and leveraging these when making predictions (Warton et al. 2015). Third,  
52 focusing on the responses of fish communities at the catchment and policy implementation scale may

53 provide new information concerning effective regional management and restoration actions. Many studies  
54 examine local responses to restoration at one or a few locations. Focusing on a larger spatial scale, however,  
55 may shed light on environmental factors limiting restoration success, while providing more information on  
56 the spatial distribution of these factors, potentially guiding management at the regional policy and decision-  
57 making level. Finally, the model output should be easy to interpret by policy makers and governmental  
58 agencies responsible for designing policies and management strategies for riverine systems.

59         In this study, we integrate fish and environmental monitoring data to better understand and quantify  
60 community responses to environmental policy scenarios in Flanders (Belgium). To do so, we use the  
61 Hierarchical Modelling of Species Communities framework (HMSC; Ovaskainen et al. 2017), a joint  
62 species distribution model quantifying community-level responses to the environment. Our approach is  
63 twofold. First, we quantify the relative contribution of environmental pollution and degradation to the  
64 structuring of fish communities across all Flemish watersheds, while accounting for species associations  
65 and spatial processes. This will increase our understanding of general processes structuring fish  
66 communities, while estimating the effect of pollution and degradation on species distributions. Second, we  
67 formulate policy scenarios based on the Flemish physico-chemical and hydromorphological quality targets  
68 under the European Water Framework Directive. We compare the predicted effects of these environmental  
69 quality targets on fish community composition and species richness to better understand fish responses at  
70 the policy implementation scale. Species richness is one of the main metrics used to quantify ecological  
71 quality based on fish communities in Flanders (fish index; Belpaire et al. 2000; Breine et al. 2004), but also  
72 in other EU member states (Birk et al. 2012). Other important criteria of the Flemish fish index include fish  
73 condition and abundance (e.g. number of individuals, biomass, recruitment, number of exotic species), and  
74 trophic composition (e.g. relative abundance of omnivorous, invertivorous, and piscivorous species).  
75 Additionally, expected values take into account river type (i.e upstream zone, barbel and bream zone;  
76 Belpaire et al. 2000; Breine et al. 2004). A sensitivity analysis revealed that fish species richness is an  
77 important metric in defining final ecological quality (Bennetsen et al 2014). However, the effects of policy

78 decisions on fish species richness remain poorly understood. We therefore opted for fish species richness  
79 as the main response variable of the policy simulations.

80

## 81 **Methods**

### 82 **Study area**

83 Flanders, the northern part of Belgium, covers an area of 13 522 km<sup>2</sup> and represents one of the most densely  
84 populated areas in Europe (Fig. 1). Flemish riverine systems belong to eleven river basins draining into  
85 three main rivers, the Meuse, the Scheldt, and the Yser, all of which eventually flow into the North Sea.  
86 Approximately 57 fish species inhabit Flanders, of which 18 are considered non-indigenous (Verreycken  
87 et al. 2007). Fish are exposed to high levels of nutrients, pesticides, and metals resulting from agriculture,  
88 household, and industrial waste. The presence of barriers such as watermills and weirs obstruct migration  
89 and reduces available habitat. Consequently, the quality of Flemish rivers is highly variable.

90

### 91 **Data collection and preparation**

92 *Fish community data* - Fish community data were collected between 2003 and 2017 by the Research  
93 Institute for Nature and Forest (INBO) at 1142 unique sampling locations in the context of the Flemish Fish  
94 Monitoring Network (Van Thuyne et al. 2020). Standardized fish stock assessments were made by electric  
95 fishing (5 kW generator, adjustable output voltage 300-500 V, pulse frequency 480 Hz) in an upstream  
96 direction along 100 m of both riverbanks. The number of electric fishing devices and anodes varied with  
97 river width (Belpaire et al. 2000). Captured fish were identified to species level, counted, and released. All  
98 data is publicly available (Fish Information System, VIS, Van Thuyne et al. 2020). The total fish dataset  
99 included 2965 sampling events for the 1142 locations.

100

101 *Environmental data* - The Flemish Environmental Agency (VMM) provided two environmental datasets  
102 with physico-chemical and hydromorphological data (Table 1). The first dataset was collected as part of

103 VMM's physico-chemical monitoring network. Variables were measured monthly between 2003 and 2017  
104 and include temperature, pH, oxygen concentration, conductivity, Secchi depth, chloride, biochemical and  
105 chemical oxygen demand, nutrients (Kjeldahl nitrogen, ammonium, nitrate, nitrite, total nitrogen, total  
106 phosphorus, orthophosphate), sulfate, and suspended matter (Fig. S1, Table1).

107         The second dataset contains seven hydromorphological indices that describe various aspects of the  
108 structural quality (profile, riverbed, riverbank, flow variation, alluvial processes, longitudinal and lateral  
109 continuity) of 462 waterbodies (Table 1). The quality of each of these parameters is reflected by a score,  
110 ranging from 0 (bad quality) to 1 (excellent quality), which is derived from combinations of  
111 hydromorphological field measurements describing the structural quality of a segment of 100 – 400 m. For  
112 example, the quality score of the riverbed of a specific river section is based on the type of substrate, the  
113 presence of sediment banks, pool-riffle patterns, driftwood and aquatic vegetation. More detailed  
114 information about these indices can be found in the supplements (Table S1).

115  
116 *Data preparation* - Fish and environmental sampling locations overlapped only partially in space and time.  
117 Because we focus on fish communities, the spatio-temporal structure of the environmental datasets was  
118 adjusted to match the sampling design of the fish community data. A physico-chemical sampling location  
119 was considered identical to a fish sampling location whenever both locations were within 100 m on the  
120 same or a directly connected river branch. In other cases, physico-chemical sampling locations were  
121 connected to a fish location when within a 5 km buffer zone at the same river and when no significant  
122 discharge points were present. If multiple physico-chemical sampling locations were present within this  
123 buffer zone, the one closest to the fish sampling location was chosen. A fish sampling event was linked to  
124 a specific physico-chemical sampling event within 90 days before or 14 days after the fish sampling date.  
125 This asymmetric time window was chosen because water quality conditions after the sampling event were  
126 considered less relevant for the occurrence of fish species than water quality conditions before the event.  
127 Again, if multiple options were available, the physico-chemical sampling event closest in time to the fish

128 sampling event was chosen. Next, hydromorphological data was added based on the same criteria used to  
129 match the physico-chemical data to the fish sampling data.

130         Among the 2965 fish sampling events at the 1142 locations between 2003 and 2017, only 1013  
131 could be linked to a physico-chemical and a hydromorphological sampling event, as many environmental  
132 records only included basic physico-chemical parameters (i.e. temperature, oxygen, pH and conductivity).  
133 Additionally, environmental variables that were measured in only few locations were removed (Table 1;  
134 e.g. BOD, SO<sub>4</sub>). This quality filtering resulted in a reduced dataset comprising 695 fish observations at 320  
135 unique sampling locations. In order to minimize the temporal dimension, this dataset was further reduced  
136 to only include events between 2008 and 2012 (2965 fish sampling events at 1142 unique sampling  
137 locations). If a location was sampled multiple times during this timeframe, only the most recent sampling  
138 event was included. The final dataset comprised 218 complete records (i.e. 218 fish sampling events for  
139 218 unique sampling locations), 29 fish species, nine physico-chemical variables (temperature, pH, oxygen,  
140 conductivity, chloride, chemical oxygen demand (COD), Kjeldahl Nitrogen, total nitrogen, total  
141 phosphorus), and seven hydromorphological variables (profile, riverbed, riverbank, flow variation, alluvial  
142 processes, longitudinal and lateral continuity). Among the 29 included fish species, five fishes were  
143 identified as ‘invasive’ (Verreycken et al. 2007) (Table S2). A detailed description of the data preparation  
144 is provided in the supplements (Fig. S2).

145         Prior to further analyses, strongly correlated environmental variables were removed to avoid  
146 collinearity (Pearson correlation coefficient > 0.6; Dormann et al. 2013) (Fig. S3). For the physico-chemical  
147 variable set, we retained four variables: COD, Kjeldahl nitrogen, oxygen and conductivity. Chemical  
148 oxygen demand measures the amount of oxygen used to oxidize organic matter. Kjeldahl nitrogen (hereafter  
149 referred to as nitrogen) is the sum of organic nitrogen, ammonia and ammonium and will be treated as a  
150 proxy for nutrients due to its strong correlation with other nutrient-related variables. Conductivity is a  
151 general water quality parameter and indicates the concentration of ions. For the hydromorphological  
152 dataset, we included three variables thought most relevant for the hydromorphological quality of the  
153 environment (i.e. profile, riverbed, and flow variation), and two variables that quantify connectivity (i.e.



154 longitudinal and lateral continuity) (Table 1, Table S1). The profile index summarizes the width/depth ratio,  
155 variation in width and profile type of the riverbank. The riverbed index combines substrate type and the  
156 presence of sediment deposits, pool-riffle patterns, aquatic vegetation, duckweed, and algae. The flow  
157 variation index includes flow variation and the presence of obstructions to flow. A low score for lateral  
158 continuity results from embankment and the presence of lateral barriers. Longitudinal continuity includes  
159 the presence of interruptions and migration barriers along the measured segments (Table 1, Table S1).

160

### 161 **Joint species distribution model**

162 We built a hierarchical joint species distribution model based on the Hierarchical Modelling of Species  
163 Communities (HMSC) framework described in Ovaskainen et al. (2017). We used probit regression to  
164 model the presence-absence of each fish species at each sampling location. Species environmental niches  
165 were described using the environmental covariates measured at the sampling location level (physico-  
166 chemistry, hydromorphology, and connectivity). We included sampling location (representing the stretch  
167 of 100 m over which the electric fishing was performed), river, and basin as hierarchical random levels,  
168 thus estimating species-to-species association matrices and residual variation at these three levels. Sampling  
169 locations were modelled through spatially structured latent factors to account for spatial autocorrelation  
170 (Ovaskainen et al. 2016). To do so, we first calculated pairwise waterway distances using the Network  
171 Analyst extension in ArcMap 10.7, and then rescaled the resulting distance matrix to x and y coordinates  
172 using Multidimensional Scaling (MDS).

173 The model was fitted using the R-package Hmsc 3.0 assuming the default priors described in  
174 Supporting Information of Tikhonov et al. (2020). Two Monte Carlo Markov chains (MCMC) were run for  
175 150 000 iterations each, out of which the first 50 000 were discarded as transient, and the remaining were  
176 thinned by 100 to yield 1000 posterior samples per chain. MCMC convergence was evaluated by visual  
177 assessment of posterior trace plots, and by computing Gelman diagnostics and the effective size of the  
178 posterior sample. We evaluated the explanatory and predictive power (the latter based on two-fold cross-  
179 validation) of the model by the measures implemented in the R-package Hmsc 3.0: root mean square error

180 (RMSE), the area under the receiver operating characteristic curve (AUC), and the coefficient of  
181 discrimination (Tjur  $R^2$ ).

182

### 183 **Ecological inference from the fitted joint species distribution model**

184 To evaluate the relative importance of the environmental variables (fixed effects) in explaining species  
185 occurrences, we partitioned the variation explained by the model into contributions of each group of  
186 environmental variables and the random effects at each hierarchical level. The random effects represent  
187 variation in species occurrences which cannot be attributed to the environmental variables included, and  
188 represent unmeasured environmental variation and random spatial effects as well as species co-occurrences.

189 To better understand the origin of the random effects, we measured pairwise species associations  
190 at each of the three hierarchical random levels by correlation matrices derived from the loadings on the  
191 latent factors (Ovaskainen et al. 2016). These include information about the positive or negative co-  
192 occurrences of species and yields an indication of the importance of species interactions. A positive residual  
193 correlation indicates that two species co-occur more often than expected from their shared environmental  
194 response, and a negative correlation indicates that two species co-occur less often than expected.

195

### 196 **Model-simulated policy implementation scenarios**

197 We evaluated the response of species richness to two sets of nine policy scenarios, one related to each  
198 environmental covariate (Table 2). Species richness was chosen as the main response variables for these  
199 scenarios, because it represents an important metric under the Flemish implementation of the WFD, and  
200 because the effects of policy decisions on this metric are poorly understood (see Introduction).

201 In the first set of scenarios, the value of the focal variable was set so that it corresponded to ‘good’ quality  
202 according to the EU WFD for each specific sampling location (standards differ depending on river type  
203 which includes variation in size and location). In the second set of scenarios, the value for each  
204 environmental variable was set to a ‘very good’ status, again specific for each river type. Since quality  
205 standards are specific to each member state, the chosen quality values were based on the Flemish WFD

206 targets. The values of the non-focal variables were set to the baseline values representing the observed  
207 values for each sampling location. Some locations already met the required quality standards and were not  
208 included (Table 2). We used the fitted HMSC model to predict posterior-mean species- and site-specific  
209 occurrence probabilities for each scenario, and summarized these predictions in terms of expected species  
210 richness by summing over the species-specific occurrence probabilities.

211

## 212 **Results**

### 213 **Model performance**

214 The model discriminated well between presences and absences for most species (mean AUC = 0.94, s.d. =  
215 0.037, mean Tjur  $R^2$  = 0.35, s.d. = 0.17). The highest coefficients of discrimination (Tjur  $R^2$ ) were observed  
216 for *Lampetra planeri* (0.89) and *Perca fluviatilis* (0.72), and the lowest for *Leucaspius delineatus* (0.066)  
217 and *Platichthys flesus* (0.088) (Table S3).

218

### 219 **Structure of Flemish fish communities**

220 *Variance partitioning* - More variance in species occurrences was attributed to environmental filtering  
221 represented by the fixed effects, than to biotic filtering and random processes represented by the random  
222 effects operating at the sampling location, river, and basin levels (Fig. 2, Table S4). The amount of variation  
223 explained by the fixed effects varied among species, ranging from almost 99% for *Lampetra planeri* to 22.6  
224 % for *Pseudorasbora parva*. Physico-chemistry explained the largest part of the variation (mean = 50.7%,  
225 range = 9.8 – 98.7%). Within the physico-chemical group, conductivity was the most important variable on  
226 average (mean = 34.2%, range = 1.0 – 97.5%), followed by nitrogen (mean = 9.8%, range = 0.9 – 36.4%),  
227 COD (mean = 4.4%, range = 0.2 – 17.9%) and oxygen (mean = 2.4%, range = 0.1 – 6.8%). The  
228 hydromorphological variables explained on average 14.4% of the observed variation in species occurrences  
229 (range = 1.4 – 37.7%) with lateral continuity explaining the most (mean = 4.0%, range = 0.0 – 12.4%),  
230 followed by flow variation (mean = 3.9%, range = 0.8 – 10.7%), riverbed (mean = 2.6%, range = 0.0 –

231 3.7%), profile (mean = 2.3%, range = 0.0 – 4.1%) and longitudinal continuity (mean = 1.6%, range = 0.0 –  
232 3.1%).

233 The random effects acting at the sampling location, river, and basin levels explained 34.9% of the  
234 variation (range = 0.0 – 73.9%). Most variation was explained at the sampling location (mean = 11.2%,  
235 range = 0.0 – 67.6%) and river level (mean = 11.2%, range = 0.0 – 63.8%), followed by the basin level  
236 (mean = 3.3%, range = 0.0 – 15.9%).

237  
238 *Species co-occurrences* - Residual species associations were stronger at the sampling location level than at  
239 the river and basin levels, with most species co-occurring on sampling locations more often than expected  
240 by chance (Fig. 3). At the river level, *Pseudorasbora parva*, *Gasterosteus aculeatus*, and *Pungitius*  
241 *pungitius* co-occurred more often than expected by chance, and this cluster was negatively associated with  
242 another cluster of seven species including *Abramis brama*, *Blicca bjoerkna*, *Gymnocephalus cernuus*,  
243 *Anguilla anguilla*, *Perca fluviatilis*, and *Rutilus rutilus*. At the basin level, we detected a single negative  
244 association between *Rutilus rutilus* and *Gobio gobio*.

245

## 246 **Policy scenarios**

247 *Species richness* - The policy scenarios simulating a ‘good’ status of the environmental variables revealed  
248 limited effects of the physico-chemical quality criteria on species richness (Fig. 4; Fig. S4). Many sampling  
249 locations already met the EU WFD standard for the physico-chemical parameters and were not included in  
250 the policy scenarios (Table 2). For the locations that did not meet the target, the predicted change in species  
251 richness rarely exceeded an increase or decrease of one species on average. Decreasing conductivity levels  
252 led to an average predicted increase in accumulated occurrence probability for 94 out of 96 locations (mean  
253 change = 0.26 range = -0.42 – 1.44). Decreasing nitrogen led to an average increase at all 18 locations  
254 included (mean change = 0.69, range = 0.09 – 3.54). Increasing oxygen levels increased predicted species  
255 richness in 23 out of 37 locations (mean change = 0.02, range = -0.11 – 0.21 ). Decreasing COD levels

256 generally led to a reduction in species richness in 68 out of 81 locations (mean change = -0.20, range = -  
257 1.04 – -0.37).

258 More sampling locations were included in the hydromorphological scenarios because fewer  
259 locations met the standards for these variables. Increasing the quality of the riverbed led to the greatest  
260 predicted improvement in species richness, with an increase in mean predicted species richness in 175 out  
261 of 186 included locations (mean change = 0.29, range = -0.16 – 0.99). Improving profile structure and  
262 longitudinal continuity led to predicted increases in 188 out of 203 (mean change = 0.13, range = -0.25 –  
263 0.56) and 27 out of 36 locations (mean change = 0.11, range = -0.08 – 0.61), respectively. On the contrary,  
264 improving flow variation and lateral continuity had negative average predicted effects (flow variation: mean  
265 change = -0.39, range = -0.08 – -3.27; lateral continuity: mean change = -0.59, range = -0.01 – -1.158 ).

266 Across all environmental variables and locations, improving riverbed quality led to the greatest  
267 predicted increase in species richness (greatest increase for 120 locations), followed by conductivity (45  
268 locations), profile (31 locations), nitrogen (6 locations) and longitudinal continuity (5 locations). For 10  
269 locations, none of the improvements affected predicted species richness or community composition, and  
270 for one locations multiple scenarios had similar positive effects on species richness (Fig. 4).

271 Greater predicted increases in species richness were observed when improving the physico-  
272 chemical and hydromorphological quality to a ‘very good’ status (Fig. 5; Fig. S5). A predicted increase in  
273 species richness resulted from decreasing conductivity (179 out of 185 locations, mean change = 1.29, range  
274 = -1.5375 –4.29), decreasing nitrogen input (123 out 126 locations, mean change = 0.80, range = -0.1285 –  
275 5.469), and increasing oxygen levels (66 out of 95 locations, mean change = 0.04, range = -0.2577 0.374).  
276 For the hydromorphological variables, improving riverbed quality led to a predicted increase in species  
277 richness (196 out of 208 locations, mean change = 0.53, range = -0.1140 – 1.429). The same was true for  
278 improvement of the river profile (203 out of 214 locations, mean change = 0.29, range = 0-0.7200 – 0.690),  
279 and longitudinal continuity (53 out of 71 locations, mean change = 0.13, range = -0.0918 – 0.856). However,  
280 increasing flow variation and lateral continuity generally led to a predicted reduction in species richness

281 (flow variation: 186 out of 191 locations, mean change = -0.64, range = -3.97 – 0.775; lateral continuity:  
282 168 out of 170 locations, mean change = -0.65, range = -2.12 – 0.01192).

283 When we improved quality to the ‘very good’ standard, the role of physico-chemistry became more  
284 important compared to the previous set of predictions (Fig. 5). Variables predicted to lead to the greatest  
285 improvements included conductivity (greatest increase in species richness for 115 locations), riverbed  
286 quality (61 locations), nitrogen (36 locations), and profile (5 locations). A lack of predicted improvement  
287 across all scenarios occurred for one location only.

288  
289 *Species-specific responses* - The predicted responses to most restoration scenarios differed among species,  
290 but we detected no consistent difference between native and invasive species (Fig. S6). While most species  
291 responded positively to a reduction in conductivity, eight species responded negatively (*Platichthys flesus*,  
292 *Abramis brama*, *Sander lucioperca*, *Anguilla anguilla*, *Blicca bjoerkna*, *Perca fluviatilis*, and  
293 *Gymnocephalus cernuus*). Species responses to an increase in oxygen concentration were limited and  
294 inconsistent across species: the occurrence probability increased for half of the species, while *Tinca tinca*,  
295 *Cyprinus carpio*, *Rhodeus amarus*, *Esox lucius*, *Perca fluviatilis*, *Scardinius erythrophthalmus*, *Rutilus*  
296 *rutilus*, *Pseudorasbora parva*, and *Carrasius gibelio* exhibited negative responses. The occurrence  
297 probability of almost all species responded positively to a reduction in nitrogen concentration, except for  
298 *Lampetra planeri* and *Carassius gibelio*. Predicted responses to increases in riverbed and profile quality  
299 also differed across species. Species occurrence probability generally decreased following an increase in  
300 lateral continuity and flow variation quality. Occurrence probability increased for all species as a response  
301 to an increase in longitudinal continuity except for *Anguilla anguilla*.

302

### 303 **Discussion**

304 Physico-chemical variables emerged as the main drivers of fish community structure in Flanders.  
305 Evaluation of policy scenarios targeting a ‘good’ status according to the European Water Framework

306 Directive (EU WFD) revealed that current environmental quality standards (i.e. targeting ‘good’ status for  
307 physico-chemical and hydromorphological variables) may be insufficient to improve species richness. The  
308 greatest predicted improvement resulted from more ambitious policy actions improving environmental  
309 quality to a ‘very good’ status, involving management actions reducing conductivity and nitrogen levels,  
310 and improving riverbed structure. In the following, we discuss the effects of physico-chemical and  
311 hydromorphological quality, biotic interactions, and spatial processes on community assembly in Flemish  
312 riverine fish, and provide recommendations for regional policy targets and management goals.

313

### 314 **Drivers of community assembly**

#### 315 *Physico-chemistry as the main determinant of community composition*

316 The distribution of Flemish fish species was well explained by the variables describing abiotic  
317 environmental conditions, suggesting that environmental filtering plays an important role in fish  
318 community assembly. This result is well supported in the literature (e.g. Blanchet et al. 2014; Cilleros et al.  
319 2016; Jackson et al. 2001). Physico-chemical conditions constituted a particularly strong environmental  
320 filter. Some studies reported similar results while others have instead reported a strong effect of climate and  
321 hydromorphology on species distributions (e.g. Dahm et al. 2013; Helms et al. 2009; Schmutz et al. 2015).  
322 We must note here that hydromorphology was incorporated into the analyses through quality indices  
323 summarizing several criteria. This choice might have obscured the relationship between fish diversity and  
324 some hydromorphological variables underlying these criteria.

325

#### 326 *Does variance explained by latent factors represent biotic interactions?*

327 The variation explained in the distribution of 11 out of 29 fish species was almost fully accounted for by  
328 environmental filtering, and particularly by the physico-chemical covariates. Most species in this group are  
329 present at less than 5% of the sampling locations. *Lampetra planeri*, *Salmo trutta fario*, *Leuciscus leuciscus*,  
330 *Cottus gobio*, and *Barbatula barbatula* are strongly affected by poor water quality as shown by their  
331 individual tolerance values, indicating medium to high water quality demands (Belpaire et al. 2000; Breine

332 et al. 2004). Previous studies also reported that the narrower the environmental tolerance of a species, the  
333 better and more accurate the modelling results (Bennetsen et al. 2016; Sundermann et al. 2015). *Lampetra*  
334 *planeri* and *Cottus gobio* are extremely vulnerable in Flanders and their distributions have been constrained  
335 by the lack of pristine rivers. However, structural quality and the presence of specific substrates also impact  
336 the distribution of these species, which is not reflected by our results (Belpaire et al. 2000). *Alburnus*  
337 *alburnus*, *Umbra pygmaea*, and *Lepomis gibbosus*, which are species with lower water quality demands,  
338 may perform better at polluted locations, possibly due to release from competitors and predators (Belpaire  
339 et al. 2000; Breine et al. 2004). For 11 other fish species, random effects explained more than 50% of the  
340 variation in their distribution. This group consists of more generalist species. *Pungitius pungitius*,  
341 *Gasterosteus aculeatus*, *Perca fluviatilis*, *Blicca bjoerkna*, *Pseudorasbora parva*, and *Carassius gibelio* are  
342 more tolerant to pollution and disturbed environments (Breine et al. 2004; Raat 2001). These species are  
343 probably less constrained by poor water quality and thus more affected by biotic interactions, spatial  
344 processes, or unmeasured covariates.

345         To capture the influence of such random processes, our model included latent factors which model  
346 variation of occurrence not explained by the environmental variables. Some species co-occurred more often  
347 at the sampling location level than expected by chance. Predominantly positive associations suggest that  
348 this pattern reflects shared responses to unmeasured covariates, rather than direct ecological interactions.  
349 Other studies detect similar patterns and suggest that biotic filtering is, in general, less important than  
350 environmental filtering (Giam and Olden 2016; Jackson et al. 2001), especially in highly disturbed  
351 environments (Giller and Malmqvist 1998). Moreover, using co-occurrence to make inferences about  
352 ecological interactions remains questionable (Blanchet et al. 2020). At the river level, some species were  
353 positively associated and others negatively. Most potentially interacting species were those for which the  
354 environmental covariates explained less variance, again suggesting that these residual associations may  
355 reflect responses to unmeasured covariates. Potentially important unmeasured covariates at the sampling  
356 location level include pollutants (e.g. heavy metals and pesticides), links with other biological groups (e.g.  
357 macro-invertebrates acting as a food source, or the presence of vegetation) or additional



358 hydromorphological covariates (e.g. flow rate and substrate type). Unmeasured variables at the river level  
359 may include the effect of variation at a larger spatial scale, for example the effect of migration barriers,  
360 which dramatically alter hydrodynamic properties.

361

### 362 *The importance of spatial processes*

363 Some variation explained by the latent factors is likely to reflect unexplained spatial processes impacting  
364 fish communities (Altermatt 2013; Radinger and Wolter 2015). In addition, the effect of migration barriers  
365 should be captured by the longitudinal continuity variable. However, this index focuses on small-scale  
366 connectivity only (e.g. the presence of a migration barrier within the sampled river stretch) and scored well  
367 for most sampling locations. Migration barriers such as watermills and weirs represent a significant problem  
368 globally (Grill et al. 2019). Barriers are not included among the model predictors, but may explain the  
369 distribution of migratory species such as *Anguilla Anguilla* and *Salmo trutta.*, However, weirs and  
370 watermills in Flanders have been shown to also affect population connectivity for non-migratory species  
371 (Raeymaekers et al. 2008).

372

### 373 **Recommendations for regional policy targets and management goals**

#### 374 *Are current quality criteria sufficient?*

375 The policy scenarios increasing environmental quality up to a ‘good’ standard according to the WFD had  
376 very limited predicted impact on the fish communities in terms of average species richness. Improving the  
377 hydromorphological quality to a ‘good’ status would lead to the greatest increase in species richness for  
378 most of the locations. Increasing environmental quality to a ‘very good’ status led to greater predicted  
379 increase in average species richness. Here, species richness at most locations would benefit most from  
380 improving the physico-chemical quality. For instance, half of the locations would benefit most from a  
381 reduction in either conductivity or nitrogen to a ‘very good’ status suggesting that a ‘good’ physico-  
382 chemical status might not be sufficient to significantly increase species richness.

383 Nutrient enrichment remains a major issue in Europe (EEA 2012; Grizzetti et al. 2017). However,  
384 improving nutrient levels to a ‘very good’ standard may be overly ambitious for the heavily polluted  
385 Flemish rivers. Past actions in Flanders targeting waste-water treatment have substantially increased fish  
386 diversity and abundance. However, a sustained reduction of the nutrient load, with agricultural run-off and  
387 overflows of household waste water as the primary source, remains challenging (Filoso and Palmer 2011;  
388 Grizzetti et al. 2011). Additionally, the source of enhanced conductivity is difficult to trace; it has been  
389 attributed to dissolved salt ions and inorganic material from marine sources (especially in the lowland  
390 polders and Scheldt estuary), diffuse sources from runoff such as phosphate and nitrate-based fertilizers,  
391 road salting, and point sources of industrial pollution (VMM 2019; Zang et al. 2019). The wide range of  
392 sources and natural origin in some river systems make conductivity a difficult variable to control.

393 Our results do not only confirm the importance of nutrients but also illustrate the complex nature  
394 of the various stressors affecting riverine systems (Jackson et al. 2016; Teichert et al. 2016). Furthermore,  
395 improving hydromorphological and more specifically riverbed quality to a ‘very good’ standard seems  
396 unfeasible as many rivers have been heavily modified. Hence, reaching targets will require large-scale and  
397 costly restoration actions such as channel reconfiguration, reconnecting floodplains, and the removal of  
398 migration barriers (Wohl et al. 2015). A low score for riverbed quality results from the lack of sediment  
399 banks, pool-riffle patterns, dead wood and vegetation, which are the result of the absence of natural river  
400 dynamics. This is a common problem across Europe and almost half of all waterbodies with poor quality  
401 experienced strong habitat alterations (EEA 2012). Except for reduced nutrient concentrations, which leads  
402 to the largest increase in species richness in the western part of Flanders, there was no obvious spatial  
403 structure in the predicted relative success of various restoration actions. This implies that management  
404 action are most likely effective when regional policy are combined with local management needs.

405 Interestingly, species richness is predicted to decline in response to an increase in flow variation  
406 and lateral continuity. The flow variation index does not directly include flow velocity, but includes local  
407 flow variation and the impoundment level of the river. Flow velocity, however, has often been identified as  
408 a strong determinant of fish community structure, where high flow rates may eliminate smaller species or

409 species which limited swimming capacity (e.g. Jackson et al. 2001; Toth et al. 2019). Lateral continuity, on  
410 the other hand, represents the connection between rivers and the surrounding floodplains. A stronger  
411 connection affects productivity and community composition by for example altering carbon composition  
412 and oxygen levels (Fernandes et al. 2014). A well connected floodplain is generally expected to increase  
413 species richness (Bolland et al. 2012; Paillex et al. 2009). For both parameters, values for the sampling  
414 locations were dichotomous and hence, either good (close to 1) or bad (close to 0). Moreover, the model  
415 was defined based on a dataset with small variation for both parameters, potentially suggesting that the  
416 observed effect result from poor sensitivity to these parameters. A true negative effect, however, may be  
417 explained by a strong shift in habitat conditions, following a simulation from a bad to a good standard,  
418 which in turn negatively impacts the present fish community.

419         When focusing on species-specific responses to the policy scenarios, all species responded  
420 similarly to selected variables (conductivity, nitrogen, flow variation, longitudinal and lateral continuity),  
421 but not to others (oxygen, COD, riverbed and profile). This indicates that decreasing conductivity and  
422 nitrogen levels would benefit all species across all basins, while focusing on the other variables may have  
423 a greater effect on individual species on a more local scale. Additionally, there was no coherent difference  
424 between the response of native and invasive species (e.g. *Pseudorasbora parva*, *Lepomis gibbosus*, *Umbra*  
425 *pygmaea*), suggesting that invasive species do not consistently react differently to environmental drivers.  
426 This implies that the abundance of alien fish species in general does neither benefit from general measures  
427 nor does it decrease (Eros 2007; Wohl et al. 2015).

428

#### 429 *General recommendations and future directions*

430 We quantified responses of fish communities to policy implementation scenarios across all basins within  
431 one administrative region and thus focused on a broad policy perspective, while also including local  
432 responses. By doing so, we allow local managers to optimize their management strategy and to adjust  
433 regional policy measures and decision-making, by for example setting and adjusting current water quality  
434 standards. Overall, the outcome of our model makes it clear that tackling high nutrient and conductivity

435 levels is essential. General policy advice should be adjusted to match this need because current quality  
436 targets may not capture the complete range of standards to which ecological quality will improve.

437 Our chosen modelling approach (HMSC) provided a solid framework for modelling complex  
438 dendritic systems such as rivers, adding to the available modelling approaches used as decision support  
439 tools (Bennetsen et al. 2016; Guse et al. 2015). A strength of this framework is the inclusion of both species  
440 associations and spatial processes, and the possibility of evaluating both species-specific and community-  
441 level responses to the environment. Explicit consideration of community-level responses allowed us to  
442 successfully model the distribution of rare species such as *Lampetra planeri* that were present at a limited  
443 number of sampling locations (Ovaskainen et al. 2017). Additionally, clear output in the form of  
444 informative maps should be useful tools for river managers.

445 Several challenges and problems emerged during data compilation, that could guide changes in  
446 ongoing monitoring efforts. Many data points had to be excluded due to incompleteness and differences in  
447 sampling strategies between environmental agencies. One general suggestion is therefore to collect data  
448 coherently to the fullest possible extent, as this study shows that monitoring data can be successfully used  
449 to make inferences about community structure and management strategies. Additionally, primary  
450 hydromorphological data (e.g. river width, substrate type, flow velocity) could not be included due to  
451 incompleteness. An additional future challenge includes the explicit modelling of migration barriers, as our  
452 approach to include local continuity indices might not be sufficient. Moreover, a model focusing on large  
453 scale patterns cannot include all complex and fine scale aspects, losing some realism for specific restoration  
454 actions at the local level. In future studies, our model can be easily adjusted to include variation at a finer  
455 scale with consideration of local-scale effects.

456

## 457 **Conclusion**

458 Joint species distribution modelling in combination with monitoring data can be successfully applied to  
459 understand responses of fish communities to pollution and disturbance, while accounting for species  
460 association and spatial effects. It is clear that physico-chemical quality plays an important role in heavily

461 degraded systems. Consequently, decreasing nutrient and conductivity levels, and restoring natural river  
462 dynamics should be the focal points of policy planning in Flanders. All these actions should explicitly  
463 consider the needs of biological communities.

464

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471

#### 472 **Author's contribution**

473 ID, JR, EB, GVT and FV designed the study. ID, EB, ØO, FC, JR and OO analysed the data. ID led the  
474 writing of the paper. All authors contributed to the writing and approved the final version for publication.  
475 The authors declare that they have no competing interests. Informed consent was obtained from all  
476 individual participants included in the study.

477

#### 478 **Data and code availability**

479 Data will be made available at Dryad Digital Repository. Code will be made available after acceptance.

480

#### 481 **Ethical approval**

482 All applicable institutional and/or national guidelines for the care and use of animals were followed.

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623 **Figures**

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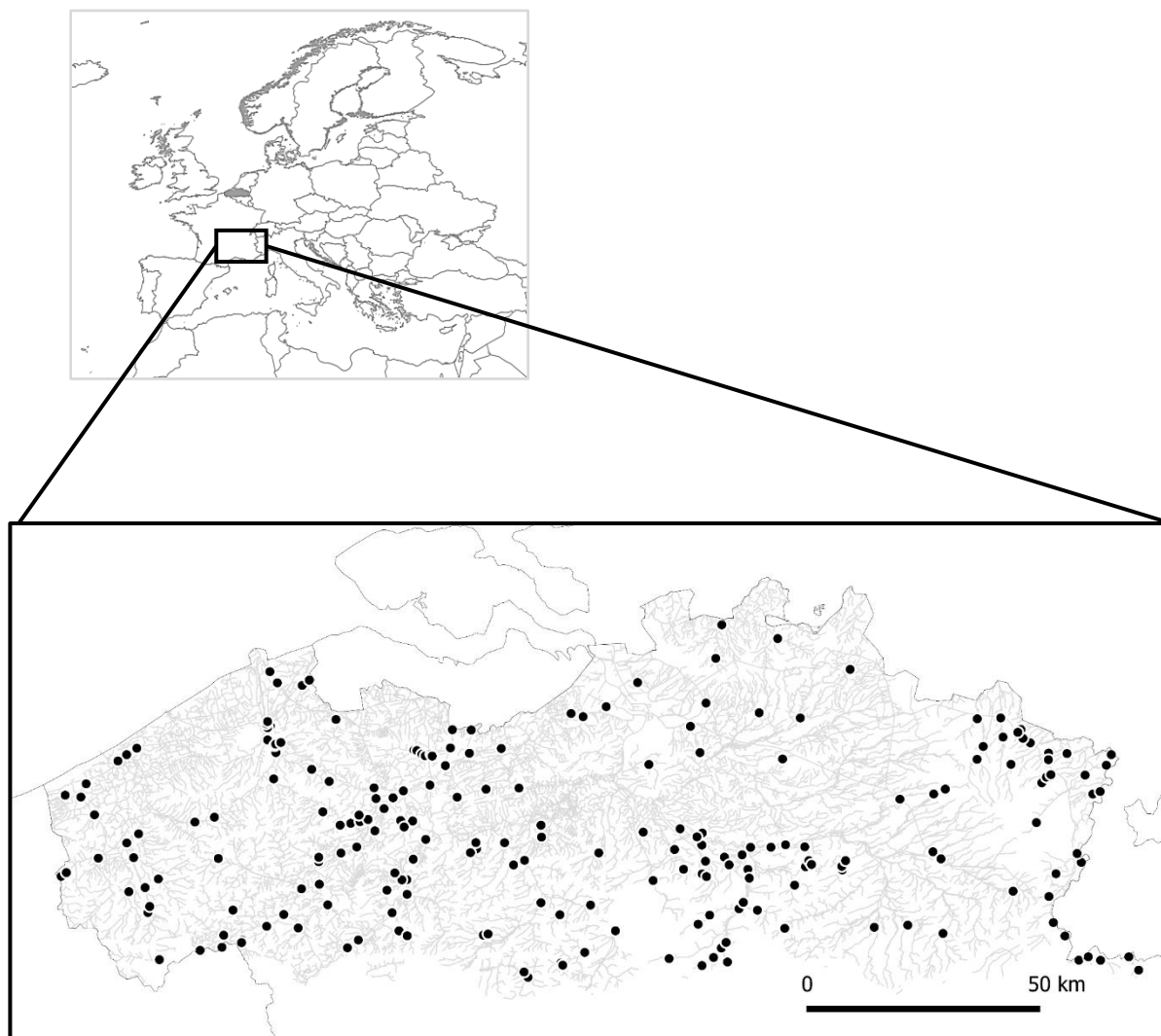
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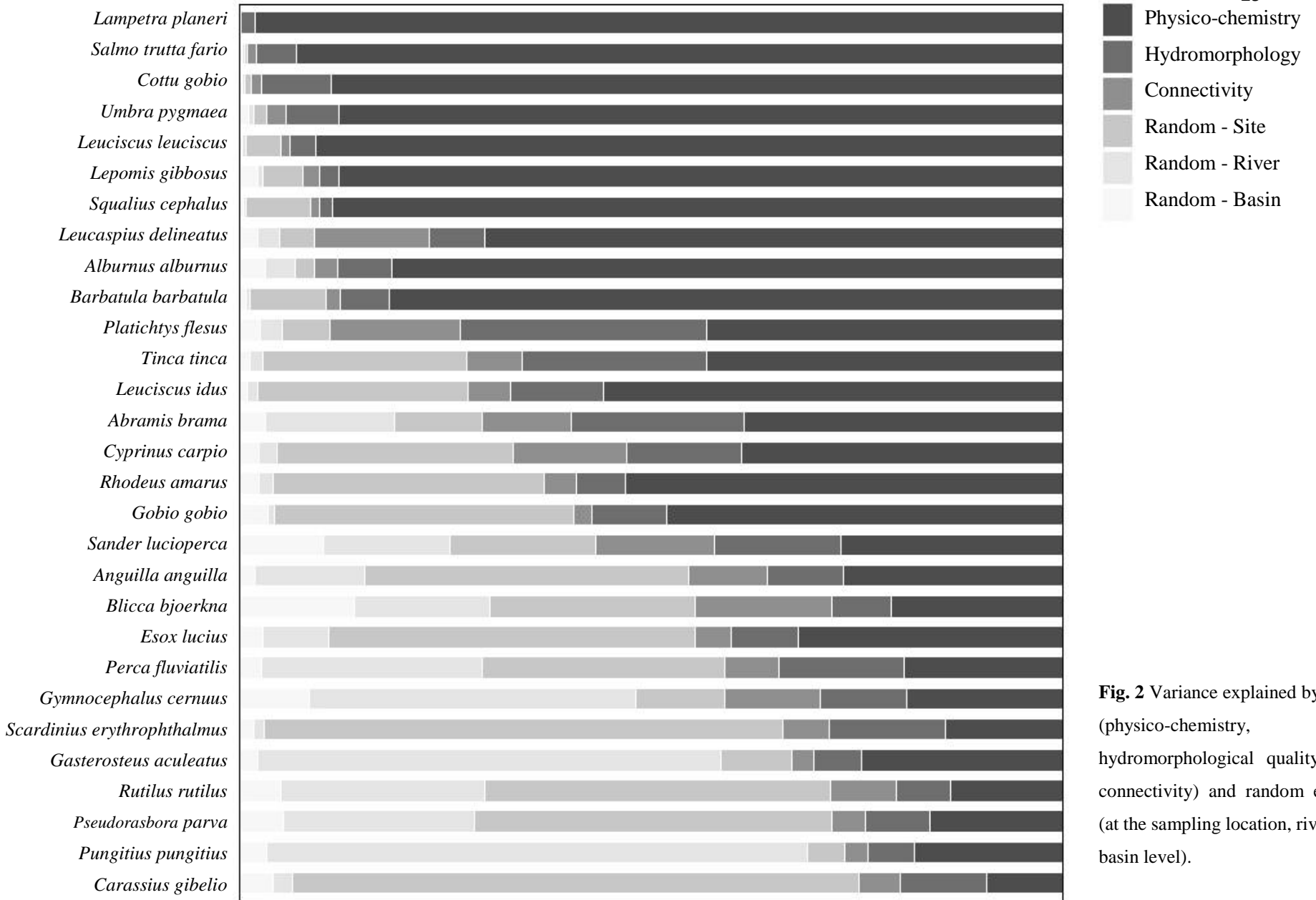
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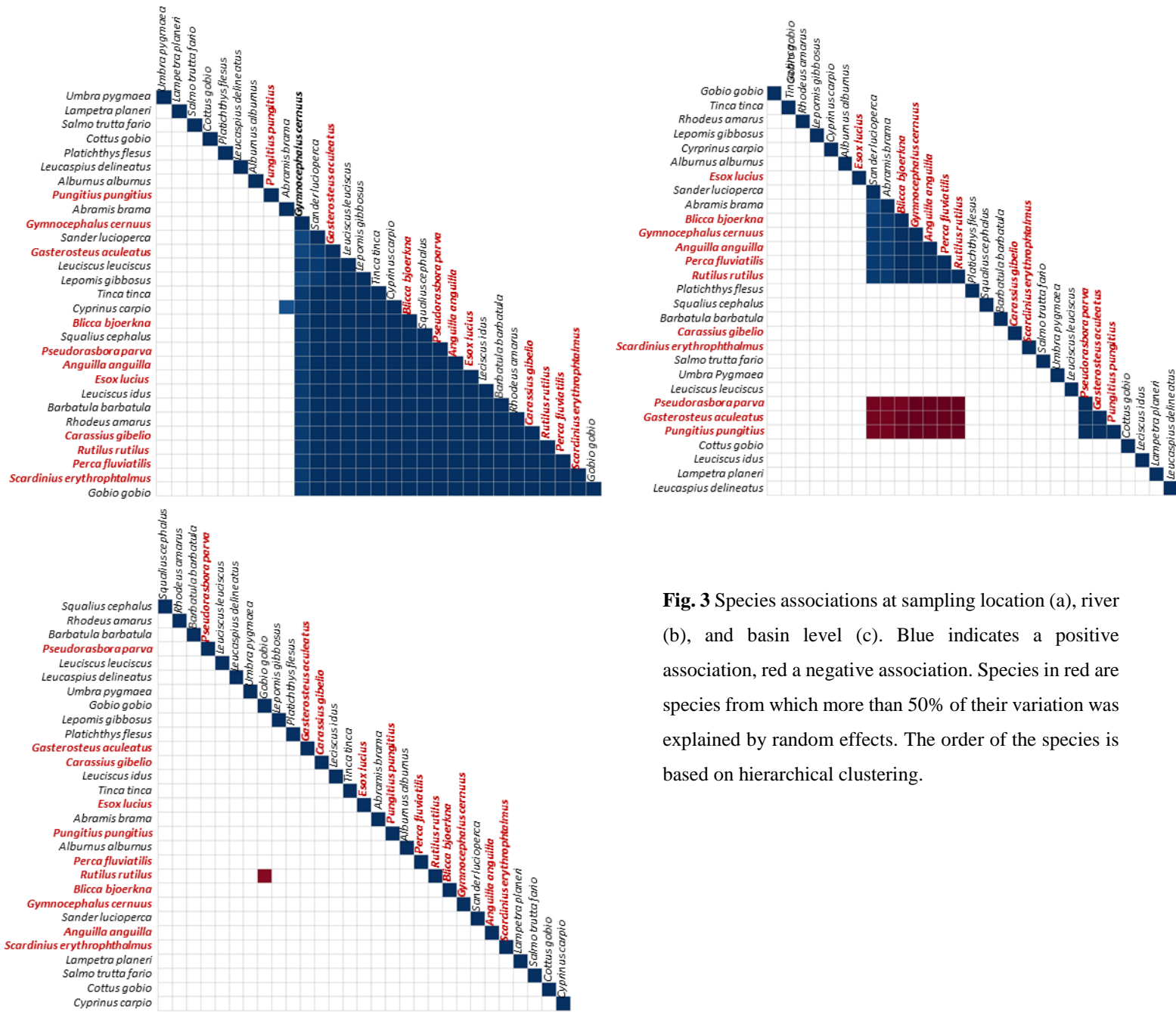
640

641 **Fig. 1** Overview of the sampling locations

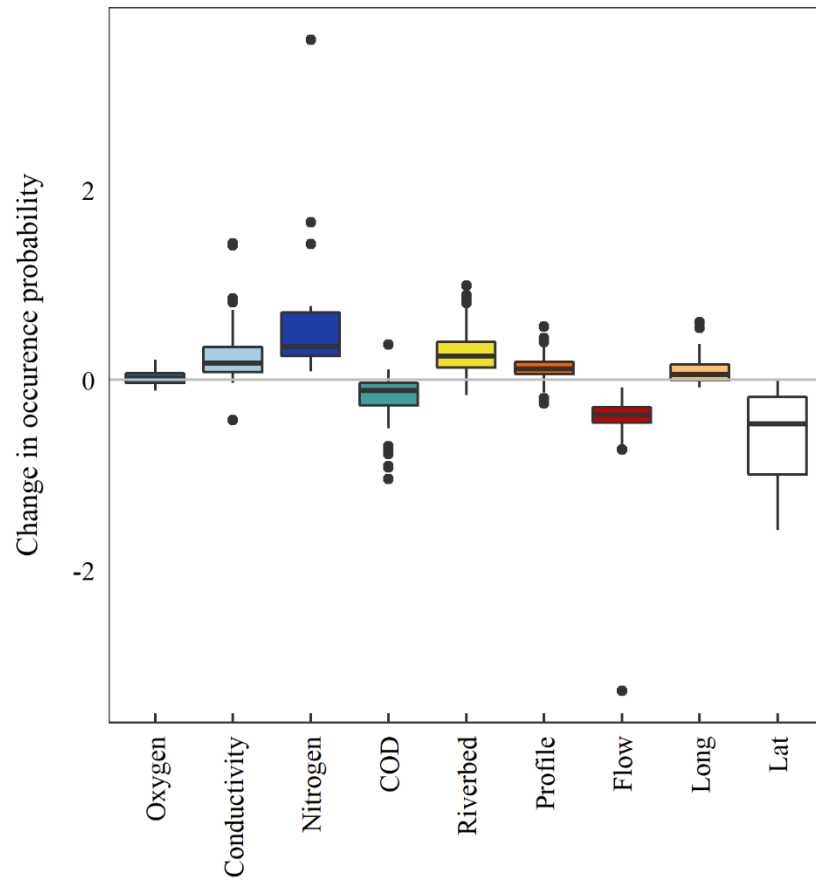
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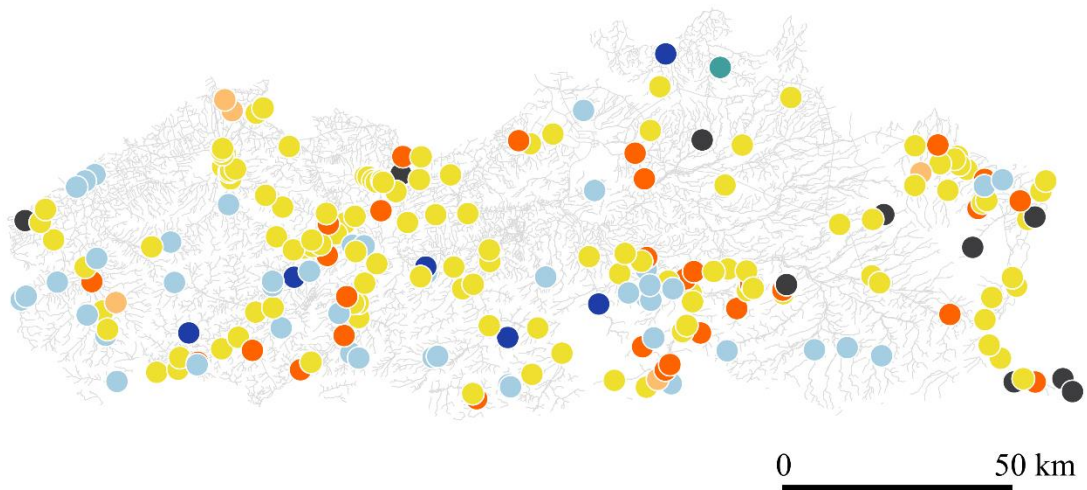
**Fig. 2** Variance explained by fixed (physico-chemistry, hydromorphological quality, and connectivity) and random effects (at the sampling location, river and basin level).



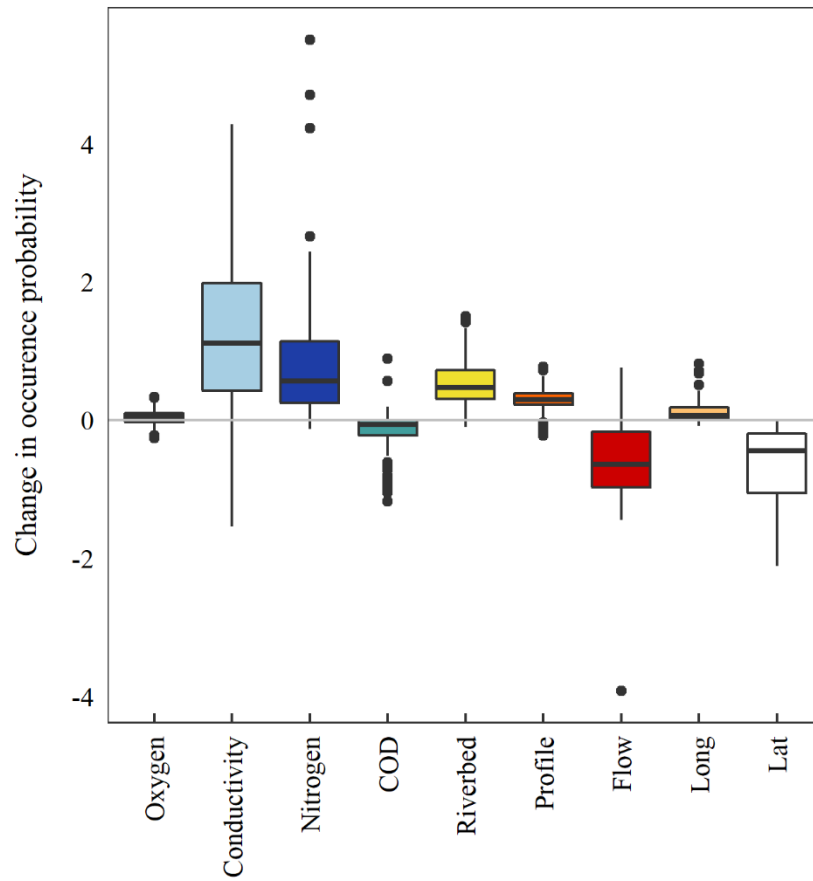
**Fig. 3** Species associations at sampling location (a), river (b), and basin level (c). Blue indicates a positive association, red a negative association. Species in red are species from which more than 50% of their variation is explained by random effects. The order of the species is based on hierarchical clustering.



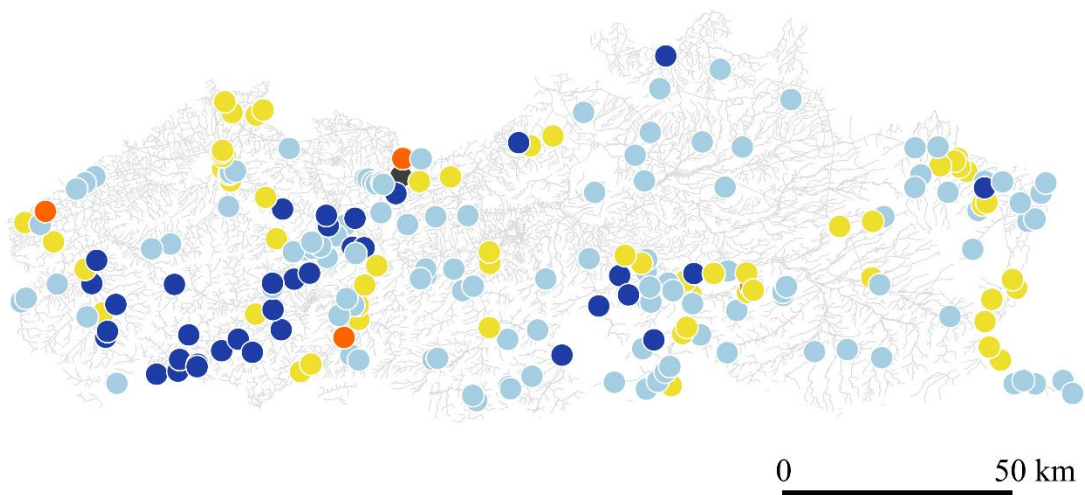
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**Fig. 4** Predicted changes in species richness under nine scenarios of improved environmental quality up to a 'good' status. Scenario leading to the greatest predicted increase in species richness for each location (a) Boxplots representing change in accumulated occurrence probability following the nine scenarios (b).



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**Fig. 5** Predicted changes in species richness under nine scenarios of improved environmental quality up to a 'very good' status. Scenario leading to the greatest predicted increase in species richness for each location (a) Boxplots representing change in accumulated occurrence probability following the nine scenarios (b).

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656 **Tables**

657 **Table 1** Minimal, average, and maximal values of the physico-chemical and hydromorphological environmental variables. A subset of the data was used for the  
 658 species distribution model, which was based on the variables in bold. Values in brackets indicate the minimal, average, and maximal value of these variables for  
 659 the subset considered. More information on the hydromorphological and connectivity variables is available in Table S1.

Category	Variable	Unit	Min	Average	Max	% NA	Reflects
Physico-chemistry	Temperature	°C	2.0	13.4	27.2	0.72	
	pH	-	6.4	7.66	9.4	0.96	
	<b>Oxygen</b>	<b>mg/L</b>	<b>0.70 (2.30)</b>	<b>7.80 (8.34)</b>	<b>24.10 (16.70)</b>	<b>0.96</b>	Dissolved oxygen levels
	<b>Conductivity</b>	<b>µS/cl</b>	<b>104 (104)</b>	<b>965.2 (928.79)</b>	<b>50100 (6860)</b>	<b>1.2</b>	Dissolved salts
	Secchi	-	-50	62.25	300	95.2	
	Chloride	mg/L	2.5	174.5	18350	0	
	Biochemical Oxygen Demand	mgO <sub>2</sub> /L	0.25	4	120	10.44	
	<b>Chemical Oxygen Demand</b>	<b>mgO<sub>2</sub>/L</b>	<b>1.5 (3.5)</b>	<b>30.53 (27.96)</b>	<b>1230 (131)</b>	<b>0.24</b>	Algal blooms
	<b>Kjeldahl Nitrogen</b>	<b>mgN/L</b>	<b>0.2 (0.375)</b>	<b>3.28 (2.63)</b>	<b>213 (18)</b>	<b>0</b>	Nutrient levels
	Ammonium	mgN/L	0.03	3.25	15	0	
	Nitrate	mgN/L	0	0.37	11	0.24	
	Nitrite	mgN/L	0.01	3.45	20.1	80.19	
	Total Nitrogen	mgN/L	0.03	1.01	70.9	0.24	
	Total Phosphorus	mgP/L	0	0.36	5.5	0	
	Orthophosphate	mgP/L	0	0.23	0.99	95.8	
	Sulfate	mg/L	0.02	82.33	2590	41.18	
	Suspended matter	mg/L	0.8	28.97	1280	2.76	
H	-	8	27.87	43	98.2		
Hydromorphology	<b>Profile*</b>	-	<b>0 (0)</b>	<b>0.28 (0.27)</b>	<b>1 (0.93)</b>	0	Substrate, sediment deposits, pool-riffle patterns
	<b>River bed*</b>	-	<b>0 (0)</b>	<b>0.28 (0.30)</b>	<b>1 (1)</b>	0	Width/depth ratio, variation in width, profile type
	<b>Flow variation*</b>	-	<b>0 (0)</b>	<b>0.62 (0.61)</b>	<b>1 (1)</b>	0	Flow variation and the presence of obstructions to flow
	Riverbank	-	0	0.62	1	0	
	Alluvial processes	-	0	0.27	1	0	

Connectivity	<b>Longitudinal continuity*</b>	-	<b>0 (0)</b>	<b>0.82 (0.83)</b>	<b>1 (1)</b>	0	Riverbank interruptions and migration barriers
	<b>Lateral continuity*</b>	-	<b>0 (0)</b>	<b>0.51 (0.54)</b>	<b>1 (1)</b>	0	Embankment and lateral barriers

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661 **Table 2** Overview of the two sets of scenarios with percentage of locations included and scenario value for each target variable.

	Scenarios 'good status'		Scenarios 'very good status'	
	% sampling locations included	Scenario value	% sampling locations included	Scenario value
Oxygen	16.9	4 - 6 mg/L	43.6	8 mg/L
Conductivity	37.2	400-15000 $\mu$ S/cm	84.9	150-1000 $\mu$ S/cm
Nitrogen	7.8	6 mgN/L	57.3	1.5 mgN/L
COD	44.5	30 mgO <sub>2</sub> /L	65.1	20 mgO <sub>2</sub> /L
Riverbed	84.9	0.6	95.4	0.8
Profile	92.7	0.6	97.7	0.8
Flow variation	55.5	0.6	87.2	0.8
Longitudinal continuity	16.1	0.6	32.1	0.8
Lateral continuity	51.8	0.6	77.5	0.8

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