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Water-controlled ecosystems as complex networks: Evaluation of network-based approaches to quantify patterns of connectivity

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Abstract

This study provides a new perspective on understanding the intricacies of water-mediated connectivity in ecosystems, bridging landscape ecology and geomorphology through network science. We highlight dryland and river-floodplain ecosystems as distinct examples of contrasting water-controlled systems. We (1) discuss central considerations in developing structural connectivity and functional connectivity networks of water-mediated connectivity; (2) quantify the emergent patterns in these networks; and (3) evaluate the capacity of network science tools for investigating connectivity characteristics. With a focus on strength (weights) and direction, connectivity is quantified using seven parameters at both network and node levels. We find that link density, betweenness centrality and page rank centrality are highly sensitive to directionality; global efficiency and degree centrality are particularly sensitive to weights; and relative node efficiency remains unaffected by weights and directions. Our study underscores how network science approaches can transform how we quantify and understand water-mediated connectivity, especially in consideration of the role(s) of weights and directionality. This interdisciplinary perspective, linking ecology, hydrology and geomorphology, has implications for both theoretical insights and practical applications in environmental management and conservation efforts.

KEYWORDS
dryland ecosystem, emergent patterns, functional connectivity, network theory, river-floodplain ecosystem, structural connectivity

1 | INTRODUCTION

Ecosystems are inherently connected systems, with intricate webs of interactions that are significantly driven by hydrological processes across scales—from the flow of water shaping individual habitats to large-scale watershed dynamics (Abed-Elmdoust et al., 2017; Czuba & Foufoula-Georgiou, 2015; Fausch et al., 2002; Laio et al., 2001; Larsen et al., 2012; Torgersen et al., 2022; Turnbull, Wainwright,

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Brazier, 2010). Connectivity defined as the degree of linkage between the various components of a system is critical in shaping the structure and function of water-controlled ecosystems (Allan & Castillo, 2007; Bracken & Croke, 2007; Corenblit et al., 2011; Turnbull et al., 2008; Urban & Keitt, 2001). Therefore, by quantifying connectivity patterns, we can better understand the controls on the characteristics of these ecosystems (Maestre et al., 2016; Taylor et al., 1999; Turnbull et al., 2008; Wiens, 2002), which is ultimately important for their management and conservation.

While conventional ecological and geomorphological methods capture valuable aspects of water-controlled ecosystems, they can face limitations in quantification of the connectivity and capturing hidden patterns of their dynamism and spatial intricacies (Jacoby & Freeman, 2016; Martensen et al., 2017; Phillips et al., 2015). Traditional approaches, such as field surveys and remote sensing, can provide detailed snapshots of ecosystem components and processes, but they may struggle to fully capture the dynamic nature and multi-scale connectivity patterns that drive ecosystem behaviour (Turnbull et al., 2018).

To address these limitations, there is a growing recognition of the need for more integrative, multi-scale approaches that can better capture the complexity and dynamism of water-controlled ecosystems (Turnbull et al., 2018). Over the last two decades, network theory has been used to explore and quantify connectivity in complex systems, where a network is graph-based representation of individual elements (e.g., habitats, local populations/communities or geomorphic units) as nodes and their interactions or potential resource flows as links (Aleta & Moreno, 2019; Barabási, 2012; Barabási et al., 2002; Tiwari et al., 2020; Turnbull et al., 2018). Tejedor et al. (2015) presented a graph-theoretic approach for studying connectivity and steady-state transport on deltaic surfaces, enabling the computation of flux distributions and the construction of vulnerability maps. Abed-Elmdoust et al. (2017) investigated the eigenvalue spectra of river network adjacency matrices, revealing distinct patterns related to the branching topology. These studies highlight the potential of network-based methods to capture the complex, multi-scale nature of connectivity in water-controlled ecosystems. The key idea behind network theory is that it is possible to obtain valuable information about system-level behaviour and pinpoint critical locations for conservation or intervention by studying system's underlying network topology (Barabási & Crandall, 2003). Once constructed, network connectivity can be quantified using mathematical graph metrics. However, the quantification and interpretation of network metrics depend on whether links are weighted/unweighted or directed/undirected (Barrat et al., 2004), where weighted networks account for connectivity strength while directed networks capture asymmetry. Network-based approaches can support two distinct modes of connectivity analysis: structural connectivity (SC) and functional connectivity (FC). SC focuses on the physical arrangements of landscape elements (Metzger & Decamps, 1997; Wainwright et al., 2011), whereas FC focusses on the connectivity arising from dynamical processes, such as flow of water, resources, organisms or energy (Bracken & Croke, 2007; Czuba & Foufoula-Georgiou, 2015; Schumaker, 1996; Tischendorf & Fahrig, 2000). Larsen et al. (2012) emphasized the importance of considering directionality when quantifying connectivity, as it provides critical information for predicting transport processes and understanding landscape responses to directional forces.

The conceptualization of water-mediated connectivity and its subsequent network-based representation can include both the ecological and geomorphic components of an ecosystem (Figure 1a). In a landscape-ecology context (referred to as an ecological perspective hereafter), connectivity is the extent to which the landscape impedes or facilitates the dispersal of organisms and gene-flow modulation (Figure 1b) (Minor & Urban, 2008; Turner et al., 2015). From a geomorphic perspective, connectivity can be linked to the flow of water and sediments between the landscape unit (Figure 1c) (Bracken et al., 2015; Wohl et al., 2019).

The representation of ecosystems as networks—to enable quantification of connectivity—is dependent on ecosystem characteristics (such as weather, system boundaries and flow pathways) and the disciplinary perspective from which connectivity is approached (i.e., whether the focus is on biotic or abiotic components of a system or on the interplay between the two) (see Table 1 for a brief overview of applications of network theory in dryland and floodplain ecosystems). The aim of this perspective article is to investigate the network-based representation of water-mediated connectivity based on the combined disciplinary perspectives of ecology and geomorphology using two contrasting endmembers of water-controlled ecosystems: drylands and river-floodplains (overview of these water-controlled ecosystems is presented in Table 1). Specifically, we address three key questions: (i) how to develop SC and FC networks of water-mediated connectivity; (ii) how to quantify the emergent patterns of connectivity in different network topologies; and (iii) what is the scope of existing network science tools for quantifying water-mediated connectivity characteristics?

The article is structured as follows: an overview of networks, network properties and connectivity metrics, in the context of ecology and geomorphology; an exploration of network structure and properties on resulting connectivity metrics; a critical evaluation of how best to represent dryland and river-floodplain ecosystems as networks; and, finally, a discussion pertaining to the usefulness of network metrics in potentially enhancing our understanding of system connectivity.

2 | NETWORK-BASED CONNECTIVITY FRAMEWORK

The network-based representation of water-mediated connectivity is primarily determined by the type of connectivity (structural and functional), system characteristics (such as weather, species traits, system boundary and flow pathways), disciplinary perspective(s) (e.g., ecology, hydrology and geomorphology), the specific research question and data availability (spatial and temporal resolution) (Figure 1 and Table 1).

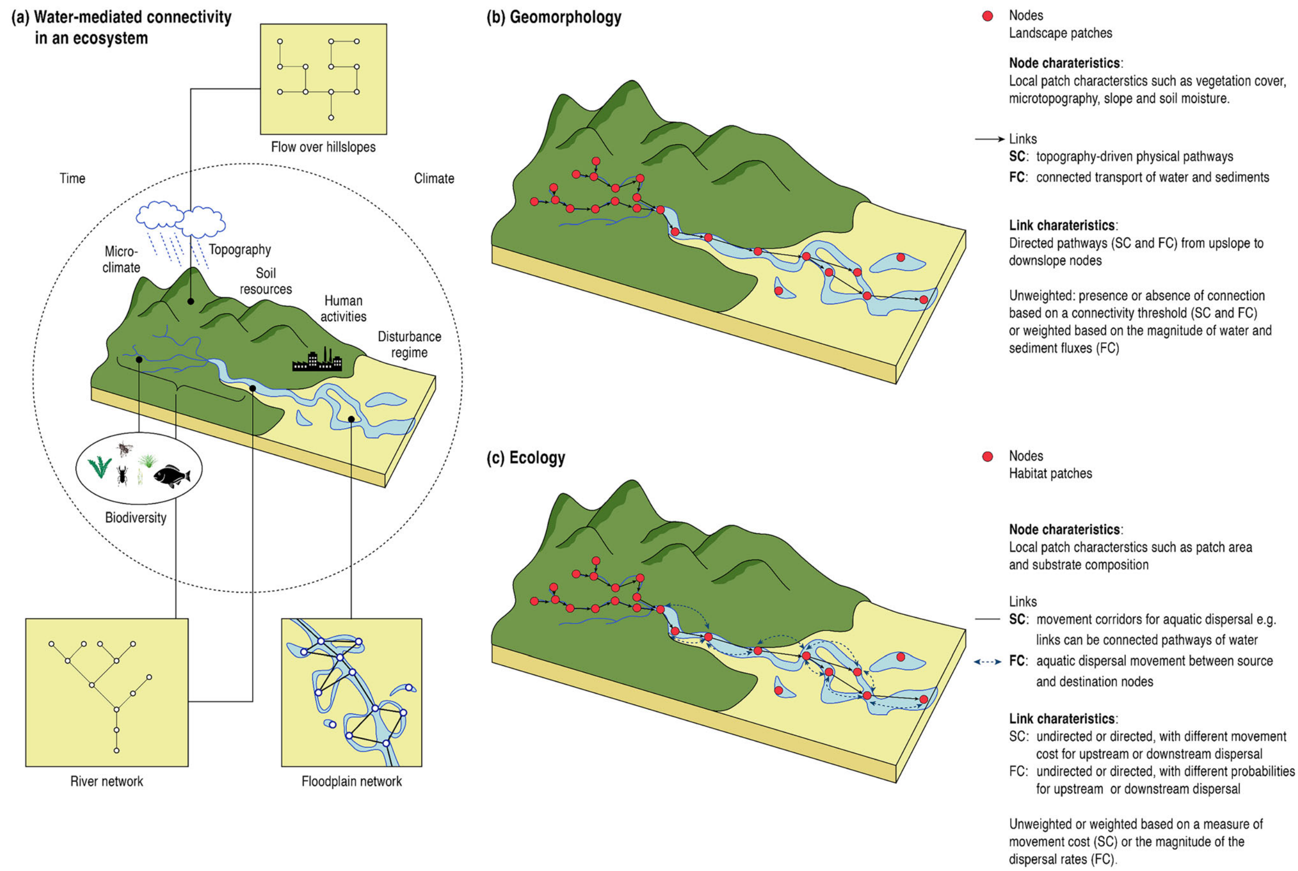

FIGURE 1 (a) Conceptualization of water mediated connectivity in an ecosystem and evaluation of connectivity and subsequent network-based representation of an ecosystem from a (b) geomorphic and (c) ecological perspective

2.1 | Network component

2.1.1 | Nodes

The first key step when building connectivity networks is to define nodes, i.e., fundamental landscape units of interest (Turnbull et al., 2018). In ecology, common approaches for delineating nodes include the following:

i. Habitat patches based on vegetation, resources and suitability for target species (Erős et al., 2012; Kupfer et al., 2015; Turner et al., 2015). Considerations include foraging, breeding and movement requirements of focus organism at appropriate spatial scales.
ii. Channel confluences/bifurcations or channel segments with uniform conditions in dendritic ecosystems like rivers, which form natural boundaries (Baldan et al., 2022; Czuba & Foufoula-Georgiou, 2015).

In geomorphology, nodes typically represent the following:

i. Fundamental landscape units like sediment sources/sinks and erosion/deposition zones shaping connectivity (Heckmann et al., 2015; Phillips et al., 2015; Turnbull & Wainwright, 2019; Wohl et al., 2019).
ii. Roughness elements affecting water and sediment flows such as vegetation induced microtopography (Abrahams et al., 1995; Wainwright et al., 2011).
iii. Landforms and boundaries where flows converge/diverge (Sarker et al., 2019).

The scale of features represented as nodes needs to align with research goals and available data (Calabrese & Fagan, 2004; Turnbull et al., 2018). Across different geographical scales, considerations vary. For example, at the hillslope scale, considerations include the availability of high-resolution topographic data/aerial imagery to delineate features such as vegetation patches or roughness elements at 1–10 m scales (Abrahams & Parsons, 1996; Turnbull & Wainwright, 2019). In rivers/floodplains, nodes often represent 100 m to 1 km segment scales based on confluences or channel cut-off boundaries (Funk et al., 2023; Sonke et al., 2022). For catchments or sub-catchments, nodes often represent hydrological response units at scales of 1–100+ km^2 (Phillips et al., 2015).

2.1.2 | Links

Links represent pathways and routes for flows and movements between nodes (landscape units) in networks. Links that form connections in the network can have directionality and weights, which allow

TABLE 1 Example of application of connectivity and network theory in various ecosystems from ecologic and geomorphic systems.

Ecosystem	System characteristics	Discipline	Network
Dryland ecosystem	Drylands are defined as areas with precipitation that is less than two thirds of potential evapotranspiration (water-limited ecosystems), with patchy vegetation cover with limited resource/nutrient distribution due to low water availability (Calvo-Cases et al., 2021; Safriel et al., 2005). **Biotic:** Patchy vegetation configuration and dynamics affecting hydrological fluxes (Calvo-Cases et al., 2021). Patches of vegetation also act as 'resource traps' (Calvo-Cases et al., 2021). **Abiotic:** water and wind (direction and velocity) as the primary medium of connectivity (e.g., precipitation, runoff and recharge), morphological traits and resources (e.g., sediments and nutrients, and topography), temperature (Mueller et al., 2014). **Spatial variability:** Drylands exhibit high spatial heterogeneity driven by the interactions between sparse vegetation patterns, geomorphic processes and variable soil properties over multiple scales (Maestre et al., 2016; Wainwright & Parsons, 2002). At fine scales, the patchy configuration of vegetation influences infiltration rates, runoff generation and sediment capture, creating sources and sinks of hydrologic connectivity (Parsons et al., 1996; Turnbull, Wainwright, Brazier, 2010). Vegetation patches accumulate resources transferred from bare interpatch areas, acting as 'islands of fertility' (Ravi et al., 2010; Wainwright et al., 2002). At broader scales, landscape features like dunes, desert pavements, gravelly surfaces and drainage networks impose structural controls on hydrologic flow paths and aeolian transport corridors (Okin et al., 2009). This spatial patterning interacts with microtopography and soil crusting to create a highly discontinuous mosaic of connected and disconnected areas (Jeltsch et al., 2014) **Temporal variability:** Water inputs to drylands are extremely variable and punctuated in time, ranging from high-intensity convective thunderstorms to prolonged multi-year droughts (Porporato et al., 2002, Post & Knapp, 2020). Rainfall patterns exhibit high variability at event, seasonal, annual and decadal scales, resulting in corresponding pulses of runoff generation, sediment transport and nutrient redistribution across the landscape (Thompson et al., 2014, Wilcox et al., 2022).	Ecology	**Node**: landscape units that can be represented as centroids of a grid-cell or patches characterized by vegetation cover (Calvo-Cases et al., 2021). **Links**: movement corridors defined as least-cost path (i.e., identified by their vegetation cover) (Khosravi et al., 2018; Wang & Liu, 2020), source-sink runoff dynamics, where sink is vegetated areas (Calvo-Cases et al., 2021). **Example:** Calvo-Cases et al. (2021) assessed the effects of vegetation configuration and erosion on runoff and hillslope connectivity processes (source-sink dynamics). In this study, the different landscapes were abstracted as grid-cells, where the runoff paths between source and sink areas (vegetation patches) were calculated using flow-routing techniques (e.g., D8). Calvo-Cases et al. concluded that soil erosion processes affect the configuration and composition of vegetation.
		Geomorphology	**Node:** Landscape patches (with variable vegetation cover). **Links:** Flow of water and sediment movement along the nodes through a resistance layer (such as surface roughness, vegetation sinks). **Example:** Turnbull and Wainwright (2019) have studied patterns of connected flow pathways of sediment and water along the grass and shrub plots in the drylands of the southwest USA. They identified key locations with land degradation feedback by using the length of connected pathways and SC-FC relationships.
Floodplain ecosystems	Floodplains are low relief and low gradient landscapes that go from the outer banks until the limits of the river valley and can have a variety of spatial scales (Opperman et al., 2017). They include lotic (river channel) and lentic (standing waters) conditions (Lewin & Ashworth, 2014). Floodplain wetlands can be frequently flooded when river flows are greater than bankfull (Xu et al., 2021). **Biotic:** aquatic, semi-aquatic, and terrestrial micro-, meso- and macro-fauna and flora (e.g., fishes, benthic macroinvertebrates, amphibians and	Ecology	**Connectivity:** degree to which the landscape facilitates or impedes the movement of biodiversity among resource patches (Taylor et al., 1993). **Node**: habitat patch (Dou et al., 2020), individual waterbodies and confluences/bifurcations (Funk et al., 2023). **Link**: movement corridors defined by surface water connections between patches, movement of individuals and proxies of dispersal (Erős & Lowe, 2019; Neufeld et al., 2018; Rinaldo et al., 2018).

TABLE 1 (Continued)

Ecosystem	System characteristics	Discipline	Network
	diatoms) adapted to different hydrodynamic conditions (Tonkin et al., 2018). **Abiotic:** alluvium or sediments, precipitation, discharge, nutrient concentrations, flow velocity and depths of the water table (Neufeld et al., 2018). **Spatial variability**: spatial patterns in floodplain morphology (e.g., channel migration and cutoff) change based on erosion and deposition processes, as well as vegetation patterns (Czuba et al., 2019; Gurnell, 2014). Inundation patterns in floodplains also depend on the magnitude, frequency and timing of flood events and on the relationship between river flows and floodplain flows (Opperman et al., 2017). **Temporal variability:** floodplains are highly dynamic systems. Floodplain inundation varies depending on the temporal scale: e.g., during an individual flood event, during cyclical events (seasonal, annual and interannual) or during long-term climatic changes (Opperman et al., 2017). Deposition and erosion processes that shape floodplain morphology also operate at multiple temporal scales (Florsheim et al., 2011).		**Example:** Funk et al. (2023) used a dynamic network approach to quantify and assess the importance of node-level connectivity for floodplain functions and restoration potential.
		Geomorphology	**Connectivity:** water flow and sediment linkages and pathways between channels and floodplain surfaces (Opperman et al., 2017). **Node:** landscape units or patches representing a river stretch or located every river confluences (Erős et al., 2012) or bar areas emerge riffles. **Link**: physical connections (e.g., via surface water), stream junctions or confluences (Erős et al., 2012) **Example**: Zhang et al. (2022) assessed the variation in water-mediated connectivity by merging disciplinary methods with network theory. Later, they discussed the effects of a dam construction on the hydrological connectivity of a floodplain system.

for a more detailed quantification of the systems' connectivity (Barrat et al., 2004; Sivakumar, 2014; Sonke et al., 2022). Weight describes the strength of the connection between nodes, such as the amount of water/sediment transport or species dispersal between two points, while directionality refers to the nature of the link, whether it is undirected or directed (Figure 1). The representation of links depends on whether SC (i.e., underlying network topology) or FC is being represented.

For SC networks, links in ecology can represent physical corridors that could facilitate species movements or habitat connectivity (Larsen et al., 2017; Taylor et al., 1993; Tischendorf & Fahrig, 2000), such as habitat corridors, channel networks or floodplain mosaics. In geomorphology, SC links indicate topological pathways for potential flows of water or sediment based on terrain structure and surface properties (Bracken et al., 2015; Turnbull & Wainwright, 2019; Wainwright et al., 2011), for example, drainage channels, gullies and rills formed by runoff. While factors including link length, width or stream order could be used as weights in certain contexts, comprehensively quantifying the strength of SC connections can be challenging due to the multitude of factors that may influence the importance of a given link. For example, in a dryland ecosystem, the strength of an SC link between two landscape patches may depend on a complex interplay of topography, surface roughness, vegetation characteristics and soil properties (Wainwright & Parsons, 2002). Capturing this heterogeneity in a single weight value is not always straightforward, as the relative importance of these factors may vary across the landscape and over time. SC links typically focus on the presence/absence of physical connections (Heckmann et al., 2015; Phillips et al., 2015).

For FC networks, links in ecology can represent confirmed routes used for migration, dispersal or gene flow of organisms, determined from tracking or genetic data (Baldan et al., 2020; Crooks & Sanjayan, 2006). In geomorphology, FC links quantify actual water/sediment fluxes and transfers measured between landscape units, often directed by elevation gradients (Czuba et al., 2019; Wohl et al., 2019). In contrast to SC links, weights for FC links can often be more directly quantified based on the magnitude of the material flux (e.g., water, sediment or organisms) between nodes, as these fluxes are the primary driver of FC (Barrat et al., 2004; Costa et al., 2019). FC links are commonly weighted based on flow magnitudes, movement costs, dispersal flux or probabilities of dispersal events derived from empirical measurements.

Both SC and FC links are important. SC provides the structural template, upon which dynamical processes yield FC (Turnbull et al., 2018). Careful and appropriate selection of links and incorporation of relevant weights/directionality is crucial for capturing connectivity across multiple scales and processes.

2.1.3 | Adjacency matrix

Mathematically, a network can be represented as an adjacency matrix, which is a matrix with rows and columns assigned to nodes. The presence or absence of a link between two nodes is represented by a numerical value (weight) in the matrix. The adjacency matrix is typically populated based on the connectivity from the source node to every other possible receptor node in the system. For undirected networks, the adjacency matrix is symmetrical, meaning the connectivity between two nodes is the same regardless of their positions as source or receptor nodes. However, for directed networks, the adjacency matrix is asymmetrical, with links represented from source nodes to receptor nodes. Overall, adjacency matrices provide a compact encoding of network connectivity and weights in a computable array structure that enables mathematical analysis and modelling (Tejedor et al., 2015).

2.2 | Network types

Networks can be categorized based on two key link properties—weights and directionality. This characterization yields four main network representations for quantifying water-mediated connectivity: unweighted and undirected (UNW + UND), weighted and undirected (WGT + UND), unweighted and directed (UNW + DIR) and weighted and directed (WGT + DIR) networks. Selecting an appropriate network representation is crucial for capturing the relevant ecological and geomorphological processes influencing water-mediated connectivity.

In early applications of networks to quantify habitat-connectivity patterns, unweighted and undirected (UNW + UND) networks were applied to quantify the emergent patterns associated to a set of habitats occupied by a population or community (e.g., Keitt et al., 1997). In this context, connectivity is assessed based on counting for the presence/absence of connected movement corridors or dispersal of individuals of particular species, ignoring characteristics of the landscape that can exert a cost for movement or amount of dispersal flow (Erős et al., 2011; Rayfield et al., 2011). However, UNW + UND networks cannot capture the connectivity of abiotic fluxes observed over a hillslope because these fluxes mostly move from a high to a low elevated node and are thus best represented by directed networks. The WGT + UND networks can also be used to quantify connectivity, with link weights representing strength of connectivity (Borrett & Scharler, 2019; Corley & Sha, 1982). There is mounting evidence that weighted networks are useful in quantifying the emergent behaviour of a system arising from strength of connectivity, which is lacking in unweighted networks because unweighted links only indicate the presence or absence of connections (Costa et al., 2019; di Summa et al., 2011; Tejedor et al., 2015; Wang et al., 2008). For instance, the asymmetrical movements of some fish species (from upstream to downstream of a river) can be represented as WGT + UND networks, weighted based on real dispersal flows (recorded animal movements), a measure of movement cost (e.g., Euclidean or watercourse distances). Furthermore, UNW + DIR networks are useful to investigate the direction-dependent connectivity in an ecosystem, such as movement of water and sediment along an elevation gradient. For example, Sarker et al. (2019) identified the location of critical nodes in the structure of river network using an unweighted and directed network. Unweighted networks are especially useful in the case of SC networks because it is difficult to quantify weights associated with SC linkages, where strength of connectivity might depend on multiple characteristics (such as slope, vegetation cover and surface roughness), as opposed to an FC network where weights are directly proportional to the magnitude of flux. It is important to note that in some applications, having an unweighted network can broaden the application of available network tools (Heckmann et al., 2015; Turnbull & Wainwright, 2019). The WGT + DIR networks are also useful to study direction-dependent connectivity in an ecosystem; for example, fluxes of water and sediment along landscape patches (or in a river) can be represented as a weighted and directed network (Marshall et al., 2016). Weighted and directed networks are especially useful for quantifying emergent behaviour in systems where strength of connectivity is important and quantifiable (e.g., an FC network), because ignoring link weights may result in the loss of potentially important network information.

In summary, the choice of network representation—ranging from simple UNW + UND to comprehensive WGT + DIR networks—depends on the research questions, study system, available data on directional biases and constraints, link weights and the underlying connectivity processes of interest (Barrat et al., 2004).

2.3 | Quantifying network properties

We explore a selection of graph-theoretical metrics previously used in various disciplines to quantify the characteristics of connectivity at both network and node levels (see Table 2 for a graph theoretical description of the proposed network metrics). Here, we explore the following network-level metrics: (i) link density (LD), which quantifies the proportion of observed links to the maximum possible links, and (ii) global efficiency (GE), which quantifies the average ease of movement across the network (inverse of shortest path lengths). At the network level, metrics like LD and GE are constrained by nodes and links. Network-level metrics do not focus exclusively on the node level but rather summarize the role of nodes and links in the context of the entire network. Compared to other disciplinary metrics (e.g., drainage density and DEBAS index [stream power DEficit on BASin slopes]), LD and GE are graph-theoretical alternatives that provide insights on the complexity and network level connectivity of ecological and geomorphic systems (Marchi & Dalla, 2005; Phillips et al., 2015).

Undoubtedly, one of the most applied network metrics is centralities (node-level metrics), which are used to rank nodes according to their importance and have practical applications for helping to prioritize management and conservation actions. The node-level metrics explored here are (i) degree centrality, which counts the number of connections per node; (ii) betweenness centrality (BC), which quantifies the importance of a node as a bridge between other nodes; (iii) page rank (PR) centrality, which is a probability-based measure of a node's importance based on the connectivity of its neighbours; (iv) length of connected pathways (LOCP), which is the total number of nodes linked upstream from a given node; and (v) node efficiency, which quantifies the ease of movement to/from a specific node (inverse of average path length to other nodes).

These metrics assign importance to each node according to their link patterns (degree centrality), their position in the network and characteristics of their connected pathways (BC, total LOCP and

TABLE 2 Interdisciplinary metrics to measure emergent patterns in dynamic ecosystems

Metric	Definition	Interpretation
Link density (network)	The link density (*LD*) is the number of connected links relative to the total number of possible links. $LD = \frac{x}{y}$, where *x* is total number of connected links and *y* is the total number of possible links.	LD represents the number of direct connections between neighbouring nodes (Canard et al., 2012). A network with a high LD has a high degree of connectivity between neighbouring nodes.
Global efficiency (network)	Global efficiency (*GE*) is defined as the average of the inverse shortest path length between all nodes in the network. $GE = \sum_{i=1}^{n} \sum_{\substack{j=1 \\ i \neq j}}^{n} \frac{1}{l_{ij}}$, where l_{ij} is the length of shortest path between node pair *i* and *j* (for weighted networks, l_{ij} is dependent on the link weights, with shortest pathways associated with path with higher weights) and *n* is the total number of nodes.	GE can be thought of as a measure of global integration or network connectivity (Latora & Marchiori, 2001) and is typically interpreted as a network's capacity to withstand change and to quantify its resilience (Zhang & Ng, 2021). A network topology that is closely connected will have a high GE and will be better able to withstand changes in local connectivity (Crucitti et al., 2003).
Degree (node)	Degree (*D*) quantifies the number of neighbouring nodes directly connected to a given node (Minor & Urban, 2008). For directed networks, this can be further separated into in-degree D_{in} and out-degree D_{out}. Furthermore, all-degree (D_{all}) is the sum of D_{in} and D_{out}, $D_i = \sum_{j=1}^{l_n} w_j$, where l_n is the number of links connected (in/out) to a node *i* and w_j is the weight of link *j* (for unweighted network, w_j is equal to one for all links).	D_{all} represents the total number of incoming and outgoing pathways associated with a node. A node with high D_{all} has high number of connected links. For weighted network, D_{all} can be linked to the net strength of connectivity associated with a given node (Phillips et al., 2015).
Betweenness centrality (node)	Betweenness centrality (*BC*) is the total number of the shortest paths between any pair of nodes that passes through a given node (Wang et al., 2008), $BC_i = \sum_{u,v \neq i} l_{xy}(i)$, where l_{xy} is the total number of shortest weighted paths from node *u* to node *v* that pass-through node *i*.	The BC can be used to quantify whether a node acts as a bridge (ability to connect two nodes) during connectivity processes. A node with high BC value has a high number of connected pathways passing through it (Sarker et al., 2019, Zetterberg et al., 2010).
Page rank centrality (node)	Invented by Google founders Larry Page and Sergei Brin, page rank (*PR*) centrality was designed for ranking web content, using hyperlinks between pages as a measure of importance. $PR_i = (1-d) + d * \sum_{y \neq i} \frac{PR_y}{D_{y,in}}$, where *d* is damping factor between 0 and 1, here $d = 0.85$ (based on Page & Brin, 1998), and $D_{y,in}$ is the outdegree centrality of node y (for weighted network, $D_{y,in}$ is weighted). Note that the page ranks form a probability distribution over all the nodes in the network, so the sum of all nodes' Page Ranks will be one.	PR centrality is a measure of a node's importance. A node is important if it is linked to other important nodes and links sparse nodes or if it has a high degree.
Total length of connected pathways (node)	In a network, the total length of connected path (*LOCP*) is the length of a node sequence in which each node is connected by a link to the next. In weighted network, the path length corresponds to the sum of weights of links in the path (Boccaletti et al., 2006). For directed networks, this can be further separated into incoming $LOCP_{in}$ and outgoing $LOCP_{out}$, $LOCP_i = \sum_{y=1}^{n} w_{iy} + \sum_{y=1}^{n} w_{yi}$, where w_{iy} is the weights of links with node *i* as source node (outgoing pathways from node *i*) and w_{yi} is the weights of links with node *i* as sink node (incoming pathways to node *i*).	The total LOCP represents a node's influence on connectivity pathways across a network. A node with a long incoming path length (LOCP) has a high impact on how local resources are distributed among other nodes in a network (Okin et al., 2009).
Relative node efficiency (node)	Relative Node efficiency (*RNE*) of node *x* is the of ratio global efficiency of the network without and with node *x* (Zhang & Ng, 2021), $RNE_i = \frac{GE_G - GE_H}{GE_G} \times 100$, where GE_G is the global efficiency of the network with node *i* and GE_H is the global efficiency of the network after node *i* is removed.	RNE is used to test a system's ability to function even after critical nodes have been attacked, disabled or degraded (Komali et al., 2008). A node with a high RNE value implies that its removal (from the network) will have a significant impact on network connectivity. Positive RNE values indicate that node removal reduces global efficiency (a measure of network connectivity), whereas negative RNE indicates that node removal increases GE.

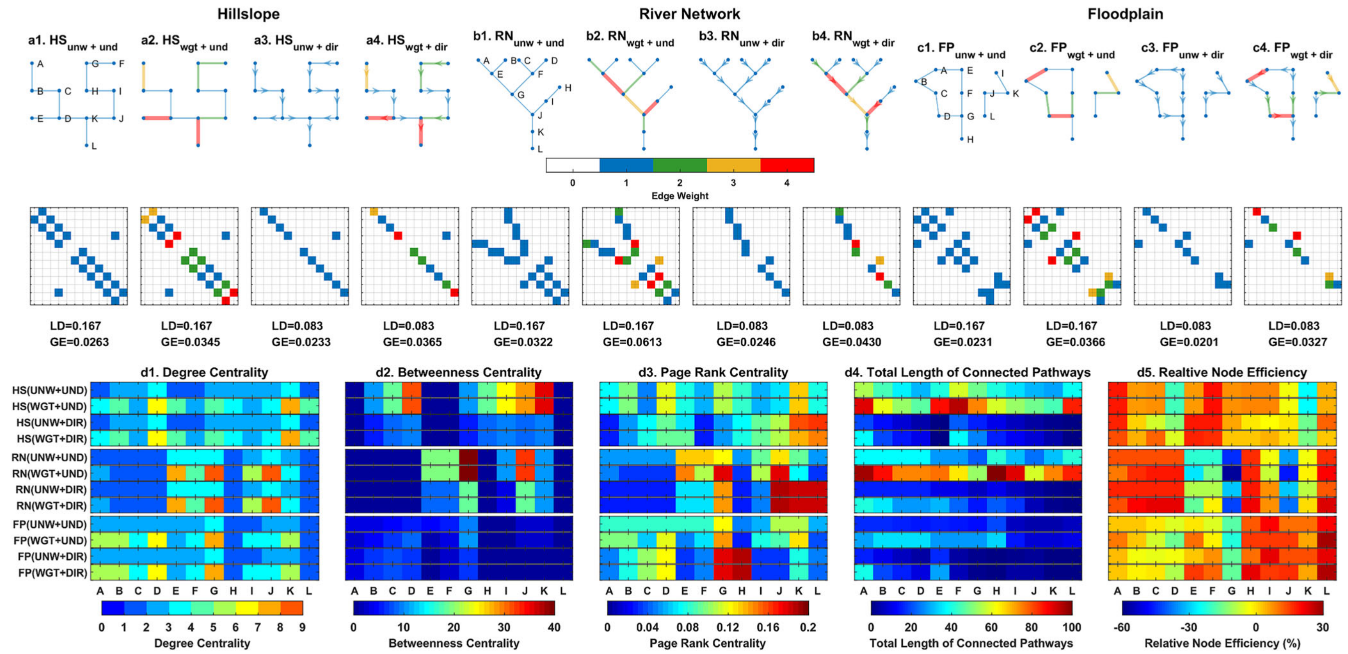

FIGURE 2 A toy example of three network classes, i.e., hillslope (a1 to a4), river network (b1 to b4) and floodplain (c1 to c4) each with four sub-types associated with water-mediated connectivity in ecosystems, i.e., unweighted and undirected network (UNW + UND) with symmetric adjacency matrix (representing undirected links) with binary elements 0 and 1 indicating the presence (1) and absence (0) of links, weighted and undirected network (WGT + DIR) with symmetric adjacency matrix with elements representing link weights (proportional to the strength of connectivity), unweighted and directed network (UNW + DIR) with asymmetric adjacency matrix (representing directed links) with binary elements 0 and 1 indicating the presence (1) and absence (0) of links and weighted and directed network (WGT + DIR) with asymmetric adjacency matrix (representing directed links) and elements representing link weights. (d1 to d5) Five node-level metrics (degree centrality, betweenness centrality, page rank centrality, total length of connected pathways and relative node efficiency) for the proposed network types. *Note*: LD stands for link density, and GE stands for global efficiency.

relative node efficiency [RNE]), while they can also account for neighbourhood configurations (PR). We focus on these metrics, as we identified them as being potentially useful in quantifying connectivity within both ecological and geomorphic systems. Besides network- and node-level metrics, we do not expand on any community-detection applications (e.g., clustering and modularity) in our ecological perspectives because they are not observed in the geomorphic perspective of water-mediated connectivity, in which water flows from upslope to downslope. Furthermore, sensitivity of the proposed metrics to link weights and directionality is explored in section 3.

3 | TOY EXAMPLE OF THE APPLICATION AND UTILITY OF NETWORK METRICS

3.1 | Model networks

We use a toy example (Figure 2), a simplified and illustrative demonstration, to highlight appropriate metrics for accounting for link directionality and weights when quantifying water-mediated connectivity. We focus on three contrasting landscape components associated with water-mediated connectivity and their underlying network topologies: a hillslope, a river and a floodplain, and demonstrate the utility of the network metrics explored. We investigate the relation between network type and network properties for three network classes: hillslope (HS), river network (RN) and floodplain (FP), each with four simple networks consisting of 12 nodes and 11 links, namely, UNW + UND, WGT + UND, UNW + DIR and WGT + DIR (Figure 2). For the hillslope network, the links represents flow in four possible directions around each node (D-4 flow algorithm, Figure 2a1–a4). The river network follows a dendritic structure, which is loop-less and resembles a hierarchical branching order (e.g., Strahler order) (Figure 2b1–b4). For the floodplain network, the sequences of nodes A–D, as well as I, K, J and L, resemble configurations of side-arm systems commonly found in floodplains (Figure 2c1–c4). The main river channel is represented by nodes E–H. Node E in the sequence of nodes A–D represents the inflow area from the main river channel to the floodplain, while node G represents the outflow area.

3.2 | Results

Analysis of network metrics for the different network topologies presented in the toy example shows that across all network types, LD is sensitive to directionality but not weights. For all three network classes, LD decreases from 0.167 for UNW + UND to 0.083 for UNW + DIR. GE is sensitive to both directionality and weights across all network types. GE decreases in a directed network and increases when the network is weighted, indicating that in these examples, undirected networks are better connected than directed networks and the presence of stronger links (weights) results in a more connected network. Furthermore, different node-level characteristics are also sensitive to changes in link directionality and weights (as shown in Figure 2d1–d5: further interpretation of these node-level metrics is presented in the Table 2). Degree centrality (D_{all}) is not sensitive to direction but can be subdivided into indegree and outdegree for directed networks based on number of incoming and outgoing pathways to/from a node (Figure 2d1). The BC and PR centrality are highly sensitive to direction and vary slightly with link weights for all three network topologies (Figure 2d2,d3), in the case of BC a node's bridging capacity is primarily determined by link direction, and in the latter, PR is a probability-based measure that does not consider the absolute value of link weights. The BC and PR centrality measures differ for all nodes in the network, highlighting the importance of network topology on local measures of connectivity. The BC corresponds to bridging capacity, so nodes in the network's centre will have high BC, whereas high PR corresponds to a node that is well connected to other well-connected nodes. Total LOCP varies with both link direction and weight (Figure 2d4). RNE is calculated relative to changes in GE and is less sensitive to link direction and weights compared to absolute node efficiency (Figure 2d5).

The node-level metrics are also dependent on the network topology. For example, in the river network example, downstream central nodes (nodes G, J and I) tended to have higher node-level metrics, while in floodplain example, nodes within looping structures (nodes D, F and G) showed high node-level metrics (Figure 2). Overall, BC and LOCP are highly sensitive to changes in network topology, with high values observed for river networks and low value for river-floodplain networks. Furthermore, D_{all}, PR and RNE are less sensitive to changes in network topology. In summary, it is important to consider link characteristics such as direction, weights and spatial scales when using network-based approaches to evaluate water-mediated connectivity.

4 | REPRESENTING DRYLAND AND RIVER-FLOODPLAIN ECOSYSTEMS AS NETWORK AND THE USEFULNESS OF NETWORK METRICS TO QUANTIFY CONNECTIVITY

Here, we evaluate how different water-controlled ecosystems can be usefully represented as networks, as well as how different network metrics can be interpreted in two end-member scenarios of water-mediated connectivity. The first scenario pertains to a dryland ecosystem from a geomorphic perspective, where water-mediated connectivity is largely controlled by the interaction between patchy vegetation and surface microtopography (Table 1). The second scenario focuses on a river-floodplain ecosystem where dispersal traits of the organism and the seasonality of flow largely control connectivity from an ecological standpoint (Table 1).

4.1 | Quantification of connectivity in dryland ecosystems: a geomorphic perspective

Drylands are 'water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs' (Noy-Meir, 1973, p. 26). Given the role of water as the main limiting resource for biological activity in drylands, the connectivity of water-driven transport of sediment and nutrients between and within vegetation patches is widely acknowledged as a key driver of dryland structure and function (Charley & West, 1975; Garcia-Moya & McKell, 1970; Ravi et al., 2010; Schlesinger et al., 1990; Stewart et al., 2014; Turnbull et al., 2008; Ye et al., 2016). Abiotic drivers such as discrete rainfall events and temperature variation influence a wide range of ecological processes in drylands, including microbial activity, nutrient cycling and species interactions (Maestre et al., 2016). Other abiotic factors, for example, topography, spatiotemporal patterns of soil erosion and soil characteristics (such as moisture and texture), significantly modulate the effects of climate on the structure and functioning of these ecosystems (Wainwright, 2009). Biotic factors, such as vegetation cover, species diversity and spatial distribution of plants and microbial communities, also influence the functioning of dryland ecosystems (Mueller et al., 2014; Steven et al., 2021; Turnbull et al., 2008). Their climatic characteristics, and the fact that their scarce resources limit biological activity for most of the year, make the processes driving the functioning of drylands rather unique compared with other ecosystems.

Dryland ecosystems have important interactions and feedbacks across fine to coarse scales (Mueller et al., 2014; Wainwright, 2009), where interactions and feedback between climate, soil, vegetation and topography develop distinct patterns of redistribution of water, soil, nutrients and vegetation (Schlesinger et al., 1990; Turnbull et al., 2008; Turnbull, Wainwright, Brazier, 2010). Due to these interactions and feedbacks, dryland ecosystems exhibit several complex system characteristics, including emergent behaviour (Mueller et al., 2014), state dynamics (Bagchi et al., 2012; Turnbull et al., 2008, 2012), self-organization (Dong & Fisher, 2019), resilience (Yuan et al., 2019) and adaptation (Okin et al., 2009; Stewart et al., 2014; Turnbull & Wainwright, 2019) (details presented in Table S1).

4.1.1 | SC-FC networks of dryland ecosystems

In developing a network-based representation of geomorphic connectivity in drylands, nodes can be defined based on the vegetation cover, surface roughness and elevation characteristics of landscape patches (Caviedes-Voullième et al., 2021; Turnbull & Wainwright, 2019). For example, Turnbull and Wainwright (2019) used a patch-based approach to define nodes in the context of geomorphic connectivity in a dryland ecosystem. The spatiotemporal definition of a fundamental unit depends on the timescale under consideration and associated feedback. For instance, to understand the effect of vegetation (cover type) on the connectivity of water and sediment at hillslope scales, nodes should represent the landscape patches with size no larger than the vegetation patch (i.e., the scale of the 'island of fertility';

Charley & West, 1975; Schlesinger et al., 1990; Schlesinger & Pilmanis, 1998).

Once the fundamental unit has been defined, the SC between two landscape patches can be determined by their elevation profile as well as the presence of sinks in the connectivity pathway between them (e.g., a vegetation patch not associated with a topographic high, acting as a sink that essentially forms a barrier within the water-flow network and thus disconnect flows). The FC between two nodes can be evaluated based on the connected fluxes of water, sediment and nutrients.

Dryland ecosystem networks can be constructed using data derived from empirical field measurements, numerical model output and remote sensing. Empirical field measurements provide direct observations of the ecosystem, but it can be challenging to collect dynamic flux data such as surface-water flow and sediment transport data at appropriate spatial and temporal scales (Mueller et al., 2014). Numerical models, on the other hand, provide spatial estimates of fluxes that can be used to build networks for more robust quantification of connectivity at appropriate spatial and temporal scales (Mueller et al., 2014; Stewart et al., 2014; Wainwright et al., 2008a, 2008b, 2008c). Once the data sources have been organized into fundamental units and fluxes, the network consisting of nodes and links can be constructed (Phillips et al., 2015), from which the network and associated adjacency matrix can be examined using a variety of metrics as outlined in Section 2.

4.1.2 | Network-based analysis of emergent patterns in drylands

Network-level metrics are critical for understanding how local connectivity patterns between vegetation patches scales up to influence landscape-level characteristics in drylands. In dryland SC networks, high LD indicates more physical connections between patches that could facilitate water/sediment flow (Okin et al., 2009). For FC networks, LD shows the extent of active transport pathways present under given conditions. Comparing LD across rainfall scenarios or between areas with different vegetation cover can reveal regimes where landscape connectivity is promoted or limited (Turnbull & Wainwright, 2019), although it does not take into account the strength of connectivity (i.e., link weights). GE is a useful metric as it allows quantification of the net capacity of a system to withstand any change (Zhang & Ng, 2021) and is thus potentially useful as a way to quantify the resilience of an ecosystem to different perturbations (e.g., climatic or anthropic). For example, a water-mediated connectivity network with a high GE value will be more resilient to changes in individual node characteristics (such as changes in local vegetation cover) that the one with a low GE value.

In the context of node-level metrics, degree represents the total number of incoming and outgoing flow pathways and can be weighted based on the associated discharge. Patches with high degree act as sources (predominantly outgoing links) or sinks (predominantly incoming links) in the water/sediment flux networks. Such hotspots of external inputs/outputs exert disproportionate influence on dryland functioning. Time series of degree changes can track shifts in source/sink patch importance. BC can be used to quantify whether a node acts as a bridge during transportation processes across connected flow pathways (Bodin & Saura, 2010), whereby a node with high BC value has a high number of water and sediment-transport pathways passing through it. Disruptions to these critical patches could disconnect different components of the landscape. Instead of highlighting individual bridging nodes, PR highlights the importance of densely interconnected patch clusters that are hubs of water/sediment transport in the landscape. Shifts in these regions over time could indicate reorganization of dryland hydrological regimes. Incoming LOCP (same as LOCOP by Okin et al., 2009) can be used to demonstrate the role of vegetation cover in propagating different types of structural and FC. High LOCP in FC network denotes a node that receives water and sediment fluxes from a high number of nodes. RNE can be linked to the effect of node removal on the overall connectivity of the system (Veremyev et al., 2015). RNE quantifies how crucial each patch is for maintaining the overall connectivity of the dryland network. Patches with high efficiency potentially regulate large-scale sediment/nutrient redistribution processes when their local connections change state. Monitoring efficiency reveals the most sensitive loci of dryland functioning. By comparing these network metrics across different scenarios (e.g., varying rainfall or vegetation cover) or monitoring their changes over time, we can gain valuable insights into the emergent patterns and dynamics of dryland ecosystems.

4.2 | Quantification of connectivity in river-floodplain ecosystems: an ecological perspective

River-floodplains are dynamic, disturbance-driven ecosystems governed by the lateral exchange of water, sediment, nutrients and organisms between the main river channel and its adjacent floodplain water bodies (Amoros & Bornette, 2002; Opperman et al., 2017; Tockner & Stanford, 2002; Ward et al., 2002). The frequency, magnitude, duration and spatial extent of overbank flooding events are principal drivers that shape floodplain habitats and biotic communities (Allan et al., 2021; Fausch et al., 2002; Marrin, 2020; Poole, 2002; Strahler, 1957). During high flows, floodplains become a mosaic of hydrologically connected aquatic and terrestrial habitats that facilitate dispersal, gene flow and the homogenization of communities (Amoros & Bornette, 2002; Thomaz et al., 2007) Conversely, as floodwaters recede, the landscape transitions to a more fragmented regime where discontinuous aquatic habitats form semi-isolated patches occupied by communities assembled by environmental filtering processes (Larsen et al., 2019). This water mediated exchange from the river across the floodplain (floodplain inflows or wetting) and returning back to the river further downstream (floodplain outflows or draining) are key controls of the spatial distribution of species (emergent biodiversity patterns) and ecosystem functioning (Larsen et al., 2019; Marle et al., 2022; Xu et al., 2021).

A floodplain's dynamic spatiotemporal heterogeneity in hydrological connectivity creates a shifting mosaic of suitable and unsuitable habitats for different species based on their physiological tolerances (fitness) and dispersal abilities (Auerbach & Poff, 2011; Chaparro et al., 2019; Fernandes et al., 2014; Funk et al., 2023). For example, more mobile taxa can take advantage of brief hydrological connections to colonize new areas, while less mobile species may be constrained by dispersal limitation. As a result of the continuous variation in local environmental conditions and habitat connectivity, both intricately linked to the fluctuating river discharge regime, floodplain ecosystems support high levels of biodiversity (Chaparro et al., 2018; Tonkin et al., 2016). However, understanding the role of mechanisms influencing species distribution proves particularly challenging within these dynamic systems (Chaparro et al., 2018).

4.2.1 | SC-FC networks of river-floodplain ecosystem

From a landscape ecology perspective, nodes in floodplain networks represent discrete habitat patches, river reaches/confluences determined by the spatial hierarchy of the analysis and the resolution at which organisms perceive their environment (Erős et al., 2012; Sonke et al., 2022).

SC links in floodplain ecosystems depict the physical pathways facilitating potential movements of water, sediment, nutrients and organisms between floodplain habitats. The architecture of the SC network emerges from the interplay between river geomorphology, floodplain topography and hydroperiod (Czuba et al., 2019; Lewin & Ashworth, 2014; Xu et al., 2021). River planform exerts a strong control on floodplain morphology, creating more reticulate SC patterns, compared to the more dendritic templates, with meandering and anastomosing channels that may or may not have the presence of loops (loops/cycles referring to paths of any length that start and end at the same node; Phillips et al., 2015, Tejedor et al., 2015) and disconnected components (Barthélemy, 2011; Connor-Streich et al., 2018; Hiatt et al., 2022; Lewin & Ashworth, 2014; Limaye, 2017; Xu et al., 2021). Floodplain microtopography further subdivides the landscape into a complex mosaic of aquatic/terrestrial patches, oxbow lakes, backwaters and other morphological features that become interconnected during floods (Lewin & Ashworth, 2014; Ward et al., 2002) or via through-bank inundation (Xu et al., 2021). Meanwhile, levees and banks act as barriers to the lateral exchange of water between channel and floodplain as long as water levels do not exceed their height (Opperman et al., 2017). Nevertheless, conduits that cross levees or banks, such as through-bank channels, may enable hydrological connections to the interior of the floodplain across various sub-bank flow conditions (Xu et al., 2021). The feedbacks between geomorphologic fluxes and SC are crucial, as floodplain ecosystems cycle between inundation and recession in response to flood pulses and hydroperiods (Junk et al., 1989; Ward et al., 2002). During high water stages, extensive areas become hydrologically linked, creating temporary aquatic corridors and homogenizing conditions (Thomaz et al., 2007). Low water periods leave only the main channel and subset of deepest wetlands connected, fragmenting habitats (Xu et al., 2021).

Besides low/high water periods, fluvial processes like channel migration, cut-offs and avulsions also progressively reconfigure the SC template over annual-decadal timescales by altering watercourse patterns (Czuba et al., 2019). Researchers can choose to model SC as a static baseline template relevant to central tendency conditions or incorporate time-varying links to capture dynamics over specified time periods (i.e., Funk et al., 2023). Representing the full hydroperiod may require generating an ensemble of temporally explicit SC realizations to characterize the shifting patterns of connectivity over characteristic flood cycles. The appropriate approach depends on the spatiotemporal scale, research questions and degree of process detail required.

SC networks can be represented as lattice-based models at coarse scales or vectorized morphologies derived from remote sensing (Funk et al., 2023; Zhang et al., 2022). High resolution topographic data from LiDAR enables mapping of microtopographic SC features at submeter scales (Torgersen et al., 2022). Link directionality is used to capture flow asymmetries, with weights quantifying landscape properties influencing movement 'costs' like distance, velocity, depth and roughness (Baldan et al., 2020; Czuba et al., 2019; Neufeld et al., 2018; Sonke et al., 2022). Flow directionality is usually estimated from DEMs using flow routing algorithms. However, unlike landscapes with steep terrains (as for river networks), flow asymmetries in floodplains do not necessarily follow the steepest descent (Coulthard et al., 2013; Lewin & Ashworth, 2014; Limaye, 2017). Therefore, approaches that focus on finding low pathways through the riverbed, which can descend and ascend locally to connect deeper channels through shallower parts, are more appropriate (Limaye, 2017; Sonke et al., 2022).

FC networks quantify realized movement of organisms and gene flow along the SC template, where undirected and directed links are representative for different dispersal probabilities of active or passive dispersal traits (Figure 3b4) (Neufeld et al., 2018; Song et al., 2008). At a catchment scale, dispersal processes in headwater streams are expected to be more limited than in downstream regions (Schmera et al., 2018). Likewise, central positions in floodplain networks are expected to be more influenced by mass effect (spatial mechanisms in which the high dispersal flow results in variations in local population size) (Schmera et al., 2018). During high water stages, extensive areas become hydrologically linked, creating temporary dispersal corridors and reducing dispersal limitation (Thomaz et al., 2007). Low water periods reduce aquatic habitats to the main channel and deeper floodplain waterbodies. Across scales species' traits (e.g., body size, dispersal abilities and dispersal mode) is a further important driver of metacommunity structure and the spatial distribution of species (Padial et al., 2014).

The dispersal of organisms can be empirically recorded, yet measuring movements empirically presents challenges for certain groups, such as aquatic invertebrates and algae. To address this challenge, dispersal-related FC networks may utilize movement data derived from mesocosm experiments or estimated through various numerical models, such as individual-based models, metapopulations,

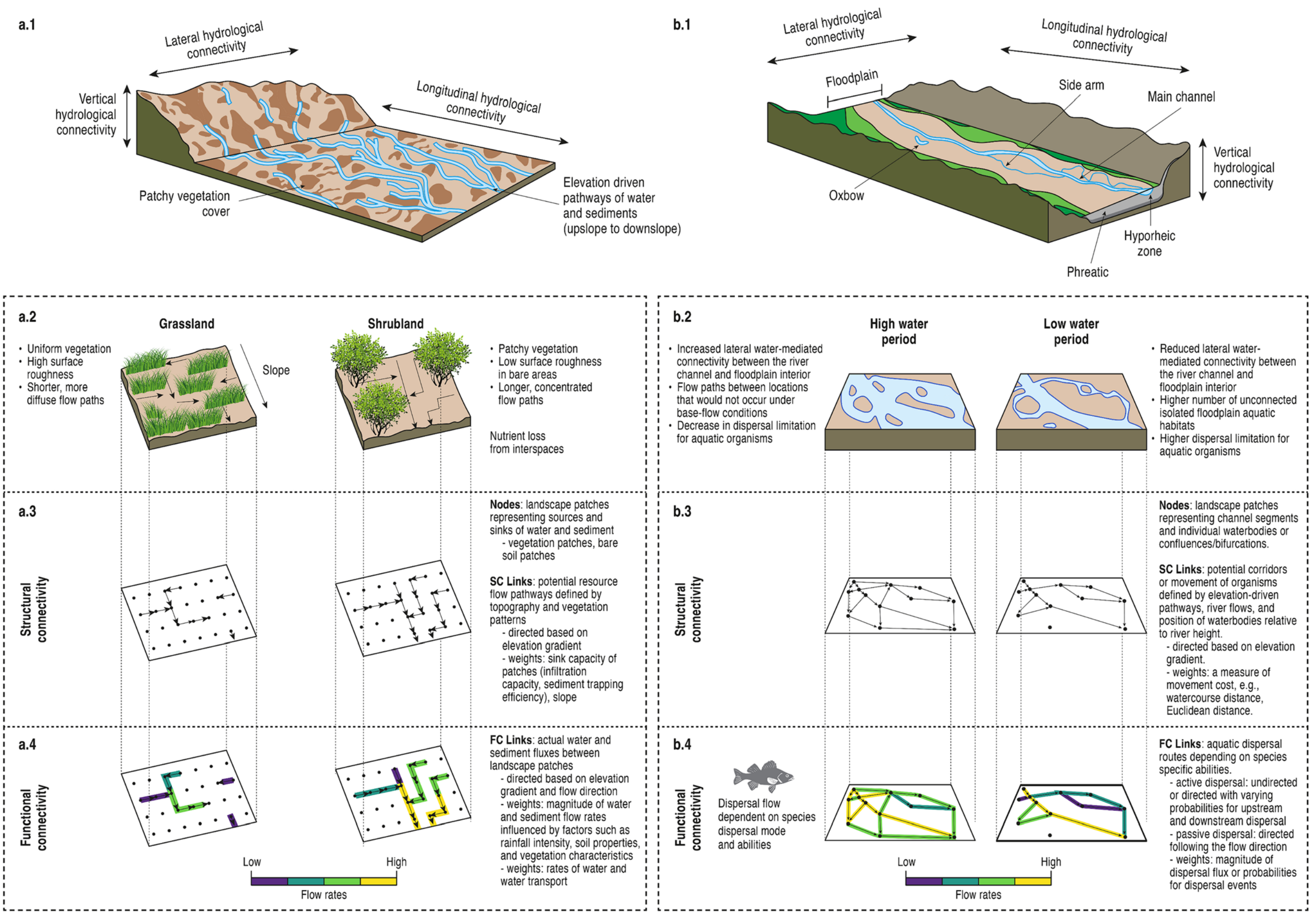

FIGURE 3 Characteristics of SC-FC network abstractions of a dryland ecosystem from a geomorphic perspective (Turnbull & Wainwright, 2019) (a) and river-floodplain ecosystem from an ecological perspective (Reckendorfer et al., 2006; Tonkin et al., 2014) (b). (a1) An example of hillslope-scale representation of a dryland ecosystem with patchy vegetation cover, elevation driven pathways and water-mediated connectivity in a longitudinal, lateral and vertical dimension. (a2) Influence of vegetation type on the length of pathways of water and sediments. (a3) Conceptualization of the structural connectivity (SC) network, based on elevation-based flow pathways and the presence of vegetation sinks, with link weights attributed to the sink capacity of a landscape patch. (a4) Conceptualization of a functional connectivity network based on the directed transfer of water and sediment between landscape patches, with link weights attributed to the rates of water and sediment transport. Moving on to river-floodplain ecosystems, (b1) exemplifies the spatial structure of a river reach and its floodplain, composed by the main river channel, as well as different side-arm systems and floodplain wetlands, with water-mediated connectivity in its lateral, longitudinal and vertical dimensions. (b2) Differences in the aquatic habitat structure during high and low water periods (determined by flood pulses).
(b3) Conceptualization of SC, with nodes representing individual reaches or waterbodies (habitat patches) and links as river at each confluence. Links are directed following the flow direction and can be unweighted or weighted based on a measure of movement cost. (b4) Functional connectivity representing dispersal processes along the structural template. FC links are weighted based on the magnitude of the dispersal flow and can be undirected or directed depending on the species dispersal traits: active dispersal better represented by undirected links and passive drift by directed links.

metacommunity dynamics models, spatial capture-recapture models and stochastic patch-occupancy models (Auerbach & Poff, 2011; DeAngelis & Grimm, 2014; Dominguez Almela et al., 2020; Duarte & Mali, 2019; Rinaldo et al., 2018; Saura & Pascual-Hortal, 2007). Figure 3b4 illustrates the versatility of probabilistic habitat reachability models, which are applicable to both single and multiple species. Probabilistic models, like the Conefor network-based model developed by Saura and Pascual-Hortal (2007), define FC through dispersal probabilities along weighted SC links based physical distances or other cost measures. Similarly, network-based metapopulation and metacommunity approaches assess habitat connectivity by assuming functional connections within species' dispersal ranges, with dispersal probabilities decreasing as they near maximum dispersal distances (Chaput-Bardy et al., 2017; Thompson & Gonzalez, 2017; Tonkin et al., 2014).

4.2.2 | Network-based analysis of emergent patterns in a river-floodplain

Network and node-level metrics are useful for quantifying the ability of an ecosystem to facilitate species dispersal (Baggio et al., 2011).

Following the views of landscape ecology and metacommunity theory, we present disciplinary interpretations of the network- and node-level metrics introduced in Section 2. The network-level metric, LD, provides an overview of dispersal processes in FC networks by describing the total number of dispersing individuals or propagules with respect to the total amount of individuals who could potentially disperse. Thompson and Gonzalez (2017) used LD to describe the structure and evolution of dispersal networks in the context of environmental change. GE measures the effectiveness of species dispersal at a network level (Baggio et al., 2011). GE evaluates the spatial redundancy of pathways from a landscape permeability perspective—networks with high efficiency can maintain crucial ecological flows even if localized disturbances disrupt specific routes.

Node-level metrics can be applied to rank floodplain areas based on their role in maintaining and facilitating dispersal (Bodin & Saura, 2010; Saura & Pascual-Hortal, 2007; Urban et al., 2009). The node rankings of the proposed metrics when applied to FC networks can be used to quantify how individuals disperse throughout the river network. In weighted FC networks, D_{in} describes the emigration potential of a node and the D_{out} the immigration potential. The weighted D_{in} and D_{out} can be used as indicators of a node's source and sink strength (Rayfield et al., 2011). BC can be used to describe the importance of a site as a stepping stone for movement (e.g., connectivity providers for dispersal) (Chaput-Bardy et al., 2017). PR surfaces highly connected local neighbourhoods that can act as ecological reservoirs or sources for spatial spreading dynamics (de Domenico et al., 2015). RNE identifies irreplaceable locations maintaining overall ecological connectivity at the landscape scale. If these bottleneck areas are lost, the entire system may undergo a rapid transition towards isolation (Osei-Asamoah & Lownes, 2014), which has potential applications in assessing the effects of man-made disturbances on the resilience of dispersal networks. Finally, ranking nodes by the total length connected path length helps differentiate areas strongly influenced by large-scale dispersal from areas where local factors primarily control community assembly.

Collectively, these metrics move beyond traditional patch/corridor concepts to formally model how patterns of ecological movements in riverine landscapes are governed by the multi-scale topological roles of habitat patches embedded within the wider architecture of hydrological connectivity. Furthermore, understanding of the emergent patterns of connectivity at a node-level can explore ecological theories such as

a. *network position hypothesis:* where the effects of local and regional drivers on community structure vary depending on the position of area of focus within the river network (Brown & Swan, 2010; Schmera et al., 2018);
b. *mass effect*: mechanisms in which the high dispersal flow of individuals homogenizes the community structure (Leibold et al., 2004; Suzuki & Economo, 2021);
c. *species sorting:* mechanisms in which adequate dispersal rates allow species to track environmentally suitable habitats (Leibold et al., 2004; Suzuki & Economo, 2021); and
d. *dispersal limitation*: where low dispersal rates might prevent species to track suitable habitats, since occupied habitats are too far away or not accessible because of the presence of disconnectivity (Altermatt, 2013; Economo & Keitt, 2010; Leibold et al., 2004).

5 | CURRENT CHALLENGES AND FUTURE DIRECTIONS

5.1 | The value of network-based approach in quantifying water-mediated connectivity

Networks provide a valuable framework for investigating the complexity of water-mediated connectivity in ecosystems, and we have shown how they can be usefully applied within two end-member systems, drylands and floodplains, to improve our understanding of connectivity. A weighted network formalism can address not only presence or absence of connectivity between system components but also emergent behaviour associated with the strength of connectivity. While the presence of a path between nodes indicates a connected network, the strength of those connections (as represented by link weights) can provide additional insights into the degree and dynamic nature of connectivity. For instance, in a river network, the presence of a channel between two locations suggests a connected system. However, the volume of water flow (which could be represented as a link weight) can vary significantly between different channels, affecting the strength of connectivity and the potential for material transport (Phillips et al., 2015; Wohl et al., 2019). Similarly, in ecological networks, the frequency or probability of species movement between habitat patches (link weights) can indicate the strength of FC, even if SC (presence of a physical path) exists. Link weights play a crucial role in quantifying the strength and dynamics of connectivity, while acknowledging that the presence of a path is the fundamental requirement for a connected network.

We have demonstrated that the network-based representation of drylands and floodplains should be informed by system characteristics and our understanding of the structure and function of these systems (naturally informed by our disciplinary perspectives) that guide how we conceptualize these systems as networks.

5.2 | Challenges in defining nodes and link characteristics

As discussed, when conceptualizing ecosystem as networks, the first challenge is defining an appropriate fundamental unit of connectivity, i.e., the node. While there is a growing body of literature on how to define a node in a system (see review in Turnbull et al., 2018), the challenge remains in considering the most appropriate scale of the fundamental unit and how this relates to different types of connectivity (SC and FC). The choice of the fundamental unit is typically based on the available input data, assuming that they accurately capture the essential connectivity features of the system.

The next area of interest is the link characteristics. Whether a directed link representation is preferable to an undirected one within a network representation is dependent on the specific material or organism in question. Given that link weights can be quantified, using weights is generally preferable because it allows for the quantification of emergent patterns associated with connectivity strength. For example, an unweighted network configuration of dispersal processes will treat low and high rates of species dispersal equally simply because of the presence of a connection, whereas incorporating dispersal rates (weights) will allow for more accurate quantification of emergent patterns (Neufeld et al., 2018). However, quantification of strength of connectivity in the SC network in a meaningful way is particularly challenging because of the presence of multiple factors that potentially impact the importance of links, such as surface roughness, the role of vegetation patches and slope for geomorphic SC in dryland ecosystems and water depth, flow velocity for hydrological SC in river-floodplain ecosystem.

In ecological networks, incorporating node characteristics such as patch area and local habitat characteristics into the quantification of emergent patterns can be critical and is an important direction of research (Baldan et al., 2020; Bodin & Saura, 2010; Engelhard et al., 2017; Neufeld et al., 2018; Saura & Pascual-Hortal, 2007). Local habitat conditions are critical because they can limit the establishment of a species and its subsequent persistence (Brown et al., 2011; Suzuki & Economo, 2021). Collecting the necessary data for questions best answered using weighted networks can be time-consuming because the data must account for dynamic strength of connectivity, which necessitates different observational and/or modelling methods at relevant spatial and temporal scales.

In the case of dryland ecosystems, empirical data scarcity limits the development of network-based representations of water-mediated connectivity in these systems. The development of dynamical FC networks requires improved spatial and temporal data on geomorphic processes within these systems. However, obtaining such high-resolution information remains a difficult task, not least because of the episodic nature and short duration of flow events. Within freshwater systems, while there is a growing body of research using network-based approaches, there is also scarcity of empirical data on the movement of organisms, and, often, static network models are applied to describe dynamic processes such as dispersal.

5.3 | Limitations of traditional measures and the advantages of network metrics

Network metrics, such as those discussed in our study (e.g., BC, PR, LD and GE), provide a more comprehensive and flexible framework for analysing connectivity patterns in complex water-controlled ecosystems compared to traditional measures like drainage density and Horton-Strahler ratios. These metrics can capture the multi-directional, weighted and dynamic aspects of connectivity, which traditional measures may not fully represent. For example, drainage density (Saco et al., 2020) provides information about the total length of channels per unit area but does not consider the direction of flow or the strength of connections between different parts of the network. Similarly, Horton-Strahler ratios (Horton, 1945) describe the hierarchical structure of river networks but do not account for the temporal variability in flow conditions or the role of non-channelized pathways in the landscape.

In contrast, network metrics can incorporate these additional dimensions of connectivity, enabling researchers to explore questions related to the resilience, efficiency and vulnerability of water-controlled ecosystems. BC measures the number of shortest paths that pass through a node, indicating its importance as a bridging element in the network, while PR assigns a probability value to each node based on the likelihood of a random walker visiting that node, considering the importance of its neighbouring nodes. Although BC and PR are calculated differently, they both provide insights into the relative importance of nodes in the network. PR values are probabilities assigned to each node, and the sum of all PR values in a network equals 1. These probabilities can be interpreted in ecological and geomorphological contexts, such as identifying critical habitat patches or key locations for sediment transport.

Furthermore, LD and drainage density are two essential measures used to analyse the characteristics and behaviour of river networks. While drainage density focuses on the total length of streams per unit area, providing insights into the efficiency of water removal and the basin's response to rainfall events, LD emphasizes the number of stream segments per unit area, reflecting the complexity and dissection of the drainage network. Both measures are influenced by various factors such as climate, geology, topography and land use within the drainage basin. Generally, a higher drainage density corresponds with a higher LD, as a well-dissected drainage network often exhibits a greater number of stream segments per unit area. By considering both drainage density and LD, researchers can gain a more comprehensive understanding of the river network's structure, function and response to hydrologic events, as well as its role in sediment transport and overall basin morphology. However, we have not considered drainage density in our analysis because it does not have much significance over hillslope-scale processes.

The value of the proposed network metrics lies in their ability to help researchers and managers:

i. Identify critical nodes and pathways for the flow of water, sediment and organisms in the landscape.
ii. Assess the resilience and vulnerability of ecosystems to disturbances or changes in connectivity patterns.
iii. Compare the efficiency of different network configurations in facilitating ecological and geomorphological processes.
iv. Develop targeted conservation and restoration strategies based on the connectivity properties of the system.

Recent studies have successfully applied network metrics to address important questions in water-controlled ecosystems, showcasing their potential to generate new insights and inform management decisions (Baldan et al., 2020; Turnbull & Wainwright, 2019; Zhang et al., 2022).

5.4 | Future directions: Multilayer-weighted networks, time-delayed connectivity and higher order interactions

Multilayer networks are a type of network representation that consists of multiple layers, each representing a different type of interaction or subsystem (Bianconi, 2018). Nodes can be connected within a single layer (intra-layer edges) or across different layers (inter-layer edges). This framework allows for the integration of multiple dimensions of connectivity, such as different types of ecological interactions (e.g., trophic, mutualistic and competitive) or different modes of transport (e.g., surface water, groundwater and sediment). In the context of water-controlled ecosystems, multilayer networks can be used to capture the complex interplay between ecological and geomorphological processes. For example, a multilayer network could represent the connectivity of habitat patches for different species (ecological layer) and the connectivity of sediment transport pathways (geomorphological layer), with inter-layer edges representing the feedback between these two subsystems. Multilayer networks can aid in the quantification of connectivity caused by changes in environmental conditions in floodplain ecosystems, such as transitions from dry to wet or from lentic to lotic conditions. Specific examples of how multilayer networks can be implemented in water-limited systems include modelling the coupled dynamics of vegetation growth and sediment transport in drylands, where the ecological layer represents plant dispersal or vegetation biomass, and the geomorphological layer represents erosion and deposition processes (Stewart et al., 2014) and analysing the effects of hydrological connectivity on the metacommunity structure of benthic macroinvertebrates in floodplain ecosystems, where different layers represent different dispersal-related traits such as flying and non-flying groups (Recinos Brizuela et al., 2024).

Approaches that integrate knowledge and expertise from multiple disciplines and systems are increasingly recognized as crucial for understanding the characteristics of connectivity of water-mediated ecosystems (Heckmann et al., 2015; Larsen et al., 2012; Pilosof et al., 2017; Turnbull et al., 2018; Voutsa et al., 2021). For example, ecogeomorphology has emerged as an important approach to understand the bidirectional feedbacks between an ecosystem's biotic and abiotic components (Allen et al., 2014; Butler & Hupp, 2013; Mueller et al., 2014; Turnbull et al., 2008). Furthermore, the concept of meta-ecosystems highlights the importance of considering the integration of spatial flows of energy, materials and organisms across ecosystem boundaries (Cid et al., 2022; Fausch et al., 2002; Padgham & Webb, 2010). This integration of biotic and abiotic components is especially relevant in interdisciplinary studies that aim to understand the connectivity between geomorphology and ecology (Viles, 2020). However, analysing connectivity in meta-ecosystems can be difficult due to the emergence of new properties and patterns that result from the interactions of different ecosystem components (Wolf et al., 2022). A network-based representation of a meta-ecosystem, for example, must account for the complexity of ecosystem components, as well as how the structure and function of each individual ecosystem contribute to the overall connectivity of the meta-ecosystem (Jacquet et al., 2022; Kheirkhah Ghehi et al., 2020). Additionally, the scale at which the analysis is conducted can significantly influence the patterns of connectivity that emerge in the network (Levin, 1992). Therefore, while the concept of meta-ecosystems provides a framework for understanding connectivity across different ecosystem components, its application to network-based representations necessitates careful consideration of emergence and scale-dependency.

Building on the weighted-directed networks explored in this paper, there are opportunities to understand better the feedbacks between ecological and geomorphic processes by developing the application of multilayer-weighted networks (Bianconi, 2018) and time-delayed connectivity responses (Voutsa et al., 2021) in water-controlled ecosystems. In a multilayer network, nodes are arranged into layers, and edges can connect nodes within the same layer (intra-layer edges) or between different layers (interlayer edges) (Pilosof et al., 2017). A weighted-directed network formalism can address connectivity not only within a single layer but also between intra-layers (multilayer network), and therefore, this approach has great potential to improve understanding of multidimensional connectivity of an ecosystem (e.g., Pilosof et al., 2017). In addition, while time-delayed connectivity (i.e., how one node at time $= t$ is connected to another node at time $= t + \mathrm{d}t$) in an ecosystem has yet to be investigated, concepts related to synchronized and sequential connectivity networks can aid in quantifying connectivity propagation in time (see Voutsa et al., 2021, for an overview of sequential and synchronized connectivity in different complex networks).

Water-controlled ecosystems are expected to exhibit higher-order interactions (Bianconi, 2021), such as non-linear feedback loops (Thompson et al., 2017; Turnbull et al., 2008) and emergent properties (Marrin, 2020; Turnbull et al., 2018), that cannot be fully captured by traditional pairwise connectivity networks. In ecology, higher order interactions can arise between multiple species in a food web (Guichard, 2017). For example, the presence or absence of a top predator can have cascading effects on the abundance and dispersal of other species in the community (Killengreen et al., 2012; Thomaz et al., 2007). In geomorphology, higher order interactions can occur between different components of a landscape, such as soil, water and vegetation (Wainwright et al., 2011). For example, vegetation can influence erosion rates and sediment transport, which in turn can influence the formation and evolution of landforms (Diehl et al., 2018; Okin et al., 2009). Researchers have developed new approaches to quantify higher order interactions in complex systems, such as network motifs, hypergraphs and graphlets, which capture patterns of connectivity between multiple nodes (Yin et al., 2018). As network science advances and data availability improves, ecologists and geomorphologists should embrace these new techniques to improve the quantification of connectivity patterns in water-controlled environments.

Overall, network science provides a diverse set of tools for studying connectivity, but due to the unique characteristics of ecosystems, only a subset of these tools is applicable. It is critical to continue developing adequate network tools and to appropriately apply existing tools to better quantify the emergent behaviour and characteristics of ecosystems.

6 | CONCLUSION

This study highlights the importance of network-based approaches in quantifying the patterns of connectivity in water-controlled ecosystems. We can better understand the emergent patterns of connectivity by carefully conceptualizing water-controlled ecosystems as networks and taking disciplinary perspectives and system characteristics into account. Our evaluation of network properties and their influence on network metrics has conclusively demonstrated that our resulting understanding of connectivity using these metrics is sensitive to how we conceptualize these systems as networks in the first place. In addition, our evaluation of network metrics in different water-controlled ecosystems has established that directionality and weighting play a crucial role in accurately quantifying connectivity patterns. We found that LD, BC and PR centrality are highly sensitive to directionality; GE and degree centrality are particularly sensitive to weights, while RNE remains unaffected by weights and directions. The study highlights the scope for network and node-level measures to shift how we quantify, and thus understand, water-mediated connectivity, especially in consideration of the role(s) of weights and directionality. Furthermore, network-based representations of system connectivity can aid in the identification of critical nodes in terms of structure and function, which can inform management and conservation efforts at specific locations. We further emphasize the importance of interdisciplinary research and collaborations in expanding our understanding of connectivity in water-controlled ecosystems.

AUTHOR CONTRIBUTIONS

Shubham Tiwari: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing—original draft; writing—review & editing. **Sonia Recinos Brizuela:** Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing—original draft; writing—review & editing. **Laura Turnbull:** Conceptualization; funding acquisition; project administration; resources; supervision; writing—review & editing. **John Wainwright:** Conceptualization; funding acquisition; project administration; resources; supervision; writing—review & editing. **Thomas Hein:** Conceptualization; funding acquisition; project administration; resources; supervision; writing—review & editing. **Andrea Funk:** Conceptualization; funding acquisition; project administration; resources; supervision; writing—review & editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article, as no new data were created or analysed in this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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