Disentangling multiple pressures on fish assemblages in large rivers

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Disentangling multiple pressures on fish assemblages in large rivers

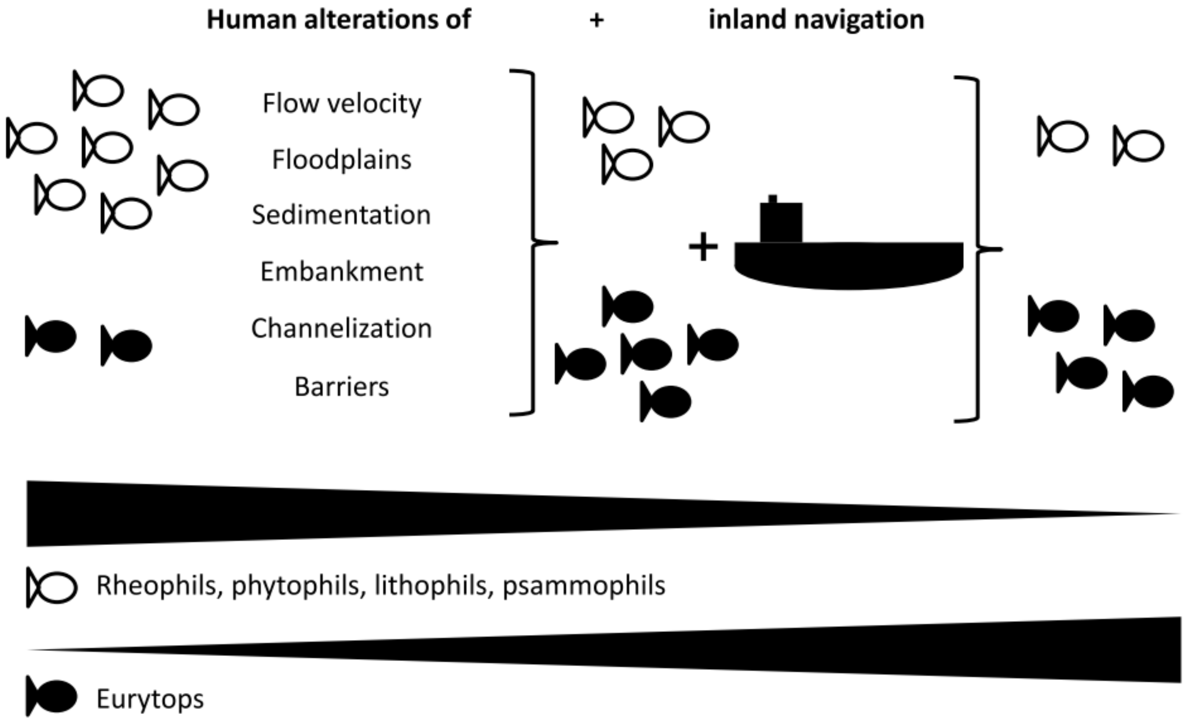
Keywords:

Waterways; inland navigation; functional guilds; fish diversity; river rehabilitation; fish-based assessment

Highlights:

- Large rivers serve as waterways with highly degraded hydromorphology
- Multiple pressures reduce densities of habitat-sensitive fish
- Inland navigation adds on top of the prevailing hydromorphological degradation
- Increased velocity, navigation intensity and loss of floodplains matter most
- Diagnostic fish population metrics were derived for specific pressures

Graphical abstract:



Abstract

European large rivers are exposed to multiple human pressures and maintained as waterways for inland navigation. However, little is known on the dominance and interactions of multiple pressures in large rivers and in particular inland navigation has been ignored in multi-pressure analyzes so far. We determined the response of ten fish population metrics (FPM, related to densities of diagnostic guilds and biodiversity) to 11 prevailing pressures including navigation intensity at 76 sites in eight European large rivers. Thereby, we aimed to derive indicative FPM for the most influential pressures that can serve for fish-based assessments. Pressures' influences, impacts and interactions were determined for each FPM using bootstrapped regression tree models. Increased flow velocity, navigation intensity and the loss of floodplains had the highest influences on guild densities and biodiversity. Interactions between navigation intensity and loss of floodplains and between navigation intensity and increased flow velocity were most frequent, each affecting 80% of the FPM. Further, increased sedimentation, channelization, organic siltation, the presence of artificial embankments and the presence of barriers had strong influences on at least one FPM. Thereby, each FPM was influenced by up to five pressures. However, some diagnostic FPM could be derived: Species richness, Shannon and Simpson Indices, the Fish Region Index and lithophilic and psammophilic guilds specifically indicate rhithralisation of the potamal region of large rivers. Lithophilic, phytophilic and psammophilic guilds indicate disturbance of shoreline habitats through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. In European large rivers, inland navigation constitutes a highly influential pressure that adds on top of the prevailing hydromorphological degradation. Therefore, river management has to consider river hydromorphology and inland navigation to efficiently rehabilitate the potamal region of large rives.

1. Introduction

Large rivers are the most severely impacted ecosystems on earth due their manifold exploitations and modifications to serve multiple human demands (Malmqvist and Rundle, 2002; Nõges et al., 2015). Up to the late 1980s, river assessments focused primarily on water quality, in particular eutrophication and pollution by chemicals and heavy metals (reviewed by Meybeck and Helmer, 1989). Meanwhile, the focus has shifted to ecological quality as alterations of hydrology, morphology, habitat availability and connectivity have been recognized as key pressures on surface water bodies (EEA, 2012; Melcher et al., 2007).

More recently, the importance of impacts by multiple pressures and their interactions became increasingly acknowledged and addressed by research (Hering et al., 2015; Jackson et al., 2016; Milošević et al., 2018; Radinger et al., 2016; Segner et al., 2014), as single pressures could barely account for the vast amount of observed ecosystem changes (Vaughan et al., 2009). For example, 90% of lowland rivers in 14 European countries are affected by a combination of four pressure groups referring to alterations of water quality, hydrology, morphology and connectivity (Schinegger et al., 2012). Disentangling the effects of these pressure groups and their interactions on fish assemblages were broadly explored since then (Schinegger et al., 2016, 2013; Trautwein et al., 2013). However, pressure groups subsume common types of degradation which might neglect intensity and direction of the underlying single pressures (Schinegger et al., 2012). Further, local-scale pressure variables can have a high influence on fish communities (Sagouis et al., 2017). Therefore, knowledge on the effects of single pressures is required to provide management advice and enhance restoration success (e.g., Friberg et al., 2016). Moreover, previous studies primarily focused on small and medium sized rivers, while large rivers were rather underrepresented (Schinegger et al., 2013). Since large rivers constitute complex hydrological, ecological, economic, political and social systems (Campbell, 2016), they receive multiple impacts both from the upstream catchment and at the reach scale (Wolter et al., 2016). Therefore, in large rivers, the lack of knowledge on dominance, interactions and impacts of human pressures constitutes a particular research gap.

Assessing the impact of multiple pressures across large rivers is challenging, because sampling methods are extremely resource-demanding and not standardized and data availability is limited (Milošević et al., 2018; Nõges et al., 2015; Oliver and Morecroft, 2014).Not surprisingly, large rivers are significantly under-researched. Hence, extraordinarily little is known about impacts and interactions of multiple pressures in large rivers (Hering et al., 2015).

A common approach to assess effects of pressures is the comparison of impacted sites with reference sites resembling unimpaired conditions (e.g., Pont et al., 2006). This approach works well in small rivers and streams, where less disturbed or near natural reference reaches still exist. In contrast, almost all large rivers are so heavily degraded (e.g., Malmqvist and Rundle, 2002) that near natural reference channel reaches do not exist anymore (Birk et al., 2012). For instance, in Europe nearly all large rivers are rectified, channelized and regulated, and hence substantially modified in hydromorphology (e.g., Petts et al., 1989). Channelization invokes artificial embankment and steepening of shorelines, thus a loss of important shallow nursery areas for fish. Further, channelization concomitantly increases flow velocity as a result of the straightened and deepened river channel. Together with meander cut-offs and levee constructions these changes result in the wide-spread loss of periodically inundated floodplains (e.g., Strayer and Findlay, 2010). As a consequence of the high overall degradation of large rivers, a comparative assessment approach was chosen along a gradient of more or lesser disturbed river reaches to identify single pressure impacts on fish assemblages (e.g., Clapcott et al., 2012).

Large rivers are commonly maintained as waterways for commercial navigation. Navigation-induced physical forces are well-known to impact on various riverine taxa mainly in shallow areas along the banks (Gabel et al., 2017; Söhngen et al., 2008) that often represent suitable habitats for reproduction (Wolter et al., 2004). Impacts of navigation-induced forces have in particular been shown for aquatic plants (Ali et al., 1999; Asplund and Cook, 1997; Murphy and Eaton, 1983), benthic invertebrates (e.g., Gabel et al., 2012), and juvenile fish (e.g., Arlinghaus et al., 2002; Huckstorf et al., 2011; Wolter and Arlinghaus, 2003). Hydraulic forces causing drawdown (Liedermann et al., 2014), shear stress and dewatering (Wolter and Arlinghaus, 2003) affect important shallow nursery areas of fish larvae and juveniles along the banks (Huckstorf et al., 2011). Vessel-induced return currents commonly exceed the critical swimming speed of young fish resulting in dislocation (Wolter and Arlinghaus, 2003), stranding (reviewed by Nagrodski et al., 2012) and direct mortality (Adams et al., 1999; Pearson and Skalski, 2011). Accordingly, inland navigation constitutes a key limiting factor for littoral fish recruitment in waterways (Wolter and Arlinghaus, 2003). Therefore, navigation intensity provides a significant pressure on fish assemblages of large rivers, which moreover interacts with the hydromorphological degradation of the river channel. Surprisingly, inland navigation has not been considered in analyzes of multiple pressures so far, except the study by Leclere et al. (2012). The authors modeled occurrence of fish species based on environmental parameters. They reported that inland navigation and physico-chemical disturbances both negatively influence the occurrence of juveniles of selected fish species (Leclere et al., 2012).

Most studies on the impacts of "multiple" pressures considered pairwise interactions of two pressures based on predefined hypotheses (reviewed in Crain et al., 2008; Darling and Côté, 2008; Jackson et al., 2016). Further, such studies often aimed to untangle the direction of the expected interaction (e.g., antagonistic, synergistic, additive; reviewed in Piggott et al., 2015). In contrast, this study aimed to identify dominant pressures and their potential interactions in large rivers, rather than addressing specific interactions and their directions. To our knowledge this is the first study, which explicitly considered potential additional effects of inland navigation on fish assemblages in relation to the other prevailing pressures on European large rivers.

We analyzed the effects of 11 ranked pressure variables on ten fish population metrics (FPM) referring to biodiversity (e.g., species richness, Simpson Index), river type specific species composition (Fish Region Index, FRI), and densities of sensitive life history traits (e.g., rheophils, lithophils). Thereby, we expected to identify indicative FPM for specific types of degradation, serving as valuable ecological tools for the fish-based assessment of large rivers. Both pressure variables and FPM (fish samplings were conducted 250 times in total) were available for 76 sites in eight European large rivers. It was hypothesized: i) that inland navigation intensity appears as a significant pressure on fish assemblages in large rivers and ii) that impacts of vessel operation positively correlate with hydromorphological degradation of the river channel. The expected impacts of inland navigation comprise decreasing densities of habitat-sensitive guilds that require shoreline areas for reproduction. Hence, it was expected that Inland navigation appears as a very specific pressure, which accordingly offers potential for targeted rehabilitation of large rivers and the recovery of the inherent fish communities.

2. Methods

2.1 The large river database

The large river database (LRDB) has been compiled within the EU project "Improvement and Spatial Extension of the European Fish Index" (EFI+, EC 044096) and further completed since. It compiles 2693 fish samplings conducted at 358 sampling sites in 16 European large rivers, i.e., rivers with a catchment size >10,000 km² (Berg et al., 2004). Samplings were carried out using different sampling methods, in different seasons and during both day and night. From this vast and unique dataset of fish samplings across European large rivers, a representative subset of comparable sites and samplings was extracted as follows: We selected fish samplings that (i) were obtained by boat electrofishing along the banks during daytime, which was found well representing the fish assemblages of large rivers (Zajicek and Wolter, 2018), (ii) originated from large rivers draining into the North Sea and Baltic Sea to ensure generally comparable fish species inventories (e.g., Sommerwerk et al., 2017), (iii) conducted under low flow conditions in autumn to avoid seasonal bias (Schmutz et al., 2007), (iv) had covered a minimum fished length of 100 m and (v) captured at least 100 fish (Flotemersch et al., 2011). The resulting dataset used for analyzes consisted of 250 fish samplings assembled at 76 sites in eight large rivers between 1996 and 2008 (Fig. 1). The average length fished per site was 1659 ± 100 m (mean ± standard error). The area fished varied according to the size of the anode used and was on average 5287 ± 456 m² per site. Therefore, all samplings have been standardized as fish densities per 100 m² prior analyses. Fifty percent of the sites were sampled only once, 93% less than 10 times, and 7% between 10 and 26 times. The vast majority (96%) of the sampling sites was at least 1 km apart of each other and the distance between sampling sites by far exceed 1 km in most cases (compare x-axis in Fig. 2). All sites were situated in comparable river reaches allowing for representative fish based-assessments (Wolter et al., 2016).

Each sampling site was characterized by a set of 26 pressure variables ranked on a scale from 1 to 5 associated with little (class 1), intermediate (class 3) and severe (class 5) alteration of the natural state, respectively. Pressure ranks were assigned by the local water authorities in accordance with national survey standards and the requirements of the European Water Framework Directive (2000/60/EC, WFD) and provided with the fish data. Pressure variables with insufficient gradient among sites, i.e., with >95% of the observations in the same class, have been excluded prior analyses. Ten pressure variables remained (Table 1 and Fig. 2). In addition, for each site the intensity of inland navigation was determined based on counts of annually passing cargo vessels at the nearest ship lock. Vessel counts at ship locks were provided by the Water and Navigation Authority (wsv.de) in Germany and by the Ministry of Infrastructure and the Environment (rijkswaterstaat.nl) in The Netherlands. Navigation intensity has been classified in accordance to the other pressures as 1= 0 – 3000 passing vessels per year, 3= 3.001 – 33.000 and 5= 33.001-133.000.

2.2 Data analyzes

For each sampling, we determined ten diagnostic fish population metrics (FPM) for the ecological status of river systems (Noble et al., 2007; Welcomme et al., 2006; Wolter et al., 2013): Densities of eurytopic (EURY), rheophilic (RH), lithophilic (LITH), phytophilic (PHYT) and psammophilic (PSAM) fish as well as species richness (SPR), Shannon Index (SHA), Evenness (EVE), Simpson Index (SIM), and the Fish Region Index (FRI). All FPM were calculated based on standardized fish densities (fish per 100 m^2 sampled area, referred to as Ind. / 100 m^2). The assignment of fish species to guilds and to the species-specific Fish Region Index followed the classification provided by Scharf et al. (2011). For species not listed there we used Dußling et al. (2004) and EFI+ Consortium (2009) (compare appendix, Table A.1).

Five FPM refer to habitat preferences for flow velocities (rheophilic and eurytopic fish) and for spawning substrates (lithophilic, phytophilic and psammophilic fish). Rheophilic fish prefer flowing river reaches and are thus considered sensitive to the impairment of fluvial dynamics and habitats. In contrast, eurytopic fish show no flow preferences and are further tolerant to low oxygen saturation. Therefore, high densities of eurytopic fish are commonly considered as indicators for the degradation of natural river dynamics (Dußling et al., 2004b; Wolter and Vilcinskas, 1997). However, in large rivers, low densities of eurytopic fish could as well indicate degradation through rhithralisation of typically slow flowing potamal river reaches. Lithophilic fish are gravel spawners with benthic larvae. They are considered most sensitive to the impairment of hydromorphological processes, especially of sediment sorting and the provision of coarse gravel (Wolter et al., 2016). Psammophilic (sand spawning) and phytophilic (plant spawning) fish also form guilds with obligatory spawning substrate requirements. Both guilds are sensitive to habitat degradation, especially to losses of shallow littoral areas with low flow conditions and submerged and emerged macrophytes. Plant spawners further suffer from the loss of periodically inundated floodplain habitats. Guild densities were calculated for each sample as the number of fish with the respective flow or habitat preferences per 100 m².

The other five FPM refer to measures of alpha diversity, dominance structure and river type specific species composition: Species richness, the Shannon Index and the Evenness according to Spellerberg (2008), the Simpson Index (Somerfield et al., 2008) and the whole-sample Fish Region Index (Dußling et al., 2004). The FRI is a species-specific metric, which characterizes the preferred longitudinal distribution of a species within a river course, from the trout region in the headwaters to the ruffe-flounder region close to the estuary. It serves to characterize river reach specific fish communities (e.g., Schmutz et al., 2000). Species-specific FRI values have been derived from empirical occurrence data for all common European fish species (Dußling et al., 2004; Wolter et al., 2013, appendix Table A.1). The whole-sample or total FRI was calculated according to Dußling et al. (2004) based on the species-specific FRI and abundance of each species captured at a sampling site. It describes the correspondence of the entire fish assemblage of a sampling site to the respective river region. The total FRI is a generic index, which can be applied in different biogeographic regions. In large rivers, the total FRI (referred to as FRI in our study) is especially valuable for fish-based assessments as it indicates both rhithralisation and potamalisation, i.e., bi-directional hydromorphological changes (Schmutz et al., 2000; Wolter et al., 2013).

The metrics were calculated for each sample as follows:

$$\text{Species richness } (SPR) = number\ of\ species$$

$$\text{Shannon Index } (SHA) = -\sum \left(\frac{n_i}{N}\right) \log \left(\frac{n_i}{N}\right)$$

$$\text{Evenness } (EVE) = \frac{SHA}{\log SPR}$$

$$\text{Simpson diversity Index } (SIM) = 1 - \sum \left(\frac{n_i}{N}\right)^2$$

$$\text{Fish Region Index } \left(FRI_{(total)}\right) = \frac{\sum_{i=1}^{s} \left(FRI_i \frac{n_i}{S^2 FRI_i}\right)}{\sum_{i=1}^{s} \frac{n_i}{S^2 FRI_i}}$$

where n_i = n individuals of species i; N = all individuals per sample; FRI_i = FRI of species i; S^2FRI = variance of the FRI of species i (Wolter et al., 2013).

2.3 Statistics

Boosted regression tree (BRT) models were applied to identify most influential pressures and their interactions on the fish population metrics (FPM). BRTs determine the relative influence of explanatory variables on a response variable as the contribution of each explanatory variable in reducing the overall model deviance (Lewin et al., 2014). Major advantages of BRTs are their ability to handle collinearity, nonlinearity, outliers and to automatically identify interactions between explanatory variables (Elith et al., 2008). BRTs therefore constitute a powerful tool to investigate relationships between the environment and ecological responses (Dahm and Hering, 2016; Pilière et al., 2014; Segurado et al., 2016) and hence to identify the impact of multiple pressures in aquatic environments (Feld et al., 2016; Lewin et al., 2014). To model the continuous response variables (the FPM), a BRT model with a Gaussian distribution was selected as loss function for minimizing squared errors. To improve homogeneities of variances, all guild densities were log(x+1) transformed, EVE was arcsine-, SHA was exponential-, and SIM was arcsine-exponential- transformed. To obtain robust estimates, we followed recommendations of Feld et al. (2016) and Elith et al. (2008) and set bagfraction to 0.7, tree complexity to 5 and learning rate to 0.001 so that at least 1000 trees contributed to the final model. All BRTs were modeled with the default 10-fold cross-validation. The 11 pressure variables (Fig. 2) were included as ordered factors. The relative importance (%) of each pressure variable in each BRT was quantified based on the number of times each of the variables was used for splitting, weighted by the squared improvement at each split and averaged over all trees (Elith et al., 2008). We calculated 500 parametric bootstrap simulations of each BRT model to obtain confidence intervals (95%-CI, percentile method, Carpenter and Bithell, 2000) of the relative importance of each explanatory variable and its effects on the response variable. Model quality (Mac Nally et al., 2017) of each BRT model was determined as goodness-of-fit (R^2_{COR}) based on the linear correlation between fitted and observed values (Cameron and Windmeijer, 1996).

Data were analyzed in R 3.3.1 (R Development Core Team, 2016) using the R packages ‘gbm’ (version 2.1.1; Ridgeway, 2016) and ‘dismo’ (version 1.1-4; Hijmans et al., 2016) to calculate the BRTs, and the R package ‘boot’ (version 1.3-19, Canty and Ripley, 2017) to calculate bootstrap simulations. Figure 1 was drawn using ArcMap, version 10.5.1.

3. Results

3.1 Catch composition

The 250 samplings at 76 sites in 8 large rivers yielded 148,964 fish belonging to 55 species (including three lamprey species referred to as fish in the following). The most abundant species were roach *Rutilus rutilus*, bleak *Alburnus alburnus* and perch *Perca fluviatilis,* which contributed 26%, 14% and 13% to the total catch, respectively (appendix, Table A.2). The most frequently occurring species were roach, perch and ide *Leuciscus idus* captured in 99.6%, 98.8% and 94.4% of all samplings, respectively (see appendix, Table A.2 for detailed catch statistics).

Eurytopic fish dominated the total catch with 67% of all fish. The habitat sensitive ecological guilds of rheophils, lithophils, phytophils and psammophils comprised 32%, 11%, 5% and 8% of the total catch, respectively. Eurytopic and rheophilic fish were captured in all samplings and at all sampling sites. Lithophilic, phytophilic and psammophilic fish were captured in 92% 87% and 59% of all samplings, and at 95%, 88% and 75% of all sites, respectively (see appendix, Table A.3 for detailed guild composition).

Rivers Rhine, Lek and Meuse had the lowest average densities of fish in all of the guilds studied (compare Fig. 3 for the between-river variation of guild densities and appendix, Fig. A1 for a site-specific overview). Rivers Havel and Spree had the lowest densities of fish in the sensitive guilds of rheophils (average: <= 1.71 Ind. / 100 m^2) and lithophils (<= 0.25 Ind. / 100 m^2), low densities of psammophils (<= 0.06 Ind. / 100 m^2) and higher densities of eurytops (>= 24.84 Ind. / 100 m^2). The rivers Rhine and Meuse had the lowest densities of psammophils (<= 0.02 Ind. / 100 m^2). Thus, these five rivers, Rhine, Lek, Meuse, Havel and Spree experienced the highest overall degradation indicated by the guild composition. Rivers Elbe and Oder had higher densities of fish in most sensitive guilds (rheophils: >=7.79 Ind. / 100 m^2, lithophils: >= 1.98 Ind. / 100 m^2, psammophils >= 1.87 Ind. / 100 m^2) than the aforementioned rivers. Phytophilic fish were more abundant in the rivers Elbe, Ems, Havel, Spree and Oder (>= 1.66 Ind. / 100 m^2) than in the rivers Rhine, Lek and Meuse (<= 0.25

Ind. / 100 m²). Highest densities of rheophils (23.45 Ind. / 100 m²), lithophils (12.91 Ind. / 100 m²) and psammophils (9.36 Ind./100 m²) were estimated in the River Ems. However, in the River Ems, the average Fish Region Index was below 6.5 indicating a more rhithral fish assemblage corresponding to the so-called barbel river region. All other river systems had comparable mean Fish Region Indices (>6.5) indicating similar fish assemblages corresponding to the common bream river region. Biodiversity metrics indicated degradation trends widely similar to the guild composition (e.g., lower species richness, Shannon Index, Evenness and Simpson Index and a higher Fish Region Index in the rivers Rhine, Meuse, Havel and Spree compared to the rivers Ems, Elbe and Oder) but the between-river variability was much less pronounced (Fig. 4). The River Lek had the highest Evenness of all rivers and a higher Simpson Index than the rivers Rhine, Meuse, Havel, Spree and Oder.

3.2 Modeled pressure influences

Variation between classes of single pressures was as expected rather low (Fig. 2). Across all 11 pressures considered, pressure class 1, 3 and 5 indicating little, intermediate and high alteration occurred on average at 31 ± 11% (mean ± SE), 36 ± 10% and 41 ± 14%) of the sampled sites, respectively (Table 1). Goodness-of-fit (R^2_{COR}) of 500 bootstraps of each regression tree model ranged between 0.54 and 0.88 and was highest for models fitting Evenness and the eurytopic and phytophilic guilds (means: 0.88, 0.84, 0.83, respectively) and lowest for the Fish Region Index, species richness and the psammophilic guild (0.54, 0.60, 0.64, respectively; compare Table 2).

Increased flow velocity, navigation intensity and loss of floodplains had the strongest mean relative influence (39%, 16% and 11% respectively) on all ten fish population metrics (FPM). Thereby, mean influence of increased flow velocity was higher on the five biodiversity metrics (55%) than on the five guild densities (23%) and vice versa for the influence of navigation intensity (23% on guild densities and 10% on biodiversity metrics). These three pressures as well as increased sedimentation, channelization, organic siltation, the presence of artificial embankments and the presence of barriers downstream and within a 5 km upstream segment had a relative influence >10% on at least one FPM. Thereby, each FPM was strongly influenced by one to five pressures (Table 2).

Shannon and Simpson indices were strongly influenced (68% and 62%, respectively) by one dominating pressure only: increased velocity. Species richness and the Fish Region Index were likewise dominated by the influence of increased velocity (54% and 70%), but navigation intensity had also a strong influence (19%) on species richness, and the loss of floodplains had also a strong influence on the Fish Region Index (16%). The influence of increased velocity dominated on lithophilic (40%) and psammophilic fish (49%) but these FPM were also both strongly influenced by navigation intensity (20% and 25%) and by the loss of floodplains (16% and 10%). Densities of phytophilic fish were strongly influenced by navigation intensity (34%) and organic siltation (33%). The influence of inland navigation dominated on densities of rheophilic fish (24%) but was followed by equally strong influences of barriers downstream (15%), channelization (13%), loss of floodplains (12%) and by the presence of barriers within a 5 km upstream segment (11%). The Evenness and densities of eurytopic fish were each comparably strongly influenced by five pressures (Table 2).

Six pairwise interactions between pressures affected each fish population metric (FPM, Table 3). The most frequent pairwise interactions occurred between navigation intensity and loss of floodplains and between navigation intensity and increased velocity, both affecting 80% of all FPM. Further, the 60 interactions identified in total were dominated by the pressures increased velocity (involved in 47% of the interactions), navigation intensity (38%) and loss of floodplains (35%).

Pressure impacts were both positive and negative, depending on the fish population metric affected. Fig. 5 and Fig. 6 illustrate the impacts on the guild compositions and on biodiversity metrics, respectively. For example, increased flow velocity was associated with significantly higher biodiversity, higher densities of psammophils and lithophils, a lower Fish Region Index and lower densities of eurytops, all indicating rhithralisation. Inland navigation was associated with a significant decline in densities of lithophils and phytophils already at intensities of >3000 vessels per year, corresponding to an average of >8 cargo vessels per day. Rheophils, psammophils, eurytops and biodiversity (species richness, Shannon Index, Simpson Index) significantly declined at high navigation intensities, i.e. at >33,000 vessels per year or an average of >90 vessels per day. A partial loss of floodplains was associated to significantly lower densities of rheophilic and phytophilic fish and to a higher Evenness. A total loss of floodplains was associated with significantly lower densities of eurytopic fish and higher densities of lithophilic fish. Densities of rheophilic fish significantly declined in response to the presence of barriers (both upstream and downstream).

4. Discussion

This study aimed to identify key pressures and their interactions that contribute to lower densities of fish in diagnostic guilds and to lower biodiversity in European large rivers while explicitly accounting for inland navigation. It further aimed to derive diagnostic fish population metrics (FPM) for key pressures in large rivers. Increased velocities, navigation intensity and loss of floodplains had the highest influences on FPM. Increased flow velocities resulting from shortening and straightening rivers accompanied by faster discharging runoff downstream appeared as the most dominating pressure, strongly fostering higher biodiversity and higher densities of fish relying on sediment sorting for spawning (lithophils, psammophils). Navigation intensity of more than eight vessels per day resulted in density declines of lithophilic and phytophilic fish. This finding corresponds surprisingly well with results obtained by Holland (1987) using experimental air exposure to study dewatering effects on walleye (*Stizostedion vitreum*) and pike (*Esox lucius*) larvae: A significant mortality due to dewatering events was observed at a dewatering frequency of 3 h, corresponding to the simulated passage of eight commercial tows per day (Holland, 1987). Floodplain degradation resulted in lower densities of eurytops, rheophils and phytophils. Moreover, the high influence of these three pressures was resembled in the most frequent interactions. Further important pressures identified like increased sedimentation, channelization, organic siltation, the presence of artificial embankments and migration barriers were well in line with the findings of Schinegger et al. (2012), with the latter becoming significantly improved by adding the impact of inland navigation to the pressures on large rivers. Among others, the strictly comparative analytical design as well as the special consideration of navigation intensity allowed identifying FPM that were diagnostic for certain types of human alterations in large river systems. Hence, our study contributes to disentangle the effects of multiple pressures in large rivers, even if most of the significant pressures impacted more than one fish population metric and most fish population metrics significantly responded to more than one pressure.

4.1 Limitations of the study

We acknowledge some limitations of our study in regard to the pressure variables analyzed. Several pressures had to be excluded, because their rank of severity did not vary within rivers and was also very low between rivers. In addition, the gradient of potential impacts was generally limited, because near natural and low disturbed sites were lacking in the large rivers studied. Accordingly, several pressures on river fishes reported from smaller rivers (e.g., Schinegger et al., 2012) could not be considered and analyzed here. Hence, their potential impact might have been underestimated. However, the overall rather severe degradation and little variation along river courses constitute a key character of the rather monotonous waterways. All European large rivers are highly degraded (e.g., Aarts et al., 2004), which was empirically confirmed here by very low densities of all sensitive reproduction guilds in all river systems studied.

Secondly, the classification of pressure ranks was conducted by the local water authorities and delivered with the site descriptions. In Europe, there are more than 100 assessment methods for river hydromorphology in use (Belletti et al., 2015). We have neither information, which particular method has been used to assess the different sites, nor on how detailed single variables have been recorded. We still know that experts can reliably discern between suitable and unsuitable habitat conditions, while they are less precise in addressing differences at finer scales (Radinger et al., 2017). Therefore, we cannot exclude that other experts would have classified a certain pressure state differently. However, at this spatial scale and reporting level on pressures, our data set still remains the best available data set for European large rivers.

4.2 Between-river variation of fish population metrics

All sampled sites, except those located in the river Ems, belonged to the same longitudinal river region (mean Fish Region Index >6.5) and therefore indicate comparable fish assemblage compositions. Hence, the observed between-river variation of the fish population metrics indicates a higher degradation of hydromorphology in the rivers Rhine, Lek, Meuse, Havel and Spree than in the rivers Elbe and Oder. Despite representing another river region, the hydromorphological degradation of the river Ems seemingly corresponds to the rivers Elbe and Oder. However, the River Ems provided the majority of sites that are not affected by commercial navigation, a rather unique situation in large rivers.

The rivers Lek, Rhine and Meuse had all the lowest densities of all sensitive reproduction guilds and comparable species richness. However, the river Lek had a higher Evenness and Simpson Index than rivers Rhine and Meuse, resembling a comparable number of species with lower densities of fish in the river Lek than in rivers Rhine and Meuse.

4.3 Highly influential pressures

The potamal region of large rivers is typically dominated by generalist species (Aarts and Nienhuis, 2003), which are well adapted to higher temperatures, nutrient loads and lower oxygen content and thus, are also successful in disturbed ecosystems (Pool et al., 2010). Nevertheless, our study indicated higher biodiversity with higher flow velocities in large rivers. High velocities can exceed the critical swimming speed of juvenile fish, with rheophilic species tolerating higher flow velocities than eurytopic species (Del Signore et al., 2014), resulting in a proportional increase of rheophils. Accordingly, increased velocities contributed to decreased density of eurytopic fish and particularly strongly to a decreased FRI which indicates rhithralisation (Wolter et al., 2013), i.e., a change from naturally slow to faster flowing conditions. Hence, increased velocities provide favorable habitat conditions for rheophilic fish species which contribute to higher diversity. Similarly, in reconnected meanders of a large river, Lorenz et al. (2016) observed increased diversity of rheophilic macroinvertebrates due to higher flow velocities therein. In our study, increased velocities were found having considerably higher influences on biodiversity metrics than on guild densities. However, lithophilic and psammophilic fish were also both strongly positively influenced by increased velocities. Hence, both lithophilic and psammophilic fish constitute indicative functional metrics for the inherent sediment sorting caused by high flow velocities. Consequently, biodiversity in large rivers (species richness, the Shannon Index, the Simpson Index) and the Fish Region Index constitute the most sensitive fish population metrics and densities of lithophils and psammophils constitute the most sensitive functional metrics for rhithralisation as a consequence of the hydrological degradation of the rather stagnant potamal region of large rivers.

The Navigation-induced Habitat Bottleneck Hypothesis (NBH, Wolter and Arlinghaus, 2003) states that littoral fish recruitment is limited in waterways due to navigation-induced hydrodynamic forces along the banks. Correspondingly, densities of all guilds requiring shallow structured habitats for reproduction most strongly declined in response to navigation intensity. Our study further refined the NBH by indicating that limited recruitment of juvenile fish along shoreline habitats propagates to lower densities of habitat-sensitive fish in the adult stages. Exemplified by the River Rhine with its prevalent floodplain loss, channelization and artificial embankments, it was further indicated that commercial navigation inevitably co-occurs with these pressures mentioned and that inland navigation impacts on top of the degradation of river hydromorphology. Concomitantly, navigation intensity was part of all most frequent interactions, affecting 80% of fish population metrics in combination with increased velocity and also affecting 80% of fish population metrics in combination with the loss of floodplains. Therefore, inland navigation is a highly influential and river-type specific pressure in large rivers which moreover interacts with the degradations of river hydromorphology. Further, densities of the sensitive reproduction guilds of lithophils and phytophils were strongly influenced by commercial navigation and declined already at intensities >8 vessels per day. Densities of psammophils were also very low in all navigated rivers, indicating that psammophilic fish were similarly affected by vessel-induced hydrodynamic forces. Therefore, low densities of lithophils, phytophils and psammophils constitute most indicative metrics for the disturbance of shoreline spawning areas through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. However, the influence of the solely vessel-induced wave action was shown to be strongest on phytophilic fish.

Recently, the presence of natural floodplain areas has been associated with an overall higher ecological status of European rivers (Grizzetti et al., 2017). Floodplains are less disturbed by hydraulic forces caused by inland navigation and they support the exchange of terrestrial and aquatic resources. Therefore, floodplains serve as an expansion of the littoral shoreline (Strayer and Findlay, 2010) providing additional spawning and nursery habitats that increase abundances of adult and juvenile fishes (Lorenz et al., 2013). Moreover, floodplains increase the diversity of fish larvae after flood events (Silva et al., 2017) and offer favorable conditions for macrohabitat generalists (Galat and Zweimüller, 2001; Schomaker and Wolter, 2011). High flow intensities and frequencies that result in extensive flooding of adjacent floodplains are related to higher species richness (Poff et al., 1997). Floodplains are however often degraded in large rivers and detached from the rivers' main channels by levees. Correspondingly, the loss of floodplains was associated with lower densities of eurytops, rheophils and phytophils in this study. Densities of lithophilic fish appeared to increase when floodplains were heavily degraded. This is plausible as shorelines are often stabilized with hard substrate, e.g, rip-rap structures (stones/boulders) that might at least partially serve for the reproduction of lithophilic species (Erős et al., 2008). The loss of floodplains further contributed to a decreased Fish Region Index indicating rhithralisation, mainly because levees commonly co-occur with straightened river courses, which in turn increase flow velocity, but primarily reduce habitat complexity and the availability of shelter along the banks.

Densities of eurytopic and rheophilic fish were comparably strongly influenced by five and four pressures, respectively. Eurytopic fish decreased in response to artificial embankment, increased velocity, loss of floodplains and navigation intensity. This finding firstly suggests that densities of eurytopic fish are also prone to decline if multiple pressures including inland navigation affect the potamal region of large rivers. Secondly, high densities of generalist species constitute less suitable fish population metrics to indicate the impacts of one dominating pressure. Instead, high densities of eurytops rather indicate the prevalence of multiple pressures and thus, the overall hydromorphological degradation of large rivers. However, lowered densities of eurytopic fish in the naturally slow flowing potamal river region can also indicate rhithralisation (as was indicated by a decline in densities of eurytopic fish in response to increased velocity). Rheophilic fish were comparably strongly influenced by navigation intensity, loss of floodplains, channelization and by upstream and downstream barriers. Barriers constitute a strong pressure preventing migration of rheophilic fish (e.g., Branco et al., 2017), but in their impoundments especially change the hydromorphological conditions towards lower flow velocities, sedimentation of fines, and loss of coarser spawning substrates.

4.4 Conclusions

Inland navigation constitutes a hitherto commonly neglected but highly influential pressure in European large rivers. In large rivers, inland navigation has an influence on fish assemblages comparable to hydromorphological alterations. Vessel operation contributes to declines of fish densities and biodiversity in addition to the hydromorphological degradation of the river channel and further interacts with the prevailing hydromorphological alterations. Reproduction guilds (densities of lithophilic and phytophilic fish) were most sensitive to navigation impacts but psammophils, rheophils, eurytops and biodiversity were also affected. The loss of floodplains has integral consequences for the ecological integrity of large rivers due to vanishing habitat complexity providing shelter, nursing and spawning habitats. Increased velocity as a consequence of channelization and bank stabilization results in rhithralisation of the potamal region of large rivers. Increased biodiversity (species richness, Shannon Index, Simpson Index), a decreased Fish Region Index and increased densities of lithophilic and psammophilic guilds are indicative fish population metrics for rhithralisation of the potamal region of large rivers. Declines in lithophilic, phytophilic and psammophilic guilds indicate disturbance of shoreline habitats through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. High densities of the eurytopic guild indicate the influence of multiple pressures, but in large rives, eurytops can also decline as a consequence of rhithralisation. Inland navigation requires particular attention in river rehabilitation and management. Therefore, a holistic river management has to consider both river hydromorphology and inland navigation to achieve a more efficient rehabilitation of the potamal region of large rives.

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Table 1. Pressure variables: classification and description

Pressure	Abbreviation	Classes	Labels	Sites [%]	Description
Barriers catchment down	BCD	1 / 3 / 5	No / Partial / Yes	18 / 82 / 0	Barriers within the catchment downstream
Barriers segment up	BSU	1 / 3 / 5	No / Partial / Yes	93 / 0 / 7	Barriers within 5km upstream
Channelization	CHA	1 / 3 / 5	No / Intermediate / Straightened	7 / 5 / 88	Alteration, straightening of natural river plan form
Cross section	CRS	1 / 3 / 5	No / Intermediate / U-profile	0 / 5 / 95	Alteration, enlargement of cross-section
Embankment	EMB	1 / 3 / 5	No or local / Permeable / Impermeable	0 / 22 / 78	Artificial embankment
Loss of Floodplains	FLO	1 / 3 / 5	Little / Severe / Extinct	12 / 21 / 67	Floodplain degradation
Inland navigation	NAV	1 / 3 / 5	Low / Intermediate / High	14 / 59 / 26	1: 0 - 3000; 3: 3.001 – 33.000; 5: 33.001-133.000 cargo vessels / year
Organic siltation	ORS	1 / 3 / --	No / Yes / --	12 / 88 / --	Presence of organic siltation
Riparian vegetation	RIV	1 / 3 / 5	High / Intermediate / Rare	88 / 12 / 0	Cover of riparian vegetation
Sedimentation	SED	1 / 3 / 5	No / Weak + Medium / High	76 / 20 / 4	Increased sedimentation
Velocity increase	VEL	1 / 3 / --	No / Yes / --	20 / 80 / --	Artificially increased velocity, Rhithralisation

Table 2. Relative influence [%] of each pressure on fish population metrics. Each column represents one boosted regression tree (BRT) model with the fish metric as response variable (EURY = eurytopic fish, RH=rheophilic, LITH = lithophilic, PHYT = phytophilic, SPR = species richness, SHA = Shannon Index, EVE = Evenness, SIM = Simpson Index, FRI = Fish Region Index). The last row provides goodness-of-fit measures (R^2_{COR}) for each BRT model. Values in parenthesis provide the upper and lower limit of the 95% confidence interval of each parameter based on 500 bootstrap simulations of the respective BRT model. Bold font highlights pressures with the strongest relative influence (>10%) on the fish population metrics.

Pressures	EURY	RH	LITH	PHYT	PSAM	SPR	SHA	EVE	SIM	FRI
Barriers catchment down	4.0 (3.6-4.6)	**15.1 (14.3-18.4)**	2.8 (2.0-3.2)	4.1 (3.8-4.4)	2.1 (1.3-2.2)	3.6 (3.6-4.1)	4.1 (4.2-4.8)	**16.7 (15.8-18.5)**	6.6 (5.7-6.6)	3.6 (3.5-3.7)
Barriers segment up	1.3 (0.8-1.6)	**11.1 (10.6-14.3)**	1.8 (1.6-1.8)	0.6 (0.5-0.8)	0.3 (0.2-0.3)	2.7 (2.4-2.9)	0.7 (0.7-1.3)	2.2 (1.4-2.5)	1.0 (0.9-1.6)	0.4 (0.2-0.5)
Channelisation	9.4 (9.1-9.8)	**12.5 (9.7-13.0)**	6.1 (2.8-6.6)	3.8 (3.7-4.3)	3.7 (0.7-4.1)	8.8 (8.9-10.2)	2.3 (2.3-3.0)	**16.4 (15.6-16.7)**	5.0 (4.7-5.5)	0.5 (0.3-0.6)
Cross-section	0.2 (0.2-0.3)	0.9 (0.5-1.0)	0.7 (0.6-0.8)	0.1 (0.1-0.1)	0.1 (0.0-0.1)	0.3 (0.3-0.4)	0.2 (0.2-0.3)	0.7 (0.7-1.1)	0.3 (0.2-0.4)	0.1 (0.1-0.2)
Embankment	**16.5 (15.9-18.7)**	6.4 (4.9-6.6)	4.7 (2.6-5.3)	0.9 (0.7-1.2)	2.7 (0.5-3.1)	0.9 (0.9-1.3)	1.0 (0.8-1.4)	0.6 (0.4-1.5)	0.8 (0.7-1.3)	0.3 (0.2-0.5)
Loss of floodplains	**14.0 (13.3-14.8)**	**11.5 (10.1-12.4)**	**16.4 (15.9-17.2)**	8.6 (8.2-10.1)	9.5 (4.7-11.0)	5.9 (5.8-6.4)	5.5 (5.3-6.2)	**13.3 (11.5-13.3)**	4.4 (4.0-5.3)	**16.3 (15.9-17.0)**
Inland navigation	**10.7 (10.3-11.0)**	**23.6 (23.0-26.9)**	**20.1 (19.6-20.8)**	**33.8 (33.2-34.6)**	**25.4 (25.1-26.7)**	**18.6 (18.2-18.8)**	8.5 (8.6-9.6)	7.4 (6.5-8.9)	8.1 (7.7-9.1)	5.7 (5.0-6.0)
Organic siltation	0.1 (0.0-0.2)	0.4 (0.2-0.5)	0.1 (0.0-0.2)	**32.9 (30.8-33.6)**	0.2 (0.1-0.3)	0.5 (0.3-0.8)	0.2 (0.1-0.3)	1.2 (0.7-1.3)	0.7 (0.5-1.3)	0.0 (0.0-0.1)
Riparian vegetation	2.1 (1.5-2.4)	4.0 (3.6-4.2)	2.6 (1.3-3.3)	8.7 (7.8-9.2)	3.5 (1.6-4.1)	1.6 (1.4-1.7)	2.8 (2.5-3.0)	6.8 (6.4-7.8)	3.9 (3.8-4.5)	0.5 (0.4-0.6)
Sedimentation	**23.3 (22.6-24.3)**	7.2 (4.8-7.7)	4.9 (3.1-5.6)	5.8 (5.4-6.2)	3.8 (1.8-4.4)	2.9 (2.8-3.5)	6.7 (6.7-7.9)	**15.9 (15.3-16.7)**	7.3 (6.6-8.3)	2.5 (2.1-2.7)
Velocity increase	**18.4 (16.6-18.8)**	7.1 (6.5-7.3)	**40.0 (36.0-49.8)**	0.7 (0.6-1.2)	**48.8 (45.2-62.1)**	**54.1 (51.0-54.1)**	**68.0 (63.1-67.7)**	**18.7 (17.3-20.5)**	**61.9 (57.4-63.8)**	**70.0 (68.7-71.7)**
Model fit (R^2_{COR})	0.84 (0.84-0.85)	0.74 (0.73-0.77)	0.73 (0.73-0.76)	0.83 (0.83-0.83)	0.64 (0.63-0.67)	0.6 (0.6-0.61)	0.72 (0.71-0.72)	0.88 (0.87-0.89)	0.79 (0.78-0.79)	0.54 (0.54-0.54)

Table 3. Pressure-interactions and their effect sizes on each fish population metric (FPM). Each column represents the results of one boosted regression tree model. BCD = barriers catchment downs; BSU = barriers segment up; CHA = channelization; EMB = artificial embankment; FLO = loss of floodplains; NAV = navigation intensity; ORS = organic siltation; RIV = cover of riparian vegetation; SED = increase of sedimentation; VEL = increase of flow velocity). Note: effect sizes are not comparable across different FPM.

Eurytopic fish		Rheophilic fish		Lithophilic fish		Phytophilic fish		Psammophilic fish		Species richness		Shannon Index		Evenness		Simpson Index		Fish Region Index	
Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size
CHA * SED	2.02	EMB * CHA	11.43	NAV * FLO	7.94	NAV * ORS	7.71	NAV * VEL	18.02	NAV * VEL	316.7	NAV * VEL	10.52	CHA * VEL	0.11	CHA * VEL	0.35	FLO * VEL	1.11
NAV * VEL	1.35	NAV * BSU	9.07	FLO * VEL	6.53	ORS * SED	1.4	FLO * SED	5.33	NAV * FLO	170.98	FLO * VEL	8.72	SED * BCD	0.04	RIV * VEL	0.23	NAV * FLO	0.42
NAV * FLO	1.29	CHA * VEL	8.93	EMB * CHA	3.49	NAV * FLO	1	EMB * CHA	3.46	FLO * VEL	109.17	NAV * FLO	7.67	RIV * VEL	0.03	NAV * VEL	0.17	FLO * BCD	0.11
NAV * EMB	1.16	VEL * BSU	5.15	NAV * VEL	2.22	NAV * SED	0.63	NAV * FLO	3.11	VEL * BSU	78.79	VEL * BCD	5.74	FLO * SED	0.02	VEL * BCD	0.12	VEL * BCD	0.08
FLO * SED	1.1	NAV * ORS	4.56	FLO * SED	0.62	ORS * RIV	0.39	FLO * EMB	0.64	CHA * VEL	22.39	RIV * VEL	4.05	NAV * FLO	0.01	NAV * SED	0.09	FLO * SED	0.02
NAV * BCD	0.81	NAV * VEL	4.36	VEL * BCD	0.46	ORS * CHA	0.23	SED * BCD	0.45	FLO * RIV	16.69	CHA * VEL	2.88	NAV * VEL	0.01	FLO * VEL	0.09	SED * VEL	0.01

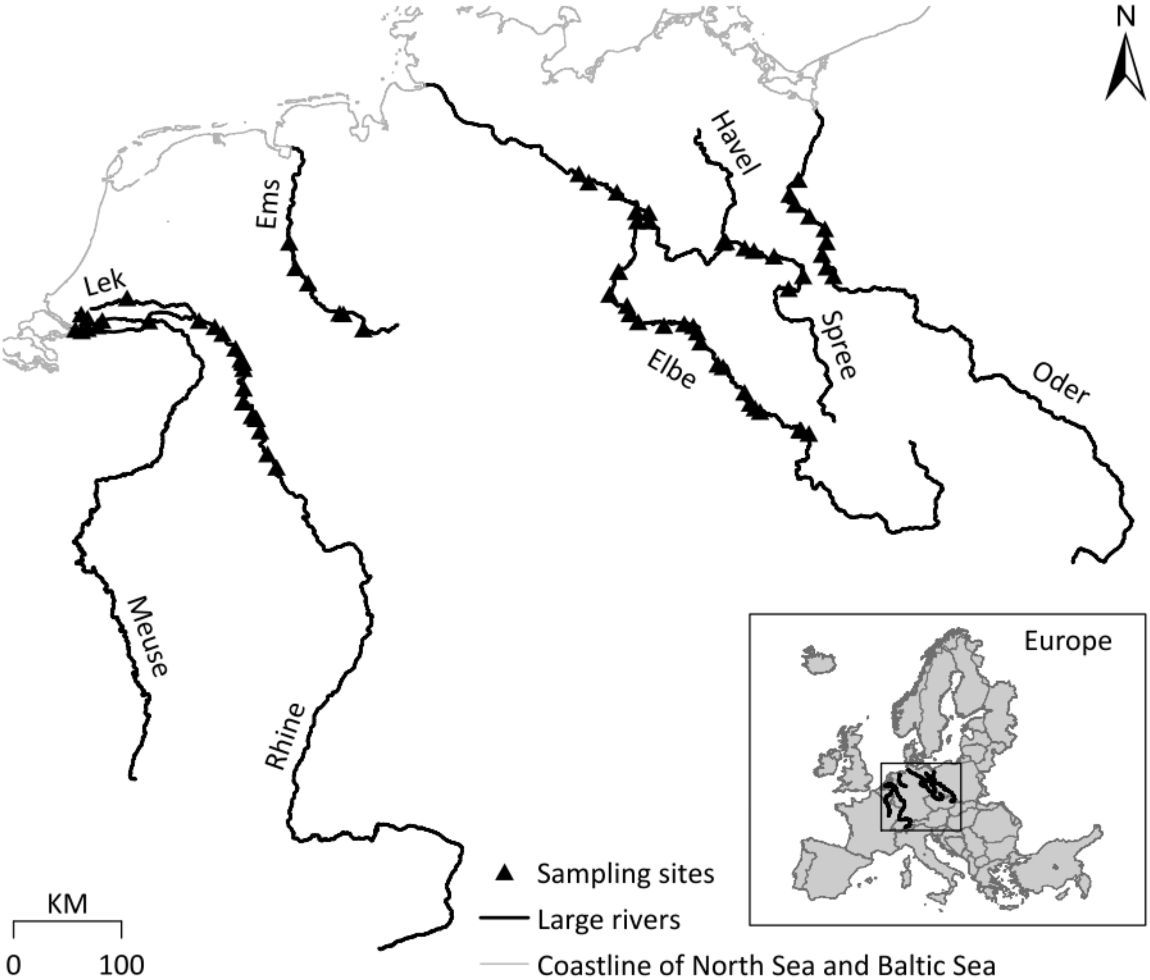

Figure 1. Location of sampling sites.

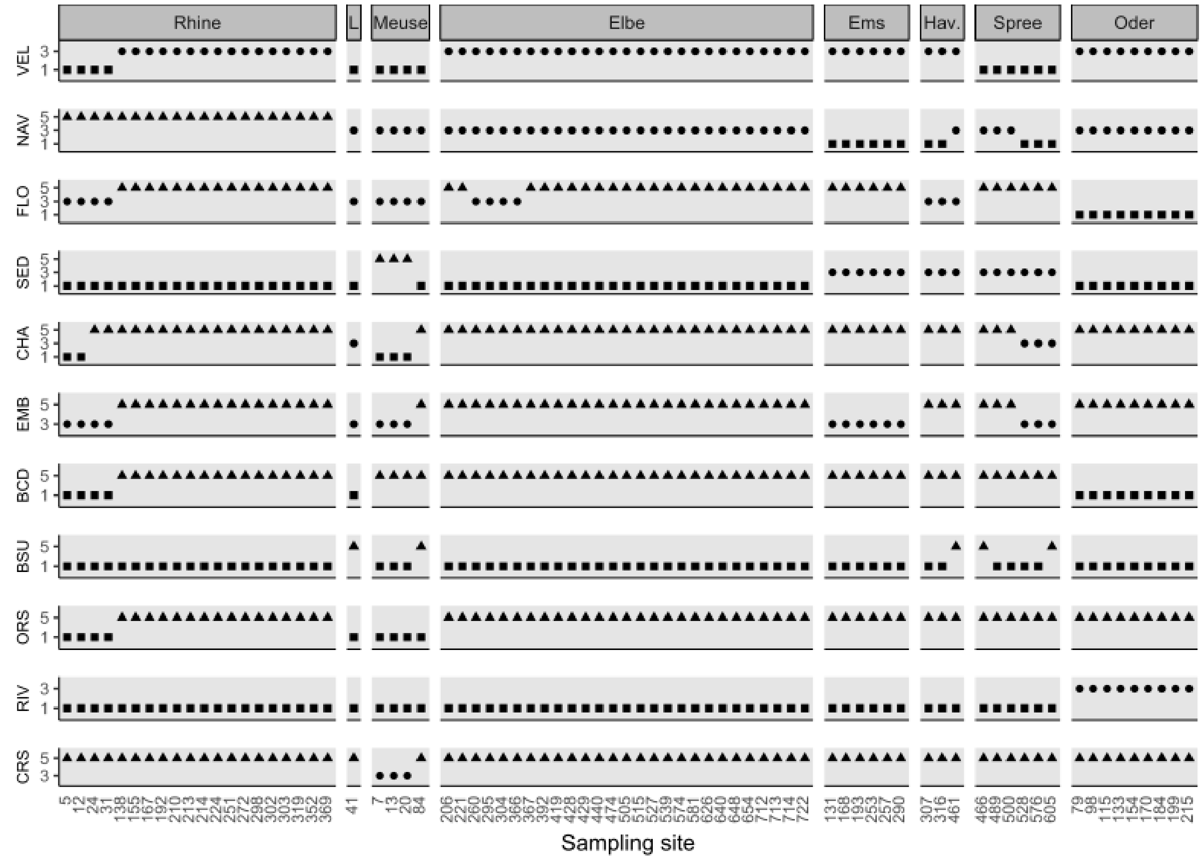

Figure 2. River-specific classification of sampling sites by pressures. L = Lek; Hav. = Havel. VEL = increase of flow velocity; NAV = navigation intensity; FLO = loss of floodplains; SED = increase of sedimentation; CHA = channelization; EMB = artificial embankment; BCD = barriers catchment down; BSU = barriers segment up; ORS = organic siltation; RIV = cover of riparian vegetation; CRS = cross-section. Alteration of the natural state increases from one to five (different symbols are used for better visualization: 1 = square: low or no alteration; 3 = circle: intermediate alteration; 5 = triangle: high alteration, compare Table 1). The x-axis labels show the distance of each sampling site to the Ocean in kilometers.

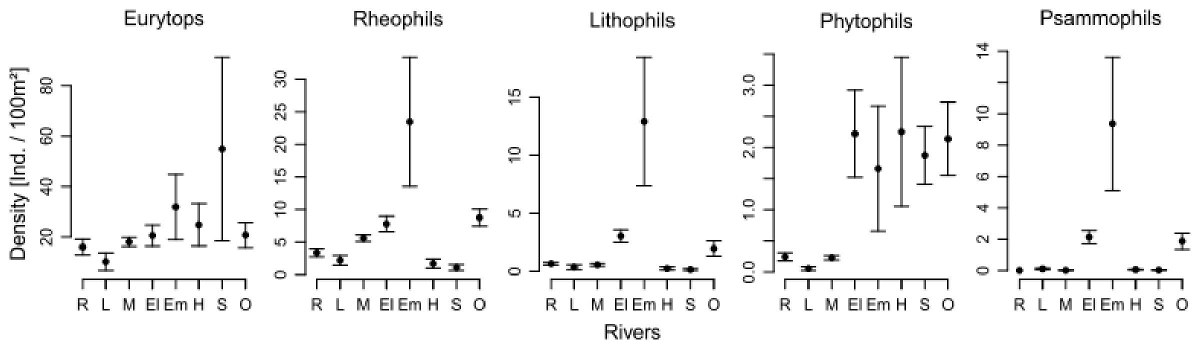

Figure 3. River-specific estimates of guild densities. R: Rhine (number of samplings: 41); L: Lek (5); M: Meuse (62); El: Elbe (100); Em: Ems (7); H: Havel (4); S: Spree (8); O: Oder (23). Means +/- standard errors are shown. Note: Figure A.01 in the appendix provides a site-specific overview.

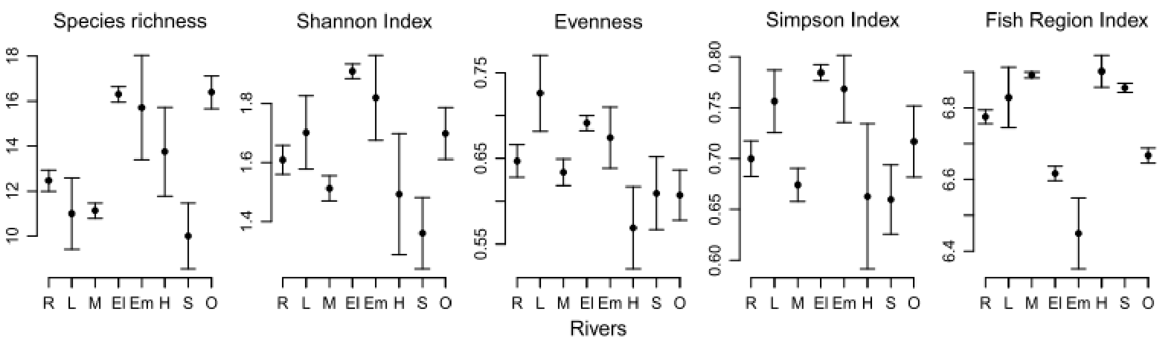

Figure 4. River-specific estimates of biodiversity metrics. R: Rhine (number of samplings: 41); L: Lek (5); M: Meuse (62); El: Elbe (100); Em: Ems (7); H: Havel (4); S: Spree (8); O: Oder (23). Note: Figure A.01 in the appendix provides a site-specific overview.

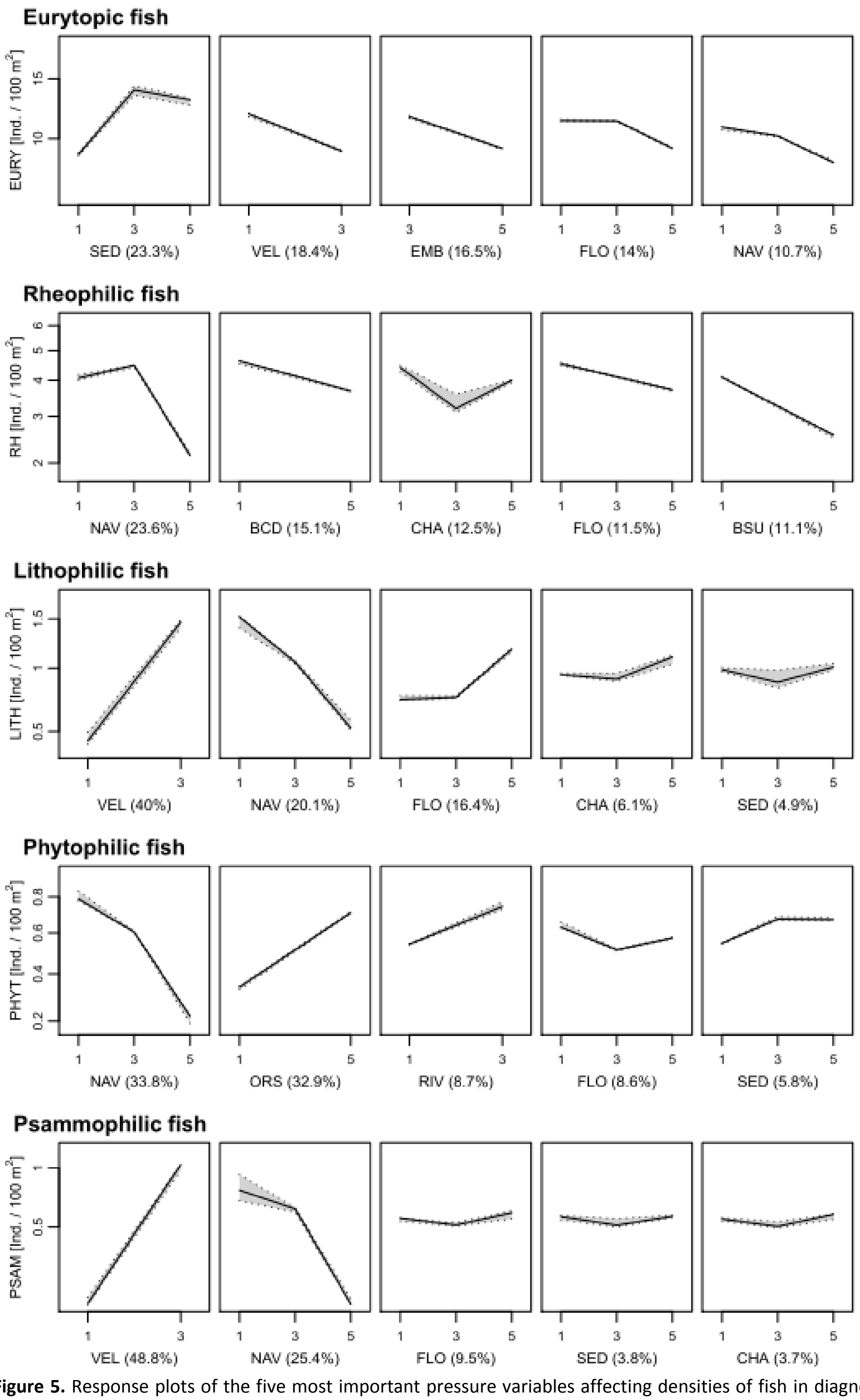

Figure 5. Response plots of the five most important pressure variables affecting densities of fish in diagnostic guilds. Each row represents one boosted regression tree (BRT) model with a given fish metric as response. Solid lines represent results obtained from the original BRT model; dashed lines and grey areas show the 95% confidence interval based on 500 bootstrap simulations of each BRT model. X-axes show ranked pressure classes (BCD = barriers catchment down; BSU = barriers segment up; CHA = channelization; EMB = artificial embankment; FLO = loss of floodplains; NAV = navigation intensity; ORS = organic siltation; RIV = cover of riparian vegetation; SED = increase of sedimentation; VEL = increase of flow velocity) with 1 = low or no alteration; 3 = intermediate alteration; 5 = high alteration. Percentages in parenthesis indicate the relative variable importance of each pressure in the respective BRT model.

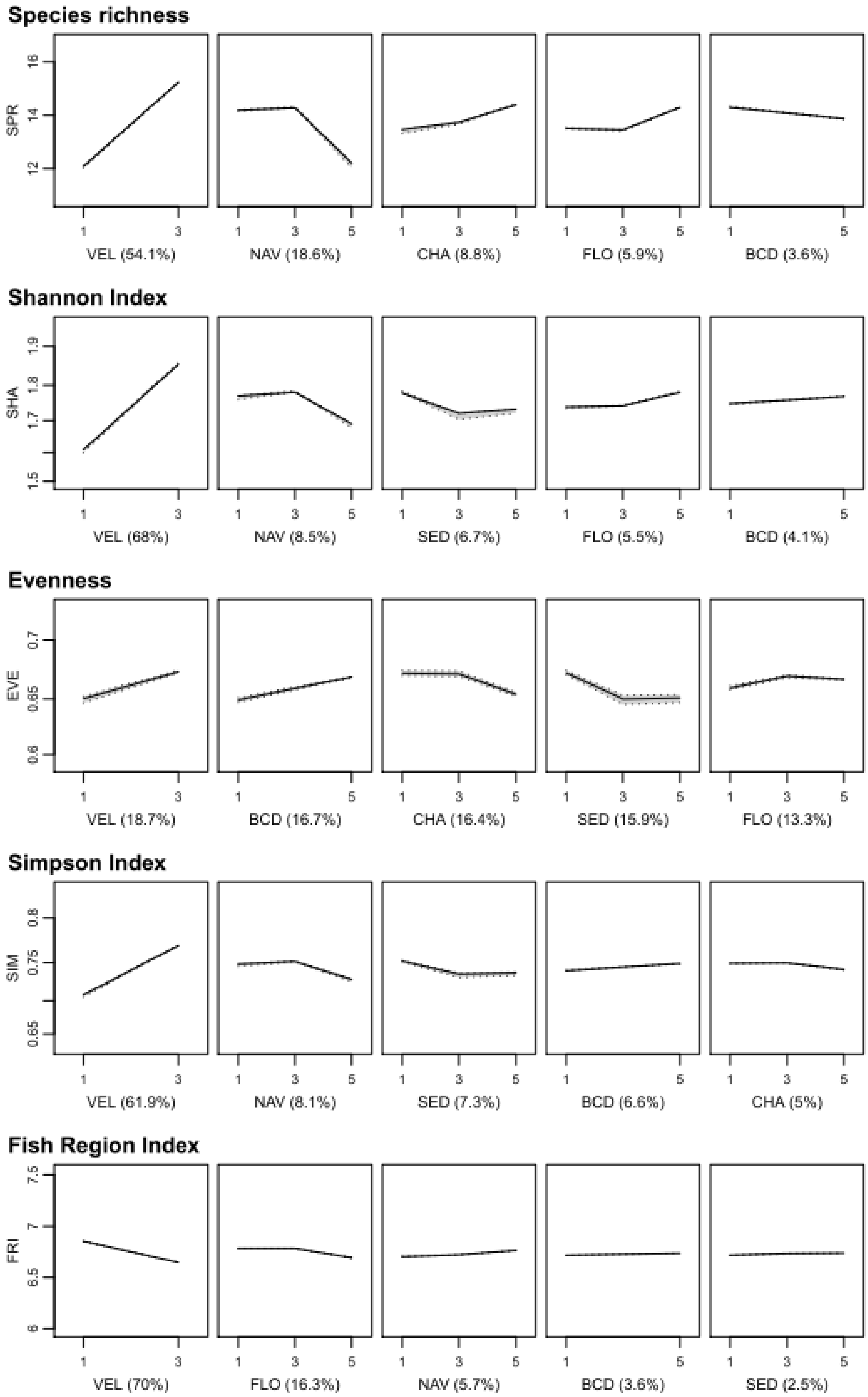

Figure 6. Response plots of the five most important pressure variables affecting biodiversity metrics. Each row represents one boosted regression tree (BRT) model with a given biodiversity metric as response. Solid line represents results obtained from the original BRT model; dashed lines and grey area show the 95% confidence interval based on 500 bootstrap simulations of each BRT model. X-axes of each plot show ranked pressure classes (BCD = barriers catchment down; CHA = channelization; FLO = loss of floodplains; NAV = navigation intensity; SED = increase of sedimentation; VEL = increase of flow velocity) with 1 = low or no alteration; 3 = intermediate alteration; 5 = high alteration. Percentages in parenthesis indicate the relative variable importance of each pressure in the respective BRT model.