Original Articles

River continuum disruptions in a highly altered system: The perspective of potamodromous fish

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ABSTRACT

In this study, we explored how barriers such as dams have affected the longitudinal connectivity of riverine habitats from the perspective of potamodromous fish. For this purpose, connectivity changes are investigated in the central part of the Austrian Danube system, where the national reporting for the EU Water Framework Directive provides detailed information on the position and characteristics of barriers as well as the distribution range of native fish species. This assessment is based on an estimation regarding the quantitative upstream and downstream passability of individual barriers, where we further investigate three different passability scenarios to account for uncertainties. We then apply several combinations of passability scenarios and assumptions on dispersal distances to calculate a series of network-based reach and catchment connectivity indices. On average, the estimation of barrier passability indicated a high downstream passability, while upstream passability was substantially lower across scenarios. Furthermore, existing fish passes were estimated to have increased passability on average between 20 % and 24 %. Overall, the results indicated a strong effect of barriers on the longitudinal connectivity of the investigated river network. Catchment scale indices revealed a loss of connectivity, which increased with dispersal distance. Reach connectivity indices displayed a strong disruption of the natural connectivity gradient along the river network and indicated that individual river reaches have, on average, become more isolated in addition to the overall decrease in connectivity. The average loss of connectivity across scenarios was estimated at 72 % (SD = 16 %) when taking into account all connections to other reaches and 66 % (SD = 7 %) when only connections to upstream reaches were considered. We conclude that longitudinal connectivity in the Austrian Danube system is still severely compromised, making it increasingly challenging for potamodromous fish species to complete their life cycle. This issue is further amplified by the severe loss of fish habitats as a consequence of river engineering.

1. Introduction

Movements between habitats during reproduction, life-history transitions, or dispersal represent a central component within the life cycle of riverine fish species (Lucas et al., 2001; Panchan et al., 2022). Consequently, in addition to environmental filtering (abiotic conditions selecting against certain species; Cadotte and Tucker, 2017; Radinger et al., 2019) and species interactions (Peoples and Frimpong, 2015),

movements via habitat connections mediate species distribution and diversity on multiple levels (Baldan et al., 2023; Beger et al., 2022; Borthagaray et al., 2020; Shao et al., 2019; Stoffers et al., 2022). The extent and the ecological implications of these movements are defined by the quantity and quality (e.g. intermittent versus continuous habitat connections) of the underlying pathways (structural component) and how organisms respond to landscape elements that have the potential to function as habitat connections (functional component; Tischendorf and

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Fahrig, 2000). Together, those two aspects define an ecosystem's degree of connection, or connectivity, which is one of the building blocks explaining ecological patterns, especially on large scales such as the meta-ecosystem level (Cid et al., 2021). Regarding rivers, this concept is especially applicable as the dispersal of fish and other aquatic organisms is mainly limited to the river network, and thus, pathways are clearly defined. Naturally, this also includes migratory movements such as spawning migrations conducted by potamodromous fish to reach suitable habitats. In the case of the barbel (*Barbus barbus*) and the nase (*Chondrostoma nasus*), for example, Steinmann et al. (1937) showed that before the construction of barriers in the Austrian Danube, over 20 % of tagged and recaptured fish from each species migrated at least 50 km in one direction while some individuals covered distances of up to 300 km. Due to this extensive use of habitat connections throughout their life cycle, potamodromous fish seem to be severely affected by anthropogenic barriers, the consequential loss of longitudinal connectivity, and thus, habitat fragmentation.

Even though the concept of connectivity and its implications for terrestrial and aquatic ecology has long been established, river management has mostly failed to mitigate the effects of longitudinal connectivity loss at the landscape scale (Cooper et al., 2016). One of the main reasons relates to the mostly dendritic structure of river networks, where a single barrier can potentially disconnect large parts of the river system. Another reason might be that quantifying and interpreting structural and functional connectivity changes can be challenging due to the inherent complexity and limited data availability regarding, for example, the position and passability of barriers (Belletti et al., 2020). Nevertheless, multiple metrics have been designed to capture the effects of barriers (Cooper et al., 2017), and with the introduction of network theory to landscape ecology (Minor and Urban, 2007; Urban and Keitt, 2001), a wide range of network-based connectivity indices have been developed and implemented (Baldan et al., 2022; Cote et al., 2008; Erős et al., 2011; Pascual-Hortal and Saura, 2006; Rayfield et al., 2011; Rodeles et al., 2021; Tiwari et al., 2023). Among other metrics, these indices facilitate the concept of closeness centrality (Newman, 2017), which measures the mean distance from a node (reach) to others within a given (river) network and can be extended to capture detailed aspects of the ecological connectivity gradient. This is accomplished by integrating structural components like the network topology, habitat characteristics, or the spatial distribution and passability of barriers, as well as functional components such as the distance and direction of organism dispersal. A sensitivity analysis of those parameters, as it is conducted in this study, can then serve as a tool to assess connectivity changes under specific assumptions regarding, for example, the movement of organisms. The assessment of connectivity changes is today more relevant than ever since, in Europe alone, more than one million barriers have been estimated to fragment the river network (Belletti et al., 2020).

Even though barriers are known to fragment habitats, cut off habitat connections, and alter the hydrological, thermal, solute, and sediment regime (Chen et al., 2023), the ecological importance of an uninterrupted river continuum is only gradually recognized by decision-makers. Nevertheless, legislation such as the European Water Framework Directive (European Commission, 2000), the European Biodiversity Strategy (European Commission, 2020) or the recently proposed European Nature Restoration Law (European Commission, 2023; Stoffers et al., 2024; Hering et al., 2023) has been or will accelerate efforts towards restoring longitudinal connectivity in the future. These efforts include, for example, the demolition of obsolete barriers and the installation of technical fish passes or nature-oriented bypass channels. Furthermore, other measures, such as rakes, are implemented to guide fish safely past the turbines of hydropower plants during downstream movements, avoiding injury or mortality (Pracheil et al., 2016). However, restoring longitudinal connectivity represents a highly laborious endeavor due to the enormous densities of barriers, let alone the challenge of implementing functional measures that restore quantitative upstream and downstream barrier passability for all relevant species

(Noonan et al., 2011). Furthermore, in the case of hydropower plants, the installation of rakes and the flow diversions through fish passes result in a loss of generated electricity. Therefore, economic interest can represent another obstacle in the way of restoring longitudinal connectivity. However, hydropower plants are far less common relative to continuum disruptions with the purpose of flood protection, such as sills which prevent the incision of the riverbed. Nevertheless, in large rivers, barriers have been constructed almost exclusively for hydropower utilization, and therefore, the ecological impact of such barriers is disproportionally high. One of the reasons is that reaches located in the main stems of the river network are also those with a higher closeness centrality and are thus most relevant for the movements of fish between different sections. Unfortunately, the rising demand for renewable energy due to a changing climate and geopolitical instabilities has further accelerated the expansion of the hydropower sector, increasing the risk of continued or even increased loss of longitudinal connectivity. This conflict between sustainable river management and the undisputed need for increased renewable energy production is demonstrated by the plan of the European Union to reduce the dependence on fossil fuels and accelerate the transition to renewable energy sources (REPowerEU; European Commission, 2022). This strategy does not rule out a further expansion of the hydropower sector, even though the overall technical potential for generating hydroelectric power in Europe is expected to decrease as a result of climate change (Gernaat et al., 2017). Moreover, Europe's current hydroelectric power generation is already approximately 90 % greater than the estimated ecological, economic potential (Gernaat et al., 2017). Therefore, the goals of REPowerEU may conflict with the goals of the European Biodiversity Strategy, the European Water Framework Directive and the recently proposed European Nature Restauration law.

In Austria, the implementation of a national river basin management plan (RBMP) in the context of the EU Water Framework Directive has produced an extensive data set addressing different aspects of surface water bodies (BMLRT, 2021b). This also includes the position and critical characteristics of barriers, such as the height, the overall passability, and the attributed public sector from which the usage (e.g., hydroelectric power production) can be delineated. This data set provides a valuable opportunity to analyze connectivity on a large scale with analytical detail and includes information on 64,476 anthropogenic barriers as well as 6642 natural barriers for fish in Austria. According to this information, the majority (75.5 %) of anthropogenic barriers have been built for flood risk management, 6.3 % are associated with the production of hydroelectric power, and 8.9 % are related to other (e.g., transportation, urban or agricultural infrastructure) or unknown uses (9.3 %). More importantly, however, 51 % of anthropogenic barriers are still not supporting the movements of fish. Establishing passability is therefore urgently needed since 44.9 % of natural watercourses in Austria have failed to achieve a good ecological status (BMLRT, 2021b), which is linked to multiple stressors including the effects of barriers (Schinegger et al., 2018). Overall, the Austrian Danube system is in urgent need of management solutions that balance flood protection, renewable energy production, as well as ecosystem restoration and conservation in order to improve the situation of aquatic biodiversity and provide valuable ecosystem services (Funk et al., 2020).

In this study, we conduct a detailed large-scale assessment of connectivity changes from the perspective of potamodromous fish in the Austrian Danube system, motivated by the following research objectives: In order to understand how the movement possibilities of potamodromous fish have changed, we investigate (1) how barrier passability and different dispersal probabilities are affecting connectivity on the reach and catchment scale. Furthermore, we identify the status quo of connectivity by assessing (2) the state of natural centrality patterns and (3) how much connectivity has been decreased due to the presence of artificial barriers relative to the naturally connected state of the system.

2. Methods

2.1. Spatial framework

Based on the official river network of the RBMP and the distribution ranges indicated by the fish index Austria (FIA; Haunschmid et al., 2009), we selected the combined Austrian habitat of three potamodromous, rheophilic fish species, the nase (*Chondrostoma nasus*) the barbel (*Barbus barbus*) and the Danube salmon (*Hucho hucho*). All three species are rheophilic gravel spawners conducting pronounced spawning migrations (Steinmann et al., 1937) and have later been classified as mid-distance (30–300 km) migratory fish species (Waidbacher and Haidvogl, 1998; BMLRT, 2021a). Several reaches in neighboring countries further extended the resulting river network to connect watercourses that are only partially located on Austrian territory. Larger foreign rivers of neighboring countries (Jihlava, Svratka, Morava, Myjava) were also added as long as they were included in the official river network of the RBMP. In addition, reaches of the Danube were included beyond the Austrian territory until the upstream and downstream hydropower plants in Straubing (Germany) and Gabčíkovo (Slovakia), respectively. The previous two processing steps were conducted to reduce edge effects that occur when reaches are clipped from a river network due to the spatial limitations of the analysis. By removing reaches from a river network, connections to the remaining reaches are also removed, which decreases their connectivity, especially in the case of those close to the ones removed. Furthermore, any watercourses of the previously identified river network, except for the Austrian Danube, that are either partially located outside or along the border of the Austrian territory were only used to calculate connectivity indices but were excluded from their subsequent analysis. The reason for this decision was that the species distribution ranges indicated by the Fish Index Austria only covered the Austrian part of the river network. In addition, the spatial representation of watercourses did not include most tributaries located outside the Austrian territory where also the available information on barriers was less detailed (Section 2.2).

Furthermore, the river network was simplified towards a dendritic structure except for two major side channels (the Marchfeld Canal in lower Austria and the Danube Canal in Vienna). Reaches were delimited either by confluences or barriers. In addition, reaches >10 km were split into segments of approximately 10 km to increase the resolution of the analysis. Finally, water courses located in the Drava catchment were clipped from the network as the confluence of the river Drava with the Danube is located far downstream in Croatia.

2.2. Barriers

We compiled a subset of natural and artificial barriers included in the database of the Austrian river basin management plan (BMLRT, 2021b) by selecting all barriers intersecting the previously constructed river network. This precise selection method was applicable since the barriers data set and the data set from which the river network was extracted originated from the same database and were generated in support of each other. Barriers on foreign territory were selected from the AMBER database (Belletti et al., 2020; accessed on 15.12.2023) if located within 5 meters of the river network. The resulting data set was then investigated for overall plausibility by identifying duplicates, missing attributes, and wrongfully selected or missing barriers. For this purpose, the position of barriers was validated based on satellite images included in the regularly updated "World Imagery" layer published by ESRI Inc, 2009. In the case of reaches located on foreign territory, this validation was conducted for every individual barrier extracted from the Amber database in addition to screening all river reaches for missing barriers. On Austrian territory, satellite images of barriers were screened if an association with the hydropower sector was indicated. This was done to distinguish hydropower plants from other associated barriers, such as sills, which are occasionally installed below a dam to reduce river bed erosion. In addition, 277 barriers had an indicated drop height of zero, which in the case of 32 hydropower plants was identified as likely errors in the data set following a validation based on satellite imagery. Thus, the respective drop height was changed from zero to "NA". No further validation based on satellite images was conducted for barriers located on Austrian territory.

In the next step, we estimated the quantitative upstream and downstream passability for all barriers following an expert judgment regarding the overall capabilities of the three investigated fish species. For national barriers, estimates were based on several attributes included in the RBMP barrier data set, such as the drop height and whether passability for fish was indicated. We further considered whether a barrier had been equipped with a fish pass, which was generally assumed to be functional if not indicated otherwise. It was further assumed that if a fish pass had been installed and barriers were reported to be passable at the same time, the reported passability had been established by the fish pass. In this case, passability was estimated to be lower compared to barriers without a fish pass, that were nevertheless reported to be passable. This assumption was based on the review from Noonan et al. (2011), which demonstrated that even barriers with functional fish passes were impeding, to some extent, the passage of a large variety of fish species. This review also contained data on the families *Salmonidae* and *Cyprinidae*, to which the species investigated in this study belong. Finally, we considered whether barriers were associated with hydropower production, and if so, the estimated downstream passability was reduced to account for turbine-induced mortality (Pracheil et al., 2016). In this case, it was assumed that upstream passability was fully inhibited without a fish pass, and if passability was reported to be given, the barrier must have been equipped accordingly.

Naturally, such an approach only yields a rough estimation of barrier passability (Baudoin et al., 2015) and does not account for differences between the three investigated species regarding their ability to overcome barriers. Therefore, we further investigated three different scenarios ranging from more conservative to somewhat optimistic estimations of barrier passability (Table 1).

Regarding barriers outside of the Austrian territory, a less detailed approach was used, as the variables mentioned above were not available, except for the drop height of barriers in some cases. However, this was not assumed to be problematic since river reaches on foreign territory only served to reduce edge effects and were excluded from the analysis of calculated connectivity indices.

Finally, we estimated the increase in barrier passability due to the installation of fish passes. For this purpose, the estimation of barrier passability was repeated after changing the binary passability attribute from the national river basin management plan to "non-passable" for all barriers equipped with a fish pass. The consequential lower estimates of passability were interpreted to reflect the passability without the effect of fish passes and were subsequently compared to the previous estimation of passability.

2.3. Connectivity indices

Connectivity indices were calculated at the reach and catchment scale based on the previously estimated scenarios, describing the upstream and downstream passability of barriers. For this purpose, we utilized the 'riverconn' R package (Baldan et al., 2022). This package applies a network approach and provides implementations of several connectivity indices. These indices extend the concept of closeness centrality (average distance to other reaches) by integrating the passability and position of barriers, limitations regarding the mobility of organisms (e.g. dispersal distances), and weights to consider, for example, the greater importance of connections to reaches with high amounts of available habitat. In this regard, the shortest path from a reach i to a reach j is interpreted as the coincidence probability I_{ij} of an organism to disperse along this path within a given network. Using the function `index_calculation`, the three previously described

passability scenarios (Table 1) were assessed by supplying the upstream and downstream passability estimates to the function through the `pass_u` and `pass_d` arguments, respectively. The argument `dir_fragmentation_type` was set to "asymmetric", indicating asymmetric barrier passability. In addition, connectivity indices were calculated for a "naturally connected" and a "zero passability" scenario. Here, all artificial barriers were taken to be either fully passable or fully impede the movement of fish, respectively. The passability of natural barriers, contrastingly, was still estimated according to the previously described method (Section 2.1). Furthermore, indices were set to reflect five symmetric (`dir_distance_type` = "symmetric") dispersal distances, formulated as distance thresholds of an exponential dispersal kernel (`disp_type` = "exponential") where the probability of dispersal has decreased to 10 %. Therefore, in contrast to the global measure of closeness centrality, the resulting indices do not quantify connectivity of a reach exclusively according to its position within the entire river network but further take into account spatial limitations regarding the movements of individuals. For this purpose, the argument `param` (kernel parameters) was set to $0.1^{1/T}$ where T is the 10 % probability threshold for dispersal in kilometers. The selected dispersal thresholds ranged between 10 km and 90 km and reflect distances covered by short- to mid-distance migratory fish species during spawning migration. While those species have been found to migrate annually up to 30 km and 300 km in one direction, respectively (Steinmann et al., 1937; Waidbacher and Haidvogl, 1998), dispersal

distances >90 km were not considered due to the limited spatial extent of the investigated river network, which covered approximately 350 km (length of the Austrian Danube). Furthermore, the length w_j of a reach j was used to approximate the amount of potentially available habitat in this reach. Therefore, w_j was used as a weight for the connection from a reach i to a reach j along the network (`weight` = `w`). Finally, for each combination of dispersal distance and barrier passability scenario, two reach connectivity indices (RCI; Eq. 1; `index_type` = "reach") and two catchment connectivity indices (CCI; Eq. 2; `index_type` = "full") were calculated:

$$RCI_i = \sum_{j=1}^{n} I_{ij} \frac{w_j}{W} \tag{1}$$

$$CCI = \sum_{i=1}^{n} \sum_{j=1}^{n} I_{ij} \frac{w_i w_j}{W^2} \tag{2}$$

With W being the sum of w_j over all n reaches, the coincidence probability of dispersal I_{ij} is calculated as the product of c_{ij} and B_{ij}, which are calculated according to Eq. 3 and Eq. 4, respectively:

$$c_{ij} = \prod_{m=1}^{k} p_m^{eq} \tag{3}$$

$$B_{ij} = \left(0.1^{1/T}\right)^{d_{ij}} \tag{4}$$

Table 1

Estimation of barrier passability in upstream- and downstream directions where 1 equals full passability and 0 equals no passability. The column "Height" indicates the drop height of a barrier, while the column "Hydropower?" indicates whether a barrier is associated with the production of hydroelectric power. Furthermore, the column "Passable?" indicates whether a barrier is considered passable for fish according to the Austrian reporting for the EU Water Framework Directive. Moreover, the column "Fish Pass?" indicates whether a barrier had been equipped with a fish pass, which, in the case of barriers associated with hydroelectric power production, was assumed to be necessary to establish passability. "NA" indicates no data availability.

| Height [m] | Hydropower? | Passable? | Fish pass? | Passability scenario | | | | | |
| | | | | High | | Medium | | Low | |
				↑	↓	↑	↓	↑	↓
NA	No	Yes	No	1.0	1.0	0.7	1.0	0.6	0.9
< 0.3	No	Yes	No	1.0	1.0	0.9	1.0	0.8	1.0
0.3–1	No	Yes	No	1.0	1.0	0.8	1.0	0.7	1.0
1–2	No	Yes	No	1.0	1.0	0.7	1.0	0.6	0.9
2–4	No	Yes	No	1.0	1.0	0.6	0.9	0.5	0.8
> 4	No	Yes	No	1.0	1.0	0.5	0.8	0.4	0.7
NA	No	Yes	Yes	0.8	1.0	0.6	0.9	0.5	0.7
< 0.3	No	Yes	Yes	1.0	1.0	0.9	1.0	0.7	1.0
0.3–1	No	Yes	Yes	0.9	1.0	0.8	1.0	0.6	0.9
1–2	No	Yes	Yes	0.8	1.0	0.6	0.9	0.5	0.8
2–4	No	Yes	Yes	0.7	1.0	0.5	0.8	0.4	0.6
> 4	No	Yes	Yes	0.6	1.0	0.4	0.7	0.2	0.4
NA	No	No	–	0.2	0.8	0.1	0.7	0.0	0.6
< 0.3	No	No	–	0.7	1.0	0.4	1.0	0.1	1.0
0.3–1	No	No	–	0.3	1.0	0.2	0.9	0.0	0.8
1–2	No	No	–	0.0	0.9	0.0	0.7	0.0	0.6
2–4	No	No	–	0.0	0.7	0.0	0.5	0.0	0.4
> 4	No	No	–	0.0	0.5	0.0	0.3	0.0	0.2
NA	Yes	No	–	0.2	0.7	0.1	0.6	0.0	0.5
< 0.3	Yes	No	–	0.7	0.9	0.4	0.9	0.1	0.8
0.3–1	Yes	No	–	0.3	0.8	0.2	0.7	0.0	0.6
1–2	Yes	No	–	0.0	0.7	0.0	0.5	0.0	0.4
2–4	Yes	No	–	0.0	0.6	0.0	0.4	0.0	0.3
> 4	Yes	No	–	0.0	0.5	0.0	0.3	0.0	0.2
NA	Yes	Yes	–	0.8	0.9	0.6	0.7	0.5	0.6
< 0.3	Yes	Yes	–	1.0	1.0	0.9	0.9	0.7	0.8
0.3–1	Yes	Yes	–	0.9	1.0	0.8	0.8	0.6	0.7
1–2	Yes	Yes	–	0.8	0.9	0.6	0.7	0.5	0.6
2–4	Yes	Yes	–	0.7	0.8	0.5	0.6	0.4	0.5
> 4	Yes	Yes	–	0.6	0.7	0.4	0.5	0.2	0.4
NA	NA	NA	NA	0.7	0.8	0.6	0.7	0.5	0.6
< 0.3	NA	NA	NA	1.0	1.0	0.9	1.0	0.8	0.9
0.3–1	NA	NA	NA	0.8	0.9	0.7	0.8	0.6	0.7
1–2	NA	NA	NA	0.6	0.7	0.5	0.6	0.4	0.5
> 2	NA	NA	NA	0.4	0.5	0.3	0.4	0.2	0.3

Regarding Eq. 3, k is the number of barriers along the path from reach i to j and p_m^{eq} is the estimated upstream or downstream passability of a barrier m depending on the direction in which it is encountered. In Eq. 4, T is the previously described 10 % dispersal probability threshold in kilometers with d_{ij} being the distance between the reaches i and j. Hence, the coincidence probability of dispersal decreases exponentially with the distance between two reaches.

Both RCI and CCI were calculated with a configuration that considered all connections (upstream and downstream) to other reaches. In addition, a second configuration only took into account upstream connections describing the perspective of potamodromous fish during spawning migration. Regarding the latter, the argument `param_u` was again set to $0.1^{1/T}$ while the argument `param_d` was set to zero and `dir_distance_type` was set to "asymmetric".

Finally, we calculated the size of the sub-network accessible to individuals in a given reach without having to overcome a barrier in either direction. For this purpose, the river network was split at all barriers into sub-networks, for which the combined length of all reaches was then calculated. After assigning this value to the corresponding reaches, the resulting variable was included in the analysis as the "connected length" to represent a more simple connectivity metric.

2.4. Statistical methods

To investigate the differences in RCIs between scenarios, we conducted a non-metric multidimensional scaling (NMDS) based on Euclidean distances, followed by a cluster analysis. All indices were rescaled using the min–max normalization before running the `metaMDS()` function from the 'vegan' R package (Oksanen et al., 2022). The algorithm was run based on three dimensions indicated by the argument `k` since fewer dimensions did not lead to the identification of a likely global optimum. The result was then validated by comparing the observed distances between data points against the corresponding distances in the ordination space, which yielded an R^2 of > 0.99. Subsequently, a cluster analysis (k-means algorithm) was conducted based on the ordination coordinates using the `kmeans()` function from the 'stats' R package (R Core Team, 2023) with `nstart = 20` to avoid local optima. The number of clusters was selected based on an optimization of the total within sum of squares (elbow method).

3. Results

3.1. Barrier passability

A total of 2116 barriers on Austrian territory and 54 barriers in neighboring countries were identified along the river network described under Section 2.1. Barriers on Austrian territory, including 33 (1.6 %) natural obstructions, had a mean drop height of 1.5 m (SD = 3.0 m) with a maximum of 60 m. Furthermore, 1069 (50.5 %) barriers on Austrian territory were reported to be passable, of which 389 (36.4 %) had been equipped with a fish pass. Due to the low height of the majority of barriers, the results of the passability estimation (Fig. 1) indicated a high mean downstream passability which ranged among scenarios between 0.92 and 0.77. Contrastingly, upstream passability was much lower due to the small number of fish passes, ranging on average between 0.59 and 0.34 throughout scenarios. Furthermore, our results indicate that fish passes have increased the overall passability of barriers between 20 % to 24 %.

3.2. Connectivity

A comparison of RCIs using a non-metric multidimensional scaling and a subsequent cluster analysis produced four clusters in a three-dimensional space (Fig. 2). One of the clusters was formed by most RCIs based on the medium and low barrier passability scenario, taking into account both upstream and downstream connections. Here, a slight overlap was visible at shorter dispersal distances, with a second cluster formed mainly by RCIs describing the naturally connected state without artificial barriers (full passability), as well as RCIs based on the high barrier passability scenario, taking into account both upstream and downstream connections. Furthermore, a third cluster included most RCIs based on the zero passability scenario and those describing the high, medium, and low barrier passability scenario considering only upstream connections. The fourth cluster was almost exclusively comprised of RCIs quantifying only upstream connections. Those included configurations addressing scenarios of high, medium, low and zero barrier passability, all at low dispersal distances. In addition, this cluster also contained RCIs describing the naturally connected state at large dispersal distances. Finally, we found that the connectivity index describing the connected length (not included in the cluster analysis) was clearly distinguished from all RCI configurations.

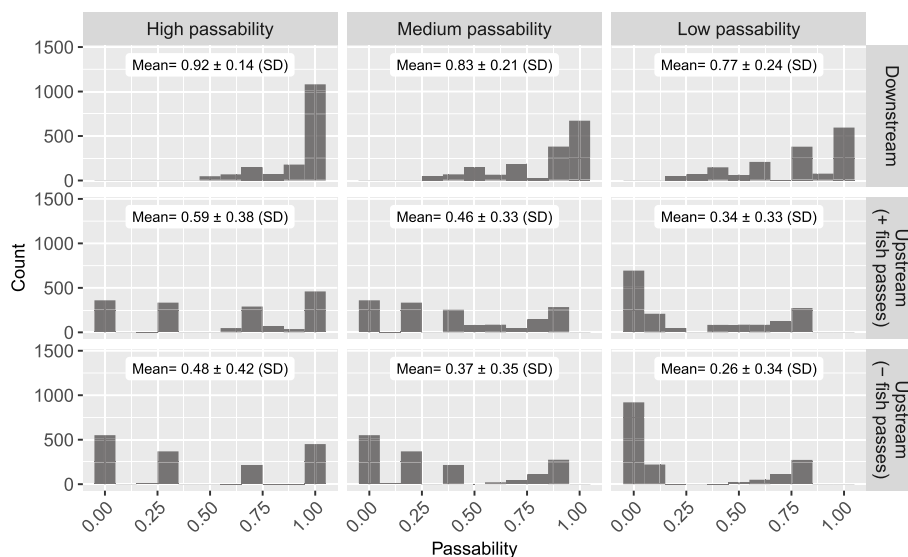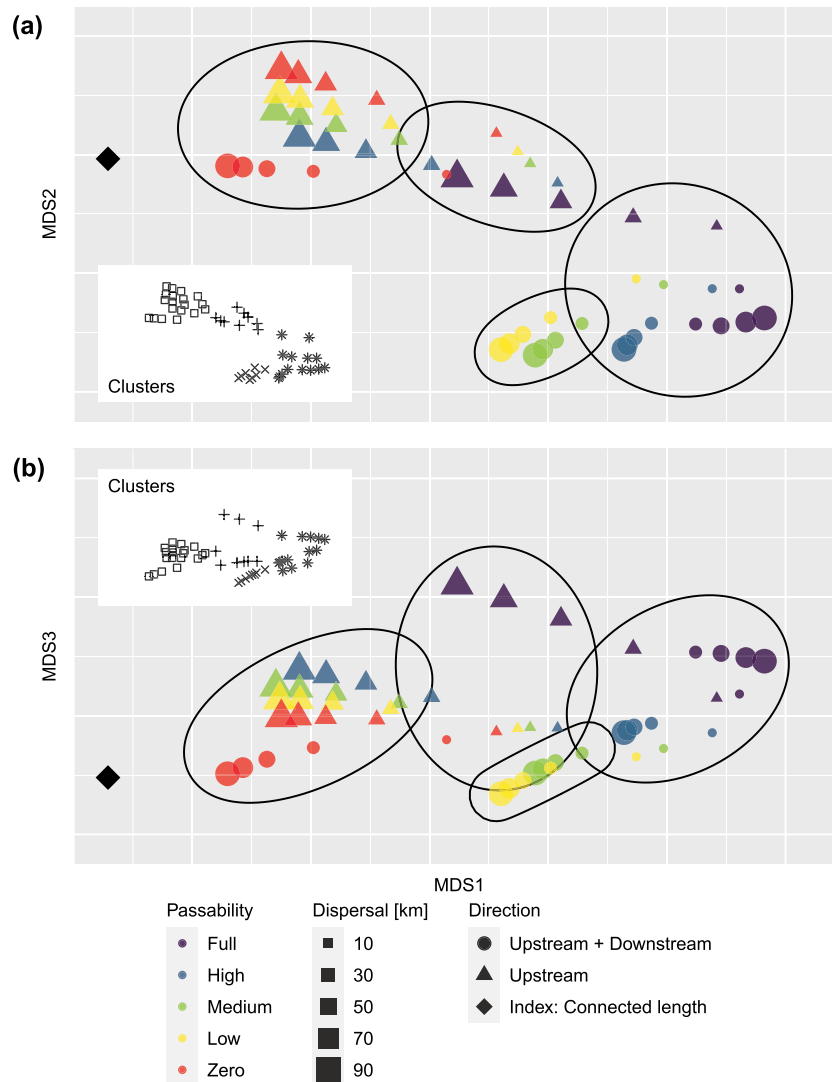CCIs showed a substantial decrease in scenarios, reflecting the effect

Fig. 1. Results of passability estimations for barriers on Austrian territory ($n = 2116$). The values indicated represent the arithmetic mean and the corresponding standard deviation.

Fig. 2. Results from non-metric multidimensional scaling (NMDS; likely global optimum identified after 780 random starts; stress = 0.035) and subsequent cluster analysis (k-means algorithm) of reach connectivity indices with four clusters, both based on three dimensions. In the "full" and "zero" passability scenarios, the passability of natural barriers has been estimated according to the "medium" passability scenario. (a) Positioning of indices on the first and second NMDS axis. (b) Positioning of indices on the first and third axis.

of artificial barriers compared to the one describing the naturally connected state of the system (Fig. 3a). This effect was small at the lowest investigated dispersal distance of 10 km but increased strongly at larger dispersal distances. Furthermore, CCIs describing the naturally connected state increased exponentially and linearly with dispersal distance when considering connections to all other reaches or only those located upstream, respectively. The effect of barriers, however, transformed the relationship between CCIs and dispersal distance into a logarithmic function. In addition to differences in connectivity at the catchment scale, the results further showed substantial differences regarding the distributions of RCIs between scenarios (Fig. 3b). Regarding RCIs considering connections in both upstream and downstream directions, the scenario describing a naturally connected state showed a transformation from a mainly Gaussian to a right-skewed and finally to an increasingly uniform distribution as dispersal distance increased. This transformation was lost as barrier passability decreased, resulting in a highly right-skewed distribution. In the case of RCIs considering only upstream connections, distributions were heavily right-skewed across all passability scenarios and dispersal distances. Merely the RCI describing the naturally connected state was slightly less skewed, especially at a dispersal distance of 10 km.

The effect of barriers further had a substantial impact on the spatial patterns of RCIs (Fig. 4). In the case of scenarios describing the naturally connected state of the system without artificial barriers, longer dispersal distances, and therefore higher CCIs, led to the emergence of a pronounced centrality pattern where RCIs increased from the upper parts of the tributaries towards the center of the river network. However, this pattern was severely disrupted by the effect of barriers, as illustrated in the case of the medium passability scenario. Moreover, several reaches were further attributed to high ranks (red) of connectivity due to the position and passability of individual barriers despite being attributed to low ranks (blue) in the full passability scenario. Hence, in today's system, even some of the naturally rather isolated reaches can be described as well-connected relative to the overall reduced degree of connectivity.

Finally, the percentage of lost connectivity relative to the naturally connected state of the river network (Fig. 5) indicated substantial losses across all barrier passability scenarios and dispersal distances. In the case of RCIs based on connections to other reaches in both upstream and downstream directions, the mean loss ranged between 36 % and 90 % with a global mean of 72 % (SD = 26 %). Regarding RCIs considering only upstream connections, the mean loss ranged between 49 % and 74 %, with a global mean of 66 % (SD = 7 %). A map visualizing spatial
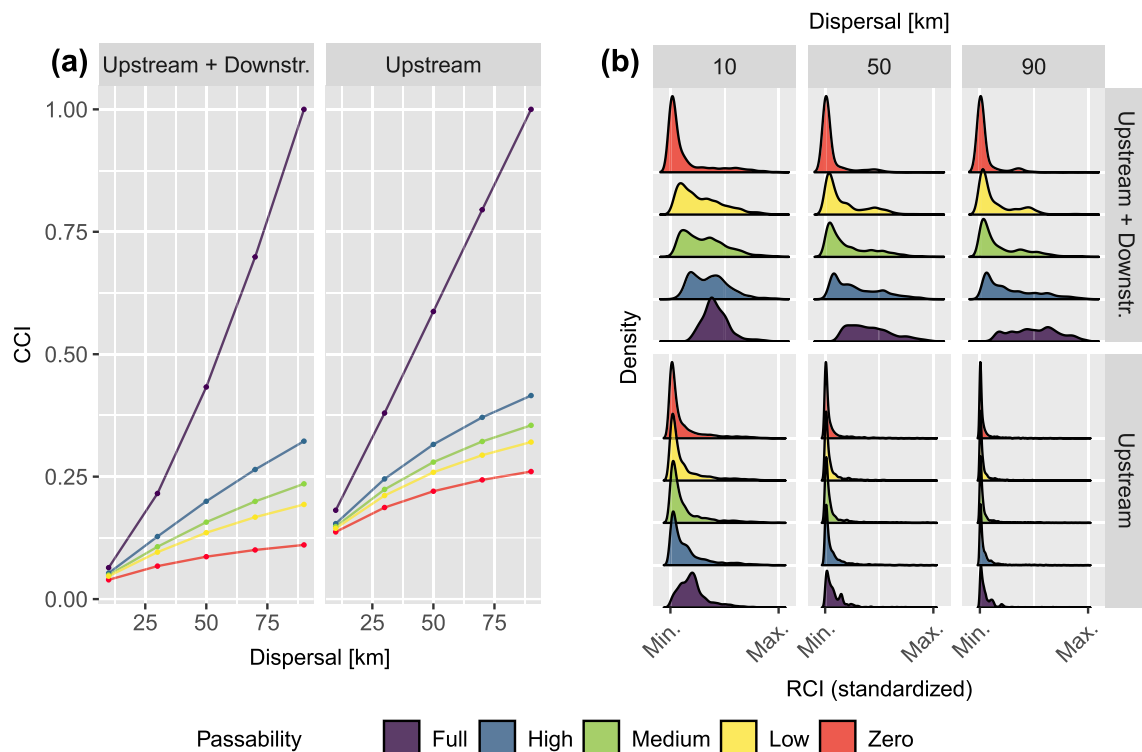
Fig. 3. (a) Normalized (maximum per plot panel) catchment connectivity indices (CCI). (b) Distribution of normalized (maximum per index configuration) reach connectivity indices (RCI) from selected dispersal distances. In the "full" and "zero" passability scenarios, the passability of natural barriers has been estimated according to the "medium" passability scenario.

patterns of connectivity loss can be found in appendix A.

4. Discussion

4.1. Ecological implications

Today, the Austrian Danube differs fundamentally from the natural conditions of high connectivity to which potamodromous fish species are adapted to. The transformation from a linear and exponential function to a logarithmic increase of CCIs with dispersal distance demonstrates how the willingness and overall capacity to spend large amounts of energy to access distant but potentially more promising habitats only pays off to a far lesser extent. While CCIs indicated only a small effect of barriers at the lowest analyzed dispersal distance of 10 km relative to larger dispersal distances, the loss of connectivity according to RCIs was substantial across all scenarios. Moreover, the increasingly right-skewed distribution of RCIs indicates that individual reaches have become more isolated, even when considering the overall decrease in longitudinal connectivity. Finally, natural centrality patterns of RCIs have been lost to a large extent, which underlines the severe effect of barriers and the fundamental change imposed on the Austrian Danube system. This issue is additionally amplified by a strong decrease in lateral connectivity, especially within the Danube where the confinement and straightening of the riverbed have led to the loss of instream habitats, the disconnection of side channels (Hohensinner et al., 2014) and floodplains (Hein et al., 2016). The consequential loss of habitats has been even further intensified by a sequence of impoundments which have induced a potamalization upstream and an incision of the riverbed downstream of barriers (Schmutz and Moog, 2018; Hauer et al., 2018). Overall, the resulting hydromorphological changes have led to a shift from primarily lotic to increasingly lentic-type conditions, resulting in a loss of characteristic habitats such as shallow gravel banks (Perle, 2023; Hohensinner et al., 2003). Rheophilic, gravel-spawning fish species, such as those investigated in this study, are strongly associated with such

habitats and are also known to conduct pronounced spawning migrations (Kottelat and Freyhof, 2007; Froese and Pauly, 2023). Therefore, these species are not only strongly dependent on habitat connections along the course of a river and into tributaries, which, as this study shows, have been severely compromised, but also depend on a habitat type that has been lost to a large extent. Furthermore, the decrease in habitat availability may require individuals to cover, on average, longer distances along this highly fragmented river network to access specific habitat types, ultimately making it even more difficult for potamodromous fish to complete their life cycle.

Another relevant aspect regarding connectivity changes from the perspective of potamodromous fish is that the distances covered, for example, during spawning migration, substantially vary within populations (Steinmann et al., 1937; Leeuw and Winter, 2008). This diversification of the migration process has been linked, in some cases, to the presence of discrete units within populations (Schindler et al., 2010) and is understood to increase its overall resilience through a so-called portfolio effect (Schindler et al., 2015). For example, as some individuals cover longer and others shorter distances during reproduction, a wider variety of individual habitats is utilized, which has the potential to compensate for local stressors such as high predation or flood events affecting reproductive success. Furthermore, stray individuals, which cover exceptionally long distances, could play a vital role in the recolonization of habitats following disturbances or facilitate the exchange of beneficial genes between populations. However, the loss of longitudinal connectivity makes it increasingly difficult or impossible for individuals to move across longer distances. The consequence is a selection towards a reduced migration portfolio (Sturrock et al., 2019; Epple et al., 2020; Carlson and Satterthwaite, 2011), likely resulting in decreased resilience and adaptability on the population and meta-population level. This is especially problematic since multiple stressors with complex interactions (Schinegger et al., 2016), in combination with a changing and less predictable climate, have already decreased the resilience of riverine fish populations against disturbances (Daufresne
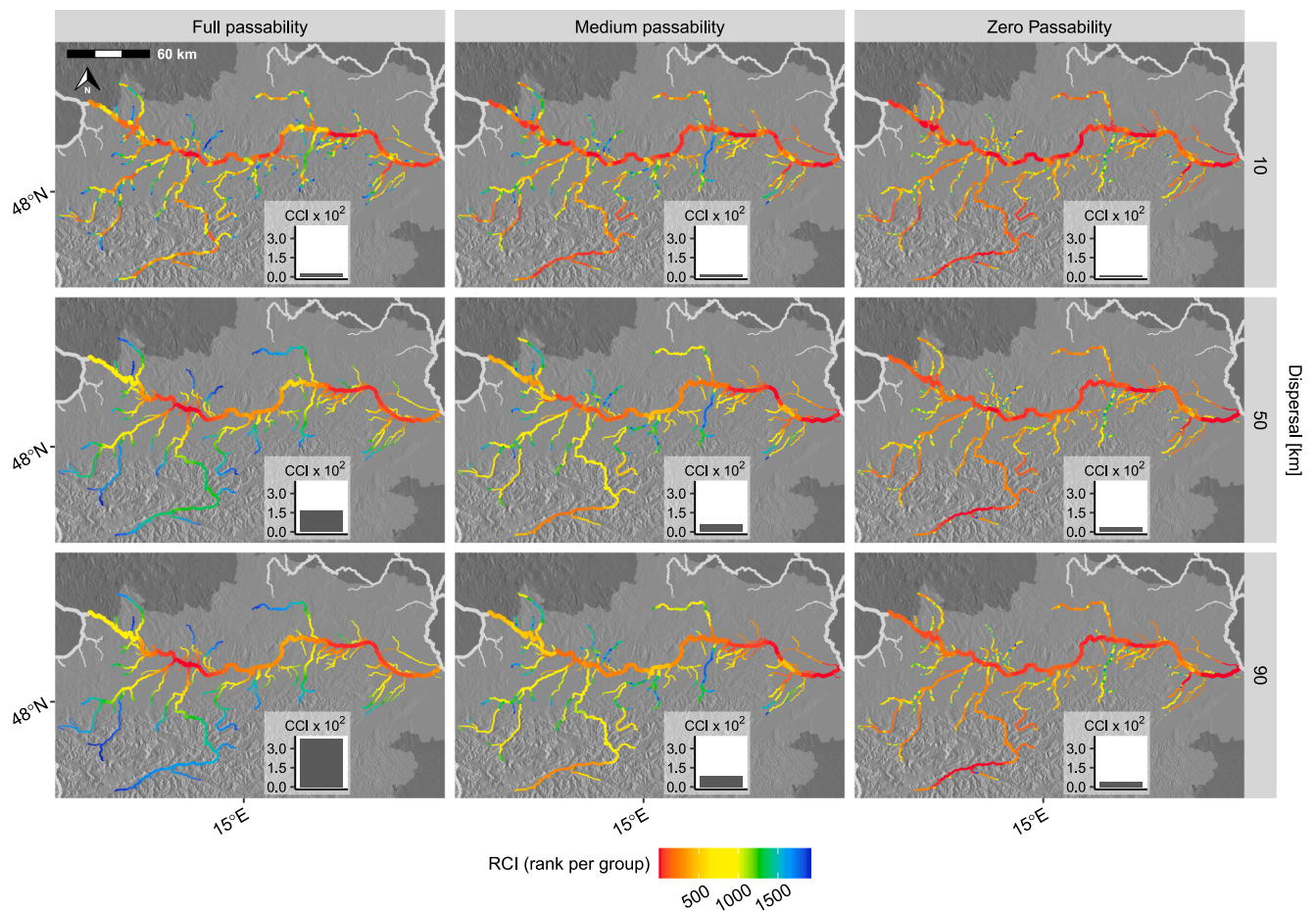
Fig. 4. Spatial patterns of reach connectivity indices (RCI) considering both upstream and downstream connections. The figure shows selected passability scenarios, dispersal distances, and associated catchment connectivity indices (CCIs; subplots). To visualize the difference in the spatial variation of RCIs between scenarios with varying degrees of catchment connectivity, RCIs have been rank-transformed per group (plot panel). Hence, on the color scale, red indicates high connectivity, whereas blue indicates low connectivity. In the "full" and vzero" passability scenarios, the passability of natural barriers has been estimated according to the "medium" passability scenario.
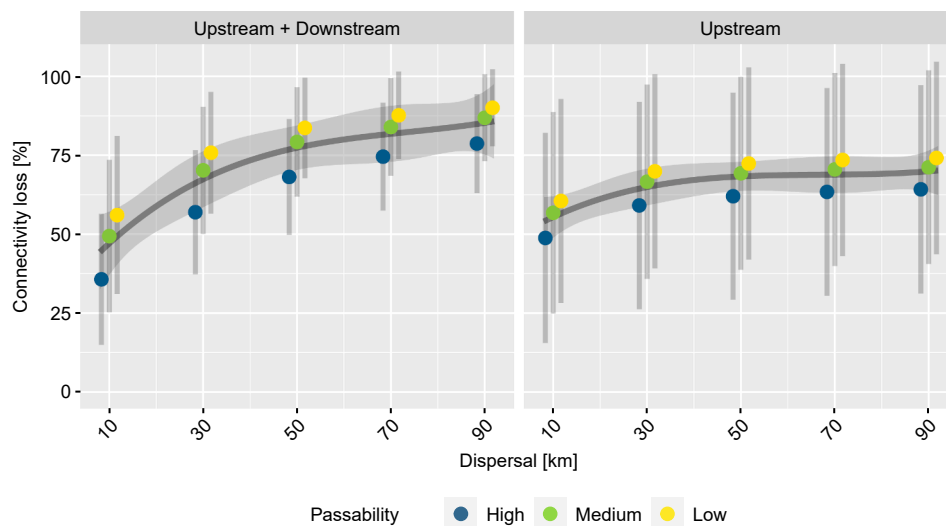
Fig. 5. Arithmetic mean of the connectivity loss across reaches according to reach connectivity indices (RCIs) from different dispersal and passability scenarios. Point positions on the x-axis have been slightly dodged to avoid overlapping. Vertical lines indicate the standard deviation.

and Boët, 2007; Hudson et al., 2014).

Finally, we want to point out that the quantitative monitoring of fish populations and their movement patterns in large rivers is challenging, in some cases impossible, and the resulting data, therefore, afflicted with potentially problematic uncertainties (Radinger et al., 2019). Moreover, the ecological connectivity gradient, which is a result of the complex

interplay between functional and structural connectivity processes, strongly depends on dispersal distances, as well as the position and passability of individual barriers (figure 2). Thus, predicting the impact that longitudinal connectivity loss has on potamodromous fish populations is extremely difficult.

4.2. Uncertainties and limitations

One of the uncertainties associated with the results of this study relates to the "naturally connected" state of the river network, where all barriers, except natural obstacles, were assigned full passability. Since this scenario describes longitudinal connectivity without the effect of anthropogenic barriers, it describes more closely the conditions to which potamodromous fish species are adapted and thus references a more natural state of the system. However, because the river network was largely simplified to a dendritic structure, connections to reaches located in side channels are disregarded. Today, the resulting river network still closely reflects the actual network topology since many lateral connections have been cut off in the course of river engineering. However, in its pristine natural state, the Austrian Danube system would have provided large quantities of additional and diverse fish habitats located in side channels, floodplains, and less confined riverbeds. When we consider the disappearance of those habitats, the actual connectivity loss in today's system would be substantially greater than the loss indicated by our results. Another aspect of uncertainty associated with the network topology is that this study was conducted for a sub-network of the Danube system clipped at its upstream and downstream ends. Even though measures were applied to reduce the consequential edge effects (Section 2.1), it should be noted that the connectivity may be slightly higher than indicated by our results. This may especially be the case regarding reaches close to the areas where the network has been clipped.

Further uncertainties are associated with the estimation of barrier passability. While this estimation only provides a rough approximation, the actual quantitative passability of barriers is highly species-specific and strongly depends on individual circumstances, such as the predation to which individuals are exposed while passing through an impoundment (Mensinger et al., 2024) or the hydraulic parameters of a fish pass (Noonan et al., 2011). In addition, the passability of sills or small weirs is not static but depends on the degree to which overflow occurs and thus on the temporal discharge variability (Shaw et al., 2016). However, compared to other studies addressing similar or larger scales, our estimation of barrier passability is much more detailed due to the high number of considered attributes, which underlines the relevance of this study. Furthermore, uncertainties regarding the passability of barriers were tackled by applying different passability scenarios. Ultimately, by estimating the barrier passability instead of conducting a monitoring-based assessment, we could investigate longitudinal connectivity changes at a spatial scale corresponding to the distances that potamodromous fish would cover during migrations under natural conditions.

Finally, the inherent complexity of functional connectivity is not fully covered by the simplified description used in this study, which defines the relevance of the specific connections from a reach i to a reach j according to the coincidence probability of an individual dispersing along this path. While this probability has been approximated based on the distance between two reaches and the length of the reach j (Section 2.3), it is rather a function of multiple variables with complex interactions. For example, the spatial distribution of a population, the resulting densities in specific reaches, as well as inherent traits (e.g., homing, straying, physiological limitations), and state variables (e.g., life stages) associated with individuals.

4.3. Management implications

Following the results of this study, we highlight the urgent need to increase the efforts aiming to restore the longitudinal river continuum in order to preserve and sustainably manage these ecosystems. The urgency of the matter is demonstrated, for example, by the population decline of the Danube Salmon, an endemic flagship species of the Danube River basin. Regarding the conservation of this species, restoring connectivity has been identified as a top priority to ensure its persistence (Pinter et al., 2024). Furthermore, we suggest that strategies for the management of potamodromous fish species facilitate a meta-ecosystem approach and thus take into account the spatial distribution, functional characteristics, and connections between specific habitats (Jacquet et al., 2022). In practical terms, this means that the overarching aim should be to provide suitable and sufficient amounts of connected habitats according to the (ideally) natural spatial distribution and movement dynamics exhibited by meta-populations. In the short term, this could be achieved by identifying, protecting, and restoring well-connected areas within a river network that provide sufficient amounts of suitable habitats for all life stages. For this purpose, nature-oriented bypass channels that reflect the size and the natural characteristics of habitat conditions in the relevant section of the river network could serve as an efficient tool to simultaneously increase the passability of barriers and mitigate the loss of fish habitat (Pander et al., 2011). However, bypass channels do not replace other necessary measures such as the restoration of shoreline and instream habitats (Schmutz et al., 2013), the removal of obsolete barriers (Stanley and Doyle, 2003), and ecologically responsible management of the sediments that are accumulating in impoundments (Tritthart et al., 2019). Most importantly, restoring one area within a river network should not lead to constructing new barriers in others. In the long-term, restoration efforts should aim to reestablish the connections between areas of high connectivity and habitat availability to facilitate the natural movement dynamics and the associated diversity within the meta-populations of potamodromous fish species. Such a management strategy may be implemented according to prioritizing barriers for removal or measures to increase their passability. A maximization of the CCI could represent an efficient way to facilitate a prioritization or complement other approaches (ICPDR, 2021). In contrast to more simplistic metrics such as the "connected length", this index can not only reflect different dispersal characteristics but can further integrate the individual needs of specific species regarding habitat suitability criteria (Rodeles et al., 2021). Furthermore, indices based on a network approach, such as the CCI and RCI, could play an important role in the process of formulating a definition for "free-flowing rivers". A precise and quantitative definition would represent a major step towards protecting the increasingly rare river networks with largely unimpacted longitudinal connectivity (Grill et al., 2019). Moreover, the lack of a precise definition has been a major criticism of the recently proposed Nature Restoration Law (Stoffers et al., 2024).

Naturally, as the catchments of large rivers are located in multiple countries, we want to point out further that sustainable and integrative management of such river systems requires international collaborations. This is especially relevant when it comes to longitudinal connectivity and should, for example, address the monitoring of fish migration patterns, the mapping and the ecological assessment of barriers. One of the benefits would be the ability to conduct a catchment-wide and detailed assessment of longitudinal connectivity, which could then be used as the baseline for efficient planning of restoration- and conservation measures. In the case of the Danube, collaborations have been formed, for example, under the International Commission for the Protection of the Danube River (ICPDR) and the EU Strategy for the Danube Region (European Commission, 2010).

Finally, it should be noted that this study has focused exclusively on potamodromous fish species, disregarding other life-cycle strategies such as anadromous migration. Species associated with such strategies are even more sensitive to longitudinal continuum disruptions and can today only be found in the lower parts of the Danube catchment (Friedrich, 2018). However, any measures affecting the longitudinal

connectivity of a river network should consider all naturally occurring species, including those that have become locally extinct.

5. Conclusion

Following the results of this study, we conclude that despite the implementation of numerous measures to increase barrier passability, longitudinal connectivity in the Austrian Danube system is still severely compromised. Therefore, potamodromous fish species are forced to survive under circumstances that make it increasingly challenging for them to complete their life cycle, which has likely decreased the resilience and adaptability of populations. The severe loss of fish habitats additionally intensifies these circumstances. Hence, we urge decision-makers and stakeholders to acknowledge the fundamental difference between today's and the long-lost natural conditions, leaving potamodromous fish species in a highly vulnerable position. Management actions should emphasize a meta-ecosystem approach that focuses on identifying and protecting the diversity and movement dynamics of meta-populations. Moreover, further measures to restore connectivity and habitats are urgently needed. While neither can replace but potentially compensate the other to some extent, the implementation of restoration measures should be planned efficiently. We therefore suggest a prioritization based on an index such as the CCI that can integrate different dispersal characteristics and local habitat availability.

CRediT authorship contribution statement

Johannes L. Kowal: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. **Andrea Funk:** Conceptualization, Supervision, Writing – review & editing.

Appendix A

Günther Unfer: Methodology, Writing – review & editing. **Damiano Baldan:** Writing – review & editing. **Gertrud Haidvogl:** Writing – review & editing. **Christoph Hauer:** Writing – review & editing. **Maria T. Ferreira:** Writing – review & editing. **Paulo Branco:** Writing – review & editing. **Rafaela Schinegger:** Writing – review & editing. **Thomas Hein:** Supervision, Funding acquisition, Project administration, Writing – review & editing.

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.

Data availability

Shapefiles corresponding to the analyzed river network and barriers, including all relevant attributes, are included in appendix B. In addition, datasets with calculated RCIs and CCIs are provided.

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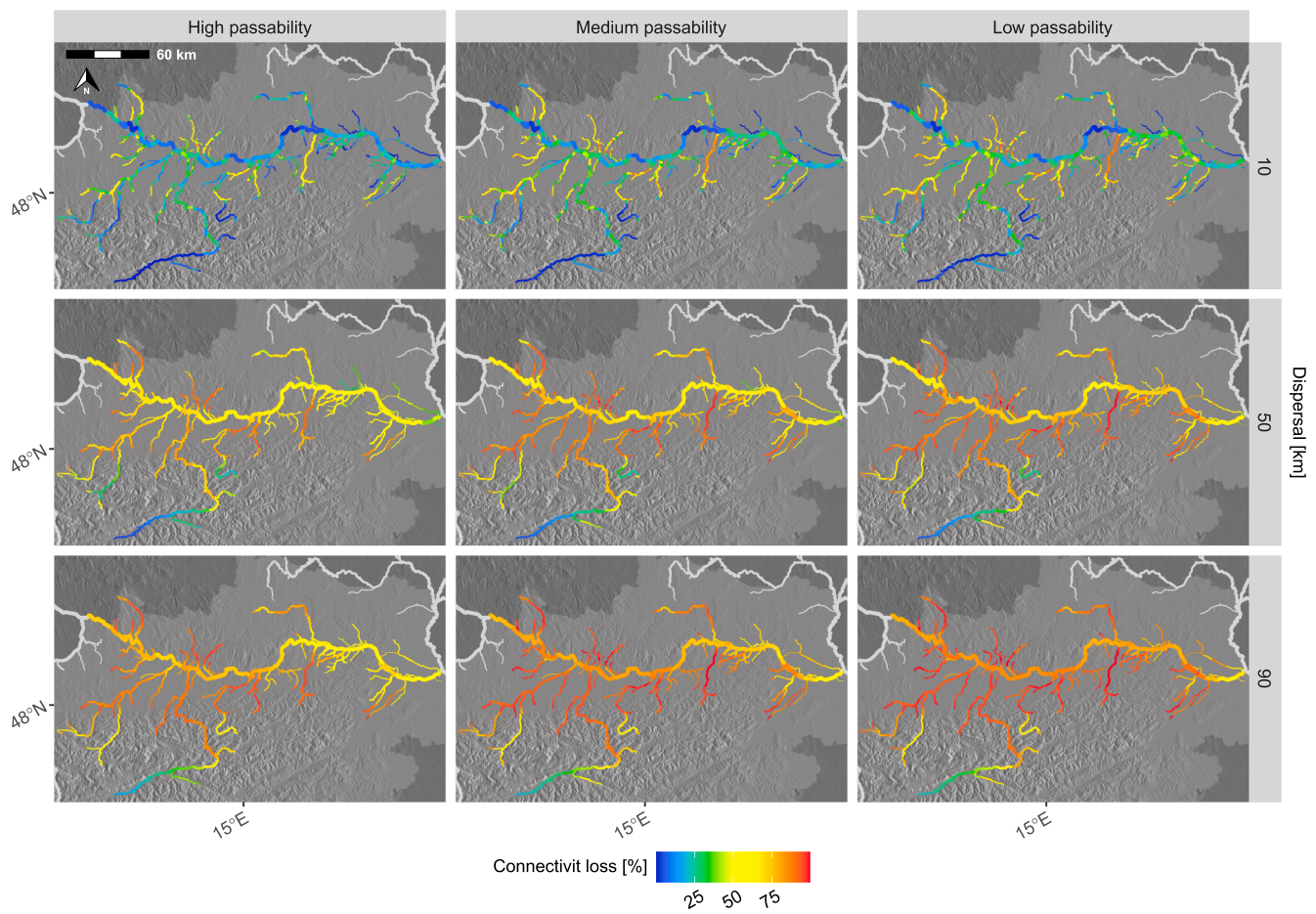
Connectivity loss based on reach connectivity indices (RCI) considering connections in both upstream and downstream directions. The map shows different scenarios regarding the results from the estimation of barrier passability in combination with selected dispersal distances.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version at https://doi.org/10.1016/j.ecolind.2024.112130.

References

Baldan, Damiano, Cunillera-Montcusí, David, Funk, Andrea, Hein, Thomas, 2022. Introducing 'riverconn': an R package to assess river connectivity indices. Environ. Model. Software 156, 105470. https://doi.org/10.1016/j.envsoft.2022.105470.

Baldan, Damiano, Cunillera-Montcusí, David, Funk, Andrea, Piniewski, Mikołaj, Cañedo-Argüelles, Miguel, Hein, Thomas, 2023. The effects of longitudinal fragmentation on riverine beta diversity are modulated by fragmentation intensity. Sci. Total Environ. 903, 166703. https://doi.org/10.1016/j.scitotenv.2023.166703.

Baudoin, Jean-Marc, Burgun, Vincent, Matthieu, Chanseau, Michel, Larinier, Michael, Ovidio, Sremski, William, Steinbach, Pierre, Bruno, Voegtlé, 2015. Assessing the passage of obstacles by fish. Concepts, design and application 37 (979-10-91047-29-6).

Beger, Maria, Metaxas, Anna, Balbar, Arieanna C., McGowan, Jennifer A., Daigle, Remi, Kuempel, Caitlin D., Treml, Eric A., Possingham, Hugh P., 2022. Demystifying ecological connectivity for actionable spatial conservation planning. Trends Ecol. Evol. 37 (12), 1079–1091. https://doi.org/10.1016/j.tree.2022.09.002.

Belletti, Barbara, Garcia, Carlos, de Leaniz, Joshua, Jones, Simone Bizzi, Börger, Luca, Segura, Gilles, Castelletti, Andrea, van de Bund, Wouter, Aarestrup, Kim, Barry, James, et al., 2020. More than one million barriers fragment Europe's rivers. Nature 588 (7838), 436–441. https://doi.org/10.1038/s41586-020-3005-2.

BMLRT, 2021a. Federal Ministry of Agriculture, Regions and Tourism Austria: Guideline for the construction of fish ladders. Bundesministerium für Land- und Forstwirtschaft, Regionen und Wasserwirtschaft.

BMLRT, 2021b. Federal Ministry of Agriculture, Regions and Tourism Austria: National River Basin Management Plan. Bundesministerium für Land- und Forstwirtschaft, Regionen und Wasserwirtschaft.

Borthagaray, Ana, Teixeira, Franco, de Mello, Giancarlo, Tesitore, Esteban Ortiz, Illarze, Mariana, Pinelli, Verónica, Urtado, Lucia, Raftopulos, Pablo, González-Bergonzoni, Ivan, Abades, Sebastián, et al., 2020. Community isolation drives lower fish biomass and species richness, but higher functional evenness, in a river metacommunity. Freshw. Biol. 65 https://doi.org/10.1111/fwb.13603.

Cadotte, Marc, W., Tucker, Caroline, M., 2020. Should Environmental Filtering be Abandoned? Trends Ecol. Evol. 32 (6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004. ISSN: 0169–5347.

Carlson, Stephanie Marie, Satterthwaite, William Hallowell, 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquatic Sci. 68(9). Ed. by Ian A. Fleming, pp. 1579–1589. doi: 10.1139/f2011-084.

Chen, Qiuwen, Li, Qinyuan, Lin, Yuqing, Zhang, Jianyun, Xia, Jun, Ni, Jinren, Cooke, Steven J., Best, Jim, He, Shufeng, Feng, Tao, et al., 2023. River damming impacts on fish habitat and associated conservation measures. Rev. Geophys. 61(4). ISSN, 1944–9208. https://doi.org/10.1029/2023rg000819.

Cid, Núria, Erős, Tibor, Heino, Jani, Singer, Gabriel, Jähnig, Sonja C., Cañedo-Argüelles, Miguel, Bonada, Núria, Sarremejane, Romain, Mykrä, Heikki, Sandin, Leonard, et al., 2021. From meta-system theory to the sustainable management of rivers in the Anthropocene. Front. Ecol. Environ. 20 (1), 49–57. https://doi.org/10.1002/fee.2417.

Cooper, Arthur R., Infante, Dana M., Daniel, Wesley M., Wehrly, Kevin E., Wang, Lizhu, Brenden, Travis O., 2017. Assessment of dam effects on streams and fish assemblages of the conterminous USA. Sci. Total Environ. 586, 879–889. https://doi.org/10.1016/j.scitotenv.2017.02.067. ISSN: 0048–9697.

Cooper, Arthur R., Infante, Dana M., Wehrly, Kevin E., Wang, Lizhu, Brenden, Travis O., 2016. Identifying indicators and quantifying large-scale effects of dams on fishes.

Ecol. Ind. 61, 646–657. https://doi.org/10.1016/j.ecolind.2015.10.016. ISSN: 1470-160X.

Cote, David, Kehler, Dan G., Bourne, Christina, Wiersma, Yolanda F., 2008. A new measure of longitudinal connectivity for stream networks. Landscape Ecol. 24 (1), 101–113. https://doi.org/10.1007/s10980-008-9283-y.

Daufresne, Martin, Boët, Philippe, 2007. Climate change impacts on structure and diversity of fish communities in rivers. Global Change Biol. 13 (12), 2467–2478. https://doi.org/10.1111/j.1365- 2486.2007.01449.x. ISSN: 1365–2486.

Epple, Tobias, Friedmann, Arne, Wetzel, Karl-Friedrich, Born, Oliver, 2020. The life cycle of nase (Chondrostoma nasus) before and after theconstruction of hydropower plants in the river Iller (Bavaria, Germany)and its migration behavior through fish-bypass channels. DanubeNews 22, 41.

Erős, Tibor, Olden, Julian D., Schick, Robert S., Schmera, Dénes, Fortin, Marie-Josée, 2011. Characterizing connectivity relationships in freshwaters using patch-based graphs. Landscape Ecol. 27 (2), 303–317. https://doi.org/10.1007/s10980-011-9659-2.

ESRI Inc., 2009. World Imagery (accessed on 15.12.2023, last updated on 08.12.2023). URL:https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer.

European Commission, 2000. Directive 2000/60/EC of the European parliament and of the council of 23 October 2000 establishing a framework for community action in the field of water policy or, in short, the EU Water Framework Directive. Official Journal of the European Communities L 327.

European Commission, 2010. Communication from the comission to the European parliament, the European council, the European economic and social committee and the committee of the regions: European Union Strategy for Danube Region. URL: https://eur-lex.europa.eu/legal-content/DE/TXT/PDF/?uri=CELEX:52010DC0715.

European Commission, 2020. Communication from the comission to the European parliament, the European council, the European economic and social committee and the committee of the regions, EU Biodiversity Strategy for 2030 – Bringing nature back into our lives.

European Commission, 2022. Communication from the comission to the European parliament, the European council, the European economic and social committee and the committee of the regions: REPowerEU plan. URL: https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=COM:2022:230:FIN&qid=1653033742483.

European Commission, 2023. Proposal for a regulation of the European parliament and of thecouncil on nature restoration. URL: https://environment.ec.europa.eu/publications/naturerestoration-%20law_en.

Friedrich, Thomas, 2018. Danube Sturgeons: Past and Future. Riverine Ecosystem Management. Springer International Publishing, pp. 507–518. ISBN: 9783319732503. doi: 10.1007/978-3-319-73250-3_26.

Froese, R., Pauly, D., 2023. FishBase. URL: www.fishbase.org.

Funk, Andrea, Tschikof, Martin, Grüner, Barbara, Böck, Kerstin, Hein, Thomas, Bondar-Kunze, Elisabeth, 2020. Analysing the potential to restore the multi-functionality of floodplain systems by considering ecosystem service quality, quantity and trade-offs. River Res. Appl. 37 (2), 221–232. https://doi.org/10.1002/rra.3662. ISSN: 1535-1467.

Gernaat, David E.H.J., Bogaart, Patrick W., van Vuuren, Detlef P., Biemans, Hester, Niessink, Robin, 2017. High-resolution assessment of global technical and economic hydropower potential. Nat. Energy 2 (10), 821–828. https://doi.org/10.1038/s41560-017-0006-y. ISSN: 2058-7546.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., et al., 2019. Mapping the world's free-flowing rivers. Nature 569 (7755), 215–221. https://doi.org/10.1038/s41586-019-1111-9. ISSN: 1476-4687.

Hauer, Christoph, Leitner, Patrick, Unfer, Günther, Pulg, Ulrich, Habersack, Helmut, Graf, Wolfram, 2018. The Role of Sediment and Sediment Dynamics in the Aquatic Environment. Riverine Ecosystem Management. Springer International Publishing, pp. 151–169.

Haunschmid, Reinhard, Schotzko, Nikolaus, Petz-Glechner, Regina, Honsig-Erlenburg, Wolfgang, Schmutz, Stefan, Spindler, Thomas, Unfer, Günther, Wolfram, Georg, Bammer, Vinzenz, Hundritsch, Lukas, et al., 2009. Leitfaden zur Erhebung der biologischen Qualitätselemente. de. Vienna, Austria: Bundesministerium für Nachhaltigkeit und Tourismus (BMNT), Abt. I 3.

Hein, Thomas, Schwarz, Ulrich, Habersack, Helmut, Nichersu, Iulian, Preiner, Stefan, Willby, Nigel, Weigelhofer, Gabriele, 2016. Current status and restoration options for floodplains along the Danube River. Sci. Total Environ. 543, 778–790. https://doi.org/10.1016/j.scitotenv.2015.09.073.

Hering, Daniel, Schürings, Christian, Wenskus, Franziska, Blackstock, Kirsty, Borja, Angel, Birk, Sebastian, Bullock, Craig, Carvalho, Laurence, Dagher-Kharrat, Magda Bou, Lakner, Sebastian, et al., 2023. Securing success for the Nature Restoration Law. Science 382 (6676), 1248–1250. https://doi.org/10.1126/science.adk1658. ISSN: 1095-9203.

Hohensinner, S., Habersack, H., Jungwirth, M., Zauner, G., 2003. Reconstruction of the characteristics of a natural alluvial river–floodplain system and hydromorphological changes following human modifications: the Danube River (1812–1991). River Res. Appl. 20 (1), 25–41. https://doi.org/10.1002/rra.719. ISSN: 1535-1467.

Hohensinner, Severin, Jungwirth, Mathias, Muhar, Susanne, Schmutz, Stefan, 2014. Importance of multi-dimensional morphodynamics for habitat evolution: Danube River 1715–2006. Geomorphology 215, 3–19. https://doi.org/10.1016/j.geomorph.2013.08.001.

Hudson, Alan G., Vonlanthen, Pascal, Seehausen, Ole, 2014. Population structure, inbreeding and local adaptation within an endangered riverine specialist: the nase (Chondrostoma nasus). Conserv. Genet. 15 (4), 933–951. https://doi.org/10.1007/s10592-014-0590-3. ISSN: 1572-9737.

ICPDR, 2021. Danube River Basin Management Plan. Ecological Prioritisation Approach.

Jacquet, Claire, Carraro, Luca, Altermatt, Florian, 2022. Meta-ecosystem dynamics drive the spatial distribution of functional groups in river networks. Oikos 11. https://doi.org/10.1111/oik.09372. ISSN: 1600-0706.

Kottelat, Maurice, Freyhof, Jörg, 2007. Handbook of European freshwater fishes. Publications Kottelat 646. ISBN: 9782839902984.

Leeuw, J.J.D., Winter, H.V., 2008. Migration of rheophilic fish in the large lowland rivers Meuse and Rhine, the Netherlands. Fish. Manage. Ecol. 15 (5-6), 409–415. https://doi.org/10.1111/j.1365-2400.2008.00626.x.

Lucas, Martyn C., Baras, Etienne, Thom, Timothy J., Duncan, Annie, Slavík, Ondrej, Eds., 2001. Migration of Freshwater Fishes. Wiley, pp. 66–92. ISBN: 9780470999653. doi: 10.1002/9780470999653.

Mensinger, Matthew A., Hawkes, James P., Goulette, Graham S., Mortelliti, Alessio, Blomberg, Erik J., Zydlewski, Joseph D., 2024. Dams facilitate predation during Atlantic salmon (Salmo salar) smolt migration. Can. J. Fish. Aquat. Sci. 81 (1), 38–51. https://doi.org/10.1139/cjfas-2023-0175 issn: 1205-7533.

Minor, Emily S., Urban, Dean L., 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. Ecol. Appl. 17 (6), 1771–1782. https://doi.org/10.1890/06- 1073.1.

Newman, M.E.J., 2017. Networks: An introduction. Oxford University Press, p. 181. ISBN: 9780199206650.

Noonan, Michael J., Grant, James W.A., Jackson, Christopher D., 2011. A quantitative assessment of fish passage efficiency. Fish Fish. 13 (4), 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x.

Oksanen, Jari, Simpson, Gavin L., Guillaume Blanchet, F., Kindt, Roeland, Legendre, Pierre, Minchin, Peter R., O'Hara, R.B., Solymos, Peter, Henry, M., Stevens, H., Szoecs, Eduard, et al., 2022. vegan: Community Ecology Package. R package version 2.6-4. URL: https://CRAN.R-project.org/package=vegan.

Panchan, Ruamruedee, Pinter, Kurt, Schmutz, Stefan, Unfer, Günther, 2022. Seasonal migration and habitat use of adult barbel (Barbus barbus) and nase (Chondrostoma nasus) along a river stretch of the Austrian Danube River. Environ. Biol. Fishes 105 (11), 1601–1616. https://doi.org/10.1007/s10641-022-01352-3.

Pander, J., Mueller, M., Geist, J., 2011. Ecological functions of fish bypass channels in streams: migration corridor and habitat for rheophilic species. River Res. Appl. 29 (4), 441–450. https://doi.org/10.1002/rra.1612. ISSN: 1535-1467.

Pascual-Hortal, Lucía, Saura, Santiago, 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecol. 21 (7), 959–967. https://doi.org/10.1007/s10980-006-0013-z.

Peoples, Brandon K., Frimpong, Emmanuel A., 2015. Biotic interactions and habitat drive positive co-occurrence between facilitating and beneficiary stream fishes. J. Biogeogr. 43 (5), 923–931. https://doi.org/10.1111/jbi.12699 issn: 1365-2699.

Perle, Emily, 2023. Riparian habitats of the Austrian Danube – how have they developed and what have we lost? MA thesis. In: Institute of Hydrobiology and Aquatic Ecosystem Management (IHG). University of Natural Resources and Life Sciences, Vienna.

Pinter, Kurt, Ratschan, Clemens, Unfer, Günther, Weiss, Steven, Jungwirth, Mathias, Schmutz, Stefan, 2024. History, life history, and fate of a salmonid flagship species: the Danube Salmon. Fisheries. https://doi.org/10.1002/fsh.11072. ISSN: 1548-8446.

Pracheil, Brenda M., DeRolph, C.R., Schramm, M.P., Bevelhimer, M.S., 2016. A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage. Rev. Fish Biol. Fisheries 26 (2), 153–167. https://doi.org/10.1007/s11160-015-9416-8.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. URL: https://www.R-project.org/.

Radinger, Johannes, Alcaraz-Hernández, Juan Diego, García-Berthou, Emili, 2019. Environmental filtering governs the spatial distribution of alien fishes in a large, human-impacted Mediterranean river. In: Zhan, Aibin (Ed.), Diversity and Distributions 25.5, pp. 701–714. https://doi.org/10.1111/ddi.12895. ISSN: 1472-4642.

Radinger, Johannes, Robert Britton, J., Carlson, Stephanie M., Magurran, Anne E., Alcaraz-Hernández, Juan Diego, Almodóvar, Ana, Benejam, Lluís, Fernández-Delgado, Carlos, Nicola, Graciela G., Oliva-Paterna, Francisco J., et al., 2019. Effective monitoring of freshwater fish. Fish Fish. 20 (4), 729–747. https://doi.org/10.1111/faf.12373.

Rayfield, Bronwyn, Fortin, Marie-Josée, Fall, Andrew, 2011. Connectivity for conservation: a framework to classify network measures. Ecology 92 (4), 847–858. https://doi.org/10.1890/09-2190.1.

Rodeles, Amaia A., Galicia, David, Miranda, Rafael, 2021. A simple method to assess the fragmentation of freshwater fish meta-populations: Implications for river management and conservation. Ecol. Ind. 125, 107557. https://doi.org/10.1016/j.ecolind.2021.107557.

Schindler, Daniel E., Armstrong, Jonathan B., Reed, Thomas E., 2015. The portfolio concept in ecology and evolution. Front. Ecol. Environ. 13 (5), 257–263. https://doi.org/10.1890/140275.

Schindler, Daniel E., Hilborn, Ray, Chasco, Brandon, Boatright, Christopher P., Quinn, Thomas P., Rogers, Lauren A., Webster, Michael S., 2010. Population diversity and the portfolio effect in an exploited species. Nature 465 (7298), 609–612. https://doi.org/10.1038/nature09060 issn: 1476-4687.

Schinegger, Rafaela, Palt, Martin, Segurado, Pedro, Schmutz, Stefan, 2016. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. Sci. Total Environ. 573, 1079–1088. https://doi.org/10.1016/j.scitotenv.2016.08.143.

Schinegger, Rafaela, Pucher, Matthias, Aschauer, Christiane, Schmutz, Stefan, 2018. Configuration of multiple human stressors and their impacts on fish assemblages in

Alpine river basins of Austria. Sci. Total Environ. 616–617, 17–28. https://doi.org/10.1016/j.scitotenv.2017.10.283. ISSN: 0048-9697.

Schmutz, Stefan, Kremser, Helga, Melcher, Andreas, Jungwirth, Mathias, Muhar, Susanne, Waidbacher, Herwig, Zauner, Gerald, 2013. Ecological effects of rehabilitation measures at the Austrian Danube: a meta-analysis of fish assemblages. Hydrobiologia 729 (1), 49–60. https://doi.org/10.1007/s10750-013-1511-z. ISSN: 1573-5117.

Schmutz, Stefan, Moog, Otto, 2018. Dams: Ecological Impacts and Management. Riverine Ecosystem Management. Springer International Publishing, pp. 111–127. https://doi.org/10.1007/978-3-319-73250-3_6.

Shao, Xiao jing, Fang, Yu, Jawitz, James W., Yan, Jiaguo, Cui, Baoshan, 2019 River network connectivity and fish diversity. Sci. Total Environ. 689, 21–30. doi: 10.1016/j.scitotenv.2019.06.340.

Shaw, Edward A., Lange, Eckart, Shucksmith, James D., Lerner, David N., 2016. Importance of partial barriers and temporal variation in flow when modelling connectivity in fragmented river systems. Ecol. Eng. 91, 515–528. https://doi.org/10.1016/j.ecoleng.2016.01.030.

Stanley, Emily H., Doyle, Martin W., 2003. Trading off: the ecological effects of dam removal. Front. Ecol. Environ. 1 (1), 15–22. https://doi.org/10.1890/1540-9295(2003)001[0015:toteeo]2.0.co;2. ISSN: 1540-9295.

Steinmann, P., Koch, W., Scheuring, L., 1937. Die Wanderung unserer Süÿwasserfische, dargestellt auf Grund von Markierungsversuchen. Zeitschrift für Fischerei und deren Hilfswissenschaften 35, 369–467.

Stoffers, T., Buijse, A.D., Geerling, G.W., Jans, L.H., Schoor, M.M., Poos, J.J., Verreth, J.A.J., Nagelkerke, L.A.J., 2022. Freshwater fish biodiversity restoration in floodplain rivers requires connectivity and habitat heterogeneity at multiple spatial scales. Sci. Total Environ. 838, 156509. https://doi.org/10.1016/j.scitotenv.2022.156509.

Stoffers, Twan, Altermatt, Florian, Baldan, Damiano, Bilous, Olena, Borgwardt, Florian, Buijse, Anthonie D., Bondar-Kunze, Elisabeth, Cid, Nuria, Erős, Tibor, Ferreira, Maria Teresa, et al., 2024. Reviving Europe's rivers: seven challenges in the implementation of the Nature Restoration Law to restore free-flowing rivers. WIREs Water 11, 3. https://doi.org/10.1002/wat2.1717. ISSN: 2049-1948.

Sturrock, Anna M., Carlson, Stephanie M., Wikert, John D., Heyne, Tim, Nusslé, Sébastien, Merz, Joseph E., Sturrock, Hugh J.W., Johnson, Rachel C., 2019. Unnatural selection of salmon life histories in a modified riverscape. Glob. Change Biol. 26 (3), 1235–1247. https://doi.org/10.1111/gcb.14896.

Tischendorf, Lutz, Fahrig, Lenore, 2000. On the usage and measurement of landscape connectivity. Oikos 90 (1), 7–19. https://doi.org/10.1034/j.1600-0706.2000.900102.x. ISSN: 1600-0706.

Tiwari, Shubham, Brizuela, Sonia Recinos, Hein, Thomas, Turnbull, Laura, Wainwright, John, Funk, Andrea, 2023. Water-controlled ecosystems as complex networks: evaluation of network-based approaches to quantify patterns of connectivity. https://doi.org/10.22541/au.168674584.45045056/v1.

Tritthart, Michael, Haimann, Marlene, Habersack, Helmut, Hauer, Christoph, 2019. Spatio-temporal variability of suspended sediments in rivers and ecological implications of reservoir flushing operations. River Res. Appl. 35 (7), 918–931. https://doi.org/10.1002/rra.3492. ISSN: 1535-1467.

Urban, Dean, Keitt, Timothy, 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82 (5), 1205–1218. https://doi.org/10.1890/0012-9658(2001)082[1205:lcagtp]2.0.co;2.

Waidbacher, Herwig, Haidvogl, Gertrud, 1998. Fish Migration and Fish Passage Facilities in the Danube: Past and Present: Fish Migration and Fish Bypasses. Fishing News Books, pp. 85–98. ISBN: 9780852382530.