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RESEARCH ARTICLE

Multilayer networks in landscape ecology: a case study to assess changes in aquatic habitat connectivity for flying and non-flying benthic macroinvertebrates in a Danube floodplain

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Abstract

Context In efforts to mitigate anthropogenic impacts on floodplain biodiversity, restoration measures that enhance habitat connectivity have been applied. However, these approaches have either neglected the spatial position of water bodies or the dynamic nature of the floodplain ecosystem.

Objectives This study focuses on the novel application of the multilayer network framework to assess changes in the aquatic habitat connectivity in floodplains, showcasing its application in the context of aquatic passive dispersal (drift) of two indicator groups of benthic macroinvertebrates (Oligochaetes and Chironomids)

Methods Our case study is located in the Donau-Auen National Park in Austria and follows floodplain restoration measures (side-channel reconnection) applied in the mid-1990s. Multilayer networks were constructed to represent the conditions before, short-term, and long-term after restoration to quantify habitat connectivity across inundation frequencies. Our network analyses involved multilayer correlation, static and dynamic monolayer centralities (centrality profiles), and multilayer centrality assessments. We used a Partial Least Squares Regression analysis as a variable selection tool to identify which centrality measures better explained the variance in α diversity

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and Local Contributions to Beta Diversity (LCBD) of benthic macroinvertebrates.

Results   In the short-term, our connectivity analysis indicated an increase in habitat connectivity. However, centrality profiles, multilayer correlation, and multilayer centrality techniques identified a long-term decrease in connectivity. Multilayer centralities had higher Variable Importance in the Projection scores (VIP) than their monolayer counterpart in explaining variations in α diversity and LCBD for strict aquatic dispersers. Meanwhile, for flying dispersers, monolayer centralities had the highest VIP scores for explaining α diversity.

Conclusions   This study underscores the relevance of integrating dynamic aspects of water-mediated transport beyond traditional pairwise distances. Although in this study we apply this tool by showcasing the aquatic passive dispersal mode, the application of this method can be extended to other dispersal modes and representative abilities for diverse groups of aquatic organisms. The expanding cross-disciplinary applications and open-source tool development for multilayer networks offer practical implications for planning and evaluating management measures.

Introduction

Floodplain landscapes have been subjected to long-term anthropogenic stressors, contributing to global freshwater biodiversity loss (Hein et al. 2019; Tickner et al. 2020). These stressors include the alteration of the physical structure of the landscape (e.g., river regulation and damming) and subsequent changes in flow, which in turn causes the decoupling of floodplains from the main river channel (Reckendorfer et al. 2006; Hein et al. 2019; Whipple and Viers 2019). To mitigate the detrimental effect of some of these anthropogenic stressors, an increasing number of river–floodplain restoration/rehabilitation measures have aimed to achieve more dynamic geomorphic and hydrologic processes promoting a dynamic habitat mosaic (Poff et al. 1997; Hein et al. 2016; Marle et al. 2022). However, the extent to which restoration

affects the habitat connectivity of freshwater biodiversity, especially within floodplain ecosystems, remains poorly understood (Al-Zankana et al. 2020).

Landscape ecology provides a framework based on network science to describe the relationships between ecological patterns and processes across spatial scales (Newman et al. 2019; Tiwari et al. 2023). In Fig. 1 and Table 1, we provide a conceptual model and a glossary with the main connectivity-related concepts used in this study. Notably, the widespread practical applications of network science tools in landscape ecology lie in utilizing monolayer centralities to identify areas that play the most central role and, thus, where conservation efforts can be prioritized (Kininmonth et al. 2019). However, most of the available network tools are typically applied to monolayer networks depicting static landscape properties. Like other dynamic systems, floodplain ecosystems generally exhibit multiple changes in their structural and functional connectivity (see habitat connectivity definition in Table 1), where the presence or absence of aquatic corridors depends on inundation frequencies. The novel approach of multilayer networks can help to overcome this challenge since it can include dependencies between seasonal or temporal static representations of the landscape (monolayer networks, Pilosof et al. 2017). In the case of floodplains, the multilayer network framework can help incorporate the frequency of lateral hydrological connectivity (LHC, see definition in Table 1) into connectivity calculations. While there are recent examples of applications of multilayer networks in species interaction networks (Timóteo et al. 2018; Costa et al. 2020), to our knowledge, this framework has not yet been applied to assess habitat connectivity in floodplains.

Worldwide, floodplains are among the most dynamic ecosystems, where the lateral water connections with the main river channel and fluctuations in flow are vital for determining the diversity of benthic assemblages (Larsen et al. 2019; Marle et al. 2022). The highly diverse benthic macroinvertebrate fauna of the Danube River, like in most European large rivers, is under extreme pressure (Graf et al. 2015). Compared to the early nineteenth century, the Danube River, which is the second largest river in Europe, has suffered an 80% reduction of its floodplains due to land-use change, river regulations, and damming (Hein et al. 2016; Buijse et al. 2002). To mitigate
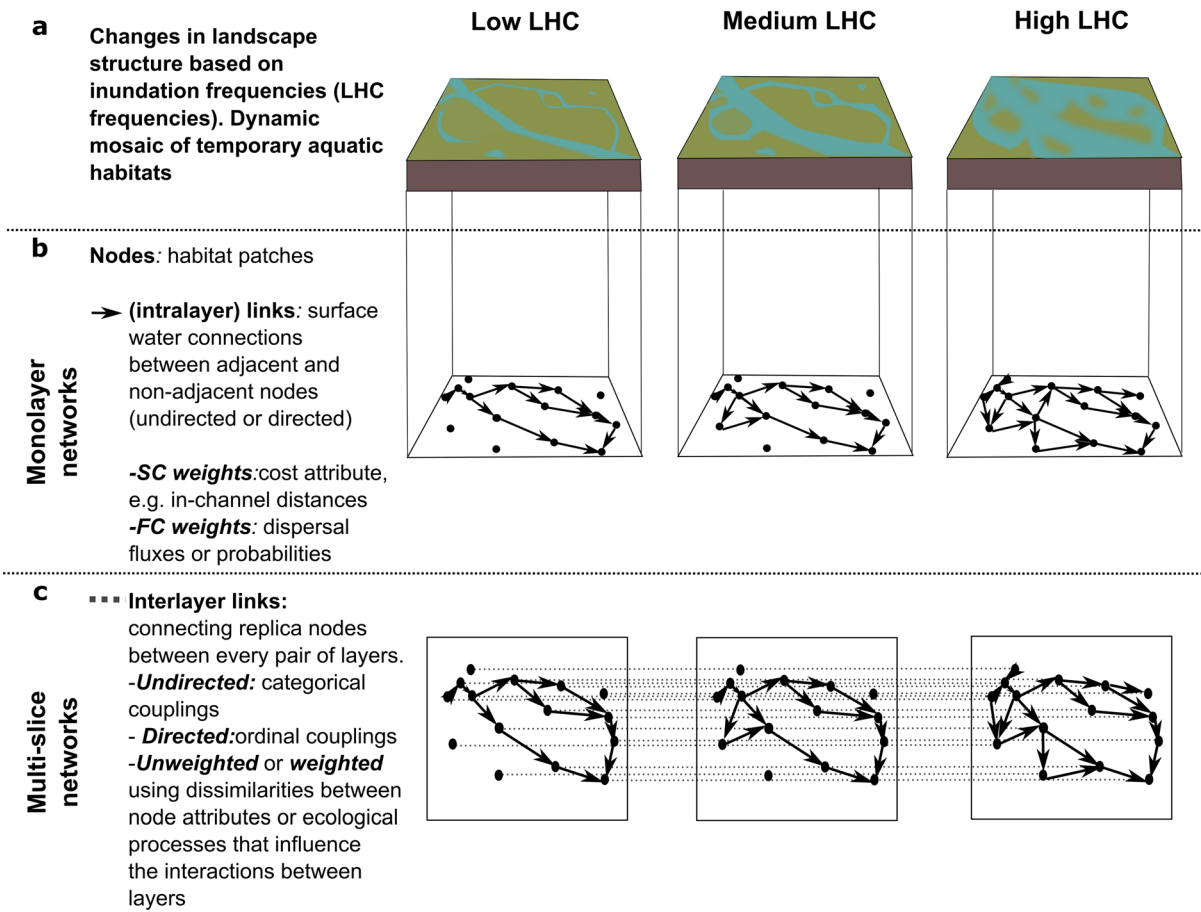
Fig. 1 Conceptual model of monolayer and multilayer network-based representations. In floodplains, functional connectivity functional connectivity will change depending on inundation frequencies (LHC frequencies that go from 0 to 365 days/year, **a**, **b**). Intralayer links in monolayer networks depict aquatic corridors (structural connectivity—SC) or routes (functional connectivity) between nodes (**b**). Intralayer links can either be undirected or directed and weighted based on costs for dispersal movements (depicting the property of landscape resistance) or by dispersal fluxes or probabilities. Some of the most commonly used cost attributes are Euclidean distance (Tonkin et al. 2017), network or in-channel distances (Grönroos et al. 2013; Chaput-Bardy et al. 2017), cost distances (Zetterberg et al. 2010), least-cost (Adriaensen et al. 2003) and resistance distances using circuit theory (McRae 2006; Bishop-Taylor et al. 2015; Dickson et al. 2019). Multilayer networks can be applied to compile dynamic LHC frequencies in landscape structures. Monolayer networks constructed for each defined LHC threshold (**b**) are compiled as layers in the multilayer network (**c**). Each layer has the same nodes (replica nodes) with different intralayer links. The interconnectedness between layers is defined by interlayer links between each pair of replica nodes (multilayer networks type multi-slice, De Domenico et al. 2015; Bianconi 2018). Interlayer links can be undirected (categorical couplings) or directed (e.g., ordinal couplings in temporal networks), unweighted or weighted

the freshwater biodiversity loss, examples of river-restoration measures in the Danube basin targeted the disconnection of floodplains from the main river channel by re-establishing hydrological connections (e.g., Tockner et al. 1999; Navodaru et al. 2005; Natho et al. 2020) and, therefore, increasing the localized hydraulic shear stress that drives changes in benthic macroinvertebrates assemblies (Paillex et al. 2013; Obolewski et al. 2016; Marle et al. 2022). A key remaining challenge for managing river–floodplain ecosystems is understanding how biodiversity relates to spatio-temporal changes in ecological patterns, processes, and habitat structure (Larsen et al. 2019). Therefore, conceptualizations of connectivity that include dynamic hydrological aspects, the spatial arrangement of habitat patches, and the patterns of their connections (network topology) can significantly improve our understanding of

Table 1 Glossary with definitions and explanations of the main connectivity-related concepts used in this study

Term	Explanation
Landscape resistance	Property of landscapes as complex systems which describes how the landscape's spatial structure facilitates/impedes animal movement (Newman et al. 2019). Landscape resistance is perhaps one of the most studied properties in landscape ecology, with an increasing number of studies applying network theory to calculate habitat connectivity (Minor and Urban 2008; Rayfield et al. 2011; Urban and Keitt 2001; Erős et al. 2012)
Habitat connectivity	Degree on which the physical configuration of the landscape [structural connectivity (SC) of the habitat] facilitates dispersal flows/movements of organisms among landscape units (patches) [functional connectivity (FC) of the habitat, Taylor et al. 1993]
Lateral hydrological connectivity (LHC)	In floodplain landscapes, LHC refers to the seasonal or permanent water-mediated linkages between the main stem of a river and the waterbodies along its floodplain (Amoros and Bornette 2002; Larsen et al. 2019). To avoid ambiguity, further on in this work, we refer to the surface water exchange between a main river channel and floodplain waterbodies as LHC and to the level of connectedness within a system as connectivity (Turnbull et al. 2018), which is measured using network analysis
Node	Landscape unit representing aquatic habitat patches (Bishop-Taylor et al. 2015)
Links	Links in a static network (for multilayer networks, physical nodes within each layer are connected with intralayer links) depict surface water connections between direct neighbouring nodes or aquatic corridors/routes between non-adjacent nodes that are within a certain distance threshold or decay exponentially with it [origin-destination (OD) links, Bera and Rao 2011; De Domenico et al. 2015; Dijkstra 2022]
Monolayer network	They are also referred to as single-layer networks. Monolayer networks are static representations of the landscape, formed by a set of nodes connected pairwise by a given set of links describing either physical connections (structural connectivity) or complex interactions (Bianconi 2018), like the dispersal of organisms (functional connectivity)
Multilayer network	Term for networks with multiple layers (Kivelä et al. 2014)
Multiplex network	Multilayer network with diagonal couplings (Kivelä et al. 2014)
Replica nodes	Corresponding nodes with the same identity but belonging to different layers (Bianconi 2018)
Multi-slice network	Multi-slice networks are multiplex networks with a one-to-one mapping of replica nodes in each layer using interlayer links (De Domenico et al. 2015; Bianconi 2018)
Centralities	Network science tools used to rank nodes according to their importance, the applicability of which depends on the type of network and the network property to be emphasised (Bianconi 2018)

how restoration affects the ecological processes shaping floodplain biodiversity (Funk et al. 2023).

In this study, we focus on the novel application of the multilayer networks framework to assess changes in the aquatic habitat connectivity in floodplains. We present a case study that follows a pilot restoration project (side-channel reconnections) implemented in the mid-90s in a river–floodplain stretch in the Donau-Auen National Park, Austria. Our main objective is to demonstrate the utility of the multilayer networks framework in capturing dynamic changes in the habitat connectivity of two indicator groups of benthic macroinvertebrates in floodplain ecosystems, showcasing the dispersal mode of passive aquatic dispersal. By integrating temporal variations and the property of landscape resistance (Table 1) into our network models, we aim to answer the following questions:

(1) To what degree do the restoration-induced enhancements of LHC influence connectivity patterns in the landscape?

(2) Do node rankings derived from monolayer networks significantly change when considering dynamic LHC aspects in the calculations (multilayer centralities)?

(3) Which measure of node-level connectivity, monolayer or multilayer centralities, best captures the variations in the taxonomic diversity (in terms of α and β diversity) of the indicator groups with dispersal-related traits?

In this case study, we pay special attention to temporal changes in the taxonomic diversity and aquatic habitat connectivity (aquatic passive) of two indicator groups of benthic macroinvertebrates with contrasting

dispersal traits: (i) individuals of the subclass Oligochaeta (strict aquatic dispersers/non-flying), (ii) individuals of the family Chironomidae of the order Diptera (flying dispersed). We selected these two taxonomic groups because they had the highest taxonomic resolution identified both before and after restoration, in both the short and long term. Oligochaetes and Chironomids communities are the most heterogeneous taxonomic groups of benthic macroinvertebrates (highest species richness) in the Danube basin (Graf et al. 2015) and have been used as indicator species since they have rapid generation times and respond to gradients in LHC (de Haas et al. 2005; Funk et al. 2017; Larsen et al. 2019). We expect that the variation of taxonomic diversity of strict aquatic dispersers would be better explained by centralities that include dynamic hydrological aspects (multilayer centralities). For Chironomids, we expect that static centrality metrics, which reflect the spatial arrangement of habitat patches, will be more important for their taxonomic diversity, as adult flying dispersers can locate nearby habitat patches independently of the hydrological network.

Methods

Case study

Our study area corresponds to a 10 km river–floodplain stretch of the Donau-Auen National Park (DANP) called Regelsbrunn (48° 20′ 30″ N and 16° 18′ 50″ E) (Fig. 2a). The DANP is 45 km downstream of Vienna along the Upper Danube River. At this location, the Danube is a ninth-order river with a mean annual discharge of approximately 1950 m³/s and a bank-full discharge of 5800 m³/s, which recurs about once a year (Funk et al. 2023). Regarding the characteristic water levels of the Austrian Danube, the mean water level (water level corresponding to the arithmetic mean of the average annual discharges for the period 1991–2020) is 281 cm, for the gauge station Wildungsmauer (viadonau 2020). Likewise, for the period 1991–2020 at this gauge station, the low navigable water level (water level that corresponds to a discharge with an exceedance duration of 94%) and the highest navigable water level (water level that corresponds to a discharge with an exceedance
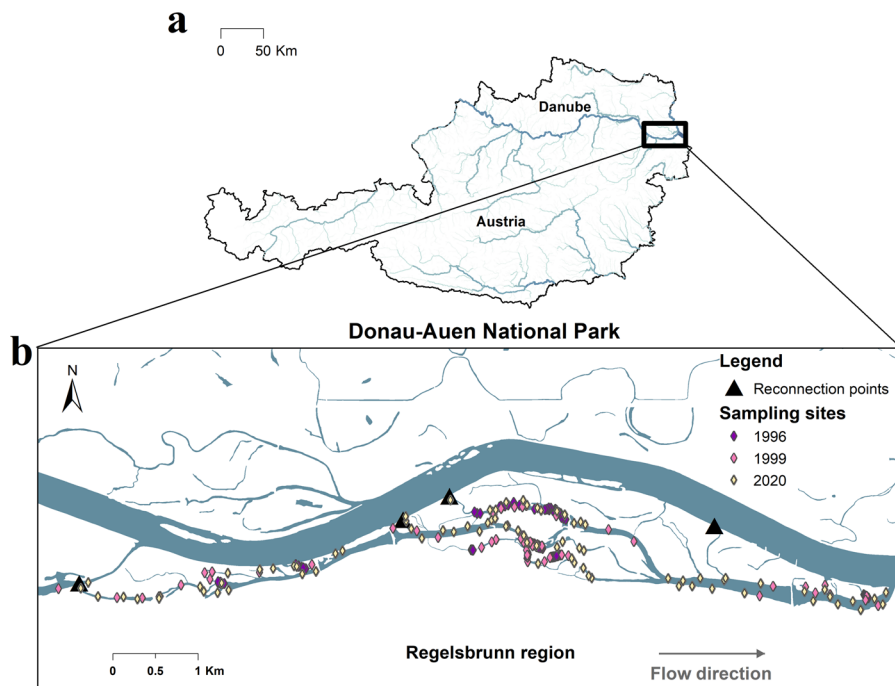

Fig. 2 Location of the Donau-Auen National Park (**a**) and the study area of Regelsbrunn. The sites where the reconnection measures were implemented are represented as black triangle symbols, and the years and locations where samples of benthic macroinvertebrates were taken are represented by coloured symbols (**b**)

duration of 1%) are 155 cm and 605 cm, respectively (viadonau 2020).

Since the mid-90s, this has been an extensively studied system, where human-made stressors date back to 1875 when large-scale regulation measures constrained a wide floodplain area (Chaparro et al. 2019). Further human alterations in the Austrian Danube (e.g., for the generation of hydropower, flood protection, and navigation) reduced floodplain ecosystems to less than 19% of their range in the nineteenth century (ICPDR 2009; Hein et al. 2019). While still impacted by these regulations, the area of what is now the DANP remained a free-flowing section (Hein et al. 2016; Chaparro et al. 2019). To mitigate human-made stressors, the region was declared a National Park in 1996, and shortly after, pilot restoration projects were implemented in the wetland of Regelsbrunn (Schiemer et al. 1999; Hein et al. 2016). The pilot restoration project consisted of the re-connection of abandoned side channels and wetlands with the main Danube channel by lowering riverside embankments, reactivating previous inflow channels, removing check dams, and creating outlets (Chaparro et al. 2019). While our study does not include specific control sites to assess the outcomes of restoration, previous studies, like the ones of Schiemer and Reckendorfer (2004), Reckendorfer and Steel (2004), and Schiemer et al. (2007, 2006), have already reported that the applied restoration measures resulted in an increase of LHC between the river and side channels (approx. 200 days/ year).

Benthic macroinvertebrates indicator groups

We built on long-term empirical datasets of Chironomids and Oligochaetes collected during sampling campaigns before (1996) and short-term after (1999) with a Gilson-corer [number of available samples: (i) 1996: N = 104; (ii) 1999: N = 47]. In 2020 (long-term after restoration), new samples were collected in Autumn, like in the previous years. Samples were collected in the littoral zone of waterbodies, spanning a LHC range from 0 to 235 days/year. The range of LHC in the sampled sites allowed us to capture a broad spectrum of connectivity conditions and habitat types.

Using a Gilson-corer at 5 to 10 cm depths (area per sample = 0.002 m^2, N = 81), samples were collected from sandy and muddy organic sediment (Funk et al. 2017). Individuals with a body size greater than 100

µm (macrozoobenthos) were identified to the finest taxonomic level possible (mostly species or genus level). Further, for all periods, the count data was harmonized to a sample area of 1 m^2.

Network analysis

We applied a multilayer network analysis to assess dynamic changes in aquatic habitat connectivity (directed connectivity). To answer our research questions, we developed monolayer and multilayer networks of a passive aquatic dispersal scenario. Multilayer networks were built with intralayer links weighted based on network distances (link cost attribute) and the probabilities for passive dispersal (link weight attribute). We applied the following topological analyses: (a) similarities between static layers representing the variation in LHC of the landscape throughout the year (edge overlap) and (b) monolayered and multilayer centralities analysis. Subsequently, using a partial least square regression analysis, we evaluated the importance of static vs. dynamic connectivity (monolayer and multilayer centralities) for explaining the variations of taxonomic diversity of the indicator groups, throughout the time periods: before, short-term, and long-term after restoration. A summary of the applied methods can be found in Fig. 3.

Building monolayer networks

Structural connectivity networks
The structural connectivity of the river–floodplain landscape is given by surface water connections between habitat patches, which was extracted from a Digital Elevation Model using flow routing in ArcMap 10.7.1. Here, nodes were mainly located every 100 m, and links were defined by the surface water connections between adjacent nodes. For each time period, the resulting structural connectivity networks were directed, following the flow direction, and weighted based on a cost attribute that acts as a constraint for dispersal movements (Rodeles et al. 2021). We used the pairwise in-channel network distances between nodes as a link cost attribute.

Potential functional connectivity
Accounting only for the connections between immediately adjacent nodes (direct neighbours) might not consider the functional interactions between non-
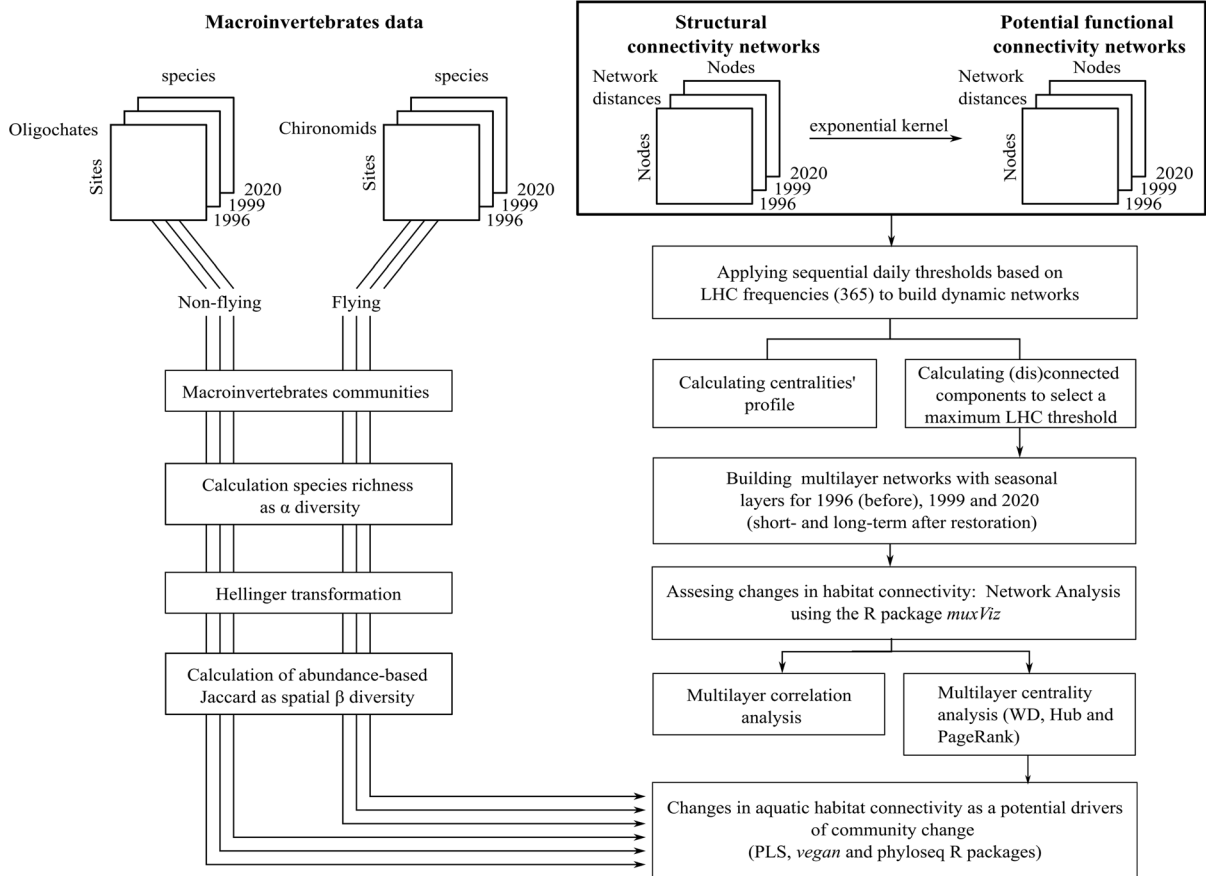
Fig. 3 Flow diagram of methods applied to assess changes in aquatic habitat connectivity for a benthic macroinvertebrates

direct neighbouring nodes (Bassolas et al. 2021). For this reason, network-based metapopulation and meta-community approaches have assessed habitat connectivity assuming functional connections between nodes. These functional connections are routes (OD-links) that are located within the species' maximum dispersal distances or where connections decay exponentially with distance (Link definition in Table 1) (Brown et al. 2011; Chaput-Bardy et al. 2017; Neufeld et al. 2018).

While in other network applications, the definition of functional connectivity networks applies to dynamic quantities (Voutsa et al. 2021), in this study, we adopt the probabilistic definitions previously applied in landscape ecological approaches by Bodin and Saura (2010) and Rodeles et al. (2021). We define potential functional connectivity for a scenario of passive aquatic dispersal (drift). Here, potential functional connectivity is the likelihood for passive drift

(flow-mediated passive downstream dispersal events), focusing on the role that structural connectivity (based on surface water connections) has in facilitating stochastic dispersal flows, where all species have the same probability of colonizing a site (Huttunen et al. 2017). We assigned dispersal probabilities as a link weight attribute that considers potential downstream/upstream dispersal pathways, following the approach of Baldan et al. (2022a) and Rodeles et al. (2021). We consider that dispersal (B_{ij}) decays exponentially with distance/resistance, where asymmetric probabilities are given by the exponential kernel:

$$B_{ij} = PD_u^{d_{ij}^u} PD_d^{d_{ij}^d}, \qquad (1)$$

where d_{ij}^u are the pairwise upstream distances and d_{ij}^d are the pairwise downstream distances between a pair of adjacent and non-adjacent nodes, while PD_u and PD_d are kernel parameters representing the mobility

abilities of the dispersers (Baldan et al. 2022a; Rode-les et al. 2021).

Aquatic passive dispersal (drift) is considered a crucial mechanism for shaping the spatial distribution of benthic macroinvertebrate communities and a fundamental ecological process with broader food web applications (Humphries 2002; Tonkin and Death 2013). For Chironomids, which exhibit aerial dispersal as adults, this dispersal scenario is only representative for their aquatic passive dispersal stage (larvae). The restoration measures primarily affected water-mediated connections, and thus, modelling aerial (overland) dispersal (i.e., using Euclidean distances between physical nodes) would not appropriately capture these changes in connectivity. Therefore, a scenario of flow-mediated passive downstream dispersal was applied for both Chironomids and Oligochaetes, to capture changes in aquatic habitat connectivity following restoration. We assumed that dispersal decays exponentially with distance, is stochastic, driven by hydraulics, and that passive dispersers (propagules) have the same probability for aquatic passive dispersal (drift). Given the location of our study area, we applied the kernel parameters $PD_u = 0$ and $PD_d = 3$ for passive lowland aquatic dispersers (see Baldan et al. 2022a). OD links and their asymmetric probabilities were calculated using network distances as costs, adapting the function B_ij_fun of the riverconn package in RStudio (Baldan et al. 2022b) for disconnected graphs. The OD-links of the resulting networks were weighted using the calculated dispersal probabilities (link weight attribute: dispersal probabilities) and network distances (link cost attribute: pairwise in-channel distances between nodes).

Building multilayer networks

We built multilayer networks of the type multi-slice based on the approach developed by De Domenico et al. (2015). For each period, multi-slice networks were built by combining temporal changes in the landscape structure, using thresholds based on LHC frequencies. LHC frequencies denote the mean annual frequency over a 20-year period of total surface connectivity between the floodplain habitats and the main river channel (inundation frequencies in days/year) (Reckendorfer et al. 2006). LHC frequencies are calculated based on the flow pattern of the main river

channel and the location of the floodplain wetlands concerning the river height (Reckendorfer et al. 2006).

We included the LHC frequencies representative for the time periods from before, short-term, and long-term after restoration, which were previously published by Funk et al. (2023) and Reckendorfer et al. (2006). We used these frequencies to define dynamic changes in the landscape structure since LHC is key in determining floodplain ecology, reflecting spatio-temporal hydrogeomorphologic conditions (Paillex et al. 2009; Funk et al. 2013; Reckendorfer et al. 2013; Marle et al. 2022).

Further, to reduce the computational cost, we built multilayer networks by applying sequential thresholds of LHC frequencies that would capture most of the variations in landscape structure. To do this, we first examined changes in landscape structure when applying daily thresholds (dynamic networks with 365 daily thresholds). For each monolayer network under daily thresholds, we calculated the number of (dis)connected components as a measure of variation in landscape structure or network fragmentation (Fig. 4). Based on the number of (dis)connected components, we then identified the maximum threshold of LHC as the threshold at which the network structures stabilized (Ishiyama et al. 2014). The maximum LHC threshold for networks before and after restoration was 89 and 181 days of LHC, respectively. However, the application of further multilayer network analysis considering daily layers can be a data-intensive procedure. Therefore, we then built multilayer networks by applying thresholds every 10 days until reaching the maximum LHC threshold. These sequential thresholds of 10 days captured most of the variability in landscape structure presented in Fig. 4. The resulting multilayer networks had a total of 10 layers for the time period before restoration and 19 for the periods after.

A monolayer network G_α in layer α is given by $G_\alpha = (V_\alpha, E_\alpha)$, which describes the interactions between the set of physical nodes V_α, where E_α is the set of intralayer links (connections between habitat patches) (Bianconi 2018). As an example, a 2-layer multilayer network can be described as $G_{\alpha,beta} = (V_\alpha, V_\beta, E_{\alpha,\beta})$, where $E_{\alpha,\beta}$ are the one-to-one interlayer links, connecting replica nodes in layer α to the replica nodes in layer β, i.e., they connect each
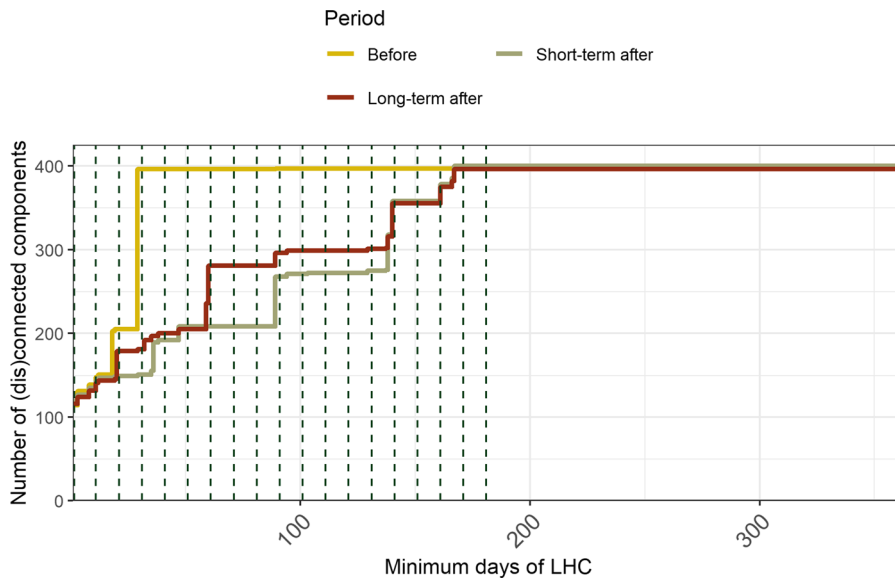
Fig. 4 Number of (dis)connected components in dynamic networks of before (yellow), short-term after (grey), and long-term after restoration (red), where layers go along 365 sequential thresholds on inundation frequencies [minimum of days of lateral hydrological connectivity (LHC)]. A (dis)connected component refers to a fully connected graph's cluster, so the more (dis)connected components there are, the more fragmented the network is. Vertical dashed lines correspond to the final thresholds selected for building multilayer networks (every 10 days until reaching the maximum LHC thresholds). A high LHC threshold will only consider connections between

nodes highly connected to the main channel, thus resulting in more disconnected networks under high thresholds. On the other hand, a low LHC threshold will consider connections between most of the nodes in the landscape. Thus, the landscape will appear as more connected. Before restoration, the network became fully fragmented at a lower LHC threshold than the other time periods. Likewise, in the long-term after restoration, the network became more fragmented at lower LHC thresholds when compared to the period of short-term after. This indicates a decrease in connectivity in the long term

node i in layer α (i, α) to its replica node (i, β) in layer β (Bianconi 2018):

$$E_{\alpha\beta} = [(i, \alpha), (i, \beta)] | i \in 1, 2, \ldots, N. \qquad (2)$$

For a N number of nodes and M number of layers, a multilayer network depiction of both intralayer and interlayer links can be represented using an $N \cdot M \times N \cdot M$ supra-adjacency matrix A (Bianconi 2018). However, standard matrices may not represent a suitable framework for interconnected multilayer networks, as they have an inherent limitation in depicting complex relationships, and information on interlayer links information can be lost (De Domenico et al. 2015). For this, De Domenico et al. (2013) uses a tensorial formalism and algebras of higher order to capture the complexity of multilayer networks (more details on the mathematical formulations of multi-slice networks can be found in De Domenico et al. 2013, 2015). Multilayer networks were built using categorical-unweighted interlayer links in the MuxViz package in RStudio (De Domenico et al. 2015).

Assessing changes in habitat connectivity

Multilayer similarity analysis
The similarities in structural properties of each layer of multilayer networks were calculated using the metric *global edge overlap* proposed by De Domenico et al. (2015). This metric was used to assess structural similarities in connection patterns between each one of the layers composing the multilayer networks from before, short- and long-term after restoration. For further details on all network metrics used in this study, refer to Table 2.

Centrality analysis
Centrality measures are used to find the most central nodes, which are important for maintaining connectivity at the network level (De Domenico et al. 2015). Multiple centrality measures can also be applied in multilayer network models (De Domenico et al. 2015). Each one has the potential to quantify the importance of replica nodes (see definition in Table 1) and highlight different aspects of habitat connectivity

Table 2 Description of the network theoretical metrics used in this study, examples of applications in Landscape Ecology, and assigned acronyms

Network metric	Description	Ecological applications	Acronyms
Edge overlap: RStudio *MuxViz* package (De Domenico et al. 2015)	Edge (link) overlap is a measure of similarity in the structural properties of two static networks (layers, De Domenico et al. 2015) For a given pair of nodes (i, j), the edge overlap is given by the fraction of layers in which the edge/link (i, j) exists (De Domenico et al. 2015): $o_{ij} = \frac{1}{M}\sum_{\alpha=1}^{M} a_{ij}^{[\alpha]}$ where α_{ij} is the adjacency matrix of the aggregated network associated with a M-layer multilayer network; an edge/link between i and j exists in the aggregated topological network only if it exists in at least one layer α on which $\alpha_{ij}^{[\alpha]} \neq 0$	The edge overlap describes the persistence of the edge/link pattern (De Domenico et al. 2015) throughout the year in our multi-slice networks. This is highly relevant to assess the effects of floodplain restoration measures that aimed to increase LHC, thus creating more dynamic hydrological conditions in the landscape.	Edge overlap

Network metric	Description	Ecological applications	Acronyms
Strength or **weighted Degree**: RStudio *igraph* package (Csardi et al. 2006) and *MuxViz* package (De Domenico et al. 2015)	Also known as Strength, it measures node importance based on the strength of its connections. Single-layer strength refers to the averaged sum of the weights of the links arriving (in-strength) and departing a specific node (out-strength, Jacoby and Freeman 2016). This metric was applied to networks weighted using dispersal probabilities (importance) and the inverse of the cost attribute (network distances). The WD formulations for multilayer networks are presented in De Domenico et al. (2015)	For networks where links are weighted based on constraints of flow (network distances), WD can indicate the tendency of a node to receive and transmit ecological flows based on landscape resistance. Likewise, for networks weighted based on dispersal probabilities, this metric is used to describe the strength of a node concerning the likelihood of emigration/colonisation processes (Minor and Urban 2007; Rayfield et al. 2011)	• `WD_cost`: for monolayer networks with links weighted based on network distances • `WD_disp`: for monolayer networks with links weighted based on dispersal probabilities • `multiWD_cost`: for multilayer networks with intralayer links weighted based on network distances • `multiWD_disp`: for multilayer networks with intralayer links weighted based on dispersal probabilities

Network metric	Description	Ecological applications	Acronyms
PageRank centrality: RStudio *igraph* package (Csardi et al. 2006) and *MuxViz* package (De Domenico et al. 2015)	This metric was applied to networks weighted based on cost attributes. PR centrality for a node x_i in a single-layered network can be seen as aethe stationary distribution of a random walk with additional random jumps (Halu et al. 2013) and it is given by: $x_i = \alpha^A \sum_j A_{ij}\frac{x_j}{g_j} + (1-\alpha_A)\frac{1}{N'}$ where N is the number of nodes in the network; A_{ij} are the elements of the adjacency matrix that are 1 whenever a node j points to node	Developed by Google's search engine, PR is a centrality metric based on a random walk (Brin andPage 1998; De Domenico et al. 2015). PR metrics calculate how well connected a node is with the rest of the network while considering the neighbourhood configuration (Kininmonth et al. 2019). When applied to our multi-slice network, PR assesses the role of a node as a connector between different parts, within and between layers, throughout a	• `PR`: for monolayer networks with links weighted based on network distances • `multiPR`: for multilayer networks with intralayer links weighted based on network distances

Table 2 continued

Network metric	Description	Ecological applications	Acronyms
	i or are 0 otherwise; g_j is given by $g_j = \max ?(1, k_j^{out})$, being k_j^{out}) the out-degree of node j; α_A is the probability that a random walker in site j jumps to another j's k_j^{out} out-neighbours (Halu et al. 2013). PR also describes the transition when a random walker (i.e., a generic propagule) jumps to a neighbouring node with a rate r and then aeteleports to any other possible node with a rate r' (De Domenico et al. 2015). The PR formulations for multilayer networks are presented in De Domenico et al. (2015)	year (node versatility, Costa et al. 2020)	

Network metric	Description	Ecological applications	Acronyms
Closeness centrality: RStudio *igraph* package (Csardi et al. 2006) and *MuxViz* package (De Domenico et al. 2015)	This metric was applied to networks weighted based on cost attributes. Closeness is the inverse of the sum of the shortest paths of node I to all other nodes in the network (Opsahl et al. 2010). Adaptations for multilayer networks are proposed by De Domenico et al. (2015), where 0 is assigned if the node is isolated and 1 if the node is connected to all other nodes in the network	Closeness assumes that a node is critical if it is located at a short distance from other nodes in the network (Bianconi 2018), thus having a favoured position to receive dispersal flows from other parts of the system (Borgatti 2005; Funk et al. 2023)	• `closeness`: for monolayer networks with links weighted based on network distances • `multiCloseness`: for multilayer networks with intralayer links weighted based on network distances

Network metric	Description	Ecological applications	Acronyms
Kleiberg's hub centrality scores (Hub): RStudio *igraph* package (Csardi et al. 2006) and *MuxViz* package (De Domenico et al. 2015)	This metric was applied to networks weighted based on the importance attribute. Node importance is defined by the principal eigenvector of AA^T, where A is the adjacency matrix of a graph (Kleinberg 1999). The mathematical formulation of multilayer Hub centralities is described in De Domenico et al. (2015)	This is a measure of how influential a node is, based on the principle that nodes with links pointing to an important node will generally have other links pointing to other important nodes (De Domenico et al. 2015). Influential habitat patches are responsible for a faster propagation of ecological flows in the network (Fang and Huang 2013; De Domenico et al. 2015)	• `Hub`: for monolayer networks with links weighted based on dispersal probabilities • `multiHub`: for multilayer networks with intralayer links weighted based on dispersal probabilities

[i.e., nodes located in central regions of the network are assigned higher importance than nodes in the periphery (marginal nodes)]. In this study, the selected centrality metrics calculate node-level connectivity using link attributes resembling costs and weights/importance (Tiwari et al. 2023). The definitions, applications, and acronyms used for each centrality metric are presented in Table 2. The centrality

measures *Strength* or *weighted degree*, *PageRank*, *Closeness*, and *Kleiberg's Hub centrality* were applied for monolayer networks (monolayer centralities; see Tiwari et al. 2023) and multilayer networks (multilayer centrality) using the R packages MuxViz and igraph (Csardi et al. 2006; De Domenico et al. 2015). As an additional step, we calculated the network-level average of each centrality (centrality profile) to the dynamic networks with 365 daily thresholds presented in the previous section "Building multilayer networks".

Comparing monolayer and multilayer centralities in capturing taxonomic diversity variations

We first described changes in the taxonomic diversity of the indicator groups of benthic macroinvertebrates for each of the time periods. Taxonomic diversity was defined in terms of:

- α **diversity**: observed species richness at each site, for each year separately (RStudio, package vegan Oksanen 2010). Significant differences in α diversity between years were assessed using the Kruskal–Wallis test and a post hoc pairwise comparison using Wilcoxon tests with p-values adjusted using Bonferroni correction.
- β **diversity**: pairwise dissimilarities in species composition among sampling units for a given region and spatial scale (spatial β diversity) (Anderson 2006). Significant differences in β diversity (Jaccard-based dissimilarities) between years were calculated using an analysis of similarities (ANOSIM) with 999 permutations (RStudio, packages vegan, and phyloseq Oksanen 2010; McMurdie and Holmes 2013). Recent studies (e.g. Heino and Grönroos 2017; Legendre and De Cáceres 2013) suggested the metric Local Contribution to beta diversity (LCBD) as a way to assign a β diversity uniqueness score to each assemblage in the study area. Following this approach, species abundances were Hellinger-transformed to calculate the LCBD using the abundance-based Jaccard index (Heino and Grönroos 2017) using the function "beta.div" of the package adespatial in RStudio (Dray et al. 2018). This function summarises each site's β diversity as the average of the pairwise dissimilarities between the focal site and all other sites in the study area.

To evaluate the relative importance of the different centrality metrics in explaining the variations on α diversity and LCBD, we used variable selection methods based on Partial Least Squares Regression (PLSR; Dobbert et al. 2021; Funk et al. 2023). To do so, we related the sampled sites' α diversity and LCBD (response variables) with their corresponding monolayer and multilayer centralities (predictors) using PLSR models (RStudio, packages pls, caret and mdatools Wehrens and Mevik 2007; Kuhn 2008; Kucheryavskiy 2020). PLSR is robust when many variables are considered for the calculations since it can perform well in front of multicollinearity and non-normally distributed data (Liu et al. 2018; Harnqvist et al. 2021). For the analyses, we scaled (normalised from 0 to 1) and centered all predictors.

We defined the model coefficients by (i) splitting the entire dataset into calibration (80%) and validation datasets (20%); (ii) determining the optimal number of components, as well as their significance, based on a permutation analysis on the calibration set (randtest function of the package mdatools in RStudio); (iii) calibrating the model using the external leave-one-out cross-validation on the calibration set; (iv) estimating performance statistics using the external validation set; and (v) estimating the inherent uncertainties of the models' performance based on jackknife variance estimates such as t-tests, standard error, p-values and 95% confidence intervals of the regression coefficients (Burnett et al. 2021). Further on, we evaluated the statistical importance of monolayer and multilayer centralities based on their Variable Importance in the Projection (VIP) scores and standardized regression coefficient (Crone et al. 2019). The VIP scores assess the contribution of each predictor variable as a cumulative measure of their influence in the relevant n number of components of the PLSR (Crone et al. 2019). VIP values > 1 are statistically important and were selected to build reduced PLSR models.

Results

Effects of LHC change on the structural properties of the floodplain landscape

For the time periods 1996, 1999, and 2020, we calculated the similarities in the intralayer links of each layer composing the multilayer networks. The
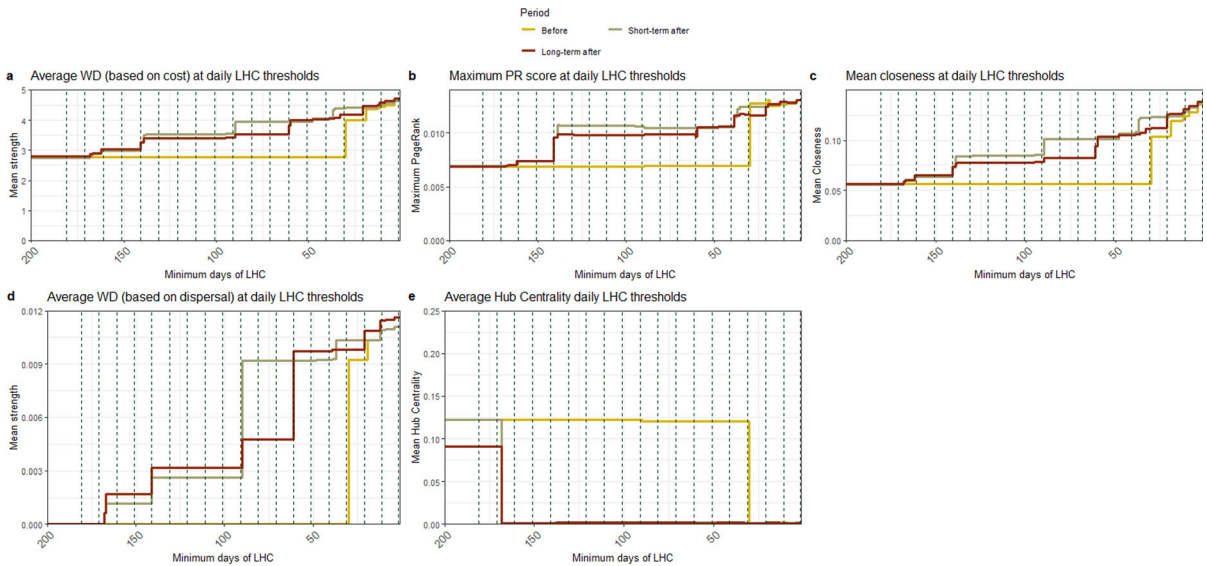
Fig. 5 Centrality profiles in dynamic networks, where layers follow daily sequential thresholds on inundation frequencies [minimum of days of lateral hydrological connectivity (LHC)]. Centralities working with a measure of link cost are **a** *weighted degree* (WD), **b** *PageRank* (PR), and **c** *closeness* centrality. Centrality works with dispersal probabilities as link weights are **d** *weighted degree* and **e** *Hub* centrality. Vertical dashed lines correspond to the thresholds used to build the multilayer networks (every 10 days until reaching a maximum threshold). The profile of each time period is represented with the colours yellow (before restoration), grey (short-term after restoration), and red (long-term after restoration). For all centrality metrics except Hub centrality, node-level connectivity was the highest for the time periods after restoration. However, in the long term, there was a decrease in connectivity

highest edge/link overlapping of multilayer networks was found in 1996 (45.67%), followed by 2020 (38.57%), and the lowest in 1999 (36.85%). The reason for this is that the network before restoration got fragmented at lower LHC thresholds (see Fig. 4). Hence, regardless of increasing LHC thresholds, network topologies of the layers remained similar at high LHC. On the contrary, the overlapping for the structural connectivity networks after restoration was lower, indicating more dynamic changes in landscape structure caused by the enhancement of LHC frequencies. The overlapping in structural connectivity networks decreased by 8.8% short-term after restoration, concerning before restoration. However, in the long term, it only decreased by 7.1% (compared to the time before restoration).

Key landscape areas for maintaining connectivity at a network level

To quantify changes in node-level connectivity and identify central areas crucial for maintaining connectivity, we ranked nodes using four centrality metrics:

weighted degree (WD), *PageRank* and *Closeness centrality*, and *Hub centrality* (Figs. 5, 6, 7). First, we examined how monolayer centralities changed along daily LHC thresholds. In Fig. 5, we present the differences between the average values of monolayer centralities at each time period. For visualization reasons, the x-axis starts with a minimum of 200 days of LHC a year (this includes only nodes highly connected to the main river channel) to 0 days a year (including all the nodes present in the river–floodplain landscape). For monolayer centralities, except for *Hub centrality*, the highest values were found short-term after restoration. The ten days/yr thresholds used to build the layers in multi-slice networks captured most of the yearly variability in the centrality metrics (represented as dashed lines in the plots of Fig. 5).

In the case of centralities working with a cost measure as a link attribute, significant differences were found between the rankings obtained from multilayer networks and those obtained from monolayer networks. Regarding centrality metrics working with a measure of cost as a link attribute, the rankings of *WD*, *PageRank*, and *Closeness centrality* differed
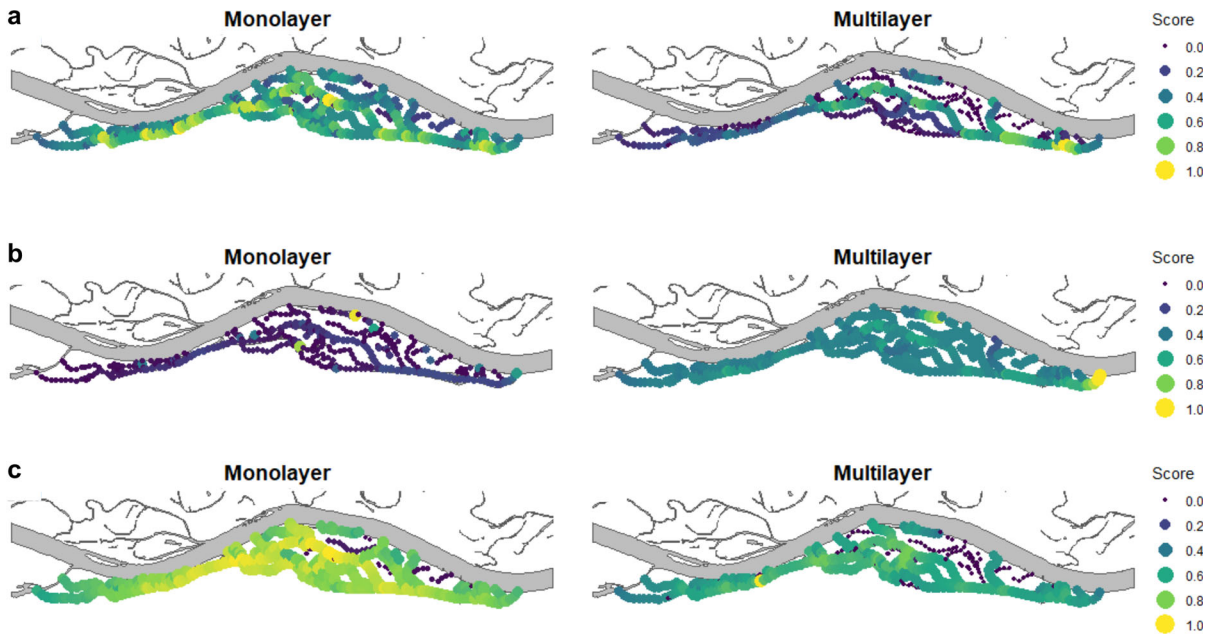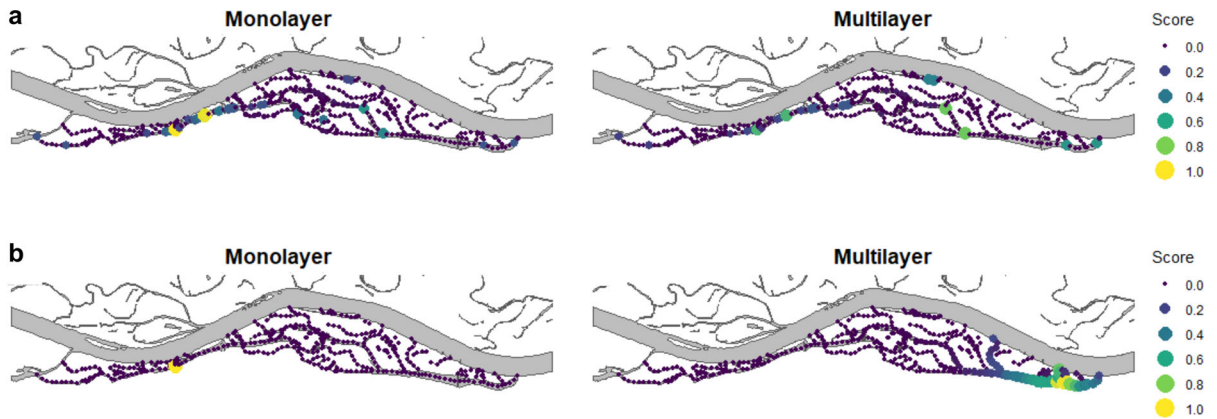
Fig. 6 Spatial distributions of monolayer and multilayer centrality scores (the time period of 2020) for centrality metrics working with network distances as link cost attribute: **a** Strength or weighted degree, **b** PageRank and **c** Closeness centrality. Monolayer weighted degree and PageRank highlight the topological network characteristics with high scores at junctions and the largest connected components, while Multilayer weighted degree shows local connectivity patterns resembling inundation frequencies [lateral hydrological connectivity (LHC)] and Multilayer PageRank assigned a higher importance to downstream regions. Monolayer closeness centralities assigned the highest importance to central regions in the network

Fig. 7 Spatial distributions of monolayer and multilayer centrality scores (time period of 2020) for centrality metrics working with dispersal probabilities as link weights: **a** Strength or weighted degree and **b** Hub centrality. In the case of weighted degree, both Monolayer and Multilayer types ranked similar areas with high importance. Monolayer Hub centrality found fewer hubs than the Multilayer type

between monolayer and multilayer types. The spatial distribution of high scores also changed for multilayer centralities, which considered LHC frequencies (Fig. 6). The scores of monolayer *WD* (WD_cost, Fig. 6a) highlight the topological characteristics of the network, assigning high scores at junctions and at the largest connected component (the biggest fully connected graph cluster). However, the spatial distributions of multiWD_cost show local connectivity patterns that resemble those of LHC frequencies

(Fig. 6a; Fig. S1a of the Supplementary Material). In a similar way, monolayer *PageRank* (PR) centrality assigned high rankings to similar areas (Fig. 6c), regardless of the time periods (Fig. S2 of the Supplementary Material). However, for multiPR, there was a difference in the rankings between the time period from before restoration and the ones after restoration (Fig. S2 of the Supplementary Material). For *Closeness centrality* (closeness), high scores derived from monolayer networks were more distributed more in the central regions of the landscape in comparison to multiCloseness. However, for monolayer and multilayer *Closeness centralities*, the scores varied slightly between time periods (Fig. S3 of the Supplementary Material).

As for metrics working with **dispersal probabilities** as link importance attribute, the rankings of the centralities *WD* and *Hub centralities* also differed between monolayer and multilayer types. In the case of *WD*, both monolayer WD_disp and multilayer multiWD_disp ranked similar areas with high importance (Fig. 7a). The differences between time periods are more marked in multiWD_disp (Fig. S1b of the Supplementary Material). As for *Hub centralities*, monolayer centralities found fewer hubs than multilayer centralities (Fig. 7b). In the time periods after restoration, multiHub found more Hubs in the most downstream regions of the landscape (Fig. S4 of the Supplementary Material).

Comparing monolayer and multilayer centralities for habitat connectivity in benthic macroinvertebrate communities

Overview of changes in α and β diversity of indicator groups

The number of Oligochaeta and Chironomidae taxa found over the years, respectively, was 36 and 52 in 1996; 41 and 44 in 1999; and 61 and 72 in 2020. In 1996, the dominant Chironomid taxa were the genera *Tanytarsus* and *Procladius*. By 1999, the dominance of the genus *Polypedium* had increased, whereas by 2020, *Procladius* emerged as the dominant genus. Meanwhile, for Oligochaetes, the family Tubificidae remained the most dominant taxon throughout all years. In 1999, there was an increase in the dominance of *Amphicaeta ledigii*, whereas by 2020, there was an increase in the dominance of the genus *Nais*.

Mean values of α and β diversity were the highest after restoration (Table 3). For α diversity, significant differences were found between all time periods for Chironomids (H = 33.936, d.f. = 2, $p < 0.001$). As for Oligochaetes, significant differences were found in α diversity for all time periods, except between 1999 and 2020 (W = 2030, d.f. = 1, $p > 0.05$, Table 3). Regarding the dissimilarities in community composition between sites (spatial β diversity), we observed significant differences between all time periods for Oligochaetes (ANOSIM: R = 0.160, $p = 0.001$), as well as for Chironomids (ANOSIM: R = 0.216, $p = 0.001$). For both groups, spatial β diversity changed following the restoration, where the year with the highest dissimilarities was 1996. The list of taxa for each year and visualizations of ANOSIM for β diversity between years are provided in Table S1 and Figs. S5, S6 of the Supplementary Material.

Partial least squares regression (PLSR)

The performance statistics of PLSR models are presented in Table 4 and Table S2 of the Supplementary Material. When considering all years together, the PLSR models that combined both monolayer and multilayer centralities had the highest performance for predicting the variance in α diversity of Oligochaetes (variance explained = 23.41%) and LCBD of Chironomids (variance explained = 19.68%, Table 4). However, when calculating PLSR models of each centrality type separately, multilayer centralities were better predictors of the variance in LCBD of Oligochaetes (variance explained = 7.83%). In contrast, monolayer centralities were better predictors of the variance in α diversity of Chironomids (variance explained = 19.20%).

The importance of different centrality metrics for explaining taxonomic diversity varied between indicator groups. As in our expectations, the most important predictors for the taxonomic diversity of Oligochaetes (VIP scores > 1) were mainly multilayer centralities (Figs. 8c, d, 9c, 9d). For both α diversity and LCBD of Oligochaetes, multiWD_cost was the strongest predictor and had the highest VIP scores (Figs. 8c, 9c; Table S3), while multiHub and multiPR were also strong predictors. In contrast, our expectations were confirmed only for the α diversity of Chironomids, as the variance in α diversity was better explained by centralities calculated based on static representations of the landscape (monolayer

Table 3 Kruskal–Wallis test and Wilcoxon test as a post hoc test with Bonferroni-corrected p-values for observed species richness (α diversity), as well as the results of Analysis of Similarities (ANOSIM) for β diversity between years

Diversity metric	Statistical test						
α Diversity: observed species richness				Chironomidae		Oligochaeta	
	Average ± sd	Year group					
		1996		4.92 ± 3.2		5.39 ± 2.5	
		1999		5.86 ± 2.5		9.21 ± 3.2	
		2020		7.96 ± 3.5		9 ± 4.2	
	Kruskal–Wallis test	Year group	df	H	p-value	H	p-value
		1996/ 1999/ 2020	2	33.936	4.275e−08***	55.268	9.973e−13***
	Wilcoxon (post hoc) tests	Year group	df	W	p-adjust	W	p-adjust
		1996/ 1999	1	1534.5	0.0665	863.5	5.276e−10***
		1996/ 2020	1	1850	5.097e−08***	2057.5	6.204e−09***
		1999/ 2020	1	1178	0.007**	2030	1
β Diversity: LCBD	Average ± sd	Year group					
		1996		0.011 ± 0.005		0.01 ± 0.003	
		1999		0.023 ± 0.009		0.021 ± 0.009	
		2020		0.013 ± 0.005		0.012 ± 0.004	
	Analysis of Similarities (ANOSIM)	Year group	df	R	p-value	R	p-value
		1996/ 1999/ 2020	2	0.208	0.001***	0.132	0.001***
		1996/ 1999	1	0.087	0.012*	0.095	0.014*
		1996/ 2020	1	0.255	0.001***	0.149	0.001***
		1999/ 2020	1	0.265	0.001***	0.152	0.001***

H Kruskal–Wallis test statistic, *W* Wilcoxon post hoc test statistic, *p-adjust* (Wilcoxon tests): Bonferroni-corrected p-value, *R* ANOSIM test statistic

Statistical difference: *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

centralities), `closeness` being the most important predictor (Fig. 8a; Table S3 of the Supplementary Material). In contrast, multilayer centralities had higher importance for LCBD of Chironomids. In this case, the variables with the highest scores were `multiHub`, `multiCloseness`, and `multiPR`

Table 4 Fit Partial Least Squares Regression (PLSR) statistics for the optimal number of components (ncomp) with α diversity and Local Contributions to Beta Diversity (LCBD) as response variables

Chironomids

PLSR model		α Diversity: observed species richness							LCBD: abundance-based Jaccard						
		ncomp	α (signif.)	$RMSEP_c$	$RMSEP_v$	R^2_c	R^2_v	Y var.	ncomp	α (signif.)	$RMSEP_c$	$RMSEP_v$	R^2_c	R^2_v	Y var.
Combined	Full	1	0.001	3.322	3.3427	0.1106	0.0414	13.60%	2	0.007	0.1794	0.174	0.1968	0.1445	19.68%
	Reduced	1	< 0.001	3.253	3.2488	0.1429	0.0637	14.29%	1	< 0.001	0.1842	0.1696	0.153	0.15	15.30%
Only monolayer	Full	2	< 0.001	3.075	3.7593	0.192	0.0217	19.20%	1	0.006	0.1941	0.1995	0.0507	0.005	6.44%
	Reduced	2	0.011	3.147	3.661	0.1539	0.0461	15.39%	1	< 0.001	0.1905	0.2017	0.0574	0.0032	7.54%
Only multilayer	Full	1	0.001	3.374	2.9343	0.1436	0.0891	8.78%	1	< 0.001	0.187	0.1744	0.1161	0.1245	11.61%
	Reduced	1	< 0.001	3.411	2.945	0.0792	0.0767	7.92%	1	< 0.001	0.1857	0.1722	0.1288	0.1492	12.88%
Oligochaetes															
Combined	Full	2	0.033	3.433	3.0051	0.2082	0.3682	23.41%	1	0.013	0.843	0.698	0.046	0.1628	5.89%
	Reduced	1	< 0.001	3.369	3.4439	0.204	0.0983	20.82%	1	0.011	0.8487	0.7408	0.1275	0.0494	4.60%
Only monolayer	Full	1	0.031	3.154	3.4373	0.1501	0.10609	4.40%	1	> 0.05	0.8419	0.8714	0.004	0.0117	0.40%
	Reduced	1	0.009	3.686	3.4861	0.0528	0.0701	5.28%	1	> 0.05	0.8415	0.8713	0.0049	0.0079	0.75%
Only multilayer	Full	1	< 0.001	3.424	3.2874	0.1938	0.1509	19.38%	1	0.002	0.7804	0.8295	0.0232	0.0019	7.83%
	Reduced	1	<0.001	3.363	3.3483	0.2223	0.1488	22.23%	1	< 0.001	0.8214	0.8417	0.0837	0.0001	8.37%

α (*signif.*) significance of the selected component (Wiklund et al. 2007), $RMSEP_c$ root mean squared error of prediction for the calibration set, $RMSEP_v$ root mean squared error of prediction for the validation set, R^2_c variance explained in the training data for the calibration set, R^2_v variance explained in the training data for the validation set, *Y explained var.* variance of the response variable cumulatively explained by the selected components
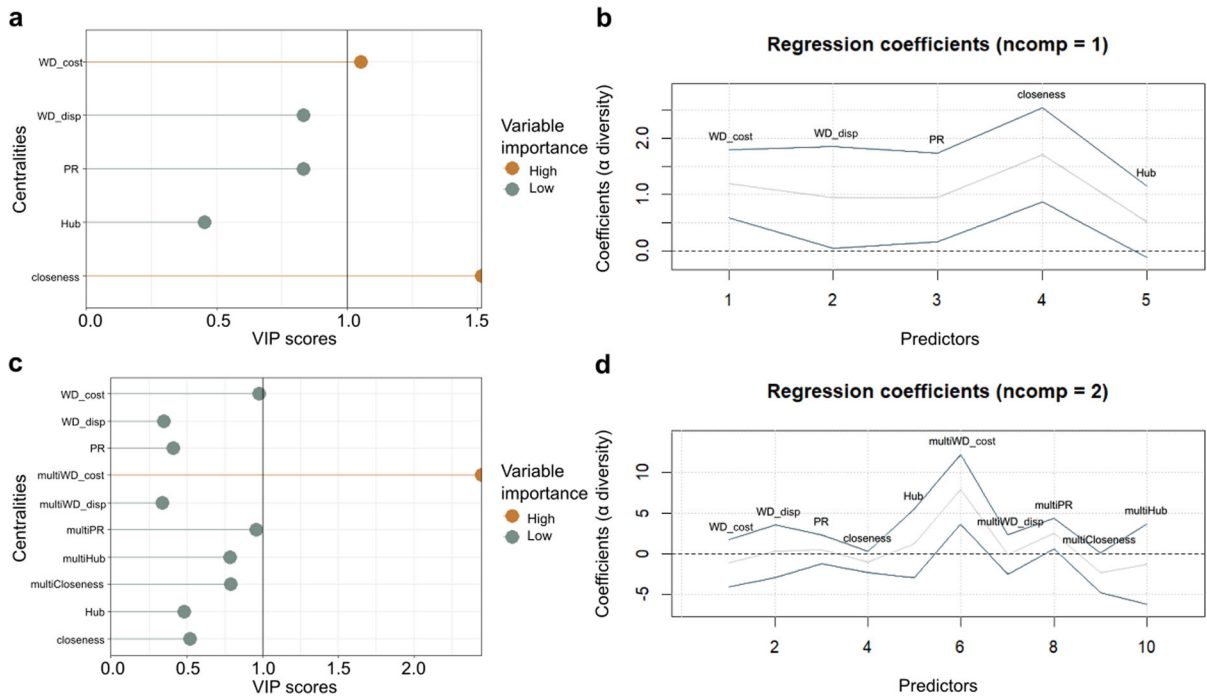
Fig. 8 Variable Importance in the Projection (VIP) and standardized regression coefficients (SRC) for the optimal number of components (ncomp) in full partial least squares regression (PLSR) models that best explained the variation in the α diversity of Chironomids and Oligochaetes. VIP scores for PLSR models (orange: VIP > 1; grey: VIP < 1) for Chironomids (**a**) and Oligochaetes (**c**), as well as the standardized regression coefficients (grey line) for Chironomidae and Oligochaetes (**b**,

d) with their 95% confidence intervals based on jackknife analysis (blue lines). For Chironomids, WD_cost and closeness were the most important variables, reflecting the importance of the spatial arrangement of habitat patches for this group. For Oligochaetes, multiWD_cost was the only important variable, which shows the importance of dynamic changes in LHC. Centrality metrics had positive relationships with α diversity in both indicator groups

(Fig. 9a; Table S3 of the Supplementary Material). Notably, regression coefficients in Fig. 8b, d indicate that the centrality metrics had positive relationships with α diversity in both indicator groups, within the context of the observed changes over time. The results of PLSR models for each year separately are presented in Tables S2 and S4 of the Supplementary Material.

Discussion

Our results emphasize the importance of incorporating pertinent hydrological factors, such as inundation frequencies, in calculating water-mediated connectivity, extending beyond only considering the pairwise distances between habitat patches. For monolayer networks (network-based representations of static aquatic corridors), there was an increase in node-level connectivity after restoration, except for *Hub*

centrality. Similarly, centrality profiles showed an increase after restoration, except for *Hub* centrality. For centrality profiles, the increase in connectivity was the highest in the short-term and decreased over the long-term. Multilayer centralities captured, simultaneously, the link additions and the increase in more dynamic LHC conditions after the restoration. Similar to centrality profiles, the highest values were found short-term after restoration, with a slight decrease in the long-term. Meanwhile, the network-level metric *Edge overlap* also supported these findings. For this metric, the highest dissimilarities between layers were found in the short-term due to the increase of aquatic corridors. The observed reduction of connectivity in the long-term aligns with previous findings documented by Klasz et al. (2013), Pessenlehner et al. (2016) and Tockner et al. (1999). These studies point to the riverbed incision of the Danube channel as the possible cause of the decrease in LHC and gradual
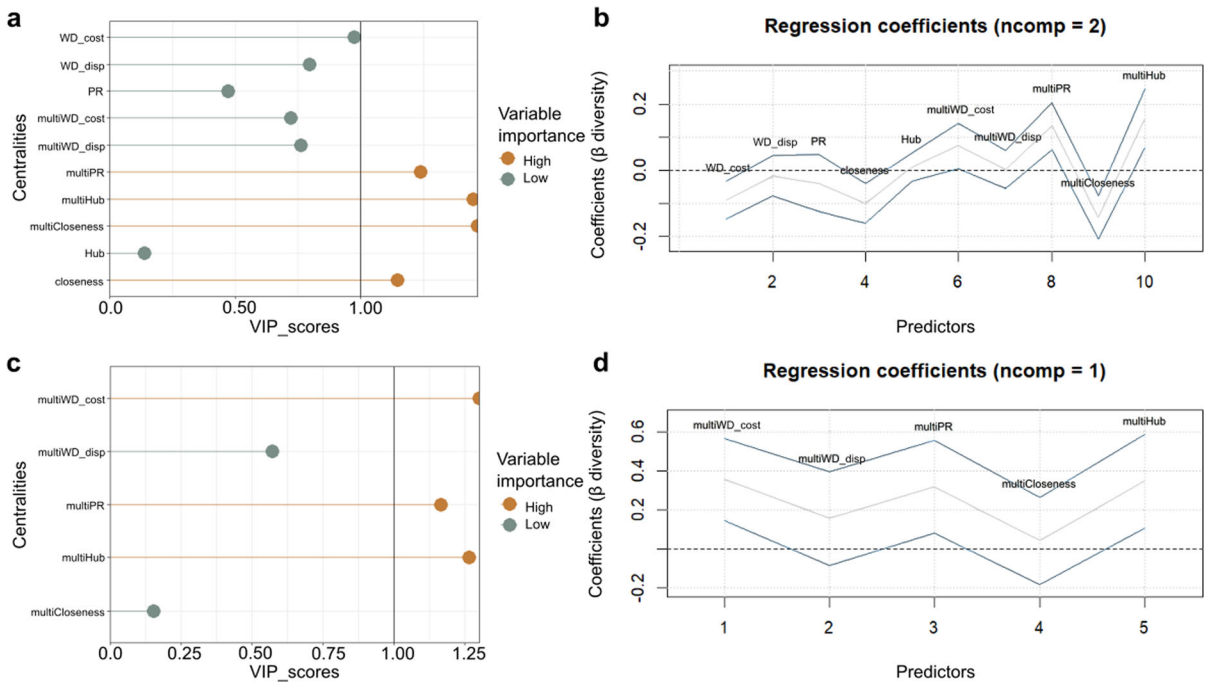
Fig. 9 Variable Importance in the Projection (VIP) and standardized regression coefficients for the optimal number of components (ncomp) in full partial least squares regression (PLSR) models that best explained the variation in the Local Contributions to Beta Diversity (LCBD) of Chironomids and Oligochaetes. VIP scores for PLSR models (orange: VIP > 1; grey: VIP < 1) for Chironomids (**a**) and Oligochaetes (**c**), as well as the standardized regression coefficients (grey line) for Chironomidae and Oligochaetes (**b**, **d**) with their 95%

confidence intervals based on jackknife analysis (blue lines). For Chironomids and Oligochaetes, multilayer centralities had higher importance, which shows the importance of dynamic changes in lateral hydrological connectivity (LHC) for LCBD. For Chironomids, the variables with the highest scores were `multiHub`, `multiCloseness`, and `closeness`, while for Oligochaetes, the most important variables were `multiWD_-cost`, `multiHub`, and `multiPR`

decoupling of side-channel systems in the Donau-Auen National Park.

In dynamic systems such as floodplains, assumptions of monolayer networks can emphasize key spatial features such as the arrangement of habitat patches and a patch's importance based on its network position. However, these networks often ignore potential temporal variation in the presence/absence of dispersal corridors or habitat patches, which can bring misleading insights into the overall habitat patch's importance (monolayer centrality scores, Bishop-Taylor et al. 2018). In their work, Bishop-Taylor et al. (2018) and Funk et al. (2023) evaluated centralities derived from static network approaches versus those derived from dynamic networks. Bishop-Taylor et al. (2018) highlight the value of assessing connectivity in spatiotemporally variable landscapes using a more data-intensive dynamic network approach. The multilayer network framework stands

out by simultaneously considering all layers and their interconnected structures when calculating centralities, which enables it to emerge as a powerful alternative (De Domenico et al. 2015; Bianconi 2018). In their work, De Domenico et al. (2015) introduced the mathematical formulations of centrality metrics, including those utilized in this study, adapted to multilayer networks. They found that multilayer centralities can avoid the limitations of approaches that aggregate the information into a single layer or of dynamic approaches that compute centralities individually for each layer of a dynamic network [e.g., limitations may include neglecting the interconnections between replica nodes, thus overestimating the importance of the most marginal nodes (nodes in the periphery)]. The capability of accounting for interconnected structures between layers is crucial for evaluating the importance of nodes within systems characterized by complex relationships (De Domenico

et al. 2015), as seen in the case of evaluating the importance of habitat patches in dynamic landscapes. Thus, multilayer centralities are suggested to be good descriptors of dynamic aspects of empirical network topologies, which are inherently multilayer (De Domenico et al. 2015).

Temporal changes in habitat connectivity and benthic macroinvertebrate community

For both indicator groups, α and β diversity changed significantly between time periods. The year with the highest dissimilarity ranks in spatial β diversity was 1996. A possible explanation for these high dissimilarity ranks is that, before restoration, less connected communities had greater variability in species composition. By re-establishing more dynamic LHC conditions, the side-channel reconnection measures increased the importance of stochastic ecological processes in localised areas of the network, thus reducing dispersal limitation. Restoration measures could also affect both stochastic and deterministic processes that shape Benthic Macroinvertebrate assemblages (Larsen et al. 2019). For this same study area, Funk et al. (2023) found that node-level directed connectivity affects sediment transport and composition, which is a key determinant of habitat heterogeneity for benthic macroinvertebrates (Johnson 1984; de Haas et al. 2005). However, it is important to notice that habitat heterogeneity is also shaped by other factors such as riparian vegetation, patches of macrophytes, topography, or other autogenic processes (Junk et al. 1989; Tockner et al. 2000; Chaparro et al. 2018). In the short-term, restoration might have influenced both deterministic and stochastic factors, creating heterogeneous young communities. However, in the long-term, more mature communities might be shaped predominantly by deterministic processes (e.g., habitat filtering and resource requirements) (Larsen et al. 2019). Additionally, the ongoing river bed incision and associated long-term decrease in connectivity (decrease in the duration and frequency of the inflows into the side-arms) may simultaneously increase the prevalence of species sorting. This complex interplay highlights the necessity for including detailed environmental data to better understand the dynamics at play.

For Chironomids, both monolayer and multilayer centralities were good predictors of the variance in α diversity and LCBD, respectively. The metrics `closeness` and `multiCloseness` had the highest importance for α diversity and LCBD of Chironomids. Monolayers and multilayers *closeness* centralities depicted different aspects of habitat connectivity. According to *closeness*, nodes of high importance are located in the central regions of the network (Bianconi 2018), where they are at shorter network distances to other nodes. Thus, `multiCloseness` captures how this importance changes depending on the presence/absence of aquatic corridors, although is less influenced by LHC conditions compared to other metrics. Both *closeness* centralities are significantly related to Chironomids' taxonomic diversity, which indicates that the effect of spatial patterns, like the spatial arrangement of habitat patches, is more influential to their community assemblages than other connectivity properties (Cáceres and Soluk 2002; Armitage et al. 2012). For this group, the variance in LCBD was better explained by both types of connectivity predictors than the variance of α diversity. Chironomids present variations in dispersal modes and abilities depending on their life cycle (Milošević et al. 2022). Chironomidae larval dispersal occurs passively, driven by water currents, while the imago exhibits limited flying ability to disperse overland (Davies 1976; Armitage et al. 2012). Therefore, adult dispersal may enable Chironomids to colonise habitat patches, with less reliance on aquatic corridors and more on the proximity to other neighbouring patches.

Our findings show that the property of landscape resistance, captured by multilayer centralities `multiWD_cost` and `multiPR`, was the most influential property for Oligochaeta (strict aquatic dispersers) assemblages. Both multilayer centralities are based on notions of landscape resistance (cost link attribute). The `multiWD_cost` centrality calculated the strength of the connections of a habitat patch along dynamic LHC conditions, while the other, `multiPR`, relied on random walks. The notable significance of both `multiWD_cost` and `multiPR` in terms of variable importance can be attributed to the greater dispersal limitation observed in Oligochaetes compared to Chironomids (Petsch et al. 2017; Armendáriz et al. 2022). Oligochaetes are strict aquatic dispersers with a passive dispersal mode, their life cycle is mainly restricted to sediments (Martin et al. 2008; Petsch et al. 2017). For this indicator group, metrics

that included dynamic LHC conditions were expected to be more influential (Zilli and Marchese 2011). While, overall, multilayer centralities explained most of the variance in taxonomic diversities, the variance in LCBD was explained to a lesser extent than the one of Chironomids. Schmera et al. (2018) found that the variance in non-flying benthic macroinvertebrates taxa was explained to a lesser extent by environmental and spatial predictors than that of flying taxa. This might be explained by (i) the fact that distinct taxa might respond differently to isolation effects; (ii) the timing of sampling can impact the relative influence of environmental and spatial factors; (iii) the scale dependency in the spatial distribution of sampling sites or incomplete detection; (iv) individual systems might exhibit substantial variability in the relative significance of environmental or spatial predictors (Göthe et al. 2013; Tonkin et al. 2016; Schmera et al. 2018).

In our approach, by focusing exclusively on flow-mediated passive downstream dispersal events, we ensured that the connectivity changes due to restoration are appropriately captured. We exemplified with a scenario the applications of monolayer and multilayer network approaches, reducing the complexity of dispersal processes for Chironomids and Oligochaetes to downstream movement. However, we acknowledge that the assumptions in our scenario model limit the representation of adult Chironomid dispersal capabilities and the upstream dispersal of Oligochaetes. While this approach simplifies our model, it remains an area for future research to incorporate different dispersal modes and abilities to gain a more complete knowledge of the habitat connectivity of benthic macroinvertebrates. Further steps can include investigating the performance of different combinations of upstream/downstream kernel parameters to represent different modes and abilities to reflect taxon-specific dispersal within the water column (see Borthagaray et al. 2015). Additionally, while the methodological focus of our paper emphasizes the novel application of multilayer networks to assess habitat connectivity in floodplain ecosystems, we also acknowledge that it is crucial to include local environmental factors and have a designated control group for assessing the outcomes of restoration on benthic macroinvertebrates (Larsen et al. 2019; Al-Zankana et al. 2020). Therefore, we interpret our findings within the context of observed changes over time in our model scenario rather than

attributing them solely to restoration activities. Nonetheless, in this study area, the immediate effects of restoration in enhancing dynamic LHC conditions in the short-term are evident in Schiemer and Reckendorfer (2004), Reckendorfer and Steel (2004), Schiemer et al. (2007), and Reckendorfer et al. (2006). Considering changes in deterministic and stochastic factors and their effect in shaping various facets of benthic macroinvertebrates biodiversity (e.g., taxonomic, functional, or phylogenetic diversity) will help in understanding how restoration affects both assembly mechanisms and the spatiotemporal scales on which these mechanisms operate. This is appropriate for testing hypotheses referring to community assembly theory and ecological succession (Paillex et al. 2013; Larsen and Ormerod 2014; Larsen et al. 2019).

Applications for management

Restoration projects that seek to maintain and enhance habitat connectivity to support biodiversity are crucial for endangered ecosystems such as floodplains (Hein et al. 2016). Yet, for this case study, the planning of restoration projects must include long-term solutions to the current connectivity loss trends that result from the ongoing bed degradation of the main river channel (Reckendorfer et al. 2006; Klasz et al. 2013). Consequently, the effective conservation and restoration of natural areas requires an integrated view of how biota interact with their habitats (Timóteo et al. 2018).

The toolset used to model connectivity changes induced by restoration measures, designed to restore connectivity, should recognise the dynamic nature of floodplain landscapes. In this study, we recommend the use of multilayer network analyses since it brings the potential to prioritize restoration efforts and monitor their effectiveness over time. This framework represents an appropriate tool for assessing connectivity in highly dynamic ecosystems like floodplains, as it integrates both spatial and temporal dimensions into connectivity analyses (Pilosof et al. 2017; Hutchinson et al. 2019; Costa et al. 2020), thereby providing a more accurate measure of the effects of restoration on reducing dispersal limitations for aquatic biodiversity.

The contributions of multilayer network toolsets are expanding with increased availability of freely accessible resources (e.g. Dormann et al. 2009; De

Domenico et al. 2015; Farage et al. 2021. Previous works by De Domenico et al. (2013, 2015) introduced a mathematical framework to compute multilayer centralities using a tensorial approach and provided an open-source tool for connectivity analyses using multilayer networks (R package MuxViz De Domenico et al. 2015). This has influenced recent methodological developments in ecology that go beyond monolayer centralities (Timóteo et al. 2018; Finn et al. 2019; Costa et al. 2020; Farage et al. 2021), which offers practical applications for planning management measures.

Evaluating restoration measures is a crucial aspect of management. Connectivity factors play an important role but can be overshadowed by the significance of local environmental factors (Schmera et al. 2018; Saigo and Marchese 2021; Tiwari et al. 2024). Therefore, to understand the potential effects of changes in water-mediated connectivity in floodplains, it is essential to differentiate the roles of environmental and connectivity factors, as well as their combination and cascaded effects (Funk et al. 2023). For future research directions, we suggest that future studies follow the important guidelines provided by Al-Zankana et al. (2020) in order to assess restoration outcomes using responses from benthic macroinvertebrates: (i) employing a Before–After-Control-Impact (BACI) study design; (ii) accounting for seasonal or annual variations that could affect Benthic Macroinvertebrate community composition; (iii) conducting multi-habitat sampling of the Benthic Macroinvertebrate community; (iv) include diversity indices that go beyond the most commonly used taxonomic diversity indices, such as unbiased estimators (Hurlbert 1971), ecosystem functional indicators (Reckendorfer et al. 2006; Neale and Moffett 2016; Funk et al. 2017), and functional diversity indices (Coccia et al. 2021; Magneville et al. 2022).

Conclusions

Multilayer networks provide a novel and promising approach for integrating dynamic changes in LHC conditions to assess floodplain ecosystems' habitat connectivity. In this study, we present the first application of multilayer networks under a flow-mediated passive dispersal scenario to estimate changes in habitat connectivity in floodplain ecosystems. The tools used in this study were appropriate for assessing the changes in aquatic habitat connectivity for the selected groups of benthic macroinvertebrates, following floodplain restoration measures. Our centrality analysis and edge overlap metric indicated a short-term increase in aquatic habitat connectivity after restoration, which decreased slightly in the long-term. Multilayer centralities, which incorporated LHC frequencies, outperformed monolayer centralities in explaining changes in taxonomic diversity, particularly for Oligochaetes (α diversity and LCBD) and Chironomids (LCBD). Post-restoration, the taxonomic diversity of both groups increased, with multilayer centralities proving most significant for Oligochaetes. For Chironomids, both monolayer and multilayer centralities, which capture the spatial arrangement of habitat patches within the network, were the most influential. In future steps, adopting a Before–After-Control-Impact (BACI) study design, as well as including both environmental and other deterministic and stochastic factors that shape different facets of benthic macroinvertebrates diversity is recommended to gain insights into how restoration impacted their community assemblages.

Data availability The code for network analysis, as well as the count of Oligochaetes and Chironomids, is archived on Github-https://www.github.com/ESR-Sonia/MLLC.

Declarations

Conflict of interest We declare that this research was conducted in the absence of any business or financial relationship that may cause a conflict of interest.

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