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Connectivity as a driver of river-floodplain functioning: A dynamic, graph theoretic approach

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A B S T R A C T

Connectivity is a crucial property of the river-floodplain ecosystem. Reduction of connectivity, fragmentation and isolation effects, impacting ecological functions and biodiversity, is one of the most critical threats to floodplain systems. We use a graph theoretical approach for analyzing possible transport pathways in the system (directed, undirected, overland, seepage) and relate them to ecosystem functions in a river-floodplain system impacted by engineering structures (Danube River, Vienna, Austria). We studied essential ecological functions using indicators on sediment composition and quality, hydrochemical conditions, and macrophyte coverage. Our results indicate that sediment transport and composition are widely driven by directional flow and connectivity. In contrast, the exchange of water and nutrients is dominated by seepage exchange in the system. Macrophytes are dominating in water bodies which are not relevant for directed transport. The graph theoretical approach solely based on remotely sensed data can be used to classify floodplain water bodies related to their essential function and importance in the network and identify main deficits and potential restoration measures. It can, therefore, be an essential tool for prioritizing systems for management measures and restoration actions.

1. Introduction

Connectivity is a crucial property of the river-floodplain ecosystem, first described in terms of "hydrological connectivity" (HC) as the exchange of matter, energy and biota between different elements of the riverine landscape via the aqueous medium (Amoros and Roux, 1988). This water-driven transport of materials between and within landscape patches is a major driver of floodplain system structure and function (Marren et al., 2014). Hydrological connectivity controls floodplain functions, including erosion, sedimentation, nutrient uptake and (re) suspension (e.g., Heiler et al., 1995; Christensen et al., 2020), resulting in services such as floodwater or nutrient retention (Natho et al., 2013; Schober et al., 2015). Besides hydrologic connectivity, geomorphic connectivity, i.e., the spatial arrangement of the water bodies in a floodplain and the potential pathways that connect them to the main channel, can control ecosystem functions and services. Graph theory has used graph-based representations of ecosystems (also known as spatial networks) to calculate landscape level and local connectivity through the lens of complex systems. In this regard, centrality measures are graph theoretical tools already widely used in landscape geomorphology as well as landscape ecology to calculate connectivity patterns in various ecosystems (e.g., Baldan et al., 2022; Uroy et al., 2021; Wohl et al., 2019). The approach is also developing towards a meta-system sense (metapopulation, metacommunity, meta-ecosystem; Bondar-Kunze et al., 2022) context, e.g., metacommunity networks (Borthagaray et al., 2015) or specifically for riverine systems (e.g., Henriques-Silva et al., 2019). Surprisingly, the interplay between hydrological connectivity and centrality/isolation is rarely analyzed in studying river-floodplains as networks and using tools provided by graph theory. This is particularly relevant because hydro-morphological alterations due to

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engineering works dissociated most of the large river channels from their previously integrated floodplains, making hydrological and geomorphic connectivity loss one of the most relevant pressures in river-floodplain systems (Blanton and Marcus, 2009; Knox et al., 2022).

Traditionally, hydrological connectivity is defined using a non-spatial approach, e.g., as the presence of upstream or downstream connection at mean water level of the main river (Amoros and Roux, 1988), especially for fragmented systems (Cid et al., 2022). Recent geomorphological studies show that graph theory is a promising tool for identifying hydromorphologically important channels and understanding morphodynamics in braided river systems (e.g., Marra et al., 2014, Connor-Streich et al., 2018). Many ecosystem functions in floodplains, such as trophic conditions and sediment dynamics, are determined by the interplay between the water source and nutrient transport (seepage, river water and groundwater; Heiler et al., 1995; Reckendorfer et al., 2013; Tockner et al., 1999), the source of primary production (macrophyte or plankton derived; (e.g. Guillon et al., 2019; Janauer et al., 2013; Keruzoré et al., 2013), the source of matter and sediments (river-borne, autumnal leaf fall and autochthonous production, e.g. Guillon et al., 2019; Reckendorfer et al., 2013), and the balance between erosion and sedimentation (e.g. Hohensinner et al., 2022; Riquier et al., 2015, Riquier et al., 2017). All these factors strongly depend on the location of a water body and its hydrological connectivity with the river (Li et al., 2021; Reckendorfer et al., 2013). Focusing on the interaction of hydrology and geomorphology, Covino (2017) summarized the importance of hydromorphological connectivity for biogeochemical fluxes (flow, exchange, pathway of nutrients) from the view of landscape geomorphology. At the river-floodplain scale, three fluxes are specifically important: i) subsurface exchange is bidirectional (from the river and to the river) and dynamically dependent on the flow conditions of the river but widely independent from the channel network (e.g., Krause et al., 2022; Roley et al., 2012). ii) surface flow in the river-floodplain is also bidirectional, dependent on channel network morphology and dynamically changing direction, from the river to floodplain during high flow and reverse during low flow conditions (e.g., Kondolf et al., 2006). Finally, there is iii) a longitudinal directional component (Vannote et al., 1980) relevant in the river-floodplain hydrological connectivity, i.e., the longitudinal downstream connectivity, also dynamically depending on the flow conditions during common flow conditions dependent on the channel network and during flooding, it might be independent of the network (Tockner et al., 1999).

In this paper, we develop a new innovative graph theoretic approach to characterize the importance of water body position (and thus different flow pathways) for floodplain functions and restoration potential. We test our approach using indicators describing ecosystem functioning in terms of trophic state, hydrochemical and sediment grain size and organic matter content. We hypothesize that i) main pathways of transport (water, sediments, nutrients) in a river-floodplain system can be identified as well as their importance for functioning, ii) local functions and habitat in an altered but still dynamic river-floodplain system can be sufficiently explained by its connectivity; using few most widely used connectivity indices from landscape geomorphology. Finally, iii) the approach can be used to classify floodplain water bodies according to their main deficits and restoration potential. We use an already intensely studied floodplain system as a model system, which is ideal for assessing the potential of the graph theoretic approach compared to more traditional analysis based on hydrological connectivity parameters. To our knowledge, this is the first application of graph theory as an indicator for transport pathways, ecosystem functions and restoration potential of floodplain water bodies.

2. Methods

2.1. Study system

At Vienna, the Danube is a ninth-order river with a mean annual discharge of about 1950 m3 s^{-1} and a bank-full discharge (recurrence time of approximately 1 year) of 5800 m3 s^{-1}. The average slope in this section is 0.45. Historically braided, the river–floodplain system has been constrained by the major regulation schemes that began in 1875 including extensive channelization and active disconnection of the floodplain through levees, culverts and weirs (Reckendorfer et al., 2006). The individual floodplain water bodies are, therefore, isolated from each other by culverts, weirs or earth dams.

Table 1
Indicators for floodplain water body functioning.

Indicator	*Unit*	*Method*	*Indicator value*
Electrical conductivity	µS/cm	field measurement via probes	Relative importance of groundwater versus river water/seepage water inflow in an aquatic system. For the case study system river water has lowest conductivity whereas groundwater has the highest (e.g. Heiler et al., 1995).
P-PO4	µg/L	APHA (2005)	Nutrient conditions of aquatic systems. For the case study system, nutrient rich water comes from the main river channel (e.g. Heiler et al., 1995)
N-NO3	µg/L	APHA (2005)	Nutrient conditions of aquatic systems. For the case study system, nutrient rich water comes from the main river channel (e.g. Heiler et al., 1995)
Dissolved organic matter (DOM) peak B	a.u.	Baker 2002	Tyrosine-like/ protein-like component (Coble, 2007). Strongly correlates with bioavailable, autochthonous DOM and biological processes (Coble, 2007, Inamdar et al., 2012). It can be considered as microbial by-product-like matter (Chen et al., 2003, Hosen et al., 2014).
fine-sediment content	percentage weight	fine-sediment content (grain size < 0.075 mm) (Reckendorfer et al., 2019)	describes the accumulation of fine-sediments (organic and inorganic)
Organic Matter (OM) content sediment	percentage weight	organic matter in a sediment core /as ash free dry weight (Reckendorfer et al., 2013)	describes the accumulation of organic material mainly form internal production (macrophytes) and leaf fall
macrophyte coverage (Kohler index)	value between 0 and 5	Kohler (1978), max. of relative macrophyte cover	macrophytes are a descriptor of the trophic situation of a water body and can also be used as an indicator for productivity (Szpakowska et al., 2021)

2.2. Indicators for trophic state and sediment exchange

The following indicators were selected to account for selected essential floodplain functions related to trophic and sediment conditions (Table 1). Data were collected from different studies (e.g., Heiler et al., 1995; Hein et al., 2004; Reckendorfer et al., 2013), screened for representativeness along the whole gradient form completely isolated to completely connected sites (Supplementary material 1) and pooled per water body (mean), including only datasets in the analysis for which at least 10 records of chemical parameters are available and at least three representative records for sediment-related indicators.

2.3. Network construction

The river-floodplain network for the graph theoretic network approach was constructed using an available GIS map of the water bodies polygons of the area (updated shapefile based on Dogan-Bacher et al., 1999, but can be other representations of water bodies e.g. Copernicus riparian zones dataset, https://land.copernicus.eu/local/riparian-zones, open street map https://www.openstreetmap.org or national open spatial datasets) and a DEM (10 cm resolution for our case, but also 1 m or 5 m resolution is appropriate dependent on the size of the water bodies) available for the system (Fig. 1). Each water body, isolated from each other by culverts, weirs or earth dams, was identified as the landscape unit. A network was digitized based on the DEM using the midpoint tool of the ArcGIS Editor toolbar (ESRI, 2021). The flow direction of the network was defined based on the flow direction of the main river using the ArcGIS Editor toolbar (ESRI, 2021). Three distance matrices were built based on network distance (directed: upstream–downstream based on flow direction, and undirected in the network) and on Euclidean distances (Peterson et al., 2013). Network distances were obtained as edge-to-edge distances along the river-floodplain networks using the "OD cost matrix analysis" of the ArcGIS network analyst extension (ESRI, 2021).

2.4. Network metrics

First network independent upstream and total hydrological connectivity expressed as the average number of days per year the water body is connected to the main channel and other water bodies, where calculated (for details see Funk et al., 2013; Reckendorfer et al., 2006). The hydrological connectivity ranges from 0 when the node is never connected over an average hydrological year to 365, when the node is always connected.

Two centrality metrics were calculated based on the fully developed network using the R package "igraph" (Csardi and Nepusz, 2006). The harmonic centrality is an extension of the closeness centrality for unconnected graphs and can be seen as a particular case of the node strength, where the weight is the reciprocal of the distance between the nodes (Table 2; Barrat et al., 2004; Rochat, 2009).

Harmonic centrality for node i is calculated as:

$$HC = \sum_{i \neq j} \frac{1}{d_{ij}}$$

Where the summation is across all couple of nodes i and j and d_{ij} is the distance between them, and $d_{ij} = 0$ if no connection exists between i

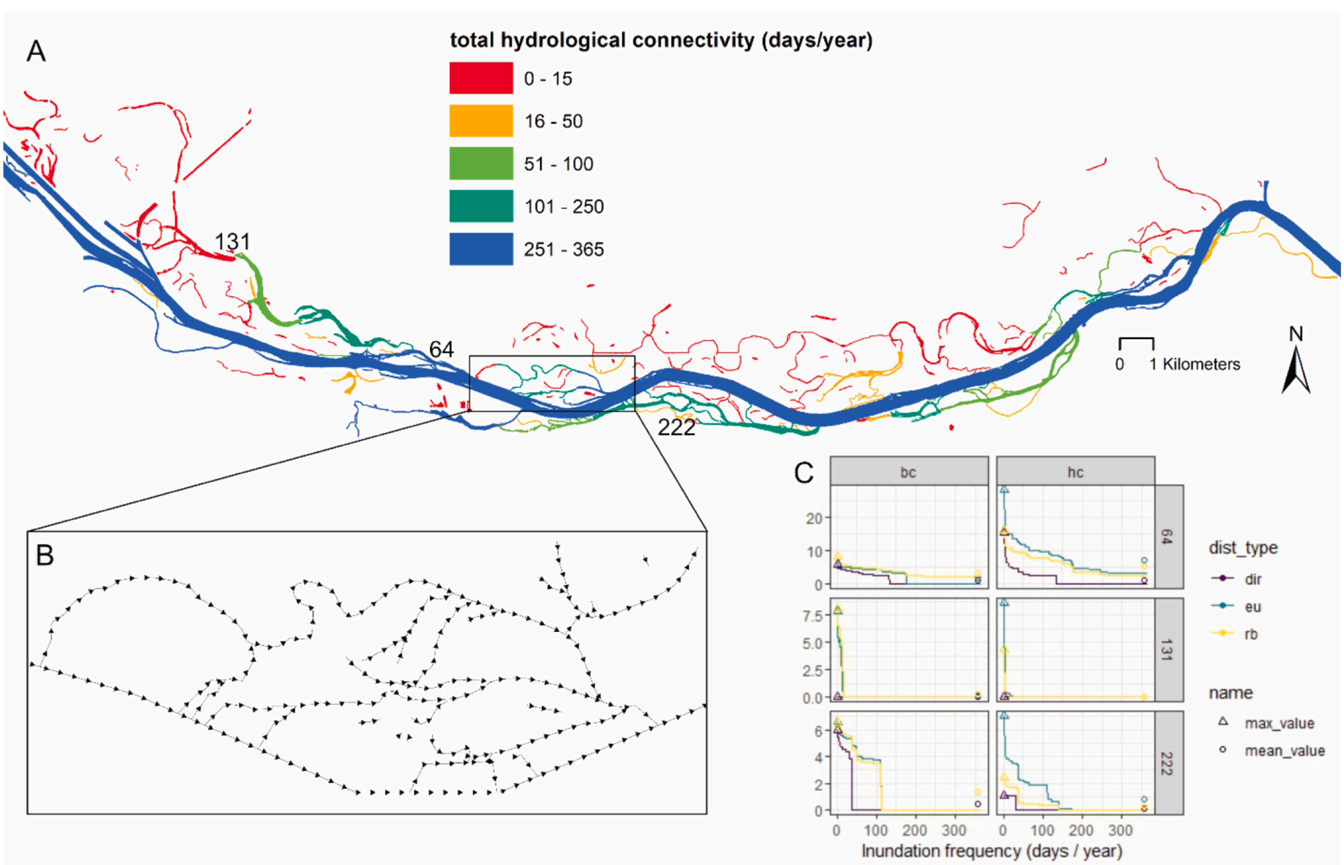

Fig. 1. Descriptions of the elements for the calculation of the dynamic centrality metrics. A) representation of the water bodies in the floodplain (projection: MGI / Austria GK East) system colored according to hydrological connectivity (days/year), B) the floodplain network used for the calculation of the river-based and directed distance matrices, as well as C) resulting centrality metrics (bc = betweenness centrality, hc = harmonic centrality) in dependence of the hydrological connectivity for selected water bodies (numbers 64, 131 and 222, see the numbers in map A for the position of the respective water bodies) in the system. For a description of the parameters of the graph theoretic approach see Table 2.

Table 2
Description of the graph theoretic approach used to quantify connectivity and transport pathways.

Pathway	*Graph representation*	*Examples*	*Code*
directional downstream	distance in directed channel network	downstream transport of sediments (Tockner et al., 1999, Covino, 2017)	dir
dependant on channel morphology	distance in channel network	bidirectional transport of nutrient (Tockner et al., 1999, Covino, 2017)	rb
independant from channels	euclidic distance	subsurface transport, flood transport (Tockner et al., 1999, Covino, 2017)	eu
dynamics	***graph representation***	***potential examples***	
dynamic (water level dependant)	dynamic network change with hydrology (average per water body)	nutrient exchange dependent on hydrological connection with the main river (Covino 2017)	d
static (at specific stage e.g. flood)	full network	erosion during high flow (Covino 2017)	s
position in the network	***graph representation***	***potential examples***	
critical for flow	betweenness centrality	This metric characterizes the importance of a node in the organization of flows in the network (Marra et al., 2014, Borgatti, 2005).	bc
central position	harmonic centrality	Indicates nodes that have a central position in the network (Rochat, 2009) and therefore receive flows that disperse in the system first (Borgatti 2005).	hc

and j.

The betweenness centrality (Table 2; Barrat et al., 2004) is giving higher importance to nodes that act as connectors for different parts of the network (Table 2, Bishop-Taylor et al., 2018).

The betweenness centrality (Barrat et al., 2004) was calculated as:

$$BC = \sum_{s \neq i \neq t} \frac{\sigma_{st}(i)}{\sigma_{st}}$$

where the summation extends to every couple of nodes s and t different from i; σ_{st} is the number of shortest paths connecting s and t passing through i and $\sigma_{st}(i)$ is the total number of shortest paths connecting s and t.

To incorporate the time-dependence of connectivity, multiple (365) network objects were created, corresponding to all possible inundation frequencies and the calculation of the metrics was repeated (range from 0, meaning all the nodes were included to 365, meaning only nodes connected over all the year were included). For each node in the metric, a frequency-centrality diagram was obtained, where the centrality metric was set to zero when the water body gets disconnected (Fig. 1C). In our approach we calculated the yearly mean (Fig. 1) as a relevant variable but also other representative statistics of the diagram can be calculated or in a temporal approach the 365 sets can be used individually.

2.5. Statistical analysis

To analyze the importance of the different connectivity metrics for the indicators of floodplain functioning we applied Partial Least Squares regression (PLSR) using the 'plsr' function of the 'pls' package (Mevik et al., 2011), including scaling and centering of explanatory variables and 10-fold cross-validation of the models using the available settings of the 'plsr' function. This multiple regression method is specifically suitable when there are a large number of highly correlated explanatory variables, i.e., high collinearity, which is the case for the calculated connectivity metrics. This technique is an extension of multiple regression approaches that analyze the effects of combinations of multiple predictors on a response variable, extracting latent factors from the predictor variables that maximize the explained variance in the dependent variables (Carrascal et al., 2009). As measures of the model performance root mean squared error (RMSE) and R2 of the model's cross-validation were calculated. The optimal number of components for each model was selected so that the cross-validation error (RMSE) was minimized.

The 'VIP' (variable importance in projection) algorithm implemented in the 'plsVarSel' package (Mehmood et al., 2012) was used to select all relevant variables using the standard settings of the function. VIP scores greater than one are commonly interpreted as being important in the PLS regression model, as the average of squared VIP scores equals 1 (Chong and Jun, 2005). Therefore, only variables with a VIP score greater than one were retained for the reduced model and reduced PLS models and used for prediction. Further, for comparison, PLS models were also calculated using only the classical "hydrological connectivity" variables (hydrological connectivity model) as well as only static network metrics (static network model), respectively.

Finally, water bodies were classified based on the predicted values for the indicators of floodplain functioning using k-means clustering using the base function 'kmeans' using R (R Core Team, 2023). The number of clusters was determined using the gap statistics (Tibshirani et al., 2001) using the 'fviz_nbclust' function of the 'factoextra' R package.

3. Results

The full PLS model as well as the reduced model show moderate to good performance across all indicators (Table 3, Fig. 2). Compared to the models based on "classical" hydrological connectivity all spatial graph-based models perform equally to significantly better. The model based only on the static unweighted network (static network model) shows performance comparable to the full model.

The importance of the different connectivity/centrality measures for the indicators of floodplain function differs among models (Fig. 2). Hydrochemical conditions (conductivity, phosphorus and nitrate concentrations) of water bodies were mainly determined by metrics based on euclidic distances (eu_s_hc and eu_d_hc), i.e., by flows independent from the network, subsurface and overbank flows, as well as by nodes critical for undirected flow (rb_s_bc), like inflow of nutrient-rich water with low conductivity from the Danube as well as inflow of nutrient-poor water with high conductivity from the groundwater, dependent on the water level of the Danube and therefore directions of flows. For peak B the overall connectivity is important (high VIP score of eu_d_hc and eu_s_hc, as well as dir_d_bc, dir_d_hc, dir_s_bc, dir_s_hc and rb_d_hc, rb_s_hc). The negative coefficients (Fig. 2) indicate that peak B and thus bioavailable, autochthonous DOM production, reaches the highest levels in overall isolated sites across all dimensions.

Fine sediment content was mainly determined by the directional connectivity in the system, especially betweenness centrality in flow direction, so the most relevant nodes for directional transport in the systems had the lowest levels of fine sediment contents. For the percentage of organic matter (OM) in the sediment, the overall connectivity in flow direction was important (high VIP score of dir_d_hc and dir_s_hc) but also network connectivity and independent connectivity were relevant (VIP score of eu_d_hc, eu_s_hc and rb_d_hc, rb_s_hc greater than 1). Therefore, the share of OM decreases with the connectivity in the water bodies and was only found in water bodies with overall high isolation, i.e., where no regular transport happens. Higher macrophyte cover was restricted to water bodies with low directional overall connectivity as well as critical nodes for transport and erosion had low macrophyte cover (Fig. 2).

Based on the predicted values of the seven indicators, water bodies were grouped using cluster analysis resulting in five groups (Fig. 3).

Table 3
Results of the partial least square regression (PLS) showing standard estimates of model quality and test statistics based on cross-validation. RMSE: root mean squared error, RMSECV: RMSE under cross-validation, R2: variance explained in the training data set, Q2: R2 under cross-validation; n comp: Number of components in the model. For indicator description see Table 1.

Full model	*Conductivity*	*P-PO$_4$*	*N-NO$_3$*	*DOM peak B*	*Fine-sediment content*	*OM sediment*	*Macro-phyte*
n comp.	4	3	4	2	2	5	3
RMSEtrain	50.45	0.76	0.49	0.03	6.27	1.00	0.71
RMSECV	67.49	0.89	0.63	0.04	7.29	1.71	0.82
R2	0.69	0.59	0.69	0.55	0.62	0.92	0.65
Q2	0.44	0.45	0.47	0.47	0.49	0.78	0.55
Reduced model							
n comp.	2	2	2	1	1	1	2
RMSEtrain	59.18	0.80	0.51	0.34	7.26	1.72	0.72
RMSECV	66.62	0.86	0.60	0.37	7.82	1.85	0.79
R2	0.57	0.55	0.66	0.51	0.50	0.78	0.62
Q2	0.45	0.49	0.54	0.44	0.42	0.73	0.56
hydrological connectivity model							
n comp.	2	1	1	1	2	2	2
R2	0.43	0.29	0.56	0.53	0.55	0.76	0.47
Q2	0.27	0.16	0.47	0.50	0.46	0.69	0.41
Static network model							
n comp.	2	3	3	1	1	1	2
R2	0.54	0.49	0.66	0.49	0.49	0.75	0.63
Q2	0.44	0.40	0.49	0.46	0.45	0.72	0.56

Cluster 1 water bodies are critical for the flows in the system (high directional bc), have the highest overall connectivity, lowest fine-sediment contents (organic and inorganic), lowest macrophyte cover but highest nutrient loads (phosphate and nitrate) due to their overall central position in the floodplain system. Cluster 2 includes all water bodies where directional transport is relevant, with high total connectivity, but the water bodies are not critical for flow, consequently, it shows medium fine-sediment contents with a low share of organic matter, low macrophyte cover, and relatively high nutrient concentrations. Cluster 3 is characterized by high fine sediment but mainly inorganic (river-based) sediments, medium densities of macrophytes, high input of nutrients and high unidirectional and network-independent connectivity. Cluster 4 also lacks directional connectivity and has also reduced unidirectional as well as network-independent connectivity. Therefore, the proportion of organic material in the sediment is higher, macrophyte cover is relatively high and peak B as a microbial by-product-like matter and an indicator for microbial activity is gaining in importance. Cluster 5 comprises the overall disconnected sites with the highest proportion of organic matter in the sediment, the highest potential for high macrophyte densities, high importance of microbial activity (peak B) and low nutrient content in the water (sites with higher isolation).

4. Discussion

The graph theoretic approach performs well in predicting indicators for essential ecosystem functions in the selected floodplain system. Compared to approaches based exclusively on hydrologic connectivity, the approach allows for determining the most important transport pathways for sediments and nutrients, proving that besides hydrological connectivity the spatial position of the water bodies and the relative position of a water body in a floodplain is of high importance for ecosystem functions (Reckendorfer et al., 2013). Further, water bodies could be classified by indicators for their trophic state and sediment composition, based on nutrient and dissolved organic matter concentration, sediment grain size and organic content as well as macrophyte coverage. The primary elements necessary for a functional floodplain ecosystem are connectivity between the river channel and floodplain, but also connectivity within the system, a variable flow regime that incorporates a range of flow levels, and sufficient geographic scale for key processes (Opperman, 2012). This can provide a habitat mosaic that includes topographic features such as side channels and oxbows, areas characterized by erosion and deposition processes, and moderately connected sections that are connected during flood events and exhibit high productivity and functional processes (e.g., sediment retention, primary production). In this study, we calculated relevant connectivity parameters gained by a graph theoretic approach and correlated them with indicators for floodplain functions to evaluate the main pathways of transport and the spatial distribution of functions and habitat conditions.

4.1. Functional patterns

Our analyses revealed that the flux of water and nutrients (conductivity, P-PO4 and N-NO3) in the system is dominated by transport, independent from the network (Fig. 2), such as seepage exchange or overbank inflow during increased water levels, network-based and directed transport is of limited relevance. Additionally, water bodies with a more central position in the network show a single (cluster 1, Fig. 3) or high relevance (cluster 2 and 3, Fig. 3) for nutrients. This underlies earlier findings, that the position within the floodplain with respect to the surface topography and the groundwater table is essential for nutrient transport (Hein et al., 2004; Malanson, 1993; Tockner et al., 1999; Trémolières et al., 1993).

Side-channels where erosion is most important, indicated by the lowest amount of fine sediments, are characterized by high betweenness centrality (BC) in flow direction. BC has already been shown to be a good indicator of channel importance for flow and transport in large braided rivers (Connor-Streich et al., 2018; Marra et al., 2014). Channels with high BC are more spatially stable and morphodynamically more important to the network due to their high levels of connectivity to other channels; they are most relevant for flow discharge distribution and material transport (Marra et al., 2014). These sites often have phases with high organic turbidity (algal blooms) due to pulses of nutrient input and lack of dense macrophyte growth (Guillon et al., 2019; Heiler et al., 1995; Reckendorfer et al., 2013). This is also well in line with our result, that macrophyte cover is mainly related to directional flow, but negatively correlated with these indices (Fig. 2). Macrophytes are often limited in these sites to the banks where fine-sediment content is higher, while in deeper parts sediments are frequently eroded and sediments are coarse (cluster 2, Fig. 3), and therefore disadvantageous for the growth of higher aquatic vegetation (e.g., Janauer et al., 2013).

Sites, which are not critical for directional flow are characterized by accumulation of fine sediments, whereas inorganic compartments are

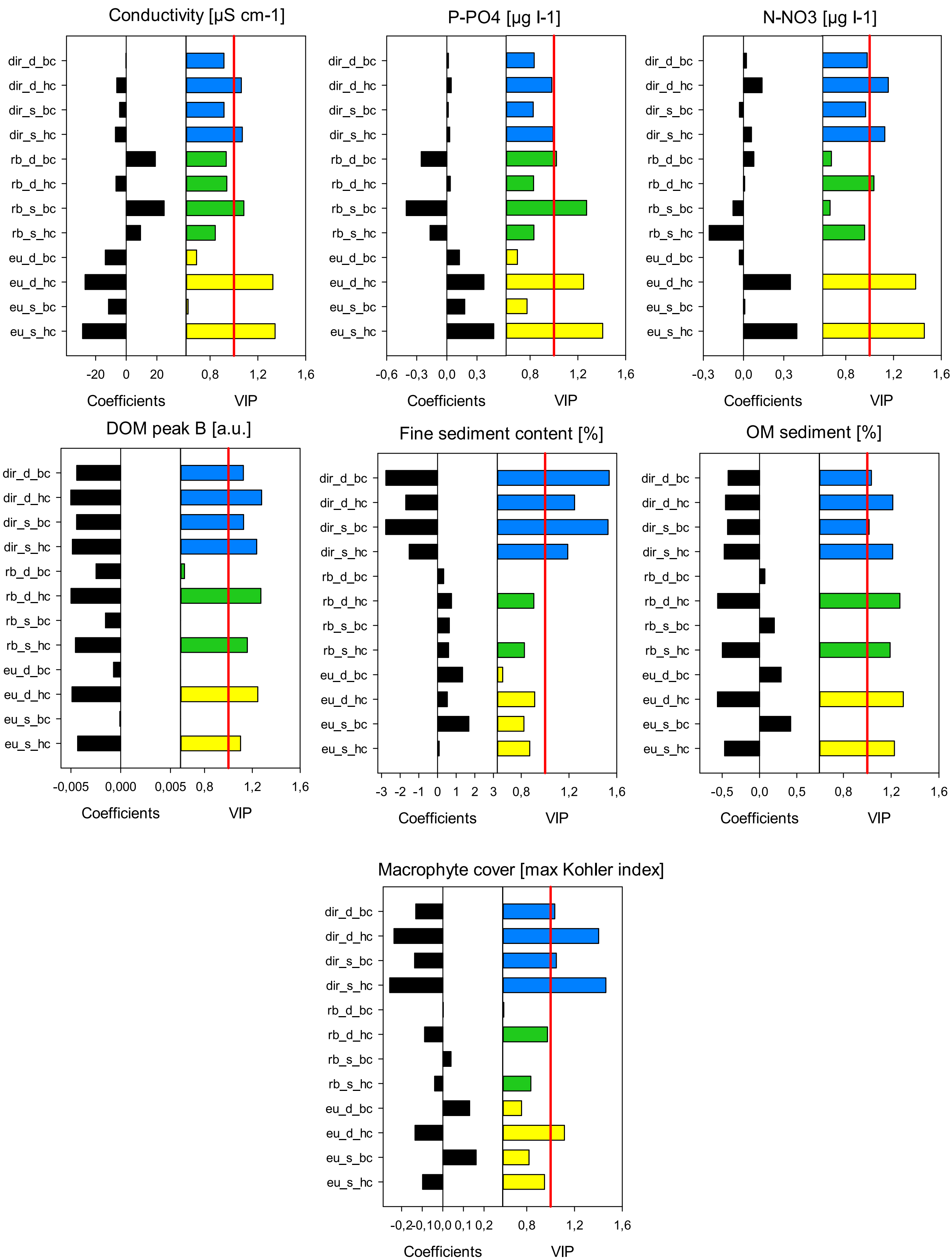

Fig. 2. Result of the PLS of the full model showing VIP (variable importance in projection) score as a measure of importance and regression coefficients (black bars, left graphs) to show the strength and direction of the dependency of the different connectivity variables in the models. The red line marks the value of the VIP score (VIP = 1) that is interpreted to be the threshold for important variables in the model. For the description of the six indicators see Table 1, for connectivity/centrality indices, see Table 2 and for the parameters of model quality see Table 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

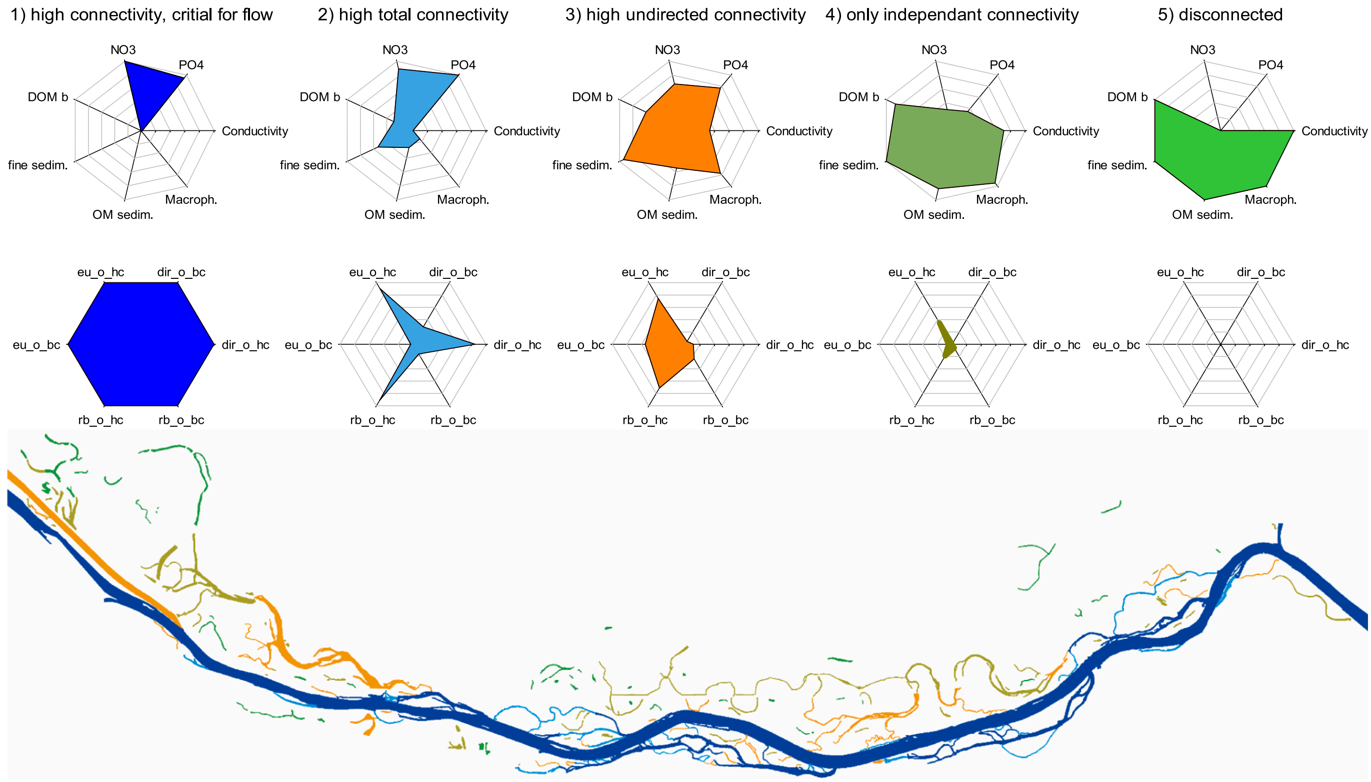

Fig. 3. Result of the cluster analysis based on the predicted values of the seven indicators for floodplain water body functioning, the five clusters are characterized by averaged, normalized (0–1) mean indicator values (see Table 1 for indicator definitions and description) and connectivity measures (see Table 2 for abbreviations and definitions) using spider diagrams. The map shows the assignment of the five functional clusters to the water bodies in the system.

dominating in systems that have high connectivity independent from flow direction (cluster 3, Fig. 3), accumulation of organic sediments is dominating in water bodies with overall low network connectivity (cluster 4, Fig. 3) (Amoros, 2001; Guillon et al., 2019; Reckendorfer et al., 2013). This pattern of aggradation is already well known from a side channel system in the study area which has no upstream connection but a downstream connection, transforming the system into a sediment sink (Hohensinner et al., 2022; Reckendorfer et al., 2013) and common to other floodplain systems with restricted connectivity due to dykes or other engineering structures where highest sedimentation rates occur in channels with low intensity of upstream overflow events compared to high intensity of backflow events (Riquier et al., 2015, Riquier et al., 2017, Ward and Stanford, 1995). Additionally, the relevance of macrophytes and dissolved organic matter (shown as DOM peak B) increases, whereas the potential for high macrophyte densities increases with an overall decrease in connectivity/centrality in the system. Systems that lack directional connectivity but also with decreasing overall connectivity, have the highest potential to be dominated by macrophytes throughout the year, in concordance with findings from other studies (Keruzoré et al., 2013). Water bodies with a total lack of connectivity (cluster 5, Fig. 3), show the highest percentage of organic matter in the sediment, highest densities of macrophyte cover, have the lowest nutrient contents and are primarily fed by groundwater (highest conductivity in the water) (Guillon et al., 2019). Our data also show a high relevance of DOM peak B in those areas which can indicate an organic matter pool with more protein-dominated and therefore more bio-available (labile) carbon, which is potentially usable for the microbial community (Lynch et al., 2019; Peduzzi et al., 2008). However, a combined decrease in nutrient concentrations and hydrologic connectivity can lead to a nutrient-limited microbial community, which cycles DOM less efficiently, which is indicated by the highest amount of peak B in those disconnected systems. Here carbon release into the atmosphere is promoted rather than incorporation into microbial biomass (Lynch et al., 2019).

Our results, therefore, point to the fact, that geomorphic complex floodplain systems have an increased heterogeneity in metabolic opportunities for DOM processing, autochthonous productivity, hydrologic connectivity, and the maintenance of different flow paths (Lynch et al., 2019).

4.2. *Implication for restoration*

The developed indices are useful to study the potential effects of changes in connectivity patterns in floodplains. Many floodplains were disconnected over time and now reconnection is considered as a way of improving ecological conditions. The indices we developed can be useful in guiding management actions:

Cluster 1 and 2 are proposed to be most relevant for reconnection to the main river channel as they have a central position in flow direction and we expect higher erosion and deposition after reconnection (Riquier et al., 2015, Riquier et al., 2017). Water bodies of the **cluster 1** type are expected to be stable and persistent as they are morphodynamically important in the network due to their high level of connectivity to other systems (Marra et al., 2014). **Cluster 2** types are expected to be important for the relocation of substrate and rejuvenation of the system after reconnection and thus most active/dynamic zones, as changes in network position are more relevant in channels with low bc (Marra et al., 2014).

Water bodies in **Cluster 3** are expected to have the shortest life span due to strong aggradation processes by riverine fine sediments and are also prone to eutrophication due to incoming river water (Van Denderen et al., 2019; Riquier et al., 2017). Due to their position in the network, an upstream reconnection is complicated. Therefore, technical measures such as active sediment management via excavation, sediment trapping for water entering the system or flood water management with weirs can be an option (e.g. Baptist et al., 2004; Breedveld et al., 2006;

Reckendorfer et al., 2013).

Cluster 4 water bodies are less threatened by sedimentation of riverine fine-sediments (and nutrient input) as the sedimentation already happens in the more connected sites of the floodplain channel network (cluster 3) and thus, this type can be expected to be more persistent (Van Denderen et al., 2019). Here, macrophytes are already dominating compared to the cluster 3 type, often impacted by algal blooms (Reckendorfer et al., 2013). In the long run management measures such as those for cluster 5 sites can be relevant.

Cluster 5 sites are most dependent on groundwater levels and expected to be threatened by the lowering of groundwater levels (e.g. climate driven), as well as internal terrestrialization and succession processes due to the intense macrophyte growth or accumulation of terrestrial organic material. At the water body scale, such systems could benefit from measures that raise the groundwater tables, such as artificial water supply or removal of sediment e.g. due to excavation (e.g., Baptist et al., 2004; Breedveld et al., 2006; Reckendorfer et al., 2013).

5. Conclusions

The graph theoretic approach is a promising innovative indicator tool to characterize the ecological functioning of floodplain systems by characterizing and quantifying the position of water bodies as well as the main transport pathways in a system. Therefore, in a meta-ecosystem view, it is especially relevant as it quantifies the interaction of local and regional processes that influence the dynamics of environmental conditions and, consequently, the distribution of organisms in a landscape (Cid et al., 2022).

Basic data for the presented network approach can be desktop derived based on digital elevation models or aerial imagery (e.g. Connor-Streich et al., 2018; Marra et al., 2014) or readily available digitalization of water bodies (e.g. Copernicus riparian zones dataset https://land.copernicus.eu/local/riparian-zones, open street map https://www.openstreetmap.org or national open spatial datasets) that can be used for network generation using available GIS tools (Lewandowicz and Flisek, 2020). With software packages such as 'igraph' for R (Csardi and Nepusz, 2006), tools can apply many different relevant network metrics (e.g. Tiwari et al., submitted for publication). Therefore, the critical next steps are i) to test the graph theoretical approach for other floodplain systems with different levels of hydro-morphological alteration to show the applicability of the method as a desktop tool to assess the functioning of river-floodplain systems. ii) The integration of biota and, therefore, biodiversity for the graph theoretic approach and a further important question is iii) the case dependency of the relationship between functions and connectivity/centrality measures, i.e., is the relationship site-specific, or are there general patterns across different systems? In the studied floodplain system, the static and dynamic approach performs equally well. However, it is not clear if this is an effect of the still high concordance of spatial position and hydrological connection in the dynamic system or a general pattern intrinsic for river-floodplain systems independent from the level of human alteration, i.e., isolation of floodplain water bodies.

CRediT authorship contribution statement

Andrea Funk: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Damiano Baldan:** Conceptualization, Software, Methodology, Formal analysis, Writing – original draft. **Elisabeth Bondar-Kunze:** Conceptualization, Writing – review & editing. **Sonia Recinos Brizuela:** Software, Data curation, Writing – review & editing. **Johannes Kowal:** Data curation, Writing – review & editing. **Thomas Hein:** Conceptualization, 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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110877.

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