

Introducing 'riverconn': an R package to assess river connectivity indices

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ABSTRACT

Fragmentation affects river ecosystems worldwide by dampening the movement and dispersal of aquatic organisms and material (such as sediment, water, nutrients) across the river network. In this paper, we develop river connectivity indices to explain biodiversity patterns, prioritize reaches that need habitat restoration and barriers that need improvement. We provide a general framework for calculating connectivity indices by disentangling the contribution of the river network's physical setup (structural connectivity) from the process-driven and biota-related contribution (functional connectivity). To facilitate the calculations, the R package 'riverconn' is introduced. A prioritization of habitats and barriers is carried out for the Ebro river (North-West Iberian Peninsula) using indices setups accounting for different classes of organisms and dispersal traits. Resulting prioritizations are very diverse. 'Riverconn' can support scientists and managers working on riverscape planning and population and community ecology by providing a means to compute and compare a wide array of fragmentation indices.

1. Introduction

Free-flowing rivers host significant biodiversity (He et al., 2021), provide a wide array of ecosystem services such as water provisioning, nutrient and sediment transport, and support to fisheries harvests (Böck et al., 2018; Grill et al., 2019). Longitudinal river fragmentation is recognized as one of the major threats to freshwater systems worldwide (Dudgeon et al., 2006; Fullerton et al., 2010). The causes of longitudinal fragmentation are multiple, including the construction of barriers (Bellotti et al., 2020; Duarte et al., 2021), point source pollution (Araujo et al., 2018), stream and riparian habitat modification (Baldan et al., 2021; Fuller et al., 2015), and water withdrawals (Baumgartner et al., 2022). Longitudinally fragmented rivers are composed of successions of isolated sections, where the free movement of water, sediments, organic matter, nutrients, energy and organisms is impeded (Jumani et al., 2020). Biotic impacts of fragmentation include the decline of migratory fish populations (Birnie-Gauvin et al., 2017), genetic drifting of isolated

populations (Inoue and Berg, 2017), and increased local extinction risks (Fagan, 2002). Thus, when habitat restoration measures are implemented without adequate consideration to river network connectivity, they might fail because of the inaccessibility of the recreated habitat (Brederveld et al., 2011). River networks are particularly sensitive to connectivity losses: even local disconnections can lead to large-scale impacts due to the hierarchic and dendritic nature of such systems (Campbell Grant et al., 2007; Duarte et al., 2019). River network topologies display few possible connections for water-mediated dispersal of organisms (Altermatt, 2013; Cañedo-Argüelles et al., 2015; Tonkin et al., 2018) and increased distances between points along the network that are geographically close (Ver Hoef and Erin, 2010). Assessing the connectivity of river networks and its changes with increasing fragmentation has become a key task for scientists and practitioners.

Recent works have developed a wide array of indices to quantify longitudinal fragmentation with different complexities (Jumani et al., 2020), including the explicit modeling of the network structure of the

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landscape (Saura and Pascual-Hortal, 2007). Even simple indices can describe the structural connectivity, i.e. the set of all possible pathways linking different reaches in the landscape (Cote et al., 2009; Grill et al., 2015; Voutsas et al., 2021), at multiple scales (Duarte et al., 2021). This concept was expanded with the inclusion of functional connectivity, i.e. the component of connectivity that can be explained by biotic factors, such as organisms dispersal traits and mobility (Branco et al., 2014; Rodeles et al., 2019, 2021). Both structural and functional connectivity indices have been used to explain biodiversity patterns in highly modified catchments (Perkin and Gido, 2012), prioritize habitat patches that need improvement (Saura et al., 2014; Saura and Pascual-Hortal, 2007), and/or explain declines in fish populations (Barbarossa et al., 2020; van Puijenbroek et al., 2019). Some indices were developed to account explicitly for the directional nature of river systems for studies with anadromous fish (Rodeles et al., 2019). Asymmetric indices, that account for the river network directionality, can be used also for classes of organism with asymmetric dispersal patterns such as macro-invertebrates (e.g., active aerial such as Coleoptera or Trichoptera in the adult phase, or passive drifters such as Gasteropoda or Bivalva; Tachet et al., 2000). Empirical evidence of the impacts of fragmentation on macroinvertebrates exists (Cañedo-Argüelles et al., 2020; Monaghan et al., 2005; Wang et al., 2019), but the use of connectivity indices for this class of organism is still overlooked. Moreover, despite the large number of existing indices, a unifying framework to examine and quantify river connectivity is still missing. Such a framework would support scientists and managers to perform an informed selection of the most suitable index for a specific task, and to examine critically the implicit assumptions behind each index formulation (also based on the decision trees presented in Jumani et al., 2020).

To mitigate river fragmentation, the permeability (hence after: passability) of barriers can be improved to allow for the passage of at least some groups of organisms (King et al., 2017). This can be accomplished via structural modifications to the barrier (e.g. with the construction of fishpasses to facilitate upstream movement and migration), the removal of obsolete obstructions (Birnie-Gauvin et al., 2020), and the improvement of the streambed or the riparian habitat. Existing studies have used different fragmentation indices to support such actions via the identification of barriers with the highest reconnection potential (Buddendorf et al., 2019), the identification of optimal removal sequences (Branco et al., 2014), including in the analysis also economic constraints (King et al., 2017). However, tools and frameworks that include structural and functional information in barriers prioritization are still missing.

Given the gaps identified above, we propose an integrative framework that aims at i) generalizing existing connectivity indices, ii) providing a straightforward parametrization of several structural and functional connectivity indices, iii) implementing algorithms for prioritization of barriers for passability improvement. To this end, we present ‘riverconn’, an R package that allows for a flexible implementation of several graph-based connectivity indices and implements algorithms to prioritize reaches and barriers with the aim of improving catchment-scale connectivity. As a proof of applicability, we calculate and compare several ‘riverconn’ indices to the Ebro catchment (NE Spain).

2. Methods

2.1. Conceptual background: algorithms to estimate river network connectivity

2.1.1. River network as a graph

Following Erös et al. (2012), we conceptualize the river network as a graph $G(E, V)$, i.e. a collection of edges E and vertices V (Csardi and Nepusz, 2006). In the example provided in this paper, edges (or links) represent either barriers or confluences between reaches, while vertices (or nodes) represent reaches, i.e. river sections having relatively uniform conditions. Reaches are river sections located either between two

confluences, or between two sequential barriers. In this conceptualization, the resulting network is a directed loop-less graph whose root is the catchment outlet (Jumani et al., 2020). An alternative characterization where confluences are vertices and reaches are edges is also possible (Borthagaray et al., 2020), but might be of limited utility when multiple habitat patches within the same reach are considered. In fact, river networks can also be defined on a finer scale, for instance on channels units like riffle/pool sections or species-specific habitat patches, where vertices may represent habitat patches and links are elements representing the potential of dispersal between two habitat patches (Erös et al., 2012).

2.1.2. Generalized connectivity index

A generalized connectivity index for river networks can be defined based on Pascual-Hortal and Saura (2006). For every pair of reaches i and j in the catchment, the dispersal probability I_{ij} (see eq. (2.3)) is defined as the probability that an organism originally located in reach i can disperse to reach j . Under the assumption of steady state behavior of the system, the dependence from time can be dropped. Hence, the dispersal probability is only a function of the path (subgraph) connecting nodes i and j . Based on the Probability of Connectivity (Saura and Pascual-Hortal, 2007), we propose a catchment-level index of connectivity, the Catchment Connectivity Index (CCI) defined as the weighted sum of the dispersal probability:

$$CCI = \sum_{i=1}^n \sum_{j=1}^n I_{ij} \frac{w_i w_j}{W^2} \quad (2.1)$$

where w_i and w_j are the weights of reaches i and j , respectively, and W the sum of the weights over the n reaches. A reach-level index of connectivity, the Reach Connectivity Index (RCI) can be defined for reach i in the catchment by dropping the first summation in equation (2.1):

$$RCI_i = \sum_{j=1}^n I_{ij} \frac{w_j}{W} \quad (2.2)$$

Reaches weights can represent either abiotic properties, such as length, area, and volume, or biotic suitability scores dependent on a target organism, such as the weighted useable length or area (i.e. the length/area of the reach weighted with habitat quality or any other variable of interest; Yi et al., 2017). When directionality is included, CCI and RCI can be further decomposed by considering separately connections entering or exiting each reach.

Following Rodeles et al. (2021), we factorize the dispersal probability (I) into a component describing the structural connectivity (the presence and arrangement of barriers) and a component describing functional connectivity (species dispersal).

$$I_{ij} = c_{ij} B_{ij} \quad (2.3)$$

where c_{ij} depends exclusively on spatial configuration and number of barriers and B_{ij} depends on the spatial configuration of reaches and the dispersal capacity of the species. Both CCI and RCI range between 0 and 1. Catchments with higher CCI values have higher levels of longitudinal connectivity, meaning habitats are reachable more easily (Cote et al., 2009). Reaches with higher RCI are more reachable from other reaches in the catchment. CCI or RCI indices approaching 0 indicate a more fragmented riverscape.

2.1.3. Barriers fragmentation

Each barrier can be characterized with two passability parameters. The upstream and downstream passability (p^u and p^d , respectively) represent the probability that an organism crosses the barrier from downstream to upstream or from upstream to downstream. If the directionality of the system is ignored, the equivalent passability for the barrier m can be defined (Cote et al., 2009):

$$p_m^{eq} = p_m^u p_m^d \quad (2.4)$$

Alternatively, if the directionality of the system is considered, the equivalent passability of the barrier m can be defined as:

$$p_m^{eq} = \begin{cases} p_m^u & \text{if } m \text{ is crossed while moving upstream in the } i-j \text{ path} \\ p_m^d & \text{if } m \text{ is crossed while moving downstream in the } i-j \text{ path} \end{cases} \quad (2.5)$$

Based on the barriers equivalent passability, the Barrier Fragmentation Index (BFI) can be defined as the weighted sum of the passabilities of all the r barriers in the catchment (Jumani et al., 2022):

$$BFI = \sum_{m=1}^r (1 - p_m^{eq}) \frac{w_m}{W} \quad (2.6)$$

where w_m are the barriers weights. BFI ranges from 0 to 1, with higher values indicating higher fragmentation.

The combined passability of all the barriers in the subgraph connecting reaches i and j results from the aggregation of the equivalent passabilities of all the k barriers located in the path (Cote et al., 2009):

$$c_{ij} = \prod_{m=1}^k p_m^{eq} \quad (2.7)$$

2.1.4. Dispersal fragmentation

The contribution of species dispersal to the dispersal probability is a function of the distance between each pair of reaches. The effect of the directionality is accounted by calculating separately the dispersal for the fraction of the path between reaches i and j that proceeds upstream and downstream (d_{ij}^u and d_{ij}^d are the total distances travelled upstream and downstream, respectively). The dependence of B_{ij} from the distance can be expressed through a dispersal kernel (eqs. (2.8) and (2.10); Rodeles et al., 2021), or through a threshold on the distance (eqs. (2.9) and (2.11) Borthagaray et al., 2015). Asymmetric dispersal can be also accounted for (eqs. (2.10) and (2.11)):

$$B_{ij} = PD^{d_{ij}} \quad (2.8)$$

$$B_{ij} = \begin{cases} 1 & \text{when } d_{ij} < TR \\ 0 & \text{otherwise} \end{cases} \quad (2.9)$$

$$B_{ij} = PD_u^{d_{ij}^u} PD_d^{d_{ij}^d} \quad (2.10)$$

$$B_{ij} = \begin{cases} 1 & \text{when } d_{ij}^u < TR_u \text{ and } d_{ij}^d < TR_d \\ 0 & \text{otherwise} \end{cases} \quad (2.11)$$

where PD , PD_u and PD_d are the dispersal kernel parameters dependent on the mobility of the organism (closer to 1 for highly mobile organisms), and TR , TR_u and TR_d are the dispersal thresholds. A value of $PD_u = 0$ or $TR_u = 0$ corresponds to organisms that are passive drifters and cannot move upstream (e.g., Gasteropoda or Bivalva).

The distance d_{ij} can be both a geometric distance or a landscape-friction weighted distance. In the latter case, the inverse of the reach-scale habitat suitability score can be used as a multiplicative factor to simulate higher friction of the landscape (Inoue and Berg, 2017). Then the effective distance would coincide with the geometric distance only when the whole habitat of the reach is suitable (being bigger otherwise).

2.1.5. Barriers prioritization

Both CCI and RCI can be used to prioritize barriers based on the relative contribution to landscape fragmentation. A ‘leave one out’ approach is commonly used (Saura and Pascual-Hortal, 2007):

$$dCCI_m = \frac{CCI_{start,m} - CCI_{start}}{CCI_{start}} \cdot 100 \quad (2.12)$$

where CCI_{start} is the value of the index calculated with the current setup,

and $CCI_{start,m}$ is the value of the index calculated after removing the barrier m . An analogous index can be defined for RCI and BFI. Values of $dCCI_m$, $dRCI_m$, and $dBFI_m$ range between 0 (when the barrier m has no effect over fragmentation), and infinite (when the landscape is fully fragmented, $CCI = 0$, and all the landscape fragmentation can be attributed to m). Rankings for $dCCI_m$ and $dRCI_m$ can be used to select barriers based on the contribution to landscape fragmentation. The same approach can be used also to calculate the connectivity gain when a certain sequence of barriers is removed (in a ‘leave many out’ approach).

2.1.6. Comparison and integration with existing indices and software

The CCI can be easily parametrized to cover a wide array of already existing indices (Table 1). If the reach length is used as weights, no dispersal limitation is considered, and symmetric organisms movement, the Dendritic Connectivity Index is obtained (Cote et al., 2009). Using the reach area instead of the length yields the Probability of Connectivity index (Saura and Pascual-Hortal, 2007). Under the same settings, including the dispersal limitation term yields the Population Connectivity Index (Rodeles et al., 2021). Using the river/impoundment volume yields the River Fragmentation Index (Grill et al., 2015). Using binary dispersal probabilities (e.g. setting a distance threshold on dispersal and a binary barrier passability) yields the Integral Index of Connectivity (Saura and Pascual-Hortal, 2007). Using the stream order as nodes weights yields the Stream Continuity Index (Shao et al., 2020). Calculating RCI based on the catchment outlet yields the Breeding Habitat Connectivity Index for anadromous fish (Rodeles et al., 2019). Using the weighted suitable length as reach weight, imposing no constrain to biotic movement, and setting barriers passabilities to zero yields the Residual Core Length (Fuller et al., 2015). Recently proposed indices, such as the Catchment Area Fragmentation Index and the Catchment Area and Rainfall Fragmentation Index can be also calculated based on the BFI, specifying the upstream catchment area or annual rainfall as barrier weight (Jumani et al., 2022). Using upstream cumulative statistics as node weights can be facilitated by a wide array of software packages (e.g. the River Network Toolkit, Duarte et al., 2019). The graph-structure allows for the calculation of centrality metrics such as the betweenness centrality (Bodin and Saura, 2010) via routines implemented in the ‘igraph’ R package.

Other software packages provide graph-based calculations of connectivity index. For instance, CONEFOR (Bodin and Saura, 2010; Pascual-Hortal and Saura, 2006) implements several connectivity indices and habitat patches prioritization in directional landscapes but requires the explicit definition of the dispersal probabilities for cases different than simple dispersal kernels, while ‘riverconn’ allows for the automatic calculation of the dispersal probability. The software FIPEX (Oldford, 2020) allows for the calculation of the dendritic connectivity index, but it does not provide the possibility of defining the functional component of the dispersal probability, while ‘riverconn’ does.

2.2. ‘Riverconn’ package features

The ‘riverconn’ package relies on the functionalities of the ‘igraph’ package (Csardi and Nepusz, 2006). All ‘riverconn’ functions are designed to accept as input an ‘igraph’ object, which can be easily created in R either from a list of vertices and edges, from an adjacency matrix (Kolaczyk and Csárdi, 2014), or directly from a shapefile through the package ‘shp2graph’ (Lu et al., 2018). The ‘riverconn’ documentation shows a general workflow to generate an igraph object based on commonly available geospatial datasets. The function ‘set_graph_directionality’ assigns the directionality to the graph based on the outlet position.

The main function of the package is ‘index_calculation’ (Table 2), that calculates RCI, CCI, or BFI (equations (2.1), (2.2) and (2.6)) based on the input graph and its attributes under a variety of settings decided by the user. For instance, the functional and the structural connectivity terms can be selected or dropped from the calculations, the way

Table 1

Examples of connectivity indices that can be calculated with ‘riverconn’. Index type refers to the typologies introduced in this paper. CCI: Catchment Fragmentation Index, RFI: Reach Fragmentation Index, BFI: Barrier Fragmentation Index.

Index name	Reference	Index type	Weight	c_{ij}	B_{ij}
Dendritic Connectivity Index (DCI)	Cote et al. (2009)	CCI	Reach length	Symmetric passabilities	No
Population Connectivity Index (PCI)	Rodeles et al. (2021)	CCI	Reach length	Symmetric passabilities	Exponential symmetric dispersal kernel
Probability of Connectivity (PC)	Pascual-Hortal and Saura (2006)	CCI	Reach/Habitat Area	No	Exponential symmetric dispersal kernel
Integral Index of Connectivity (IIC)	Pascual-Hortal and Saura (2006)	CCI	Reach/Habitat area	No	Binary symmetric dispersal probabilities
Volume-based River Connectivity Index (RCIVOL)	Grill et al. (2014)	CCI	Reach volume	Symmetric passabilities	No
River Class Connectivity Index (RCI _{CLASS})	Grill et al. (2014)	CCI	Reach volume, unique reach classes	Symmetric passabilities	No
River Migration Connectivity Index (RCI _{RANGE})	Grill et al. (2014)	CCI	Potential number of migratory fish species	Symmetric passabilities	No
Stream Continuity Index (SCI)	Shao et al. (2020)	CCI	Stream order, reach length	Symmetric passabilities	No
Dendritic Connectivity Index for diadromous fish (DCID)	Cote et al. (2009)	RFI	Reach length	Symmetric passabilities	No
Breeding Area Connectivity Index (BACI)	Rodeles et al. (2019)	CCI	Habitat area	Binary passabilities	No
Residual Core Length (RCL)	Fuller et al. (2015)	CCI	Reach length	Binary passabilities	No
Catchment Area Fragmentation Index (CAFI)	Jumani et al. (2022)	BFI	Barrier upstream area	Symmetric passabilities	No
Catchment Area Rainfall Fragmentation Index (CARFI)	Jumani et al. (2022)	BFI	Barrier upstream precipitation	Symmetric passabilities	No

directionality is dealt with can be specified, the dispersal functions and related parametrizations can be defined. Functions that allow to separately calculate c_{ij} and B_{ij} are also exported from the package for diagnostic purposes ('c_ij_fun' for equation (2.6) and 'B_ij_fun' for equations 2.7 and 2.8-11). Network-based calculations (e.g. the identification of the shortest path between each pair of reaches) are performed using the highly efficient routines from the package 'dodgr' (Padgham, 2019). Even though the 'index_calculation' function was designed with the directed, loop-less graph in mind, different structures such as lattice-like networks can also be used.

The function 'd_index_calculation' calculates the improvement in the connectivity index when selected barriers are removed (equation (2.9)). The function 't_index_calculation' calculates the index change when the graph attributes are sequentially modified (e.g. to simulate some time dynamics). The functions 't_weights_sequencer' and 't_passability_sequencer' are provided to generate the metadata needed (temporal changes of nodes weights or barriers passabilities) based on simple objects of class data. frame.

The function 'd_index_calculation' can be resource-consuming for large networks. The calculation of the dCCI indices for the case study in this paper (network size: 650 reaches) took approximately 4 min on a single core of a laptop equipped with 11th Gen Intel Core i7, 3.30 GHz and 32 GB RAM. The option to parallelize calculations on multiple cores is also available.

2.3. Application of 'riverconn' to the Ebro river

We used the Ebro river (NE Iberian peninsula) as a case study for implementing the model. We used the HydroSHEDS river network for the Ebro catchment (Fig. 1; Lehner and Processes, 2013). To limit the size of the graph we retained only those sections of the river network having an upstream area greater than 100 km². We downloaded barriers shapefiles from the Confederación Hidrográfica del Ebro website (<https://www.chebro.es/>) and snapped (maximum snapping distance = 1 km) them to the pruned river network (Fig. 1). We inspected visually the results to ensure snapped barriers were retained in the proper sub-catchment. Due to the pruning of the network, 97 barriers out of the 224 in the inventory were retained for the analysis. Based on the river network and the barriers data, we generated a graph using the package

'igraph'. We included the length of each reach (units: 10 Km) and its elevation (obtained from a Digital Elevation Model and the 'elevatr' package, units: m a.m.s.l) as edges attributes. We set the upstream and downstream passabilities of barriers to 0.1 and 0.8, respectively, adding them to the graph as vertex attributes for those vertices categorized as barriers. We set the passability of confluences to 1. The size of the resulting graph was 650 edges (reaches). We used two univariate theoretical habitat suitability curves based on elevation of each reach to account for different species tolerances (Fig. 1). We defined habitat suitability scores for an organism preferring low elevation streams and for an organism preferring higher elevation streams. Finally, we used the habitat suitability scores to calculate the weighted useable length of each reach (edge; Fig. 1). A step-by-step tutorial is available at https://damianobaldan.github.io/riverconn_tutorial/.

We calculated the RCI each reach (function 'index_calculation'), and dCCI for each barrier (function 'd_index_calculation'). In the determination of the directionality for I_{ij} in RCI, we used outbound connections for each reach. Both outputs were used to prioritize reaches and dams for restoration. We interpret the RCI as the potential of each reach to act as dispersal source for the colonization of the river network: high-ranked reaches (rank one is the highest) have high potential for restoration. We interpret the dCCI as an index prioritizing those barriers whose removal or improvement would lead to highest increases in CCI. Thus, barriers that are ranked higher (rank one is the highest) yield higher improvements in catchment connectivity (Pascual-Hortal and Saura, 2006). We repeated both assessments for 8 different setups (Tables 1 and 3): (A) Dendritic connectivity index with symmetric dams passabilities; (B) Dendritic connectivity index with asymmetric dams passabilities; (C) Integral Index of connectivity (dams are not passable and a threshold on dispersal distance is used); (D) Integral Index of connectivity with uniform reach weights equal to one; (E) lowland species with active aquatic dispersal (fish), (F) upland species with active aquatic dispersal (fish); (G) lowland species with passive aquatic dispersal (invertebrate larval stage); (H) upland species with passive aquatic dispersal (invertebrate larval stage, bivalve). Additionally, for dCCI, we calculated also (I) Catchment area fragmentation index. We plotted the spatial distribution of reaches and barriers rankings, and compared the prioritization using Spearman's rank coefficient.

Table 2

Arguments of the function ‘index_calculation’. Refer to the package documentation for a full overview. Note: V = vertex attribute, E = edge attribute.

Input	Type	‘riverconn’ name	Description
river graph	-	graph	Input ‘igraph’ object
reach weight	V	weight	Graph vertex attribute to be used as w_i in eqs. (2.1) and (2.2)
nodes id	V	nodes_id	String that univocally identify each node
type of index	-	index_type	Defines if CCI or RCI is calculated
direction of RCI	-	index_mode	Defines if inbound or outbound links are used in RCI
c_{ij} calculation flag	-	c_ij_flag	Defines if the contribution of c_{ij} to CCI or RCI is calculated or not (eq. (2.3))
B_{ij} calculation flag	-	B_ij_flag	Defines if the contribution of B_{ij} to CCI or RCI is calculated or not (eq. (2.3))
c_{ij} directionality	-	dir_fragmentation_type	Defines how equivalent barriers passability is calculated (eq (2.4) or 2.5)
confluence passability	V	pass_confluence	Defines confluences passabilities
upstream barriers passability	V	pass_u	Defines upstream-to-downstream barriers passabilities
downstream barriers passability	V	pass_u	Defines downstream-to-upstream barriers passabilities
attribute used for distances	V	field_B	Graph’s vertex attribute used to be used as d_{ij} in eqs. (2.8) - (2.11)
B_{ij} directionality	-	dir_distance_type	Defines if directionality is accounted for in B_{ij} calculation (eqs. (2.8) - (2.11))
dispersal calculation mode	-	disp_type	Define if dispersal is calculated with exponential (eq. (2.8) or 2.10) or threshold (eq. (2.9) or 2.11) decay
dispersal parameter	-	param_u	Defines the upstream dispersal parameter PD_u in eq. (2.10) or 2.11
dispersal parameter	-	param_d	Defines the downstream dispersal parameter PD_d in eq. (2.10) or 2.11
dispersal parameter	-	param	Defines the dispersal parameter PD in eq. (2.8) or 2.9

3. Results

Obtained values for RCI range between $5 \cdot 10^{-5}$ and 0.38, with higher values for DCI-like indices, and lower values for PCI-like indices. The spatial distribution of RCI differs for the different setups (Fig. 2). The symmetric DCI setup is higher for reaches located in the downstream sections of the catchment (Fig. 2A), while the asymmetric setup has higher values for reaches located in the mid-to upstream sections (Fig. 2B). The IIC setup weights more reaches located in the main stem and in the main channels (Fig. 2C and D). The PCI setup for lowland fish has higher values for few sections in the main stem (Fig. 2E), while the setup for upland-preferring fish has higher values for headwater sections in the southern and northern parts of the catchment (Fig. 2F). The PCI setup for lowland-preferring passive drifter weights uniformly the downstream sections of the river (Fig. 2G), while the setup for the upland passive drifter weights more the headwaters (Fig. 2H).

Obtained values for CCI and BFI ranged between 0.005 and 0.29, with higher values for DCI-like indices and CAFI, and lower values for PCI-like indices. The spatial distribution of prioritized barriers varies

with the CCI index setup (Fig. 3). The DCI setups, both symmetric and asymmetric, assign high priorities to barriers located in the mid-section of the main stem of the Ebro river (Fig. 3A and B). The IIC setup prioritizes barriers located in the main stem (Fig. 3C), while the setup with uniform weights prioritizes more upstream barriers (Fig. 3D). The PCI setup for lowland-preferring fish has higher values for few sections in the main stem (Fig. 3E), while the setup for upland fish has higher values for headwater sections in the southern and northern parts of the catchment (Fig. 3F). The PCI setup for lowland-preferring passive drifter weights uniformly the downstream sections of the river (Fig. 3G), while the setup for the upland passive drifter weights more the headwaters (Fig. 3H). The CAFI prioritizes the most downstream barriers (Fig. 3I).

The correlation of both RCI and the barriers prioritization is highly variable. For RCI, the Spearman’s correlation ranges from negative values (-0.46 for scenarios E-H) to high congruence (0.89 for scenarios A-E, Fig. 4). For the barrier’s prioritization with dCCI, Spearman’s correlation ranges between low congruence (-0.15 for E-H) to high congruence (0.94 for A-E, Fig. 5). There seems to be a partial overlap between RCI and dCCI, as barriers located in reaches with higher RCI are also ranked higher in the prioritization.

4. Discussion

4.1. Use of the package for population ecology

Restoring river connectivity is increasingly considered as an option to improve the health of freshwater populations and the resilience of metapopulations (Tickner et al., 2020). Beneficial impacts of connectivity restoration have been documented for many fish species (Birnie-Gauvin et al., 2020; King et al., 2017; Sun et al., 2022). However, development of general connectivity-biota causal links to inform restoration planning is complicated because of species-specific dispersal and movement traits (Baldan et al., 2020). For instance, the response of organisms with limited mobility to increased connectivity might be limited. In this regard, the analysis of historical connectivity losses and the related effects on biota can be beneficial (Hall et al., 2011; Mattocks et al., 2017). Historic populations data can be reconstructed from public datasets (e.g. RivFishTIME, Carvajal-quintero et al., 2021), while qualitative methods can be used where data are not available (Duarte et al., 2022). Historic connectivity-biota relationships can be used to validate connectivity indices, especially when developed on neighbouring catchments with different degree of fragmentation. The establishment of connectivity-biota causal pathways and the validation of connectivity metrics can then be used to support population management (Schick and Lindley, 2007).

Functional and structural connectivity are influenced by seasonal to multiannual dynamics (Fullerton et al., 2010; Pont et al., 2015), including the spatial structure of the river network, orientation properties and modes of operation of barriers, species traits and spatiotemporal scales considered. Climate change can affect the structure of the mesohabitat and indirectly affect the dispersal potential of organisms (Baldan et al., 2021; Holyoak et al., 2020). Effects can be even more drastic in rivers experiencing intermittency (Datry et al., 2014; Jaeger et al., 2014). Thus, time-dependent estimates of connectivity indices might be needed to fully capture the dynamics of the system. If the relaxation time of the system (i.e. the time the system needs to reach steady state) is smaller than the time span considered (Castillo-Escrivà et al., 2020), the problem can be considered by a sequence of steady states, with the static equations implemented in ‘riverconn’ still adequate. In this case, connectivity indices can be calculated for each state of the system separately and synthetic indicators can be developed to represent the connectivity aspects (Cid et al., 2020). For highly dynamic systems such as small sized catchments and/or highly intermittent, different methodological approaches such as individual-based models or high-frequency monitoring (Pineda-Morante et al., 2022) might be needed to better capture spatial or temporal connectivity

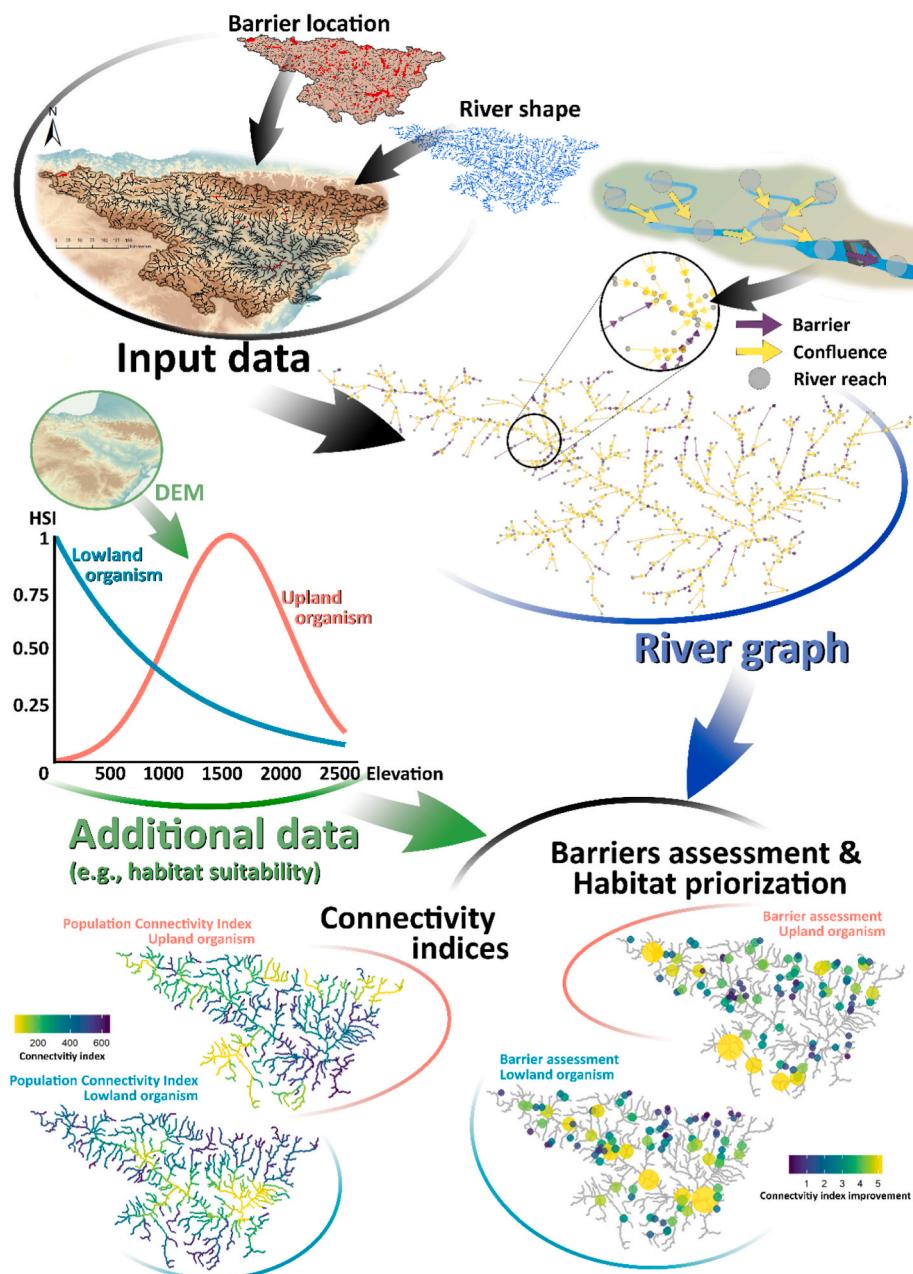


Fig. 1. Package workflow. DEM: Digital Elevation Model; HSI: Habitat Suitability Index.

patterns at the expense of higher data collection efforts and computational capacities. In these cases, connectivity patterns and barriers distribution might also be understood differently as fragmentation by drought can strongly vary in relation with river morphology, drought intensity or riffle and pool distribution (Cañedo-Argüelles et al., 2020; Sarrejane et al., 2017). The use of actual, observation-based, connectivity metrics can also be feasible for such smaller scales applications (Jumani et al., 2020).

The 'riverconn' package can be used for calculating several connectivity indices and their temporal development, and therefore can be of great support for population-level analyses. At the moment, 'riverconn' implements only equations for calculating estimates of longitudinal connectivity. However, other dimensions of connectivity exist (Cañedo-Argüelles et al., 2015; Grill et al., 2019; Tonkin et al., 2018): lateral connectivity (river - floodplains), vertical connectivity (groundwater-river-atmosphere), and temporal connectivity (constancy of the flow). The implementation of lateral and vertical connectivity would

require a modification of the base conceptualization of the river network as a directed loopless tree towards patch-based spatial graphs (Erős et al., 2012). Flow-related dependencies (the temporal connectivity aspect) could still be included in 'riverconn' by quantifying the reach- or meshohabitat-scale as a function of flow characteristics (Kakouei et al., 2018). In this regard, Indicators of Hydrological Alteration are a useful set of metrics to synthesize a wide range of hydrographs characteristics in scalar properties for spatial analyses (Olden and Poff, 2003).

4.2. Use of the package for community ecology

In fragmented landscapes, organism dispersal plays a key role in determining the local community structure (Borthagaray et al., 2015; Cañedo-Argüelles et al., 2015). Connectivity, defined as the degree to which the landscape facilitates the movement of individuals among habitat patches (Econo and Keitt, 2010; Uroy et al., 2021), is a key factor affecting dispersal. Connectivity, determined by landscape

Table 3
Scenarios definition.

Setup	Scenario name	Index acronym	Details	'd_index_calculation' setup in R ^a
A	Symmetric DCI	Dendritic Connectivity Index.	Node weights are reaches lengths.	B_ij_flag = FALSE
B	Asymmetric DCI	Dendritic Connectivity Index.	Node weights are reaches lengths. Asymmetric connectivity described in eqn. (2.5) is used.	B_ij_flag = FALSE, dir_fragmentation_type = "asymmetric"
C	IIC	Integral Index of Connectivity	Node weights are reaches lengths. A threshold of 30 km is used to calculate the dispersal probability (eq. (2.8)). Barriers passabilities are set to 0.	param = 3,disp_type = "threshold"
D	IIC with uniform weights	Integral Index of Connectivity with uniform weights	Reaches receive uniform weights (weight = 1). A threshold of 30 km is used to calculate the dispersal probability (eq. (2.8)). Barriers passabilities are set to 0.	param = 3,disp_type = "threshold"
E	PCI lowland fish	Population Connectivity Index	Nodes weights are the weighted useable length of each reach for the upland organism. Functional connectivity simulated with eqn. (2.7) setting a parameter of 0.8.	param = 0.8
F	PCI upland fish	Population Connectivity Index	Nodes weights are the weighted useable length of each reach for the lowland organism. Functional connectivity simulated with eqn. (2.7) setting a base of 0.8.	param = 0.8
G				

Table 3 (continued)

Setup	Scenario name	Index acronym	Details	'd_index_calculation' setup in R ^a
	PCI lowland passive	Population Connectivity Index	Nodes weights are the weighted useable length of each reach for the upland organism. Functional connectivity simulated with eqn. (2.8) setting a threshold of 30 km on the downstream dispersal and 0 km for upstream dispersal.	dir_distance_type = "asymmetric", disp_type = "threshold", param_u = 0, param_d = 3
H	PCI upland passive	Population Connectivity Index	Nodes weights are the weighted useable length of each reach for the lowland-preferring organism. Functional connectivity simulated with eqn. (2.8) setting a threshold of 30 km on the downstream dispersal and 0 km for upstream dispersal.	dir_distance_type = "asymmetric", disp_type = "threshold", param_u = 0, param_d = 3

^a Parameters that are not specified are assigned their default values. Additionally, for the function 'index_calculation', the following setup was added: index_type = "reach", index_mode = "from".

structure (i.e. the spatial arrangement of communities) and species' dispersal strategies is widely used to assess communities' isolation (Borthagaray et al., 2020; Horváth et al., 2019; Pineda-Morante et al., 2022). Accordingly, metacommunity theory predicts local richness and diversity to be highly influenced by the degree of isolation of the community (Heino et al., 2015; Tonkin et al., 2018). Landscape fragmentation is a factor influencing the structuring of freshwater communities (Díaz et al., 2021; Horváth et al., 2019; Perkin and Gido, 2012). Thus, deriving metrics describing communities centrality and isolation is a key task in current community ecology (Pineda-Morante et al., 2022). Recent development allowed to account for the directional and dendritic nature of the river network (Peterson et al., 2013), but still much work is needed to include longitudinal barriers indices as spatial covariates of aquatic communities (Wang et al., 2019). The RCI can be computed for each reach where community data is available and can be used as a predictor in multivariate community analysis. The effect of fragmentation on biotic communities is expected to be mediated by the spatial scales and extents analyzed (Mahlum et al., 2014). Furthermore, the use of such metrics could complement spatial covariates based on Euclidean distance, river-based distance, and flow connected distance (Ver Hoef and Erin, 2010) in a variance-partitioning algorithm to quantify the

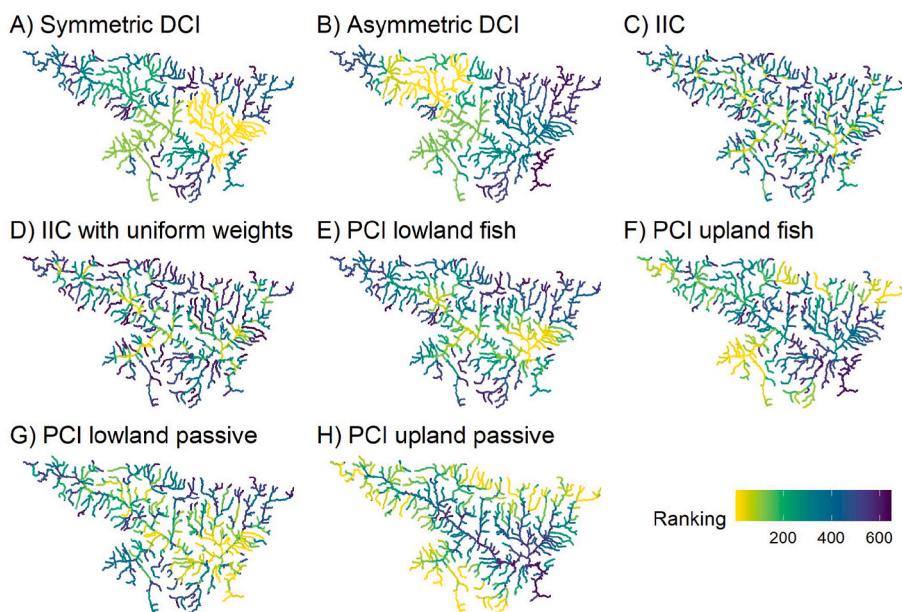


Fig. 2. Different versions of the reach connectivity index for the Ebro catchment. Refer to [Tables 1](#) and [3](#) for details on the setup of the index_calculation function. DCI: Dendritic Connectivity Index; IIC: Integral Index of Connectivity; PCI: Population Connectivity Index.

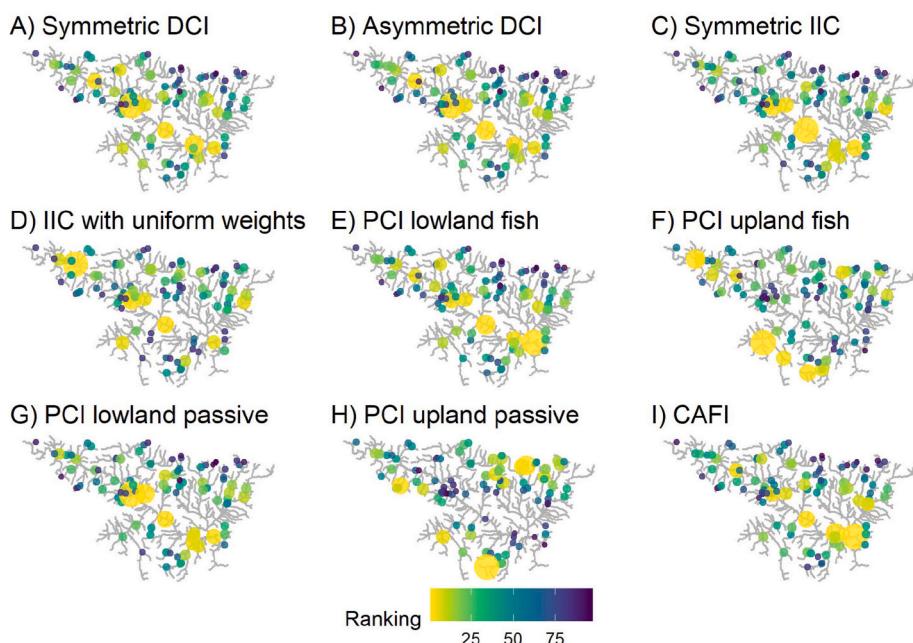


Fig. 3. Different versions of the barriers prioritization for the Ebro catchment. Higher ranking indicates a greater improvement of connectivity if the barrier is removed. Refer to [Tables 1](#) and [3](#) for details on the setup of the d_index_calculation function. The size of the points in the figure is also proportional to barriers ranking. DCI: Dendritic Connectivity Index; IIC: Integral Index of Connectivity; PCI: Population Connectivity Index; CAFI: Catchment Area Connectivity Index.

effect of longitudinal fragmentation on biotic communities and beta-diversity ([Cañedo-Argüelles et al., 2020](#); [Schmera et al., 2018](#)). Consequently, the implementation of connectivity indices for community level studies would contribute to better quantify barrier impacts at higher organizational levels and across different organisms.

4.3. Use of the package to support riverscape planning

Our results show how the use of different connectivity indices based on different assumptions on the calculation of structural and functional connectivity can lead to diverse outcomes in the prioritization of reaches

and barriers. The reaches prioritization based on the DCI has higher values for section of the catchment where few barriers exist, located more upstream when directionality is accounted for. Accordingly, barriers whose removal would increase the connected length are prioritized ([Jumani et al., 2022](#)). The DCI is length-based, and therefore it is supposed to be sensitive to the river network cropping. Therefore, the cropping of the headwater reaches might result in overlooking the connectedness of the headwaters to the river network. The CAFI partially solves this issue by using area-based weights, less sensitive to river network delineation ([Jumani et al., 2022](#)). However, CAFI is not a network based index, thus it might neglect interactions between barriers

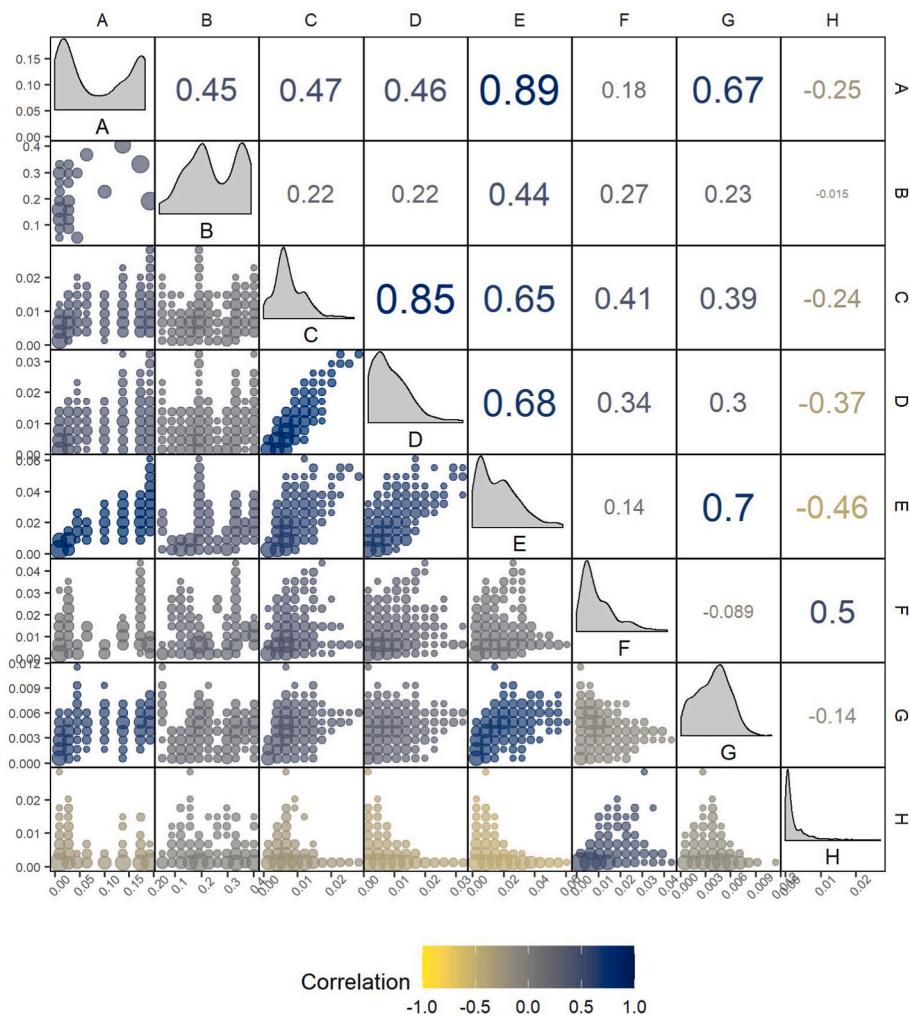


Fig. 4. Spearman's correlation diagram for the different versions of the reach connectivity index in the Ebro river. See Table 1 for the definition of the setups (Letters A-H).

placement that are accounted for in DCI and PCI (Cote et al., 2009; Rodeles et al., 2021).

The package 'riverconn', can explicitly consider the assumptions underlying the definition of each connectivity index, improving the transparency of the prioritization process. Multi-criteria analysis has the potential to generate compromise indices based on a large set of indices calculated under different setups. Further, optimization algorithms can be used to identify optimal barriers or habitat improvement sequences under economic constraints (King et al., 2017; O'Hanley, 2011).

The functions implemented in 'riverconn' can be used to support the delineation of relevant sub-catchments for conservation planning (Moilanen et al., 2008). Methods for prioritizing sub-catchment for freshwater biodiversity conservation based on optimization algorithms deal with connectivity with simplistic approaches, such as distance penalties (Beger et al., 2010), or the unobstructed distance upstream a barrier (McManamay et al., 2019). Modeling frameworks that include graph-based connectivity were recently proposed (Erős et al., 2018). The use of a wide array of connectivity indices can better incorporate multiple connectivity facets into freshwater conservation planning by explicitly including in the models organism-specific dispersal traits (Rodeles et al., 2021).

Planning and implementation of conservation actions such as habitat improvement is also carried out at the meso-habitat scale (1–100 m, Wegscheider et al., 2020). In our graph-based conceptualization of the river network, we defined a node as a whole reach. This definition allows to consider only attributes averaged over a reach and might not be

enough when the analysis seeks to follow restoration actions occurring at finer scales. However, any reach of interest could be further split in a sequence of nodes, corresponding to sequences of different mesohabitats (Erős et al., 2012). Therefore, 'riverconn' conceptualization of the river can be adapted to the specific study case and scale, allowing for fragmentation assessments by explicitly considering different scales. For instance, first a broad assessment can be conducted at the catchment scale, then a detailed analysis on a smaller area of interest (for instance, a dammed reach and the surrounding floodplains) can be performed (Erős et al., 2012).

5. Conclusions

In this paper we re-conceptualized many indices used to assess river network fragmentation under a unifying framework and we presented an R package, 'riverconn', that allows for the calculation of such indices based on a graph-based landscape conceptualization and widely available geospatial data. Functions implemented in the package can support, among others, (i) conservation planning via the identification and prioritization of barriers and habitats for connectivity improvement at the catchment scale, (ii) population ecology via the possibility to analyze historic patterns of fragmentation, and (iii) community ecology, offering the possibility to generate barriers-dependent spatial covariates for community analysis.

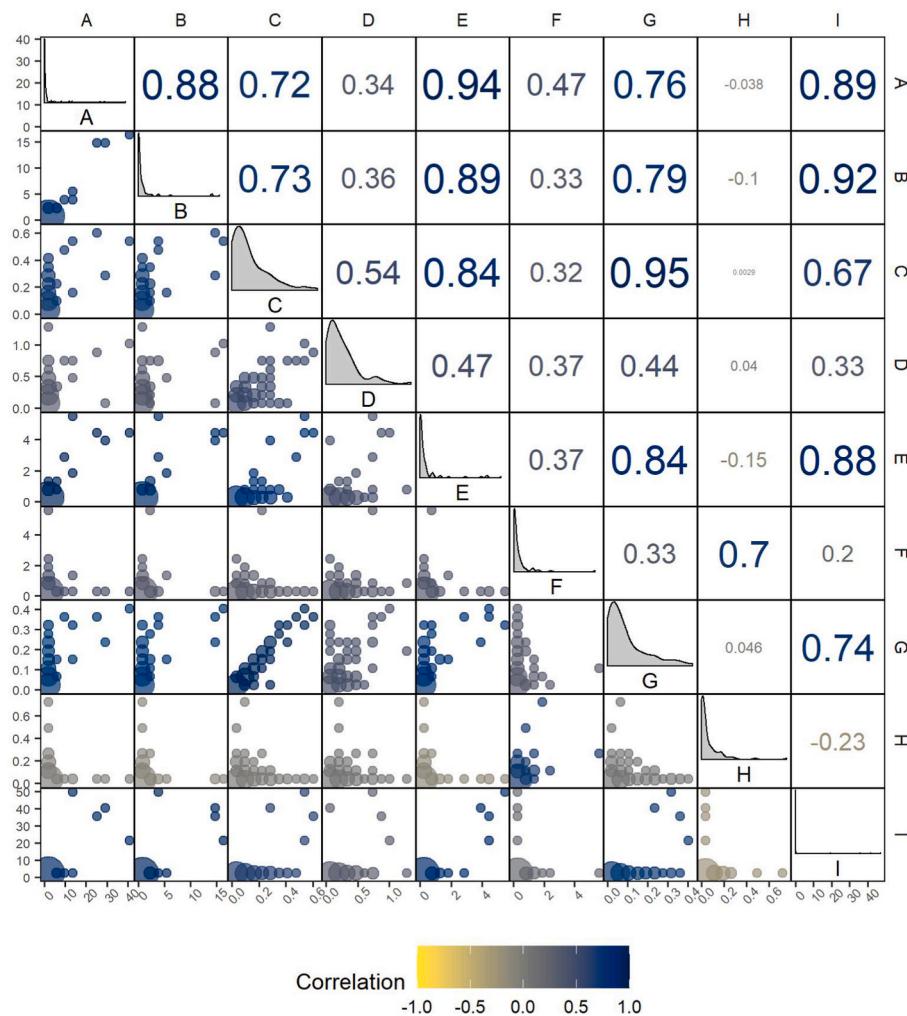


Fig. 5. Spearman's correlation diagram for the different versions of the barriers prioritization in the Ebro river. See Table 1 for the definition of the setups (Letters A-I).

Software availability

Name of the software: riverconn.
 Developer: Damiano Baldan [aut, cre], David Cunillera-Montcusí [ctb], Andrea Funk [ctb].
 Contact information: damiano.baldan91@gmail.com.
 Year first available: 2022.
 Program language: R.
 Cost: free;
 Software availability: <https://CRAN.R-project.org/package=riverconn> (last stable version); <https://github.com/damianobaldan/riverconn> (development version);
 Program size: 1.93 MB.

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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References

- Altermatt, F., 2013. Diversity in riverine metacommunities: a network perspective. *Aquat. Ecol.* 47, 365–377.
- Araujo, C.V.M., Silva, D.C.V.R., Gomes, L.E.T., Acayaba, R.D., Montagner, C.C., Moreira-Santos, M., Ribeiro, R., Pompeu, M.L.M., 2018. Habitat fragmentation caused by contaminants: atrazine as a chemical barrier isolating fish populations. *Chemosphere* 193, 24–31.
- Baldan, D., Kiesel, J., Hauer, C., Jähnig, S.C., Hein, T., 2021. Increased sediment deposition triggered by climate change impacts freshwater pearl mussel habitats and metapopulations. *J. Appl. Ecol.* 58, 1933–1944. <https://doi.org/10.1111/1365-2664.13940>.
- Baldan, D., Piniewski, M., Funk, A., Gumpinger, C., Flödl, P., Höfer, S., Hauer, C., Hein, T., 2020. A multi-scale, integrative modeling framework for setting conservation priorities at the catchment scale for the Freshwater Pearl Mussel *Margaritifera margaritifera*. *Sci. Total Environ.* 718 <https://doi.org/10.1016/j.scitotenv.2020.137369>.
- Barbarossa, V., Schmitt, R.J.P., Huijbregts, M.A.J., Zarfl, C., King, H., Schipper, A.M., 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proc. Natl. Acad. Sci. U.S.A.* 117, 3648–3655. <https://doi.org/10.1073/pnas.1912776117>.
- Baumgartner, L.J., Marsden, T., Duffy, D., Horta, A., Ning, N., 2022. Optimizing efforts to restore aquatic ecosystem connectivity requires thinking beyond large dams. *Environ. Res. Lett.* 17, 014008 <https://doi.org/10.1088/1748-9326/ac40b0>.

- Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., Possingham, H.P., 2010. Incorporating asymmetric connectivity into spatial decision making for conservation. *Conserv. Lett.* 3, 359–368. <https://doi.org/10.1111/j.1755-263X.2010.00123.x>.
- Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhusen, A., Birnie-Gauvin, K., Bussetti, M., Caroli, M., Consuegra, S., Döpico, E., Feierfeil, T., Fernández, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P.E., Kemp, P., Kerr, J., King, J., Lapińska, M., Lázaro, G., Lucas, M.C., Marcello, L., Martin, P., McGinnity, P., O'Hanley, J., Olivo del Amo, R., Parasiwicz, P., Pusch, M., Rincon, G., Rodriguez, C., Royte, J., Schneider, C.T., Tummers, J.S., Vallesi, S., Vowles, A., Verspoor, E., Wanningen, H., Wantzen, K.M., Wildman, L., Zalewski, M., 2020. More than one million barriers fragment Europe's rivers. *Nature* 588, 436–441. <https://doi.org/10.1038/s41586-020-3005-2>.
- Birnie-Gauvin, K., Nielsen, J., Frandsen, S.B., Olsen, H.M., Aarestrup, K., 2020. Catchment-scale effects of river fragmentation: a case study on restoring connectivity. *J. Environ. Manag.* 264 <https://doi.org/10.1016/j.jenvman.2020.110408>.
- Birnie-Gauvin, K., Aarestrup, K., Riis, T.M.O., Jepsen, N., Koed, A., 2017. Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers, and its implications for management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 27, 1345–1349.
- Böck, K., Polt, R., Schüttling, L., 2018. Ecosystem services in river landscapes. In: *Riverine Ecosystem Management*. Springer, Cham, pp. 413–433.
- Bodin, Ö., Saura, S., 2010. Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. *Ecol. Model.* 221, 2393–2405.
- Borthagaray, A.I., Berazategui, M., Arim, M., 2015. Disentangling the effects of local and regional processes on biodiversity patterns through taxon-contingent metacommunity network analysis. *Oikos* 124, 1383–1390. <https://doi.org/10.1111/oik.01317>.
- Borthagaray, A.I., Teixeira-de Mello, F., Tesitore, G., Ortiz, E., Illarze, M., Pinelli, V., Urtado, L., Raftopoulos, P., González-Bergonzoni, I., Abades, S., Loureiro, M., Arim, M., 2020. Community isolation drives lower fish biomass and species richness, but higher functional evenness, in a river metacommunity. *Freshw. Biol.* 65, 2081–2095. <https://doi.org/10.1111/fwb.13603>.
- Branco, P., Segurado, P., Santos, J.M., Ferreira, M.T., 2014. Prioritizing barrier removal to improve functional connectivity of rivers. *J. Appl. Ecol.* 51, 1197–1206. <https://doi.org/10.1111/1365-2664.12317>.
- Brederveld, R.J., Jähnig, S.C., Lorenz, A.W., Brunzel, S., Soons, M.B., 2011. Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *J. Appl. Ecol.* 48, 1241–1250. <https://doi.org/10.1111/j.1365-2664.2011.02026.x>.
- Buddendorf, W.B., Jackson, F.L., Malcolm, I.A., Millidine, K.J., Geris, J., Wilkinson, M.E., Soulsby, C., 2019. Integration of juvenile habitat quality and river connectivity models to understand and prioritise the management of barriers for Atlantic salmon populations across spatial scales. *Sci. Total Environ.* 655, 557–566. <https://doi.org/10.1016/j.scitotenv.2018.11.263>.
- Campbell Grant, E.H., Lowe, W.H., Fagan, W.F., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett.* 10, 165–175. <https://doi.org/10.1111/j.1461-0248.2006.01007.x>.
- Cañedo-Argüelles, M., Boersma, K.S., Bogan, M.T., Olden, J.D., Phillipsen, I., Schriever, T.A., Lytle, D.A., 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. *J. Biogeogr.* 42, 778–790. <https://doi.org/10.1111/jbi.12457>.
- Cañedo-Argüelles, M., Boersma, K.S., Bogan, M.T., Olden, J.D., Phillipsen, I., Schriever, T.A., Lytle, D.A., 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. *J. Biogeogr.* 42, 778–790.
- Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., Munné, A., Miríria, C., Pimentão, A.R., Sarremejane, R., 2020. As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *J. Biogeogr.* 47, 1861–1874.
- Carvajal-quintero, L.C.J., Tedesco, P.A., Giam, X., Brose, U., Erös, T., Filipe, A.F., Fortin, M., Irving, K., Jacquet, C., Larsen, S., Sharma, S., Ruhi, A., Becker, F.G., Casatti, L., Castaldelli, G., Stephen, R.B.D., Nathan, R.D., Anna, E.G., Keith, G., Luz, B.G., Leitão, R.P., McLarney, B., Meador, J., Milardi, M., Moffatt, D.B., Occhi, T.V.T., Pompeu, P.S., Propst, D.L., Pyron, M., Salvador, G.N., Stefferud, J.A., Sutela, T., 2021. RivFishTIME : a global database of fish time-series to study global change ecology in riverine systems. <https://doi.org/10.1111/geb.13210>, 38–50.
- Castillo-Escrivà, A., Mesquita-Joanes, F., Rueda, J., 2020. Effects of the temporal scale of observation on the analysis of aquatic invertebrate metacommunities. *Front. Ecol. Evol.* 8, 1–12. <https://doi.org/10.3389/fevo.2020.561838>.
- Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Cabot, J., Sarremejane, R., Soininen, J., Stubbington, R., Datry, T., 2020. A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *Bioscience* 70, 427–438. <https://doi.org/10.1093/biosci/biaa033>.
- Cote, D., Kehler, D.G., Bourne, C., Wiersma, Y.F., 2009. A new measure of longitudinal connectivity for stream networks. *Landsc. Ecol.* 24, 101–113. <https://doi.org/10.1007/s10980-008-9283-y>.
- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. *InterJournal, complex Syst.* 1695, 1–9.
- Datry, T., Larned, S.T., Tockner, K., 2014. Intermittent rivers: a challenge for freshwater ecology. *Bioscience* 64, 229–235.
- Díaz, G., Górski, K., Heino, J., Arriagada, P., Link, O., Habit, E., 2021. The longest fragment drives fish beta diversity in fragmented river networks: implications for river management and conservation. *Sci. Total Environ.* 766, 144323. <https://doi.org/10.1016/j.scitotenv.2020.144323>.
- Duarte, G., Branco, P., Haidvogl, G., Ferreira, M.T., Pont, D., Segurado, P., 2022. iPODfish – a new method to infer the historical occurrence of diadromous fish species along river networks. *Sci. Total Environ.* 812 <https://doi.org/10.1016/j.scitotenv.2021.152437>.
- Duarte, G., Segurado, P., Haidvogl, G., Pont, D., Ferreira, M.T., Branco, P., 2021. Damn those damn dams: fluvial longitudinal connectivity impairment for European diadromous fish throughout the 20th century. *Sci. Total Environ.* 761, 143293. <https://doi.org/10.1016/j.scitotenv.2020.143293>.
- Duarte, G., Segurado, P., Oliveira, T., Haidvogl, G., Pont, D., Ferreira, M.T., Branco, P., 2019. The river network toolkit-RivTool. *Ecography* 42, 549–557.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev. Camb. Phil. Soc.* 81, 163–182. <https://doi.org/10.1017/S1464793105006950>.
- Economou, E.P., Keitt, T.H., 2010. Network isolation and local diversity in neutral metacommunities. *Oikos* 119, 1355–1363. <https://doi.org/10.1111/j.1600-0706.2010.18272.x>.
- Erős, T., O'Hanley, J.R., Czegledi, I., 2018. A unified model for optimizing riverscape conservation. *J. Appl. Ecol.* 55, 1871–1883. <https://doi.org/10.1111/1365-2664.13142>.
- Erős, T., Olden, J.D., Schick, R.S., Schmera, D., Fortin, M.J., 2012. Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landsc. Ecol.* 27, 303–317. <https://doi.org/10.1007/s10980-011-9659-2>.
- Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83, 3243–3249.
- Fuller, M.R., Doyle, M.W., Strayer, D.L., 2015. Causes and consequences of habitat fragmentation in river networks. *Ann. N. Y. Acad. Sci.* 1355, 31–51.
- Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J., Sanderson, B.L., 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshw. Biol.* 55, 2215–2237. <https://doi.org/10.1111/j.1365-2427.2010.02448.x>.
- Grill, G., Dallaire, C.O., Chouinard, E.F., Sindorf, N., Lehner, B., 2014. Development of new indicators to evaluate river fragmentation and flow regulation at large scales: a case study for the Mekong River Basin. *Ecol. Indicat.* 45, 148–159.
- Grill, G., Lehner, B., Lumsdon, A.E., Macdonald, G.K., Zarfl, C., Reidy Liermann, C., 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environ. Res. Lett.* 10 <https://doi.org/10.1088/1748-9326/10/1/015001>.
- Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P., H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. *Nature* 569, 215–221. <https://doi.org/10.1038/s41586-019-1111-9>.
- Hall, C.J., Jordaan, A., Frisk, M.G., 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. *Landsc. Ecol.* 26, 95–107. <https://doi.org/10.1007/s10980-010-9539-1>.
- He, F., Thieme, M., Zarfl, C., Grill, G., Lehner, B., Hogan, Z., Tockner, K., Jähnig, S.C., 2021. Impacts of loss of free-flowing rivers on global freshwater megafauna. *Biol. Conserv.* 263, 109335.
- Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. <https://doi.org/10.1111/fwb.12533>.
- Holyoak, M., Caspi, T., Redosh, L.W., 2020. Integrating disturbance, seasonality, multi-year temporal dynamics, and dormancy into the dynamics and conservation of metacommunities. *Front. Ecol. Evol.* 8, 1–17. <https://doi.org/10.3389/fevo.2020.571130>.
- Horváth, Z., Ptácník, R., Vad, C.F., Chase, J.M., 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecol. Lett.* 22, 1019–1027. <https://doi.org/10.1111/ele.13260>.
- Inoue, K., Berg, D.J., 2017. Predicting the effects of climate change on population connectivity and genetic diversity of an imperiled freshwater mussel, Cumberlandia monodonta (Bivalvia: margariferidae), in riverine systems. *Global Change Biol.* 23, 94–107. <https://doi.org/10.1111/gcb.13369>.
- Jaeger, K.L., Olden, J.D., Pellant, N.A., 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13894–13899. <https://doi.org/10.1073/pnas.1320890111>.
- Jumani, S., Deitch, M.J., Kaplan, D., Anderson, E.P., Krishnaswamy, J., Lecours, V., Whiles, M.R., 2020. River fragmentation and flow alteration metrics: a review of methods and directions for future research. *Environ. Res. Lett.* 15 <https://doi.org/10.1088/1748-9326/abc37>.
- Jumani, S., Deitch, M.J., Valle, D., Machado, S., Lecours, V., Kaplan, D., Krishnaswamy, J., Howard, J., 2022. A new index to quantify longitudinal river fragmentation : conservation and management implications. *Ecol. Indicat.* 136, 108680. <https://doi.org/10.1016/j.ecolind.2022.108680>.
- Kakouei, K., Kiesel, J., Domisch, S., Irving, K.S., Jähnig, S.C., Kail, J., 2018. Projected effects of Climate-change-induced flow alterations on stream macroinvertebrate abundances. *Ecol. Evol.* 8, 3393–3409. <https://doi.org/10.1002/ece3.3907>.
- King, S., O'Hanley, J.R., Newbold, L.R., Kemp, P.S., Diebel, M.W., 2017. A toolkit for optimizing fish passage barrier mitigation actions. *J. Appl. Ecol.* 54, 599–611. <https://doi.org/10.1111/1365-2664.12706>.

- Kolaczyk, E.D., Csárdi, G., 2014. *Statistical Analysis of Network Data with R*. Springer.
- Lehner, B., Processes, G.G.-H., 2013. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. undefined, 2013, 27. Wiley Online Libr, pp. 2171–2186. <https://doi.org/10.1002/hyp.9740>.
- Liu, B., Sun, H., Harris, P., Xu, M., Charlton, M., 2018. Shp2graph: tools to convert a spatial network into an igraph graph in r. *ISPRS Int. J. Geo-Inf.* 7, 293.
- Mahlum, S., Kehler, D., Cote, D., Wiersma, Y.F., Stanfield, L., 2014. Assessing the biological relevance of aquatic connectivity to stream fish communities. *Can. J. Fish. Aquat. Sci.* 71, 1852–1863.
- Mattocks, S., Hall, C.J., Jordaan, A., 2017. Damming, lost connectivity, and the historical role of anadromous fish in freshwater ecosystem dynamics. *Bioscience* 67, 713–728. <https://doi.org/10.1093/biosci/bix069>.
- McManamay, R.A., Perkin, J.S., Jager, H.I., 2019. Commonalities in stream connectivity restoration alternatives: an attempt to simplify barrier removal optimization. *Ecosphere* 10. <https://doi.org/10.1002/ecs2.2596>.
- Moilanen, A., Leathwick, J., Elith, J., 2008. A method for spatial freshwater conservation prioritization. *Freshw. Biol.* 53, 577–592. <https://doi.org/10.1111/j.1365-2427.2007.01906.x>.
- Monaghan, M.T., Robinson, C.T., Spaak, P., Ward, J.V., 2005. Macroinvertebrate diversity in fragmented Alpine streams: implications for freshwater conservation. *Aquat. Sci.* 67, 454–464. <https://doi.org/10.1007/s00027-005-0787-0>.
- O'Hanley, J.R., 2011. Open rivers: barrier removal planning and the restoration of free-flowing rivers. *J. Environ. Manag.* 92, 3112–3120. <https://doi.org/10.1016/j.jenvman.2011.07.027>.
- Olden, J.D., Poff, N.L., 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Res. Appl.* 19, 101–121. <https://doi.org/10.1002/rra.700>.
- Oldford, G.L., 2020. *The Fish Passage Extension (FIPEx) with Dendritic Connectivity Index (DCI) for ArcGIS 10.4+ User Manual*. Nova Scotia, Halifax.
- Padgham, M., 2019. *Dodgr: an r package for network flow aggregation*. Findings 6945.
- Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: towards the prioritization of habitat patches and corridors for conservation. *Landsc. Ecol.* 21, 959–967. <https://doi.org/10.1007/s10980-006-0013-z>.
- Perkin, J.S., Gido, K.B., 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecol. Appl.* 22, 2176–2187. <https://doi.org/10.1890/12-0318.1>.
- Peterson, E.E., Ver Hoef, J.M., Isaak, D.J., Falk, J.A., Fortin, M.J., Jordan, C.E., McNyset, K., Monestiez, P., Ruesch, A.S., Sengupta, A., Som, N., Steel, E.A., Theobald, D.M., Torgersen, C.E., Wenger, S.J., 2013. Modelling dendritic ecological networks in space: an integrated network perspective. *Ecol. Lett.* 16, 707–719. <https://doi.org/10.1111/ele.12084>.
- Pineda-Morante, D., Fernández-Calero, J.M., Pösterl, S., Cunillera-Montcusí, D., Bonada, N., Cañedo-Argüelles, M., 2022. Local hydrological conditions and spatial connectivity shape invertebrate communities after rewetting in temporary rivers. *Hydrobiologia* 849, 1511–1530. <https://doi.org/10.1007/s10750-022-04799-8>.
- Pont, D., Logez, M., Carrel, G., Rogers, C., Haidvogl, G., 2015. Historical change in fish species distribution: shifting reference conditions and global warming effects. *Aquat. Sci.* 77, 441–453. <https://doi.org/10.1007/s00027-014-0386-z>.
- Rodeles, A.A., Galicia, D., Miranda, R., 2021. A simple method to assess the fragmentation of freshwater fish meta-populations: implications for river management and conservation. *Ecol. Indicat.* 125, 107557 <https://doi.org/10.1016/j.ecolind.2021.107557>.
- Rodeles, A.A., Leunda, P.M., Elso, J., Ardaiz, J., Galicia, D., Miranda, R., 2019. Consideration of habitat quality in a river connectivity index for anadromous fishes. *Int. Waters* 9, 278–288. <https://doi.org/10.1080/20442041.2018.1544817>.
- Sarreméjane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., Bonada, N., 2017. Do metacommunities vary through time? Intermittent rivers as model systems. *J. Biogeogr.* 44, 2752–2763. <https://doi.org/10.1111/jbi.13077>.
- Saura, S., Bodin, Ö., Fortin, M.J., 2014. EDITOR'S choice: stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J. Appl. Ecol.* 51, 171–182. <https://doi.org/10.1111/1365-2664.12179>.
- Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landsc. Urban Plann.* 83, 91–103. <https://doi.org/10.1016/j.landurbplan.2007.03.005>.
- Schick, R.S., Lindley, S.T., 2007. Directed connectivity among fish populations in a riverine network. *J. Appl. Ecol.* 44, 1116–1126. <https://doi.org/10.1111/j.1365-2664.2007.01383.x>.
- Schmera, D., Árva, D., Boda, P., Bódó, E., Bolgovics, Á., Borics, G., Csercsa, A., Deák, C., Krasznai, E., Lukács, B.A., Mauchart, P., Móra, A., Sály, P., Specziár, A., Sűveges, K., Szivák, I., Takács, P., Tóth, M., Várbíró, G., Vojtkó, A.E., Erős, T., 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* 63, 74–85. <https://doi.org/10.1111/fwb.12973>.
- Shao, X., Fang, Y., Cui, B., 2020. A model to evaluate spatiotemporal variations of hydrological connectivity on a basin-scale complex river network with intensive human activity. *Sci. Total Environ.* 723, 138051 <https://doi.org/10.1016/j.scitotenv.2020.138051>.
- Sun, J., Tummers, J.S., Galib, S.M., Lucas, M.C., 2022. Science of the Total Environment Fish community and abundance response to improved connectivity and more natural hydromorphology in a post-industrial subcatchment. *Sci. Total Environ.* 802, 149720 <https://doi.org/10.1016/j.scitotenv.2021.149720>.
- Tachet, H., Richoux, P.H., Bournaud, M., Usseglio-Polatera, P., 2000. *Invertébrés D'eau Douce. Systématique*, vol. 588. Biol. écologie. CNRS éditions, Paris.
- Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *Bioscience* 70, 330–342.
- Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., 2018. The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshw. Biol.* 63, 141–163. <https://doi.org/10.1111/fwb.13037>.
- Uroy, L., Alignier, A., Mony, C., Foltête, J.C., Ernoult, A., 2021. How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. *Landsc. Ecol.* 36, 2487–2504. <https://doi.org/10.1007/s10980-021-01277-9>.
- van Puijenbroek, P.J.T.M., Buijse, A.D., Kraak, M.H.S., Verdonschot, P.F.M., 2019. Species and river specific effects of river fragmentation on European anadromous fish species. *River Res. Appl.* 35, 68–77. <https://doi.org/10.1002/rra.3386>.
- Ver Hoef, J.M., Erin, E.P., 2010. A moving average approach for spatial statistical models of stream networks. *J. Am. Stat. Assoc.* 105, 6–18. <https://doi.org/10.1198/jasa.2009.ap08248>.
- Voutsas, V., Battaglia, D., Bracken, L.J., Brovelli, A., Costescu, J., Díaz Muñoz, M., Fath, B. D., Funk, A., Guiro, M., Hein, T., Kerschner, C., Kimmich, C., Lima, V., Messé, A., Parsons, A.J., Perez, J., Pöppel, R., Prell, C., Recinos, S., Shi, Y., Tiwari, S., Turnbull, L., Wainwright, J., Waxenecker, H., Hütt, M.T., 2021. Two classes of functional connectivity in dynamical processes in networks. *J. R. Soc. Interface* 18, <https://doi.org/10.1098/rsif.2021.0486>.
- Wang, J., Ding, L., Tao, J., Ding, C., He, D., 2019. The effects of dams on macroinvertebrates: global trends and insights. *River Res. Appl.* 35, 702–713.
- Wegscheider, B., Linnansäri, T., Curry, R.A., 2020. Mesohabitat modelling in fish ecology: a global synthesis. *Fish Fish.* 21, 927–939. <https://doi.org/10.1111/faf.12477>.
- Yi, Y., Cheng, X., Yang, Z., Wieprecht, S., Zhang, S., Wu, Y., 2017. Evaluating the ecological influence of hydraulic projects: a review of aquatic habitat suitability models. *Renew. Sustain. Energy Rev.* 68, 748–762. <https://doi.org/10.1016/j.rser.2016.09.138>.