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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

Introduction

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

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

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

A modelling approach, focusing on responses of fish communities to environmental pollution and degradation, may provide important insights needed to efficiently restore, protect, and enhance fish communities. An effective fish community model should consider the following issues in conservation planning. First, dispersal is important and cannot be neglected (Altermatt 2013). This requires a spatially explicit model considering the impacts of dispersal and colonization, more specifically the effect of nearby source populations. Second, the model should explicitly account for species co-occurrence patterns, either by setting constraints to the number of species that co-occur in a patch (Guisan and Rahbek 2011), or by estimating species associations and leveraging these when making predictions (Warton et al. 2015). Third, focusing on the responses of fish communities at the catchment and policy implementation scale may provide new information concerning effective regional management and restoration actions. Many studies examine local responses to restoration at one or a few locations. Focusing on a larger spatial scale, however, may shed light on environmental factors limiting restoration success, while providing more information on the spatial distribution of these factors, potentially guiding management at the regional policy and decision-making level. Finally, the model output should be easy to interpret by policy makers and governmental agencies responsible for designing policies and management strategies for riverine systems.

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

Methods

Study area

Flanders, the northern part of Belgium, covers an area of 13 522 km² and represents one of the most densely populated areas in Europe (Fig. 1). Flemish riverine systems belong to eleven river basins draining into three main rivers, the Meuse, the Scheldt, and the Yser, all of which eventually flow into the North Sea. Approximately 57 fish species inhabit Flanders, of which 18 are considered non-indigenous (Verreycken et al. 2007). Fish are exposed to high levels of nutrients, pesticides, and metals resulting from agriculture, household, and industrial waste. The presence of barriers such as watermills and weirs obstruct migration and reduces available habitat. Consequently, the quality of Flemish rivers is highly variable.

Data collection and preparation

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

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

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

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

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

Among the 2965 fish sampling events at the 1142 locations between 2003 and 2017, only 1013 could be linked to a physico-chemical and a hydromorphological sampling event, as many environmental records only included basic physico-chemical parameters (i.e. temperature, oxygen, pH and conductivity). Additionally, environmental variables that were measured in only few locations were removed (Table 1; e.g. BOD, SO_4). This quality filtering resulted in a reduced dataset comprising 695 fish observations at 320 unique sampling locations. In order to minimize the temporal dimension, this dataset was further reduced to only include events between 2008 and 2012 (2965 fish sampling events at 1142 unique sampling locations). If a location was sampled multiple times during this timeframe, only the most recent sampling event was included. The final dataset comprised 218 complete records (i.e. 218 fish sampling events for 218 unique sampling locations), 29 fish species, nine physico-chemical variables (temperature, pH, oxygen, conductivity, chloride, chemical oxygen demand (COD), Kjeldahl Nitrogen, total nitrogen, total phosphorus), and seven hydromorphological variables (profile, riverbed, riverbank, flow variation, alluvial processes, longitudinal and lateral continuity). Among the 29 included fish species, five fishes were identified as 'invasive' (Verreycken et al. 2007) (Table S2). A detailed description of the data preparation is provided in the supplements (Fig. S2).

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

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

Joint species distribution model

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

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

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

Ecological inference from the fitted joint species distribution model

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

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

Model-simulated policy implementation scenarios

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

In the first set of scenarios, the value of the focal variable was set so that it corresponded to ‘good’ quality according to the EU WFD for each specific sampling location (standards differ depending on river type which includes variation in size and location). In the second set of scenarios, the value for each environmental variable was set to a ‘very good’ status, again specific for each river type. Since quality standards are specific to each member state, the chosen quality values were based on the Flemish WFD targets. The values of the non-focal variables were set to the baseline values representing the observed values for each sampling location. Some locations already met the required quality standards and were not included (Table 2). We used the fitted HMSC model to predict posterior-mean species- and site-specific occurrence probabilities for each scenario, and summarized these predictions in terms of expected species richness by summing over the species-specific occurrence probabilities.

Results

Model performance

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

Structure of Flemish fish communities

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

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

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

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

Policy scenarios

Species richness - The policy scenarios simulating a 'good' status of the environmental variables revealed limited effects of the physico-chemical quality criteria on species richness (Fig. 4; Fig. S4). Many sampling locations already met the EU WFD standard for the physico-chemical parameters and were not included in the policy scenarios (Table 2). For the locations that did not meet the target, the predicted change in species richness rarely exceeded an increase or decrease of one species on average. Decreasing conductivity levels led to an average predicted increase in accumulated occurrence probability for 94 out of 96 locations (mean change = 0.26 range = -0.42 – 1.44). Decreasing nitrogen led to an average increase at all 18 locations included (mean change = 0.69, range = 0.09 – 3.54). Increasing oxygen levels increased predicted species richness in 23 out of 37 locations (mean change = 0.02, range = -0.11 – 0.21). Decreasing COD levels generally led to a reduction in species richness in 68 out of 81 locations (mean change = -0.20, range = -1.04 – -0.37).

More sampling locations were included in the hydromorphological scenarios because fewer locations met the standards for these variables. Increasing the quality of the riverbed led to the greatest predicted improvement in species richness, with an increase in mean predicted species richness in 175 out of 186 included locations (mean change = 0.29, range = -0.16 – 0.99). Improving profile structure and longitudinal continuity led to predicted increases in 188 out of 203 (mean change = 0.13, range =-0.25 – 0.56) and 27 out of 36 locations (mean change = 0.11, range = -0.08 – 0.61), respectively. On the contrary, improving flow variation and lateral continuity had negative average predicted effects (flow variation: mean change = -0.39, range = -0.08 – -3.27; lateral continuity: mean change = -0.59, range = -0.01 – -1.1.58).

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

Greater predicted increases in species richness were observed when improving the physico-chemical and hydromorphological quality to a 'very good' status (Fig. 5; Fig. S5). A predicted increase in species richness resulted from decreasing conductivity (179 out of 185 locations, mean change = 1.29, range = -1.5375 –4.29), decreasing nitrogen input (123 out 126 locations, mean change = 0.80, range =-0.1285 – 5.469), and increasing oxygen levels (66 out of 95 locations, mean change = 0.04, range = -0.2577 0.374). For the hydromorphological variables, improving riverbed quality led to a predicted increase in species richness (196 out of 208 locations, mean change = 0.53, range = -0.1140 – 1.429). The same was true for improvement of the river profile (203 out of 214 locations, mean change = 0.29, range = 0-0.7200 – 0.690), and longitudinal continuity (53 out of 71 locations, mean change = 0.13, range = -0.0918 – 0.856). However, increasing flow variation and lateral continuity generally led to a predicted reduction in species richness (flow variation: 186 out of 191 locations, mean change = -0.64, range = - -3.97 – 0.775; lateral continuity: 168 out of 170 locations, mean change = -0.65, range = -2.12 – 0.01192).

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

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

Discussion

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

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

Drivers of community assembly

Physico-chemistry as the main determinant of community composition

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

Does variance explained by latent factors represent biotic interactions?

The variation explained in the distribution of 11 out of 29 fish species was almost fully accounted for by environmental filtering, and particularly by the physico-chemical covariates. Most species in this group are present at less than 5% of the sampling locations. *Lampetra planeri*, *Salmo trutta fario*, *Leuciscus leuciscus*, *Cottus gobio*, and *Barbatula barbatula* are strongly affected by poor water quality as shown by their individual tolerance values, indicating medium to high water quality demands (Belpaire et al. 2000; Breine et al. 2004). Previous studies also reported that the narrower the environmental tolerance of a species, the better and more accurate the modelling results (Bennetsen et al. 2016; Sundermann et al. 2015). *Lampetra planeri* and *Cottus gobio* are extremely vulnerable in Flanders and their distributions have been constrained by the lack of pristine rivers. However, structural quality and the presence of specific substrates also impact the distribution of these species, which is not reflected by our results (Belpaire et al. 2000). *Alburnus alburnus*, *Umbra pygmaea*, and *Lepomis gibbosus*, which are species with lower water quality demands, may perform better at polluted locations, possibly due to release from competitors and predators (Belpaire et al. 2000; Breine et al. 2004). For 11 other fish species, random effects explained more than 50% of the variation in their distribution. This group consists of more generalist species. *Pungitius pungitius*, *Gasterosteus aculeatus, Perca fluviatilis, Blicca bjoerkna, Pseudorasbora parva,* and *Carassius gibelio* are more tolerant to pollution and disturbed environments (Breine et al. 2004; Raat 2001). These species are probably less constrained by poor water quality and thus more affected by biotic interactions, spatial processes, or unmeasured covariates.

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

The importance of spatial processes

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

Recommendations for regional policy targets and management goals

Are current quality criteria sufficient?

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

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

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

Interestingly, species richness is predicted to decline in response to an increase in flow variation and lateral continuity. The flow variation index does not directly include flow velocity, but includes local flow variation and the impoundment level of the river. Flow velocity, however, has often been identified as a strong determinant of fish community structure, where high flow rates may eliminate smaller species or species which limited swimming capacity (e.g. Jackson et al. 2001; Toth et al. 2019). Lateral continuity, on the other hand, represents the connection between rivers and the surrounding floodplains. A stronger connection affects productivity and community composition by for example altering carbon composition and oxygen levels (Fernandes et al. 2014). A well connected floodplain is generally expected to increase species richness (Bolland et al. 2012; Paillex et al. 2009). For both parameters, values for the sampling locations were dichotomous and hence, either good (close to 1) or bad (close to 0). Moreover, the model was defined based on a dataset with small variation for both parameters, potentially suggesting that the observed effect result from poor sensitivity to these parameters. A true negative effect, however, may be explained by a strong shift in habitat conditions, following a simulation from a bad to a good standard, which in turn negatively impacts the present fish community.

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

General recommendations and future directions

We quantified responses of fish communities to policy implementation scenarios across all basins within one administrative region and thus focused on a broad policy perspective, while also including local responses. By doing so, we allow local managers to optimize their management strategy and to adjust regional policy measures and decision-making, by for example setting and adjusting current water quality standards. Overall, the outcome of our model makes it clear that tackling high nutrient and conductivity levels is essential. General policy advice should be adjusted to match this need because current quality targets may not capture the complete range of standards to which ecological quality will improve.

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

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

Conclusion

Joint species distribution modelling in combination with monitoring data can be successfully applied to understand responses of fish communities to pollution and disturbance, while accounting for species association and spatial effects. It is clear that physico-chemical quality plays an important role in heavily degraded systems. Consequently, decreasing nutrient and conductivity levels, and restoring natural river dynamics should be the focal points of policy planning in Flanders. All these actions should explicitly consider the needs of biological communities.

Declarations

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Author's contribution

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

Data and code availability

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

Ethical approval

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

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Figure legends

Fig. 1 Overview of the sampling locations

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 (A) sampling location, (B) river, and (C) basin level. Blue indicates a positive association, red a negative association. Species in red are species from which more than 50 % of their variation was explained by random effects. The order of the species is based on hierarchical clustering.

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

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

Tables

Table 1 Minimal, average, and maximal values of the physico-chemical and hydromorphological environmental variables. A subset of the data was used for the 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 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	
	Oxygen	**mg/L**	**0.70 (2.30)**	**7.80 (8.34)**	**24.10 (16.70)**	**0.96**	Dissolved oxygen levels
	Conductivity	**µS/cl**	**104 (104)**	**965.2 (928.79)**	**50100 (6860)**	**1.2**	Dissolved salts
	Secchi	-	-50	62.25	300	95.2	
	Chloride	mg/L	2.5	174.5	18350	0	
	Biochemical Oxygen Demand	mg0$_2$/L	0.25	4	120	10.44	
	Chemical Oxygen Demand	**mg0$_2$/L**	**1.5 (3.5)**	**30.53 (27.96)**	**1230 (131)**	**0.24**	Algal blooms
	Kjeldahl Nitrogen	**mgN/L**	**0.2 (0.375)**	**3.28 (2.63)**	**213 (18)**	**0**	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	**Profile***	-	**0 (0)**	**0.28 (0.27)**	**1 (0.93)**	0	Substrate, sediment deposits, pool-riffle patterns
	River bed*	-	**0 (0)**	**0.28 (0.30)**	**1 (1)**	0	Width/depth ratio, variation in width, profile type
	Flow variation*	-	**0 (0)**	**0.62 (0.61)**	**1 (1)**	0	Flow variation and the presence of obstructions to flow
	Riverbank	-	0	0.62	1	0	
	Alluvial processes	-	0	0.27	1	0	

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

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 µS/cm	84.9	150-1000µS/cm
Nitrogen	7.8	6 mgN/L	57.3	1.5 mgN/L
COD	44.5	30 mgO_2/L	65.1	20 mgO_2/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