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Freshwater fish biodiversity restoration in floodplain rivers requires connectivity and habitat heterogeneity at multiple spatial scales

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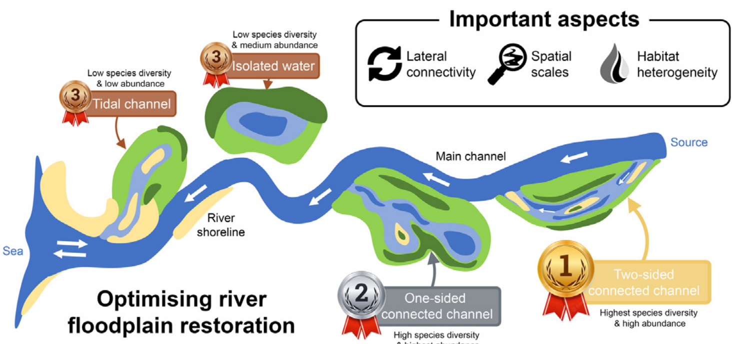
HIGHLIGHTS

- Fish recruitment and habitat conditions are studied in 46 river restoration projects.
- Flow conditions and lateral connectivity are essential for young riverine fishes.
- Multiple spatial scales of habitat heterogeneity affect both abundance and diversity.
- There is no one-size-fits-all design to restore large rivers for fishes.
- River restoration projects should be complementary to serve the entire fish community.

GRAPHICAL ABSTRACT



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ABSTRACT

With a sixth mass extinction looming and freshwater biodiversity declining at unprecedented rates, evaluating ecological efficacy of river restoration efforts is critical in combatting global biodiversity loss. Here, we present a comprehensive study of the functioning for fishes of 46 river restoration projects in the river Rhine, one of the world's most heavily engineered lowland rivers. Floodplains with permanent, either one- or two-sided lateral connectivity to the main channel, favour total fish abundance, and are essential as nursery areas for riverine fishes. Habitat heterogeneity had a strong positive effect on species richness but was negatively related with fish abundances. However, the effects of environmental variables varied between ecological groups and spatial scales. Surprisingly, richness of critical rheophilic fishes declined with large-scale habitat heterogeneity (~1000 m), while it increased at small scales (~100 m), possibly because of the presence of unfavourable habitats for this ecological group at larger scales. Clearly, there is no one-size-fits-all design for river restoration projects. Whether a river section is free-flowing or impounded dictates the scope and efficacy of restoration projects and, within a river section, multiple complementary restoration projects might be key to mitigate freshwater fish biodiversity loss. An essential element for success is that these projects should retain permanent lateral connection to the main channel.

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1. Introduction

Our planet is in the middle of a biodiversity crisis, with species numbers declining faster than at any time in human history (Barnosky et al., 2011; Cowie et al., 2022). Nowhere is this decline more severe than in freshwater ecosystems (Sala et al., 2000; Harrison et al., 2018; Reid et al., 2019), which cover 2.3 % of the Earth's surface, but contain over 10 % of the world's species, a quarter of all vertebrate species, and more than half of all fish species (Reid et al., 2019; Deinet et al., 2020; Eschmeyer et al., 2022). At present, nearly a third of all freshwater fish species are threatened with extinction, and abundances of specialised migratory fishes, such as salmons (Salmonidae), sturgeons (Acipenseridae) and eels (Anguillidae), have even declined by >75 % over the last 50 years (Deinet et al., 2020).

Rivers belong to the most affected freshwater ecosystems globally, because historically, human societies modified them for the purpose of flood safety, energy production, irrigation, and navigation. As a result, only a third of all large rivers still flow freely from source to sea (Grill et al., 2019), and an estimated 1 million barriers in the form of hydropower plants or dams fragment European rivers (Belletti et al., 2020). Furthermore, over a third of the world's wetlands and floodplains have been lost through drainage, conversion, excessive irrigation, and river normalisation and embankment since the 1970's (Tockner and Stanford, 2002; Gardner and Finlayson, 2018). This resulted in the loss of important longitudinal and lateral connectivity within river ecosystems, and in the degradation or complete loss of essential habitats for healthy river fish communities (van Puijenbroek et al., 2019; Su et al., 2021). These river modifications have contributed to a homogenisation of the world's river fish faunas, and hence to an overall decline of fish biodiversity (Villéger et al., 2011; Deinet et al., 2020; Su et al., 2021). Other imminent threats to the diversity and abundance of river fishes are: the introduction of invasive alien species (Lusk et al., 2010; Clavero et al., 2013; Gallardo et al., 2016; Pyšek et al., 2020); damaging and unsustainable fishing practises (McIntyre et al., 2016); pollution with untreated waste (IPBES, 2019); light, noise and microplastic pollution (Reid et al., 2019); and the impacts of climate change (Poff et al., 2012; Barbarossa et al., 2021).

Most river fishes rely on a sequence of inter-connected functional habitat types to complete their life history (Van Looy et al., 2019; Stoffers et al., 2022). Anadromous and catadromous fishes that have spawning migrations between seas and (upstream) rivers are particularly sensitive to the presence of longitudinal barriers (Parrish et al., 1998; Winemiller et al., 2016), whereas many sensitive rheophilic (flow-preferring) fish species are bound to the lateral connectivity of lowland rivers with their floodplains and wetlands, which they use as spawning and/or nursery habitat (Birnie-Gauvin et al., 2017; Stoffers et al., 2021). The protection and restoration of such critical (nursery) habitats is therefore essential for the recovery of river fish communities, and can be achieved through barrier removal and reconnection to wetlands and floodplains (Tickner et al., 2020).

With this aim, many diverse river restoration initiatives have been realised globally (Bernhardt and Palmer, 2011). In Europe alone, over 1400 river restoration projects in 31 countries have been implemented over the last 30 years (Environment Agency, 2022), aided by national and European environmental directives such as the EU Water Framework and Nature Directives (Szałkiewicz et al., 2018). Many river restoration projects have however failed to achieve the expected recovery of fish communities, causing global concern about their efficacy (Palmer et al., 2010; Bernhardt and Palmer, 2011; Wohl et al., 2015). For river restoration to be effective for fishes, it is essential to understand fishes' environmental requirements in terms of spatial scale and organisation of essential (micro)habitats for shelter, food and spawning (Schlosser, 1995; Van Looy et al., 2019; Stoffers et al., 2022). The fact that the spatial scale of habitat use varies with species and mostly increases with fish size further complicates effective management of (future) river restoration projects (Wohl et al., 2015; Wolter et al., 2016; Polvi et al., 2020).

Especially large temperate lowland rivers, such as the Mississippi, Danube, Rhine, and Murray-Darling rivers, have experienced and continue to face huge anthropogenic pressures (Su et al., 2021). Therefore, knowledge of the ecological functioning of river restoration project in such modified rivers is critical for implementing actions to combat global freshwater biodiversity loss (Tickner et al., 2020), but is largely inadequate. Here, we provide the first large-scale evaluation of the ecological efficacy as nursery area for riverine fishes, of 46 river restoration projects in three branches of the lower river Rhine. We introduce a novel approach, explicitly linking the effect of fish habitat to biodiversity and abundances of young-of-the-year (YOY) riverine fish communities at three relevant spatial scales. Our approach uncovers generic processes essential for the successful recruitment of riverine fishes, which are applicable for the effective restoration of modified lowland rivers around the world (Arlinghaus et al., 2016; Stoffers et al., 2022). With a potential sixth mass extinction looming (Barnosky et al., 2011; Cowie et al., 2022), studies contributing to the preservation of riverine fish biodiversity and evaluating the ecological efficacy of river floodplain restoration are of eminent importance.

2. Methods

2.1. Study area and sampling strategy

With a length of 1230 km and a catchment area of 220,000 km^2, the river Rhine is the second largest river system in Central and Western Europe (Wantzen et al., 2022). This large lowland river originates in the south-eastern Swiss Alps, and flows via France and Germany through the Netherlands before reaching the North Sea. After entering the Netherlands, the river Rhine splits into three branches: the river Waal (median annual discharge: 1473 m^3·s^{-1}), IJssel (317 m^3·s^{-1}), and Nederrijn/Lek (160 m^3·s^{-1}) (Waterinfo, 2021). The rivers Waal and IJssel are free flowing, whereas the river Nederrijn/Lek contains three weir complexes to manage water levels for water supply and navigation purposes, hereby limiting free water flow (Fig. 1A).

Over 60 floodplain restoration projects were realised in these rivers since the 1990's (approximately one per 5 km of river), aiming at improving flood protection and habitat quality (Rijke et al., 2012). All projects are outside of residential areas, and the majority of them are open to the public. There have been no marked differences in visitor numbers during the sampling period due to the COVID-19 pandemic or other developments, and therefore it is unlikely that this has impact the outcome of our study. Based on their morphology and connectivity with the main channel, restoration projects can be divided into two-sided connected channels (2SC), one-sided connected channels (1SC), tidal channels, and isolated waters. In this study, we evaluated the nursery function for riverine fishes of 46 of these restoration projects and 26 control sites (at the shoreline) in the lower river Rhine (Figs. 1B; 3A). This large-scale evaluation study took place in July from 2017 to 2020. To account for yearly variation in environmental conditions and river discharge patterns, the vast majority of the projects (41 out of 46) were evaluated at least 3 times in this period (overview in Suppl. materials A1). Sampling strategies consisted of monitoring YOY fish community and characterising the environment on three relevant spatial scales. Sampling covered all different habitat types that could be visually identified to obtain a data set that is representative for the restoration project.

2.2. Data collection

2.2.1. Fish community sampling

We collected YOY fish community data from 1253 sampling sites. To sample a wide variety of aquatic environments a combination of two sampling techniques was used: seine netting and electrofishing. We used seine nets of 25 and 75 m length, 3–4 m depth, and with a maximum stretched mesh size of 12 mm. Generally, seine netting was used in non- to slow-flowing habitats with low structural complexity. Sampling was conducted by at least two persons, one guiding the net on the shore and a second person wading (25-m seine net) or navigating a small boat through the water (75-m seine net). Electrofishing was performed from a boat (continuous DC 6A, 200 V) or wading (pulsed DC 3A, 12 V), depending on the

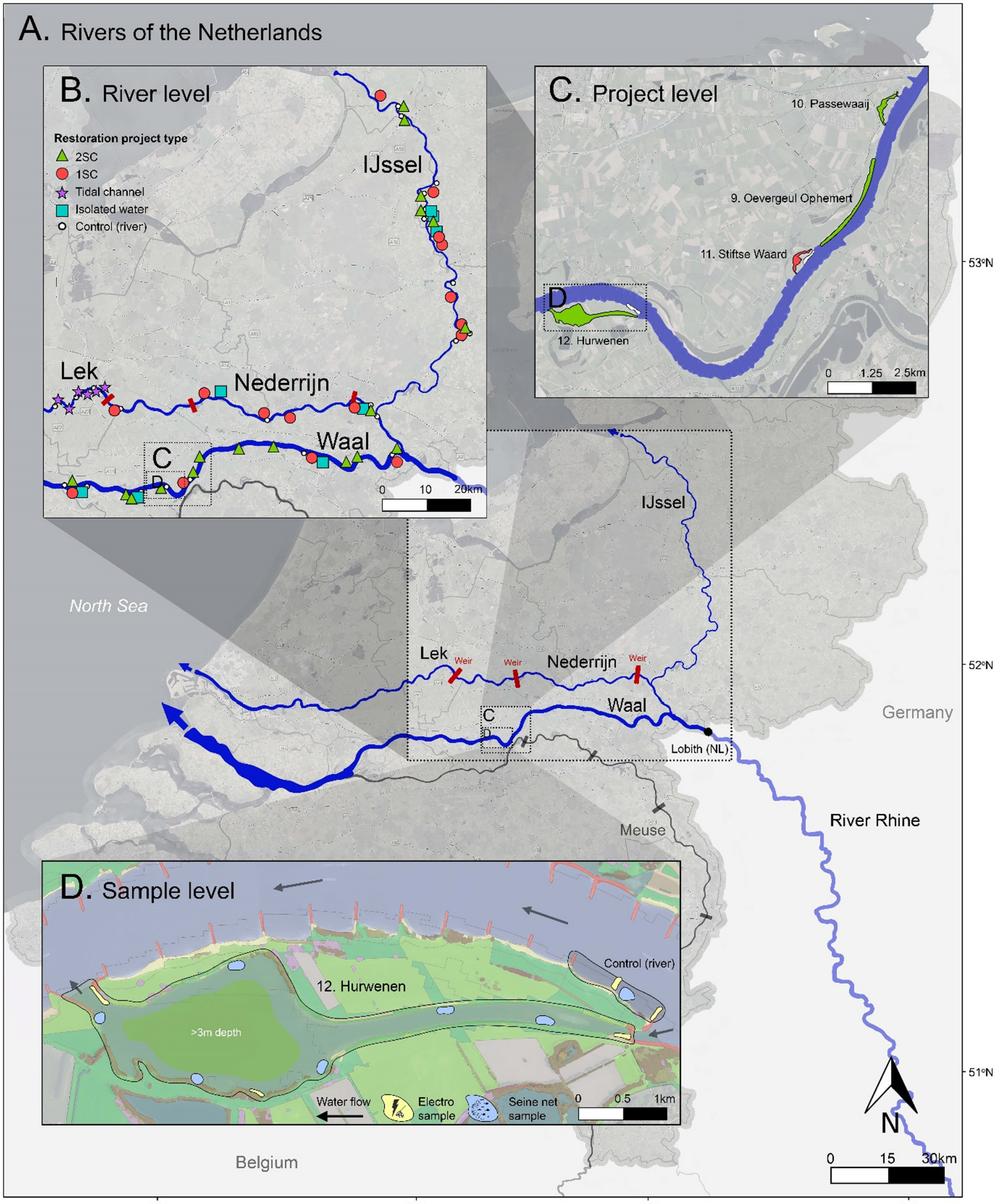


Fig. 1. Branches of the river Rhine in the Netherlands with spatial scales for floodplain restoration project evaluation. (A) Geographical location of the river branches with weirs indicated in red. (B) River level with floodplain restoration project types indicated with green triangles (2SC), red circles (1SC), turquoise squares (isolated water) and purple stars (tidal channel). Smaller white circles show control sites (river shoreline). (C) Project level with an example of the geographical position of several individual restoration projects within the river Waal. (D) Sample level with the restoration project of Hurwenen (2SC) and a corresponding control site (river shoreline) as example. The black line shows the outline of the project at average river discharge levels. Blue (seine net) and yellow (electro) areas indicate individual sampling sites.

habitat type. In general, waded sampling was used in narrow, shallow, standing waters with macrophytes, whereas electrofishing by boat was used in deeper, flowing waters with high structural complexity. For both methods, sample surface of the transect was obtained by multiplying transect area width by its length. Average surface area per seine net sample was 580 m^2, and for electrofishing 114 m^2.

The collected fishes were kept in plastic tubs until sampling was completed. Representative subsamples were taken when fish numbers caused handling time of the sample to interfere with fishes' health. This generally occurred when total fish numbers exceeded 200. Fish were identified to species level, measured to the nearest mm (total length), and released again.

2.2.2. Environmental sampling

For each sample site, we characterised 46 habitat variables on three important spatial scales for YOY fish: sample level (~0.1 km), project level (~1.0 km) and river (stretch) level (~10 km) (see also Fig. 1). We collected variables related to water quality and local habitat (sample), hydromorphology (project and river), habitat heterogeneity (sample and project), shoreline habitat (sample and project), and daily water levels (project). Many of the habitat variables were measured during field sampling, while shoreline habitat and data on habitat heterogeneity were retrieved from satellite images and aerial photographs. An overview of all habitat variables collected in this study, as well as a detailed description on collection methods, can be found in Supplementary materials.

2.3. Data analysis

2.3.1. Fish community response variables

Given the focus on the nursery function of restoration projects, species-specific cut-off sizes were used to select only YOY fishes for analysis (Suppl. materials A6). Size limits were derived from length-frequency distributions, consultation with fish ecology experts from the Netherlands, and a literature study by Stoffers et al. (2022). Hybrids and other fishes that could not be identified to species level (0.007 % of total catch) were removed prior to the analysis.

To understand the functioning of restoration projects for different aspects of the YOY fish community, we divided fish species into limnophilics (preference for stagnant water bodies), eurytopics (no specific flow preference), rheophilics (preference for flowing water), and critical rheophilics. Fish species were classified in these ecological groups according to Aarts et al. (2004) and van Treeck et al. (2020). For the critical rheophilics group we removed ide (*Leuciscus idus*), because this species is generally thought to be a less-critical rheophilic species in terms of habitat use in the lower river Rhine (Stoffers et al., 2021; Stoffers et al., 2022), while it accounted for almost 85 % of all rheophilic catches (Suppl. materials A6). For all ecological groups and for the community as a whole (all species) we calculated a set of four fish community response variables. Per sampling site, we calculated abundances (both total number of fish and number per 100 m^2) and species richness (α-diversity). For each restoration project we calculated overall species richness (γ-diversity), as well as Whittaker's species turnover rate (β-diversity) as a measure of the differentiation of species richness amoung samples within a project (Table 1). An example of these four community response variables in a project setting is given in Fig. 2 (for the 2SC of Hurwenen in the river Waal).

2.3.2. Restoration project evaluation

The functioning of different types of restoration projects as nursery areas for riverine fishes was assessed for communities as a whole (including all species), and for rheophilic, eurytopic, and limnophilic fishes. We assessed 2SCs, 1SCs, tidal channels, isolated waters, and control sites in the main channel, and performed separate analyses for the seine and electrofishing techniques. First, we calculated β- and γ-diversity per sampling year for each restoration project and control site, as well as average abundances (fish per 100 m^2) and α-diversity. Then, fish responses were summarised over all years for each project type (mean ± se), and means were tested for significant differences between project types with a Kruskal–Wallis H test (significance level $\alpha = 0.05$). Lastly, Dunn's test with Bonferroni correction was used to test for pairwise comparison between project types. These analyses were performed with R packages (rstatix v0.7.0 and agricolae v1.3.3) running on RStudio (R Core Team, 2021).

2.3.3. Habitat variable selection

Prior to the analysis, data exploration was carried out following the protocol described in Zuur et al. (2010). Herein, habitat variables were checked for extreme values (large and small) and for pairwise correlations with a correlation matrix based on Kendall's correlation coefficient (R packages: stats v4.0.2 and corrplot v0.90). Selection of habitat variables was based on three criteria: (1) Kendall correlation between variable pairs was <0.3, (2) a variable could only have one correlation >0.2 with another variable, and (3) when two or more variables were correlated, we retained the one with the clearest ecological interpretation and/or meaning for floodplain restoration project management. The correlation matrix after habitat variable selection can be found in Supplementary materials A7. Table 2 shows the final set of 20 habitat variables including description and information on assessment and data source. This set of habitat variables was used for the multivariate analysis of fish-habitat relationships (see Suppl. materials A11) and habitat requirements modelling.

2.3.4. Habitat requirements modelling

2SCs and 1SCs have the highest potential to function as nursery area for riverine fishes. For the habitat requirements modelling we therefore only used data on these two restoration project types. Modelling of fish-habitat relationships took place on the lowest possible aggregation level to ensure highest levels of detail. This means that depending on the spatial scale on which the community response variable was obtained, the scale on which we modelled was different (Table 1). For instance, fish abundances and α-diversity were modelled on sample level, whereas habitat requirements in relation to β-diversity and γ-diversity responses were assessed on restoration project scale.

Bayesian hierarchical models, using integrated nested Laplace approximations (INLA) (Rue et al., 2009; Zuur et al., 2017; Zuur and Ieno, 2018), were used to predict habitat requirements for the 12 fish community response variables. To find optimal models for each response variable, a stepwise modelling approach with INLAstep (R package: INLAutils v0.0.5) in INLA (R package: INLA v21.02.23) was used to identify: (1) data distribution type, (2) important habitat variables, and (3) non-linear habitat effects. Model validation was done according to Zuur et al. (2017). For each final model we visualised individual parametric effects of the fixed and random effects (with 95 % credible intervals) on the response variable. A detailed description of the stepwise model selection and validation procedures, as

Table 1
YOY fish community response variable information.

Response variable	Description	Spatial scale	Calculation
Abundances	Total number of fish per sample	Sample	Abundance = number of fish (and number of fish per 100m^2)
α-Diversity	Species richness per sample	Sample	α = number of species
β-Diversity	Differentiation of species richness amoung samples within a project	Project	Whittaker's species turnover: $\beta_W = (\gamma/\alpha) - 1$
γ-Diversity	Total species richness over all samples of a project	Project	γ = number of unique species

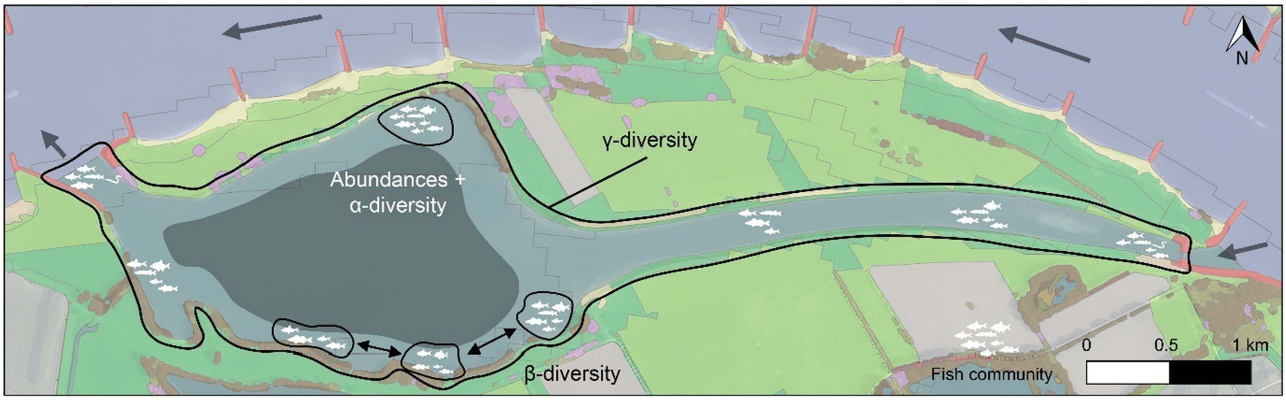


Fig. 2. An example of the quantification of fish response variables for the floodplain restoration projects (2SC) of Hurwenen.

well as a list of the optimal Bayesian models, can be found in Supplementary materials A8.

3. Results

From 2017 to 2020, we collected fish community data for 46 floodplain restoration projects and 26 control sites (river shoreline) in the lower river Rhine, resulting in 1253 sampling events. Using seine nets and electrofishing we sampled over 43 ha of potential nursery habitat and recorded 508,284 YOY fishes belonging to 38 species (overview in Suppl. materials A6).

3.1. Restoration project evaluation

Fish were recorded at each restoration project type, and species richness and abundances varied greatly (Fig. 3B). Highest overall fish abundances were found in 1SCs and 2SCs (Fig. 3B), both for seine netting and electrofishing (see Suppl. materials A12). Eurytopic abundances were on average 3 to 18 times lower at control sites and tidal channels than at 1SCs and 2SCs. Rheophilic fishes were found in significantly lower numbers than eurytopics (Suppl. materials A12) and preferred 2SCs as nursery area over 1SCs, whereas highest abundances of eurytopics were found in 1SCs.

Species richness patterns of restoration project types were similar to those of fish abundances, with highest species richness in 1SCs and 2SCs (Fig. 3; Suppl. materials A12). Both eurytopic α- and γ-diversity was on average twice as high in 2SCs and 1SCs compared to tidal channels, isolated water bodies and control sites in the main channel. Eurytopic α-diversity differed most across 2SCs and 1SCs, as β-diversity was highest here. Rheophilic species richness (both α- and γ-diversity) was highest in 2SCs. In contrast to the other ecological groups, α-diversity of rheophilics was not significantly different between control sites and 1SCs (Suppl. materials A12). Rheophilic β-diversity was highest in both 1SCs and 2SCs.

3.2. Habitat requirements modelling

3.2.1. Abundances

YOY fish abundances declined with increasing amount of shade and coarseness of the substratum at sample level (Fig. 4; Suppl. Materials B). On project level, abundances also declined but with increasing river-floodplain connectivity. A non-linear effect on abundances was observed for project shallowness (depth < 1 m) and shoreline diversity for all fishes, as well as for age and shoreline diversity for rheophilics. For abundances of critical rheophilic species such as nase (*Chondrostoma nasus*), dace (*Leuciscus leuciscus*), and barbel (*Barbus barbus*) we found an increase with small-scale shoreline diversity (50 m). Shoreline diversity on project level was not important. Increasing percentages of project shallowness and the amount of river shoreline habitat available within a 10-km radius (river shorelength) appear to be important in explaining critical rheophilic abundances.

3.2.2. Local species richness

Species richness at sample level (α-diversity) of the fish community increased with larger substratum sizes, increased organic matter coverage and water chlorophyll concentrations (Fig. 4; Suppl. Materials B). At the river scale, river shorelength had a positive effect on the α-diversity of all fishes but was negative for rheophilic species. For both rheophilics and critical rheophilics, an increase of 2SC duration and project shallowness (depth < 1 m) coincided with increasing local species richness, whereas with increasing project age and shoreline diversity, α-diversity decreased for rheophilic fishes. For critical rheophilic species however, we observed an increase in α-diversity for higher local shoreline diversity. Local species richness of critical rheophilic fishes was higher with increasing substratum sizes and larger durations of submerged woody vegetation six months prior to sampling.

3.2.3. Species richness differentiation

The differentiation of species richness among habitats within a project (β-diversity) for the fish community increased with restoration project shallowness and shoreline diversity (Fig. 4; Suppl. Materials B). Shoreline diversity also had a positive effect on the β-diversity of critical rheophilic species, but β-diversity of this group was negatively affected by project shallowness. Furthermore, increasing river-floodplain connectivity decreased β-diversity of rheophilics.

3.2.4. Project species richness

Species richness of the fish community on project level (γ-diversity) increased with river-floodplain connectivity, river shorelength and shoreline diversity, and more shallow habitats in restoration projects favours rheophilic γ-diversity (Fig. 4; Suppl. Materials B). In contrast, γ-diversity of rheophilics and critical rheophilics declined with shoreline diversity and project age.

3.2.5. Year and river effect

Despite that abundances were lowest in 2017 and highest in 2020, community responses revealed no evident year-effects (Suppl. Materials B). At the same time, α-diversities were highest in 2017, while lowest in 2020. Over half of the fish community responses were significantly affected by river branch. IJssel had the highest overall α- and γ-diversity, whereas Nederrijn had the lowest species richness. Rheophilics preferred the Waal with the highest (critical) rheophilic abundances and α-diversity. The impounded Nederrijn was least suited as nursery area for the sensitive rheophilic fishes.

Table 2
General habitat characteristics per spatial scale that were used for floodplain restoration project evaluation.

Scale	Category	Variable name	Abbreviation	Description	Type of variable	Levels	Data source
General	Geographical	River	River	Branch of the river Rhine	Class	4 classes: (1) Waal, (2) IJssel, (3) Nederrijn, (4) Lek	General information
	Temporal	Year	Year	Sampling year	Class	4 classes: (1) 2017, (2) 2018, (3) 2019, (4) 2020	General information
Sample	Water quality	Conductivity	Cond	Electrical conductance of the water at sampling site	Numeric	Range: 241–1343 mS·cm-1	Field measurements
		Turbidity	Turbidity	Water turbidity at sampling site	Numeric	Range: 1–392 Nephelometric Turbidity Units (NTU)	Field measurements
		Chlorophyll	Chlorophyll	Chlorophyll concentration of the water at sampling site	Numeric	Range: 0.3–150.0 μg·L-1	Field measurements
		O2	O2	Dissolved oxygen concentration of the water at sampling site	Numeric	Range: 4.69–21.34 mg·L-1	Field measurements
		Shade	Shade	Percentage of sampling area that is covered in shade from woody shoreline vegetation	Ordinal	5 classes: (1) 0–20 %, (2) 21–40 %, (3) 41–60 %, (4) 61–80 %, (5) 81–100 %	Field observation
	Hydro-morphological	Depth	Depth	Maximum depth at sampling site	Numeric	Range: 0.1–4.3 m	Field measurements
		Substratum	Substr	Dominant substratum type at sampling site based on particle size	Ordinal	5 classes: (1) clay/silt (<0.06 mm), (2) fine sand (0.06–0.85 mm), (3) coarse sand (0.85-2 mm), (4) gravel (2-65 mm), (5) cobbles/boulders (>65 mm)	Field observation
		Organic matter	OrgMatter	Percentage of bottom covered by a layer of organic matter (leaves, branches, etc.) at sampling site	Ordinal	5 classes: (1) 0–20 %, (2) 21–40 %, (3) 41–60 %, (4) 61–80 %, (5) 81–100 %	Field observation
		Macrophytes	Macrophytes	Presence of macrophytes and/or submerged shoreline vegetation at sampling site	Ordinal	5 classes: (1) 0–20 %, (2) 21–40 %, (3) 41–60 %, (4) 61–80 %, (5) 81–100 %	Field observation
	Spatial organisation	Shoreline diversity 50 m	ShoreDiv50	Number of shoreline habitat types within a radius of 50 m from sampling site	Numeric	Range: 0–8 habitat types	GIS analysis[a]
		Shannon index 50 m	Shannon50	Shannon-Wiener diversity index of shoreline habitat within a radius of 50 m from sampling site	Numeric	Range: 0.00–0.36	GIS analysis[a]
Project	Hydro-geographical	2SC duration	2SCduration	Percentage of time that restoration project was two-sided connected with main channel, within a period of 6 months prior to sampling	Numeric	Range: 0–100 %	River water level data[b]
		Submerged woody vegetation	SubWVegDur	Percentage of time that woody shoreline vegetation (>2 m) of restoration project was submerged, within a period of 6 months prior to sampling	Numeric	Range: 0–41 %	River water level data[b]
	Hydro-morphological	Depth < 1 m	Depth1m	Percentage of shallow water habitat in restoration project with <1 m depth at median river discharge	Numeric	Range: 1–100 %	GIS analysis[a]
	Spatial organisation	Shoreline diversity	ShoreDiv	Total number of shoreline habitat types in restoration project	Numeric	Range: 3–12 habitat types	GIS analysis[a]
		Shannon diversity	Shannon	Shannon-Wiener diversity index of shoreline habitat in restoration project	Numeric	Range: 0.09–0.29	GIS analysis[a]
	Temporal	Age	Age	Age of restoration project	Numeric	Range: 0–30 years	General information
River	Geographical	River shorelength	Shorelength	Total available shoreline habitat at restoration project side of the main channel within a 5 km radius from restoration project center	Numeric	Range: 19.2–51.1 km	GIS analysis[a]

[a] GIS analysis with river, restoration project, and shoreline habitat (ecotope) and bathymetry maps at Rijkswaterstaat (2021). See Geerling et al. (2008) for Shannon diversity calculations.
[b] Daily river water levels of the lower river Rhine, calibrated with satellite images for connectivity check of each restoration project.

4. Discussion

Understanding environmental requirements of nursery areas, as well as the spatial scale, organisation, and interconnectivity of habitat patches, is critical for successful recruitment and population restoration of fishes (Beck et al., 2001; Van Looy et al., 2019; Stoffers et al., 2022). Numerous conceptual models address habitat patch dynamics and spatial scaling in large river ecosystems from either a metacommunity perspective (Brown et al., 2011; Altermatt, 2013; Erős et al., 2017; López-Delgado et al., 2019), or a landscape ecology perspective (Wiens, 2002; Lowe et al., 2006; Erős and Lowe, 2019). Often, these models postulate how habitat properties affect riverine fishes on different spatial scales, but only a handful have supporting empirical data (Winemiller et al., 2010; Erős et al., 2019). Here, we attempt to operationalise these concepts with empirical data, using a large-scale evaluation study of the ecological efficacy of 46 river restoration projects and 26 control sites in the lower river Rhine. We introduced an innovative approach, explicitly linking field sampling data of both habitat and fish communities with spatial data derived from high-resolution satellite images, using Bayesian modelling techniques (as proposed by Kuehne et al. (2017) and Erős et al. (2019)). We explicitly addressed variable-response relationships on different spatial scales, and identified their importance in the management of river restoration efforts to increase fish population health and combat biodiversity loss in large lowland rivers.

Freshwater fishes occupy a disproportionately large share of global biodiversity (Reid et al., 2019; Eschmeyer et al., 2022), with 18,253 described species (>50 % of all known fish species) inhabiting 2.3 % of the Earth's surface. This can be explained by high levels of geographical isolation and a complex web of ecological niches in freshwater habitats (Ormerod, 2003). For our

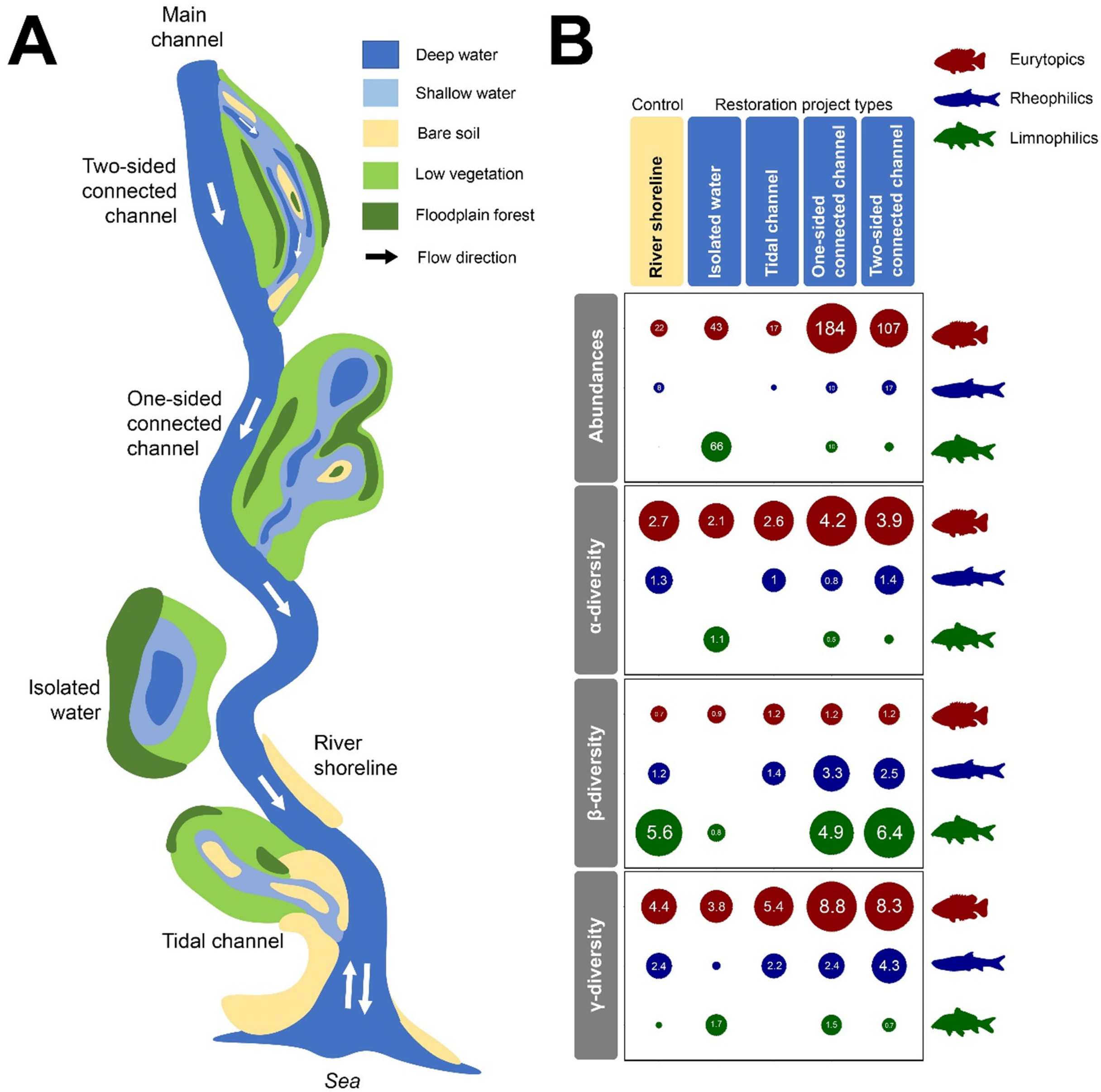


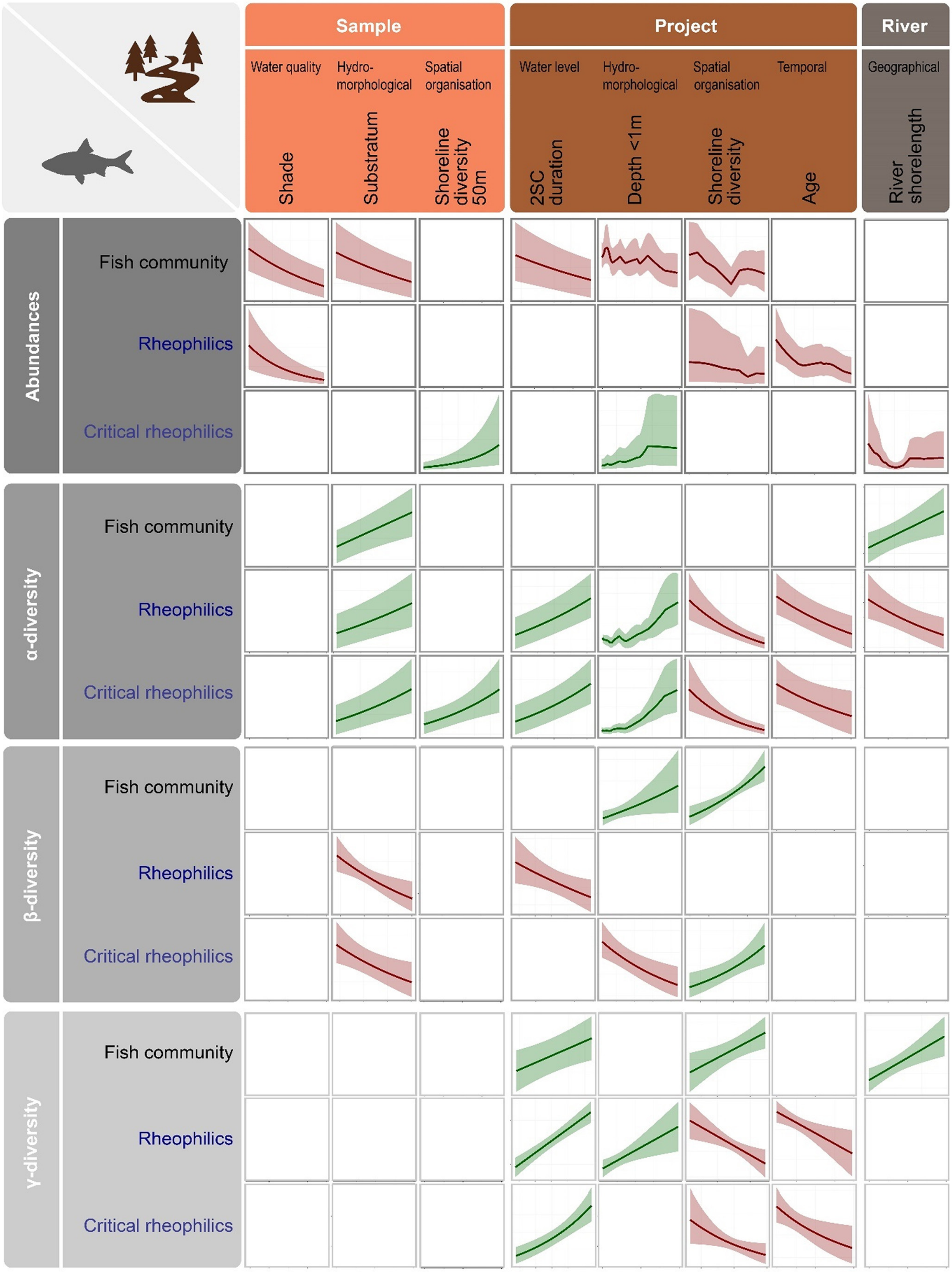
Fig. 3. Schematised overview of the nursery functioning of river restoration projects in the river Rhine, based on the detailed assessment in Supplementary materials A12. (A) Schematised lowland river with typical floodplain restoration projects: two-sided connected channel (2SC), one-sided connected channel (1SC), isolated water, tidal channel and river shoreline (control). (B) Community responses per ecological group for each restoration project and control sites in the main channel. Abundances (fish per 100 m^2) and species richness numbers were averaged across seine and electrofishing.

analysis of how fishes utilise ecological niches in floodplain nursery areas, taxonomic diversity is insufficient as indicator, and functional diversity is commonly used (Naeem et al., 2012; Mouillot et al., 2013; Craven et al., 2018; Brun et al., 2019). Riverine fishes are often classified into distinct functional groups based on diet, reproduction, and flow preference (Aarts et al., 2004). In large lowland rivers, water flow has a large influence on the physical habitat availability to riverine fishes at different phases of their lives (Welcomme et al., 2006; Baumgartner et al., 2014; Bernhardt et al., 2022), especially in early life-stages when swimming performance is limited (Wolter and Arlinghaus, 2003). Therefore, we assumed that flow is the key factor in determining the structure of YOY fish communities, and used an ecological classification of fishes based on flow preference as indicator for evaluating restoration project efficacy and nursery habitat requirements.

We also studied fish responses for critical rheophilics, in which we removed ide (*Leuciscus idus*), as this species accounted for almost 85 % of all rheophilic catches (Suppl. materials A6), and is less critical than the other 14 rheophilic species (Stoffers et al., 2021; Stoffers et al., 2022). It would seem that removing just one species would have little effect on species richness indices. However local rheophilic species richness was so low that removing ide reduced it from an average of 1.0 to 0.4 species, indicating that at many sampling sites ide was the only rheophilic species. Notwithstanding, the observed responses of critical and all rheophilic fishes were nearly identical (Fig. 4), suggesting that a wide range of rheophilic fish species have generic responses to environmental factors, such as flow and connectivity (Aarts et al., 2004; Poff and Zimmerman, 2010), water depth (Stoffers et al., 2022), and project age (Stoffers et al., 2021). There are no indications that alien and native species showed different environmental responses after being attributed to ecological groups, as abundances and species diversity showed almost identical patterns (Suppl. Materials A13).

4.1. Spatial scaling and habitat heterogeneity

Because swimming capacity in YOY fish is not yet fully developed, the proper scale, spatial organisation (heterogeneity), and interconnectivity of



Sample
Project
River
Water quality
Hydro-morphological
Spatial organisation
Water level
Hydro-morphological
Spatial organisation
Temporal
Geographical
Shade
Substratum
Shoreline diversity 50m
2SC duration
Depth <1m
Shoreline diversity
Age
River shorelength
Abundances
α-diversity
β-diversity
γ-diversity
Fish community
Rheophilics
Critical rheophilics

key nursery habitats (for foraging and sheltering) is important for their recruitment success (Schlosser, 1995; Van Looy et al., 2019) and survival through extreme drought and flood events (Guerreiro et al., 2021; Bernhardt et al., 2022). Daily activity for YOY fishes generally occurs on a spatial scale of tens to hundreds of meters, whereas dynamic ecological processes (e.g. sediment, flow, and water level dynamics) that affect their day-to-day survival typically take place at up to the river reach-scale (1–10 km) (Wolter and Arlinghaus, 2003; Thorp et al., 2006; Wolter et al., 2016). Because these processes occur at relevant spatial scales for river restoration and management (Wolter et al., 2016), it is critical to understand how spatial scaling affects fish-habitat relationships in order to effectively manage river restoration projects (Wohl et al., 2015). Here, we systematically modelled fish community response variables commonly used in the ecological evaluation of river restoration project efficacy (Ward and Tockner, 2001; Buijse et al., 2002; Erős et al., 2020) for a large data set of habitat components, including habitat heterogeneity, on three relevant spatial scales.

We defined spatial habitat heterogeneity for YOY riverine fishes as the spatial combination of shoreline habitat patches over a defined area, based on fishes' movement potential. We assumed this area to be within the project-reach scale (100–1000 m; Wolter et al. (2016)). On both sample (~100 m) and project (~1000 m) scale we used shoreline habitat diversity, the total number of shoreline ecotopes, as a proxy for spatial habitat heterogeneity. Shoreline ecotopes are mostly homogeneous landscape units defined by similarities and contrasts in vegetation structure, land use, and geomorphic and hydrologic characteristics, and ecotope maps are widely used as a reference point for policy and management river ecosystems (Geerling et al., 2009). We are confident that such an ecotope map adequately illustrates the spatial arrangement of fish nursery areas, because of the intricate interactions between the terrestrial and aquatic part of river ecosystems (Naiman et al., 1993; Weissteiner et al., 2016). The observation that project shoreline habitat diversity is important for 9 out of 12 fish community responses supports this assumption.

The observed fish community patterns provide an interesting insight into the effects of habitat heterogeneity and spatial scaling in the assessment of nursery habitat requirements. We found that the effects of environmental variables on the YOY fish community varied between ecological groups, response variables, and spatial scales. For instance, while shallow water habitats and sample-scale shoreline habitat diversity had a positive effect on critical rheophilic abundances, the presence of shallow water habitats and shoreline habitat diversity at the project scale had a negative impact on overall fish community abundances (Fig. 4). Similarly, in the lower Amazon river-floodplains, different spatial scales affected the relative contribution of food sources to (juvenile) fish biomass (Arantes et al., 2019). Food sources (e.g. benthos, macrophytes, and terrestrial plants) contributing most to fish biomass at the regional scale were often unimportant at the sample level, and vice versa.

In our study, diversity indices also revealed opposite patterns in overall fish community responses and the rheophilic group to nursery habitat variables at different spatial scales. For instance, an increasing shoreline habitat diversity within a restoration project correlated negatively with rheophilic species richness, whereas the total number of species increased. Likewise, local species richness of all rheophilics declined with the project scale shoreline heterogeneity. When looking at the smaller sample scale however, this habitat component positively affected local species richness of critical rheophilic fishes. These contrasting observations at different spatial scales, and the high contrast between preferred and non-preferred habitats (high β-diversity values), imply that rheophilic fishes require a limited number of highly specific interconnected nursery habitats within a restoration project (Schlosser, 1991; Cowx and Welcomme, 1998; Erős et al., 2017).

Spatial and temporal habitat heterogeneity are important factors affecting YOY fish growth and survival in natural rivers (Petry et al., 2003; Winemiller et al., 2010; Angeler and Allen, 2016). For instance, both species diversity and abundances of YOY fishes in natural Amazon river-floodplains benefit from habitat heterogeneity, shallow water depth, and macrophyte coverage (Petry et al., 2003). When nursery areas are permanently connected to the river, and both fish species richness and spatial-temporal habitat heterogeneity are high, fish communities are more resilient to adverse conditions such as flood pulses (Van Looy et al., 2019), and extreme temperatures (Collas et al., 2019). Riparian ecotones are particularly important nursery areas for YOY fishes in river ecosystems as they provide a variety of relatively shallow, slow-flowing habitats with a wide range of substratum sizes, are generally high in food, and warm up fast (Grift et al., 2001; Schiemer et al., 2001a; Schiemer et al., 2001b; Nunn et al., 2012; Eick and Thiel, 2013; Pander and Geist, 2018; Stoffers et al., 2022). Such heterogeneous riparian habitats are vital for well-functioning restoration projects to increase diversity and mitigate spatial homogenisation of fish communities (Schiemer et al., 2013; Arantes et al., 2019; Brennan et al., 2019; Van Looy et al., 2019).

4.2. Restoration project evaluation

Of all the investigated restoration project types, 1SCs and 2SCs provide the best nursery conditions for YOY riverine fishes (highest abundances and species richness) (Fig. 3). 1SCs and 2SCs are distinguished from other restoration projects by their permanent connection to the main channel. Permanent connection is essential for well-functioning nursery areas, as it affects fish community processes through effects on emigration and immigration, floodplain and channel habitat, and the continual interchange of biological and organic material (Opperman et al., 2010; Stoffels et al., 2022). Furthermore, as many riverine fishes show daily migrations between river and floodplain habitats for feeding (Baras and Nindaba, 1999b), predator avoidance (Copp and Jurajda, 1993; Baras and Nindaba, 1999a; Borcherding et al., 2002), and thermoregulation (Hohausová et al., 2003; Armstrong et al., 2013), permanent river-floodplain connectivity supports critical life history processes. Permanent river-floodplain connection creates a dynamic nursery area with a diverse range of interconnected and species-specific habitat patches of sufficient quality for riverine fishes (Aarts et al., 2004; Górski et al., 2011; Pander and Geist, 2018), hereby supporting high overall species richness. Rheophilic fishes are more selective about their nursery habitat, as they prefer shallow areas with flowing water and coarse substratum (Stoffers et al., 2022). This specific combination of habitat characteristics is primarily found in 2SCs, which explains why we observed highest rheophilic species richness and abundances in these project types.

Temperate lowland rivers provide a wide range of regulatory ecosystem services, such as irrigation of agricultural land, food security through freshwater fisheries (FAO, 2020; Wantzen et al., 2022), and drinking water (Opperman et al., 2018). River restoration efforts must operate within the constraints imposed by these services. This means that restoration projects are bound to the modified dynamic forces of these heavily regulated rivers, and that full recovery to an undisturbed state is not possible (Buijse et al., 2005). The context in which a restoration project operates is critical to its success and affects how much of its ecological potential is realised. For instance, we found that river restoration projects in the impounded river Nederrijn-Lek, which has limited free-flowing events and lowest median annual discharge, were very limited in their rheophilic nursery area potential (Suppl. materials B).

The timing of yearly flood pulses and discharge patterns vary considerably between temperate lowland rivers, and should be considered when evaluating the efficiency of river restoration projects in such ecosystems. During our

Fig. 4. Fish community responses for individual habitat variables obtained from INLA models. Fitted lines with 95 % credible intervals are used to indicate important trends. To provide a tool for floodplain restoration project management, only non-categorical habitat variables occurring in more than one model are presented here. Positive parametric effects on response variables are shown in green, and negative effects in red. Responses are grouped for abundances, α-diversity, β-diversity, and γ-diversity (see also Fig. 2) and habitat variables are grouped by the spatial scale they are collected on (sample, project, or river level). See also Supplementary Materials B for detailed plots and tables for all parametric effects.

study, we observed a variety of flood pulse events in early spring (February–April), the months in which many riverine fish species spawn and larvae emerge from their eggs (Suppl. materials A10). For example, in the Spring of 2020 we saw a major rise in water level that lasted about two months, filling the floodplains up to the dikes. In contrast, the annual flood pulse in 2017 was limited to a small and short peak, with a maximum water level that was >2.5 m lower than in 2020. By retreating water and creating additional slackwater habitats, major flood pulses generally result in increased nutrient enrichment and concentration in nursery areas. This boosts primary production and food availability for newly-hatched fishes (Reckendorfer et al., 1999; Hoagstrom and Turner, 2015), and could lead to strong cohorts and increased abundances of certain fish species (Górski et al., 2011; Cruz et al., 2020; Humphries et al., 2020). Following the major flooding of 2020, we observed highest overall YOY abundances whereas in 2017, we found low fish numbers. Especially abundances of the eurytopic species roach, bream and bleak were high in 2020, which could be linked to their preference for less dynamic and more productive (e.g. higher chlorophyll concentrations) habitats in the more distant parts of the floodplains, which become accessible during periods with high discharges (Suppl. materials A11).

4.3. Implications for river management

Based on decades of (traditional) ecological research, we know which ecological factors are critical for preserving riverine biodiversity and developing healthy fish communities, and therefore we know what set of restoration actions we need to carry out (Palmer et al., 2005; Bernhardt and Palmer, 2011). However, the extent to which these actions are acceptable is strongly influenced by the ecological and societal context (Palmer et al., 2014). For instance, the requirements imposed by water safety and navigation generally take precedence over the restoration of ecological processes in many large lowland rivers such as the river Rhine. Stakeholder involvement may also have an influence on the design and performance of restoration projects, which is often overlooked (Carter et al., 2007; Szałkiewicz et al., 2018). The extent to which this may have played a role in the assessed projects in this study has not been considered.

Below, we discuss what we believe are the most important steps for increasing the efficacy of lowland river restoration projects, as well as how this can be implemented to optimise large river systems to combat the global freshwater biodiversity crisis. We discovered generic processes essential for riverine fish recruitment that can be applied to improve the efficacy of river restoration projects in modified lowland rivers across the world.

First, it is essential to determine the ecological objective of the river restoration project in advance. When the objective is the restoration of riverine fish nurseries, it is then important to decide on whether the focus is on restoring fish biodiversity or on increasing abundances, and whether to focus on the whole fish community or on specific ecological guilds. As the impact of river restoration differ substantially across spatial scales and specific ecological groups (Fig. 4), the design and management of river restoration projects, as well as their ecological efficacy, are heavily dependent on these initial decisions. In short: there is no 'one size fits all' approach in floodplain restoration for fish nurseries in heavily modified lowland rivers.

Secondly, it is critical to align the restoration project's site, design, and management with the fishes' environmental requirements. We observed that different ecological groups of riverine fishes have distinct, often non-overlapping, nursery habitat preferences (Fig. 4; Suppl. materials A11). It is important that all of the target group's key nursery environments are present within the nursery area. For example, abundances of critical rheophilic fish benefit from a high percentage of shallow water habitats, while overall fish abundances were negatively impacted by this habitat characteristic. Optimising restoration projects for all fishes can be achieved by creating nurseries with varying bathymetry and sloping banks, ensuring the presence of habitats with varying water depths at a wide range of river discharge levels. A key habitat feature that benefits the majority of riverine fishes is permanent lateral connectivity with the main channel (Figs. 3; 4), and therefore restoring connectivity is essential to achieve specific ecological objectives (Stoffers et al., 2021; Knox et al., 2022). Such restoration objectives may include initiating an ecological succession process, or remaining within a specified stability range (Geerling et al., 2013). This may require a cyclic management strategy in which 'sand plugs' at the project inlet are regularly removed (Stoffers et al., 2021) or the presence of upstream sediment traps (Wohl et al., 2019). A series of restoration projects in various stages of succession, on the other hand, is required to have a diversity of nursery habitats that supports a wide range of fish species. As a result, the components of the fish community that need to be rehabilitated dictate the intended management method.

Another important aspect of well-functioning nursery areas is the spatial organisation (heterogeneity) of habitats (Brennan et al., 2019; Van Looy et al., 2019; Stoffers et al., 2022). We found that the role and spatial scale of habitat heterogeneity in restoration projects is ambiguous, as it is highly dependent on both the ecological target group and the community response variable in question (Fig. 4). Although we observed that project habitat heterogeneity increases species richness, we also found that diverse nursery areas had a negative influence on total fish abundances. We recommend to create slow flowing heterogeneous habitats by two-sided reconnection of existing floodplains, such as former sand extraction pits, rather than the construction of new restoration projects. When compared to newly constructed projects, these existing floodplains generally contain a diverse range of habitat types in an advanced stage of succession. By adding areas with flowing water to these floodplains, they become a suitable nursery area for a wide range of riverine fishes (Stoffers et al., 2021). Furthermore, former sand extraction pits can serve as important refuge areas for many fishes during extreme drought and flood events, which are predicted to become more common as a result of climate change (Lennox et al., 2019). Furthermore, river restoration efforts should be conducted in a site with the appropriate river context. For example: constructing a restoration project for rheophilic fishes, that require permanent river-floodplain connectivity and flow in their nursery, in an impounded or tidal river result in suboptimal functioning.

Finally, in attempting to face the global freshwater biodiversity crisis, we propose that river restoration efforts in heavily modified lowland rivers focus on establishing spatially heterogeneous patterns and processes in floodplain restoration projects along the river (as in natural rivers), with primarily 1SC and 2SC projects with the appropriate dimensions to retain continuous connectivity with the main channel. Floodplain channels that have been restored should develop and maintain suitable environmental conditions in order to continue to be effective for specific restoration goals, such as the presence of target species and habitats (Palmer et al., 2005). This implies that in anthropogenically modified lowland rivers, an appropriate project design is required beforehand in order to reduce the need for maintenance. When the specific objective of the restoration project is to maintain a suitable nursery area for the most critical rheophilic fishes for several decades, a management strategy involving cyclic rejuvenation through human intervention may be needed (Geerling et al., 2013). The frequency with which this must be performed is determined by the rate of sand deposition and other river-specific hydromorphological processes (Stoffers et al., 2021). Such a management strategy should result in permanent flowing conditions, lateral connection with the main channel, a variety of water depths and substratum types, and heterogeneous shoreline habitat.

CRediT authorship contribution statement

T.S.: Conceptualisation, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization, Data curation.

A.D.B.: Conceptualisation, Writing - review and editing, Supervision.

G.W.G.: Methodology, Software, Formal analysis, Writing - review and editing.

L.H.J.: Methodology, Validation, Funding acquisition.

M.M.S.: Writing - review and editing, Funding acquisition.

J.J.P.: Methodology, Software, Validation, Writing - review and editing.

J.A.J.V.: Conceptualisation, Writing—review and editing, Supervision.

L.A.J.N.: Conceptualisation, Writing - original draft, Writing—review and editing, Supervision, Funding acquisition.

Research data

The data and R-script on the restoration project evaluation and habitat requirements modelling are available at https://doi.org/10.4121/20014862

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156509.

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